for microculture of woody plant species. HortScience **16**: 453 (Abstr.) (1981). — Meier-Dinkel, A.: *In vitro* Vermehrung und Weiterkultur von Stieleiche (*Quercus robur* L.) und Traubeneiche (*Q. petraea* (Matt.) Liebl.). Allg. Forst- u. J. Ztg. **158**: 199—204 (1987). — Murashige, T. and Skoog, F.: A revised medium for rapid growth and bioassays with tobacco tissue cultures. Physiol. Plant. **15**: 437—497 (1962). — Pevalek-Kozlina, B. and Jelaska, S.: *In vitro* growth and development of oaks (*Quercus robur* and *Q. petraea*). Acta Bot. Croat. **45**: 55—61 (1986). — San-Jose, M. C.: Influencia de la situación del explanto en la planta y del tamaño del tubo de cultivo en la multiplicatión *in vitro* de *Quercus robur* L. Phyton **46**: 33—38 (1986). — San-Jose, M. C., Ballester, A. and Vieitez, A. M.: Factors affecting *in vitro* propagation of *Quercus robur* L. Tree Physiol. **4**: 281—290 (1988). — Schenk, R. H. and Hildebrandt, A. C.: Medium and techniques for induction and growth of monocotyledonous and dicotyledonous plant cell cultures. Can. J. Bot. **50**: 199—204 (1972). — Schreiner, E. J.: Maximum genetic improvement of forest trees through synthetic multiclonal hybrid varieties. Proc. 13th Northeastern Forest Tree Improvement Conference, pp. 7—13 (1966). — Shen, X.-S. and Mullins, M. G.: Propagation *in vitro* of pear, *Pyrus communis* L., cultivars "William's Bon Chretien", "Packam's Triumph" and "Beurré Bosc". Scientia Hortic. **23**: 51—57 (1984). — Strullu, D. G., Grellier, B., Marciniak, D. and Letouze, R.: Micropropagation of chestnut and conditions of mycorrhizal synthesis *in vitro*. New Phytol. **102**: 95—101 (1986). — Vieitez, A. M., Ballester, A., Vieitez, M. L. and Vieitez, E.: *In vitro* plantlet regeneration of mature chestnut. J. Hortic. Sci. **58**: 457—463 (1983). — Vieitez, A. M., San-Jose, M. C. and Vieitez, E.: *In vitro* plantlet regeneration from juvenile and mature *Quercus robur* L. J. Hortic. Sci. **60**: 99—106 (1985). — Vieitez, A. M., Vieitez, M. L. and Vieitez, E.: Chestnut (*Castanea* spp). In: Biotechnology in Agriculture and Forestry. Vol. 1. Trees 1. (ed. Bajaj, Y. P. S.), pp. 393—414. Springer-Verlag, Berlin, Heidelberg (1986). — Westwood, M. N.: The role of growth regulators in rooting. Acta Hortic. **34**: 89—92 (1972). — Yae, B. W., Zimmerman, R. H., Fordham, I. and Ko, K. Ch.: Influence of photoperiod, apical meristem and explant orientation on axillary shoot proliferation of apple cultivars *in vitro*. J. Amer. Soc. Hort. Sci. **112**: 588—592 (1987).

Family-Site Interaction in Pinus radiata: Implications for Progeny Testing Strategy and Regionalised Breeding in New Zealand

By G. R. Johnson and R. D. Burdon

Ministry of Forestry, Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

(Received 7th February 1989)

Summary

A progeny test of 170 open-pollinated families from second-generation plus trees of *Pinus radiata* was established on four sites in New Zealand in 1981. Two test s.tes were on volcanic pumice soils in the Central North Island region and two were on phosphate-retentive clay soils in the Northland region.

Assessments of volume growth, stem straightness, malformation, and branch habit were made at age 4.5 years.

Family × site interaction variance components for stem volume were highly significant ($\alpha = .01$) between pumice and clay sites, and also between the clay sites of differing fertilities, but relatively small between the two pumice sites. When the interactions for stem volume were studied in terms of genetic correlations between sites quite strong interactions were still evident between the regions, but interactions between sites within both regions were very minor, even though the Northland clay sites were of widely different fertility.

Family-site interactions for stem straightness and branch habit scores were less marked overall than for stem volume. For malformation the interactions were marked but only in relation to weakly expressed family differences.

Genetic gains were predicted, using multi-site index selection, for stem volume growth under alternative testing procedures and patterns of regionalisation. On this basis failing to test within a region would lose 50% or more of the potential gain for that region. However, it was possible to select families which performed well in both regions, such that regionalisation would only raise average genetic gain from 22% to 25%.

