

INTERNATIONAL GENE POOL EXPERIMENTS IN *PINUS RADIATA*: PATTERNS OF GENOTYPE-SITE INTERACTION

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(Received for publication 30 April 1997; revision 10 March 1998)

ABSTRACT

In 1970 an international exchange of 319 select lots of *Pinus radiata* D. Don was arranged among several countries. Most lots were open-pollinated progenies, with 31 pair-crosses, 26 polycrosses, and two bulked lots. Field experiments were planted with varying field layouts and variable representation of lots. Trials were assessed mainly at 6–8 years from planting, with one trial measured at 14 years and one remeasured at 15 years. Main emphasis was on stem diameter (dbhob), stem straightness scores, branch habit scores (primarily relating to a short-internode light-branching ideal), and malformation, with varying scales used for tree-form traits.

Pairwise genetic correlations between sites were studied, trait by trait, genotype-site interaction being manifested as departures from perfect correlation ($r_g = 1$) between sites.

Usable data came from nine sites: from New Zealand; from South Africa; and, within Australia, from New South Wales (3), from South Australia, from Western Australia (2), and from Victoria. Such data came from 47 lots at one site and from 126–238 lots elsewhere.

Within sites, repeatability of lot means (h^2_g) was good (generally >0.5) for dbhob, stem straightness score, and branch habit score, but sometimes near zero for malformation.

Estimates of between-site genetic correlations (r_g) for dbhob generally exceeded 0.5, but tended to be lower where the two Western Australian sites were involved and were often still lower for the South African site. With an adjustment for assessment-age differences between sites, however, many r_g values were increased but not radically. Some results could be interpreted, but there was often no obvious coherent pattern. For straightness, r_g generally exceeded 0.6, the main exceptions involving one Western Australian site. For branch habit score r_g tended to be still higher, except at the South African site where the scoring criterion was rather different. For malformation, r_g was often very imprecise, but mostly very high and positive. For some sites or pairs of sites inclusion of some native-population lots inflated both h^2_g and r_g , especially for dbhob.

It appears that international exchanges of select genetic material can be beneficial. However, for boosting short- to medium-term genetic gain, imported material should be chosen on appropriate selection criteria, and quite heavy culling from testing may often be needed.

Keywords: genotype-environment interaction; growth rate; tree form; *Pinus radiata*.

INTRODUCTION

Genotype-site interaction is a well-known consideration in deciding on whether genetic improvement work should be regionalised, in terms either of contiguous regions or of other definable site categories. Even where regionalisation is not required, a knowledge of the patterns of interaction can be crucial for efficient screening of selection candidates (Johnson & Burdon 1990).

Where independent tree breeding programmes exist, there is the possibility of advantageous exchanges of genetic material provided that the genotype-site interaction between certain site categories served by different breeding programmes is minor. Given the cost of starting and maintaining an intensive breeding programme with a suitably broad genetic base, the pooling of resources that could be achieved through such exchanges is very attractive. It would be very helpful to know in advance whether or not such exchanges can be expected to offer much in terms of enhanced genetic gain and/or cost savings.

Moreover, *P. radiata* breeding programmes in the main grower countries (Chile, New Zealand, and Australia) have reached the point where new planting is done wholly or predominantly with stock from seed orchards. At the same time, the primary gene resources, in the form of the natural stands, are unattractive as short-term sources of breeding material, and are under varying threats. These threats include effects of urbanisation and, very recently, the arrival and upsurge of pitch canker which can be transmitted by seed, making new seed importations from California very risky.

Between these considerations, the effective genetic management of the species as a domesticated crop is largely in the hands of, or at the mercy of, the tree breeders. International co-ordination of the management would seem highly desirable, yet this is likely to occur only if information is available as to what exchanges of genetic material will be attractive. But if

the co-ordination is not embarked on or at least planned fairly soon it may not be so effective, because such co-ordination is likely to be the key to allowing further exchanges without compromising the future control of inbreeding within the various breeding populations.

There has been limited direct evidence available as to exactly what exchanges of genetic material could be made profitably. This will depend on what material the various parties hold, and what are the patterns of genotype-site interaction among grower countries or, rather, among which regions are interactions minor.

A major initiative on international exchange of select *P. radiata* material was undertaken in 1970 by Shelbourne (1973) (*see also* Johnson 1992). Seedlots, mainly individual progenies, were exchanged among 15 agencies (14 donors, 14 recipients), in a total of nine countries (six contributing, six recipient). The recipient agencies planted out the material according to their own perceived interests. Since then, assessments have been made at various times on varying bases. The different agencies have exploited their plantings to varying degrees as sources of selections for their own breeding programmes. In New South Wales, where three