Key words: Genetic correlation, genetic gain, genotype-environment interaction, plant breeding, *Pinus radiata*, regionalisation, selection index, tree breeding.

Introduction

The question of whether or not it is necessary to select a unique set of parent clones for each region arises in almost every tree breeding programme. Gains will be maximised by regionalising, but the additional cost and effort may not be worth it, unless genotype-environment interactions are very strong. Additional gains from using regional breeds need to be weighed against the additional costs.

Over 50% of the *Pinus radiata* plantations in New Zealand (NZ) are in the Central North Island pumice region. Because of the predominant importance of this region, and the proven effectiveness of these pumice sites for screening genotypes, most progeny testing has been carried out there.

Of the remaining 'regions' throughout NZ, the phosphate-retentive (phosphorus deficient) Northland clays have shown the poorest genetic correlation with the pumice area in respect of growth of *Pinus radiata* (e.g., Burdon, 1971). Therefore the Northland clays would be a prime candidate for setting up a regional breed. If regionalisation does little to improve growth gain in Northland, then regionalisation is unlikely to improve gain much in other regions of NZ. This paper examines the effect of regionalisation on improving growth gains from progeny testing in the Northland clay and pumice regions of NZ.

Materials and Methods

Study Design

One-hundred and seventy 'second-generation' selections were tested in both the pumice and Northland clay regions using open-pollinated progeny tests. The parents were 10-year selections (the '880' series) made within open-

pollinated progeny of the '268' series of plus tree selections (see SHELBOURNE *et al.*, 1986). The families were divided randomly into five sets of 34 families each and planted in a 'sets-in-replicates' design utilising single-tree plots. Fifty replicates (reps) were planted in 1981 on each of two pumice sites (Taupo and Rotoehu) and 25 reps on each of two Northland clay sites (Moerewa 1 and Moerewa 2). Included in each set were two control seedlots, which brought the number of trees per rep/set block to 36. These 36 trees were planted in a 6-tree × 6-tree block at a spacing of 4 m × 4 m.

Locations

The trial at Taupo is located on a Taupo pumice soil with a slope of 3^0 to 10^0. Previous vegetation was monoao (*Dracophyllum subulatum*), manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*). Site preparation consisted of roller crushing and burning, followed by deep ripping and bedding in June 1981. Elevation is 570 m.

The Rotoehu site is on a Rotoehu sandy pumice with 5^0 to 35^0 slope. Previous vegetation was a plantation of *Pinus radiata*. The site was sprayed with paraquat in July 1981 to control natural regeneration and miscellaneous ground vegetation. Elevation is 260 m.

Moerewa 1 is on a relatively fertile Waiotira clay loam and Moerewa 2 is on an infertile Wharekohe clay. Both sites were covered with manuka and some *Hakea saligna* before being rotary slashed and burnt in late 1980. The sites were ripped and bedded in January 1981. At both sites the slope is 5^0 to 20^0 and elevation is 100 m.

Assessment

Before assessing at age 4½ years, all trees at the Moerewa 1, Taupo, and Rotoehu sites were pruned to two metres or one-third height (whichever was less). Trees at Moerewa 2 were too short for pruning. Twenty-five reps were assessed at Taupo and Rotoehu. Traits asssed on the pruned sites were height (HT), diameter outside bark at 1.4 m (DIA), straightness (STR) and malformation (MALF), and branch habit (BR). STR and MALF were recorded as subjective scores (1 = worst to 9 = best). BR was scored subjectively as 1 = uninodal to 9 = extreme multinodal. Only height and diameter were assessed at Moerewa 2 since straightness and malformation are difficult to assess on unpruned trees. Volume was calculated for all trees by the equation: volume (VOL) = (DIA^2) × HT × 0.0001. Although this is not true volume, it gives relative volume and results in a convenient range of values. Straightness and malformation for an entire rep were scored by the same observer, so observer bias was confounded with reps, not sets.

Data Analysis

Analysis of variance was run on each trait for each location/set subclass and for each location, using the SAS GLM procedure (SPECTOR *et al.*, 1985). Variance components were estimated using SAS Varcomp Method = Type 1 SPECTOR and GOODNIGHT, 1985). The variance components were used to estimate the narrow-sense heritabilities and family-mean heritabilities. Heritabilities were estimated as:

$$h^2 = \sigma_a^2 / (\sigma_f^2 + \sigma_e^2) \qquad \text{(Equation 1)}$$

$$h^2_{fm} = \sigma_f^2 / (\sigma_f^2 + \sigma_e^2/k) \qquad \text{(Equation 2)}$$

where: h^2 = narrow-sense heritability
h^2_{fm} = family-mean heritability
σ^2_a = additive genetic variance, estimated as $4\sigma^2_f$
σ^2_f = between-family variance component within a site
σ^2_e = residual variation
k = harmonic mean of trees per family per site

Analyses of variance were also run for each trait: firstly over sites within each region, introducing sites as a main effect and the various site interactions; and secondly over all sites, introducing regions and sites within regions as main effects with their interaction effects. Variance components were estimated as above, but covering the alternative assumptions as to whether regions and sites within regions were random or fixed effects.

For estimating covariances, and thence genetic correlations within sites, the sums of cross-products were obtained using SAS GLM Manova. The estimates of genetic correlations at a single site were calculated using the formula:

$$r_a = \sigma_{f_{xy}} (\sigma^2_{fx} \sigma^2_{fy})^{-1/2} \qquad \text{(Equation 3)}$$

where r_a = genetic correlation estimate
$\sigma_{f_{xy}}$ = between-family component of covariance between traits x and y, estimated from mean cross-products by a procedure analogous to the estimation of variance components from mean squares
$\sigma^2_{f_x}$ = between-family variance component of trait x
$\sigma^2_{f_y}$ = between-family variance component of trait y

Estimates of genetic correlations for the same trait on different sites, i and j, were calculated by adjusting the family-mean correlations using the equation (BURDON, 1977):

$$r_{a_{ij}} = r_{fm_{ij}} / (h_{fm_i} h_{fm_j}) \qquad \text{(Equation 4)}$$

where: $r_{fm_{ij}}$ = family-mean correlation for a trait between sites i and j
$h^2_{fm_i}$ and $h^2_{fm_j}$ are heritabilities (repeatabilities) of family means at sites i and j respectively.

Any interaction that tends to affect family ranking is reflected in $r_{a_{ij}} < 1$.

Genotype-environment interaction (GE) was examined primarily for one variable, volume. Its components, height and diameter, were the only variables assessed on all four sites. Also, past studies (e.g., MATHESON and RAYMOND, 1981; SHELBOURNE and Low, 1980) have shown growth rate to be subject to more GE than other economic traits.

GE was first examined by estimating both variance components and genetic intercorrelations between sites for individual traits. Differences between sites and regions are discussed.

Detailed consideration was given to the relative importance of region and sites within regions in generating GE.

The need for a Northland clay breed was examined, for stem volume only, by constructing selection indices and predicting gains for regionalising seed orchards containing reselected parents.

Selection indices were set up for both regionalising and not regionalising, adapting the method of BURDON (1979) whereby the expression of a trait at each site is handled as a separate index trait. Economic weights were the inverse of site means; thereby, percentage gains at each site were of equal economic worth. Gains for regionalising were calculated for two situations, one using only data from the region being selected for, and the other utilising the two sites in the other region as covariates. The b vectors were calculated as (LIN, 1978):

$$b = p^{-1}Ga \qquad \text{(Equation 5)}$$

where P = variance-covariance matrix of the information sources used in the index, i.e., (volume at 4 sites)

G = variance-covariance matrix of the information sources with the breeding values of the traits of interest (volume at 4 sites)

b = vector of weights used on the information sources

a = vector of assumed economic values for a unit of the particular traits being selected

Regionalising using only within-region information uses 2 × 2 P and G matrices to derive b vectors (Equation 5), and then gives the information from other two sites (b elements of zero) when gains are prediced (Equation 6) using the 4 × 4 P and G matrices. Regionalising, using information from all four sites, is done by giving economic weights of zero to sites not in the designated region (Equation 5).

Expected gain for each trait (volume at a site) was calculated as (LIN, 1978):

$$GT = Gb\ (i/\sigma_I) \qquad \text{(Equation 6)}$$

where GT = the expected genetic gain in the vector of traits in H

G = the covariance matrix of the information sources with the breeding value of the traits of interest at each site

b = vector of index weights

σ_I = standard deviation of I

i = selection intensity

Results and Discussion

Variance Components and Heritabilities

With the exception of malformation, all traits showed significant ($\alpha = 0.05$) family effects in practically every location/set subclass. The within-site variance components were used to obtain the heritability estimates shown in *Table 1*. Very little genetic variation was present in malformation, resulting in low heritabilities, and only six of the 15 location/set subclasses showed significant family effects, although over all sets family effects were significant at two of the three sites.

Estimated heritabilities for growth were similar to those calculated at early ages for other trials. However, heritabilities for the quality-related traits were comparatively

Table 1. — Estimates of narrow-sense and family-mean heritabilities.

	Site			
	Taupo	Rotoehu	Moerewa 1	Moerewa 2
Narrow-sense (h^2)				
HT	0.22	0.19	0.34	0.16
DIA	0.19	0.15	0.25	0.15
STR	0.17	0.12	0.15	-
BR	0.18	0.19	0.26	-
MALF	0.05	0.08	0.03	-
VOL	0.22	0.16	0.28	0.15
Family-mean (h^2_{fm})				
HT	0.65	0.60	0.66	0.46
DIA	0.62	0.56	0.59	0.45
STR	0.58	0.56	0.46	-
BR	0.60	0.61	0.60	-
MALF	0.29*	0.40	0.15+	-
VOL	0.65	0.57	0.62	0.45

* P = .001.
\+ P = .07.
P very small for all other cases

Table 2. — Estimated of selected variance components for stem volume ($m^3 \times 1000$) computed over four sites and over the two sites within each region (all significant at $\alpha = .01$). Effects random except as stated otherwise.

Over All Four Sites

Identity	Designation	Value
Families overall	σ^2_f	13.4
Regions fixed effect	$\sigma^2_{f'}$	24.0
Regions and sites within regions fixed	$\sigma^2_{f''}$	28.6
Family x regions	σ^2_{fr}	20.2
Families x sites within regions	$\sigma^2_{fs(r)}$	18.2
Error	σ^2_e	993.1
Families within regions	$\sigma^2_{f(r)}$	34.9
Sites within regions fixed effect	$\sigma^2_{f(r)''}$	44.3
Families within sites	$\sigma^2_{f(s(r))}$	52.2

Within each Region

Identity	Designation	Value	
		Clays	Pumice
Sites	σ^2_s	1055	1557
Reps within sites	σ^2_r	109	216
Families	σ^2_f	36	32
Families x sites	σ^2_{fs}	30	10
Error	σ^2_e	1016	978

Note: Assuming homogeneity of variances among sites the between-site correlation (r_a) conforms to:

$r_a = \sigma^2_{fam}/(\sigma^2_{fam} + \sigma^2_{fam\ x\ site})$

where: σ^2_{fam} = variance between families over all sites in question.

$\sigma^2_{fam\ x\ site}$ = family-site interaction variance.

low. This could be because these progeny were measured at age four, while the other trials were measured at ages five and six. A second possible reason is that the genetic variance of these traits had been reduced by the selection of their parents ('second-generation' selections). The third possibility is that these sites had genuinely more environmental variation.

The Moerewa 2 site gave the lowest narrow-sense heritability estimate for growth and Moerewa 1 had the highest. Trees were also much larger at Moerewa 1 than at Moerewa 2 (HT 7.1 m vs. 4.8 m). Rotoehu had lower heritability estimates for volume and straightness than Taupo, although growth was much better at Rotoehu than Taupo (6.8 m vs. 5.3 m). Because the pumice sites had 35 reps and the clays had only 25, family-mean heritabilities would be larger on the pumice for a given narrow-sense heritability.

Variance component estimates over sites for stem volume are shown in *Table 2*, although the heterogeneity of variance at the family × site-within-regions level reduces the meaningfulness of the variance components calculated over all four sites. Both the family interaction variance components were large, being of similar magnitude to the family variance component if fully random effects are assumed. On the clay sites the family × site variance component was similar to the between-family component, but among the pumice sites the interaction was much smaller than the between-family component. These relatively large interactions for the two regions suggest that regionalising could increase volume gain substantially.

Correlations

Genetic correlations between traits within each site are shown in *Table 3*. The only consistently adverse correlations were the negative correlations between volume and straightness. In other studies involving radiata pine (e.g., Shelbourne and Low, 1980) genetic correlations between growth and straightness have been variable; some studies have shown negative correlations and others positive correlations. The effect of truncation selection may have biased correlations in this study but these selections represent the current breeding population.

Table 3. — Estimates of genetic correlations between traits within each of three sites.

Site	Trait	STR	BR	MALF
Taupo				
	VOL	-0.25	0.34	0.51
	STR		0.26	0.26
	BR			0.62
Rotoehu				
	VOL	-0.25	0.33	0.04
	STR		0.20	0.48
	BR			0.26
Moerewa 1				
	VOL	-0.08	0.08	-0.24
	STR		0.32	0.32
	BR			0.69

Table 4. — Estimates of family-mean- (above diagonal) and genetic correlations (below diagonal) across sites.

	Rotoehu	Taupo	Moerewa 1	Moerewa 2
Volume				
Rotoehu	-	0.58	0.18	0.08
Taupo	0.96	-	0.31	0.17
Moerewa 1	0.29	0.52	-	0.44
Moerewa 2	0.16	0.55	0.84	
Straightness				
Rotoehu	-	0.52	0.49	
Taupo	0.91	-	0.38	
Moerewa 1	0.96	0.73	-	
Malformation				
Rotoehu	-	0.15	0.14	
Taupo	0.45	-	0.06	
Moerewa 1	0.52	0.26	-	
Branch habit				
Rotoehu	-	0.46	0.50	
Taupo	0.76	-	0.30	
Moerewa 1	0.82	0.50	-	

Note: For family-mean correlations:
$\alpha = .05$ $r = 0.15$
$\alpha = .01$ $r = 0.20$
$\alpha = .001$ $r = 0.25$

Table 5. — The relative efficiency of selecting stem volume at one site (i) for another (j).

Selecting at:	Selecting for :			
	Rotoehu	Taupo	Moerewa 1	Moerewa 2
Rotoehu	1	0.90	0.30	0.07
Taupo	1.02	1	0.51	0.14
Moerewa 1	0.28	0.53	1	0.98
Moerewa 2	0.09	0.65	0.72	1

Efficiency $= \frac{h_i r_{ij}}{h_i}$ where r_{ij} = genetic correlation between stem volume at two sites.

Estimates of family-mean- and genetic correlations across sites are shown for various traits in *Table 4.* Correlations between the two pumice sites (Rotoehu and Taupo) were strong for all traits except malformation. For growth, the two clay sites at Moerewa were very well intercorrelated. The clay site(s) showed a stronger correlation with Taupo than with Rotoehu, but the opposite was true for form. The Rotoehu site correlated better with Moerewa 1 than with Taupo for form; this may be because Moerewa 1 and Rotoehu had similar tree heights.

Predicted Genetic Gains

The expected efficiency of reselecting parents for volume on one site to improve volume on another, using heritabilities and genetic correlations, is shown in *Table 5.* For both the pumice and clay regions at was as efficient to select indirectly for the low heritability site using the higher heritability site as it was to select directly on the low heritability site itself. Considering the clay sites, Moerewa 2 was more typical of Northland clays than Moerewa 1, but Moerewa 1 would be the better site for a

Table 6. — Predicted percentage volume gains per unit i for each site from various selection indices using information from differing combinations of sites. Mean values at the respective sites are 101.5, 45.7, 84.6, and 39.1.

Location	A	B	C	D	E
Rotoehu	15.2	19.8	9.0	20.1	4.9
Taupo	20.3	21.9	15.4	20.6	11.6
Moerewa 1	29.3	19.0	31.5	13.2	30.5
Moerewa 2	23.9	14.7	26.2	9.8	25.0

A - Selection for all four sites using information from all four sites.
B - Selection for pumice using information from all four sites.
C - Selection for clays using information from all four sites.
D - Selection for pumice using information from the two pumice sites only.
E - Selection for clays using information from the two clay sites only.

progeny test since (because of its higher heritability) it would give greater gains on a wider range of sites than Moerewa 2.

To better understand how gain would be influenced by regionalising, gains using selection indices were predicted using Equation 6. *Table 6* shows predicted gains from regionalising and not regionalising.

While regionalising (*Table 6,* columns B and C relative to column A) did improve predicted gain, the increase was small (cf averages of 22.2% and 24.8%). Rotoehu had the largest increase (15.2% to 19.8%). Using all four locations to make regional selections (columns B and C) improved gain very little over using only the two locations in that region (columns D and E).

In order to cross-check the predicted gain from index selections, gain was approximated using selection differentials of the 20 New Zealand-wide selections, 20 Northland selections (4 sites) and 20 pumice selections (4 sites). Selection differentials were multiplied by twice the family-mean heritabilities to estimate gain — this allows for selection on both the male and female parents of a seed orchard. Average gain increased from 18% to 23% for regionalising, an estimate very similar to the prediction using Equation 6.

Alternative gain predictions, based on variance component estimation (*Table 2*) are shown in *Appendix 1.* The assumptions that regions and sites within regions are fixed effects accords with both the selection index predictions and the concept of the progeny test. On this assumption selecting for the separate regions would improve gain by a factor of 1.2, implying a greater relative advantage than the selection-index predictions do. Under the much less realistic assumption of regions being a random effect regionalisation would roughly double the expected gain.

It should be noted that if information from a region was ignored when making selections for that region (*Table 6,* columns D and E) the predicted volume gain was reduced dramatically, in this case by over half. Since some clonal series are tested only on pumice sites in New Zealand this means that we may be failing to identify the clones that will perform well in other regions, in particular on Northland clays. So, while regionalising may not be important, progeny testing in a variety of regions is essential.

If only one site per region is available for testing, gains for the region would be less, partly because this would create an effective confounding of family- and family-site interaction effects, and partly because families would be represented by fewer individuals (unless representation is doubled at the single site). The figures in *Table 5,* however, indicate that such losses would be small. The gain predictions (*Appendix 1*) based on variance components (*Table 2*) also indicate only marginal losses, except under the extreme assumption of the sites within regions being a random effect in which case the losses could be around 20%.

General Implications

In Northland even the clay soils are much more variable with respect to tree growth than pumiceland soils. This variability is evident from the two clay sites 1 km apart being less correlated than the two pumice sites 100 km apart and differing in elevation by 200 m.

However, these two clay sites were almost at opposing ends of the fertility scale for such soils, while altitude and rainfall are not major variables within the region. At the same time, close intercorrelations among widely differing pumiceland sites were already an established pattern (e.g., SHELBOURNE and LOW, 1980).

The study, while involving only four sites, has given one of the few indications of a really coherent pattern of genotype-site interaction for *Pinus radiata.* Other studies (e.g., MATHESON and RAYMOND, 1984; SHELBOURNE and LOW, 1980) have failed to reveal coherent patterns, although in some cases the limitations of the field experiments could have obscured real patterns.

The issue of regionalisation has been addressed solely on the basis of growth rate. The tree-form traits, straightness, malformation and branch habit have not shown any rank changes that could argue for regionalisation. However, regionalisation can be justified if relative economic weights of various traits vary according to regions (or site categories). In this case growth rate is generally of paramount importance on Northland clays, but tree form is also important on pumice sites. Inclusion of tree-form traits will not weaken the case for designating the clays as a breeding region or at least a testing region.

Producing regionalised seedlots is difficult to achieve cheaply and effectively using traditional open-pollinated seed orchards. However, it should cost very little (if any) extra if control-pollinated orchards are used.

Conclusions

1. The Northland clay and the pumiceland regions of New Zealand generated marked genotype-environment interaction, as evidenced by analysis of variance and between-site genetic correlations. However, regionalising only increased average predicted volume gain from 22% to 25%. There appear to be parent clones whose families perform well on a variety of sites although they may not always be the very best at a particular site. This group of broadly adapted clones gave predicted gains very close to those from using the very best for a particular region. The large interaction components of variance were not so much because of rank change but because of different variances at each site.

2. Although the production of regionalised seedlots does not appear to improve gain substantially, progeny testing in only one region can result in poor predicted gain for other regions. Progeny tests must be established in more than one region to ensure one is selecting clones that perform well on a variety of sites if the overall goal is to have a widely adapted breed.

3. For both regions, progeny test site selection can be crucial. Of the two sites in each region the site with the higher heritability results in the largest predicted gain for the region. While the higher heritability site was seemingly much less typical of the clay regions, it was sufficiently correlated with the other site in the region to give equal or higher gains through indirect selection than the typical site of lower heritability.

Acknowledgements

This series of trials was established by C. J. A. Shelbourne and T. G. Vincent. The following persons were involved in the field assessment: A. Firth, C. B. Low, R. Cameron, M. Miller, G. Stovold, N. Woods, R. Hahunga, G. Kuru, A. Davy or Fri and R. Sage G. Gover, C. Mothersill, A. Smart of NZFP Forests Ltd. Thanks are also due to J. N. King, C. J. A. Shelbourne and M. D. Wilcox for helpful comments on drafts.

References Cited

Burdon, R. D.: Clonal repeatabilities and clone-site interactions in *Pinus radiata*. Silvae Genetica **20**: 33—39 (1971). — Burdon, R. D.: Genetc correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genetica **26**: 145—228 (1977). — Burdon, R. D.: Generalisation of multi-trait selection indices using information from several sites. NZ J. For. Sci. **9**: 145—142 (1979). — Delong, D. M.: The CORR Procedure. In: SAS Users Guide: Basics. Version 5 Edition. SAS Institute Inc., Box 8000, Cary, NC, 27511-8000 (1985). — Lin, C. Y.: Index selection for genetic improvement of quantitative traits. Theor. Appl. Genet. **52**: 49—56 (1978). — Matheson, A. C. and Raymond, C. A.: The impact of genotype × environment interactions on Australian *Pinus radiata* breeding programs. Aust. For. Res. **14**: 11—25 (1984). — Spector, P. C., Goodnight, J. H.: The VARCOMP Procedure. In: SAS Users Guide: Basics. Version 5 Edition. SAS Institute Inc. Box 8000, Cary NC, 27511-8000 (1985). — Spector, P. C., Goodnight, J. H., Sall, J. P. and Sarle, W. S.: Ibid. (1985). — Shelbourne, C. J. A., Burdon, R. D., Carson, S. D., Firth, A. and Vincent, T. G.: Development plan for radiata pine breeding. NZ For. Serv., For. Res. Inst., Rotorua (1986). — Shelbourne, C. J. A. and Low, C. B.: Multitrait index selection of *P. radiata* progenies at five sites and associated genetic gains. NZ J. For. Sci. **10**: 307—324 (1980).

Appendix 1

Gain estimates for regionalising and not regionalising using variance components

Gain from backwards selection using half-sib families is usually expressed as:

$$\text{gain} = 2i\,\sigma^2_{fam} / \sigma_{fm} \qquad \text{(Equation 1)}$$

where: σ^2_{fam} = between-family variance component.
σ^2_{fm} = variance of family means.

When selecting across regions only the pure between-family variance component (σ^2_f) is being selected upon, therefore $\sigma^2_{fam} = \sigma^2_f$. Assuming four test sites (two in each of the two regions) each with 35 reps, the resulting gain equation is, assuming regions and sites within regions to be random effects:

$$\text{gain} = 2i\,\sigma^2_f \left(\sigma^2_f + \sigma^2_{fr}/2 + \sigma^2_{fs(r)}/4 + \sigma^2_e/140\right)^{-1/2} \qquad \text{(Equation 2)}$$

With regions a fixed effect the equation becomes:

$$\text{gain} = 2i\,\sigma^2_{f'} \left(\sigma^2_{f'} + \sigma^2_{fs(r)}/4 + \sigma^2_e/140\right)^{-1/2} \qquad \text{(Equation 3)}$$

and with both regions and sites with regions being fixed effects the equation becomes:

$$\text{gain} = 2i\,\sigma^2_{f''} \left(\sigma^2_{f''} + \sigma^2_e/140\right)^{-1/2} \qquad \text{(Equation 4)}$$

When selecting within a region the family-by-region variance (σ^2_{fr}) belongs with the pure family variance (σ^2_f). Selection takes place on both components of variance, therefore $\sigma^2_{fam} = \sigma^2_f + \sigma^2_{fr}$. Assuming two progeny test sites in a region, each with 35 reps and that sites within regions represent a random effect, the resulting gain equation for regionalising is:

$$\text{gain} = \frac{2i\,(\sigma^2_f + \sigma^2_{fr})}{\left((\sigma^2_f + \sigma^2_{fr}) + \sigma^2_{fs(r)}/2 + \sigma^2_e/70\right)^{1/2}} \qquad \text{(Equation 5)}$$

Assuming regions to be a fixed effect gain may be predicted by the following equation:

$$\text{gain} = 2i\,\sigma^2_{f(r)} \left(\sigma^2_{f(r)} + \sigma^2_{fs(r)}/2 + s^2_e/70\right)^{-1/2} \qquad \text{(Equation 6)}$$

noting that σ^2_{fr} is not really a meaningful parameter in this situation. With both regions and sites within regions being fixed the equation becomes:

$$\text{gain} = 2i\,\sigma^2_{f(r)''} \left(\sigma^2_{f(r)''} + \sigma^2_e/70\right)^{-1/2} \qquad \text{(Equation 7)}$$

Extending the argument to selecting for individual sites

Appendix Table 1. — Gain predictions from variance component estimates under alternative assumptions concerning fixed or random effects. Figures in brackets denote Appendix equations involved.

Regionalisation pattern	Assumptions concerning site effects		
	All random	Regions fixed, site (regions) random	All fixed
None	4.5 (2)	8.0 (3)	9.6 (4)
By regions only	8.9 (5)	9.2 (6)	11.6 (7)
By individual sites	11.6 (8)	11.6 (8)	11.6 (8)

within regions (assuming sites to be representative of localities) the gain equation becomes:

$$\text{gain} = \frac{2i\left(\sigma^2_f + \sigma^2_{fr} + \sigma^2_{fs(r)}\right)}{\left(\sigma^2_f + \sigma^2_{fr} + \sigma^2_{fs(r)} + \sigma^2_e/35\right)^{1/2}} \qquad \text{(Equation 8)}$$

This assumes fully random effects. Alternative assumptions regarding fixed effects do not materially alter this expectation.

Appendix Table 1 shows predicted gains after substituting in variance component estimates from *Table 2*. The gains from regionalising by the two main regions are evident by comparing solutions of Equations 5 and 2, 6 and 3, or 7 and 4 depending on the assumption concerning fixed or random effects. Correspondingly, the gains from regionalising to individual sites are evident from comparing the solution for Equation 8 with those of Equation 5, 6 or 7. The gains foregone by not regionalising can be large and depend strongly on whether fixed or random site effects are involved.

The Progression and Distribution of Graft Incompatibility in Araucaria cunninghamii Ait. ex D. Don

By R. J. Haines and M. J. Dieters

Forestry Research Centre, MS 483, Gympie, Qld 4570, Australia

(Received 9th February 1989)

Summary

The progression and distribution of graft incompatibility in *Araucaria cunninghamii* were examined using grafting records and scion assessment data which were available for a total of 199 clones in seed orchards and clone banks up to 15 years after grafting. The species displays a smooth progression in the onset of incompatibility, tailing off to a final overall incidence of 31% by 10 years after grafting. Although no sharp chronological demarcation is apparent, there is some justification for classification into "early" and "delayed" forms on the basis of the extent of scion elongation prior to the manifestation of incompatibility symptoms. Clonal repeatability for scion length at diagnosis of incompatibility was 0.50. The clonal distribution of early incompatibility is bimodal, with approximately 8% of the population highly incompatible, and the remainder highly compatible. Only two clones displaying a high incidence of delayed incompatibility were identified. Other clones clustered around a compatibility level of approximately 75%. For the severely incompatible clones, flowering race and incompatibility type seem to be associated. Clones displaying a high incidence of early and delayed incompatibility were respectively all early and late flowering. The possibility of a relatively simple genetic control mechanism is discussed, and practical implications are considered.

Key words: Araucaria cunninghamii, graft, incompatibility, scion, rootstock.

Introduction

Araucaria cunninghamii (hoop pine) is an important plantation conifer in Queensland, where over 44000 ha have been established, and is of potential value as a plantation species in several other countries (Nikles, 1980). A breeding programme has operated for approximately 30 years (Nikles and Newton, 1983), and all planting stock now used is raised from seed collected in clonal seed orchards.

Some unusual biological features of the species have had a major impact on the development of seed orchard systems (Haines and Nikles, 1987b). Like other species of *Araucaria*, *A. cunninghamii* has a rigid orthotropic-plagiotropic branching system. As a result of a differential tendency to produce female and male strobili, both orthotropic and plagiotropic ramets have been established in seed orchards, to act respectively as seed producers and pollinators. The wide interclonal variation in flowering season, associated at least partly with provenance, has resulted in the segregation of clones into "early flowering" and "late flowering" "races" for the purposes of allocation to seed orchards.

Graft incompatibility has long been recognised as a problem, but recently has been of particular concern in relation to the use of biclonal orchards for the mass production of superior full-sib families (Haines and Nikles, 1987a). Two forms of graft incompatibility in *A. cunninghamii* were described by Higgins*) (1969, unpublished). The symptoms of "early incompatibility" are profuse budding, very poor elongation and chlorosis of the scion, followed ultimately by scion death. Grafts which undergo greater elongation, but then display reduced growth rate, swelling at the union, chlorosis, necrosis and, finally, death of the scion, have been described as being afflicted by "delayed incompatibility". In terms of the time at which diagnosis can be made, the distinction between these is not sharply defined. Compatible and early incompatible ramets cannot always be distinguished with certainty until three years after grafting, and delayed incompatibility becomes apparent at a range of ramet ages.

Using data now available from a large number of clones grafted in seed orchards and clone banks, the investigation reported here was designed to examine three aspects of the phenomenon:

— the progression of the overall incidence of incompatibility with time;
— the clarity of the separation into early and delayed forms, in terms of the scion lengths at which ramets are diagnosed as incompatible; and

*) Dr. M. D. Higgins, deceased, formerly of Forestry Research Station, Imbil, Queensland.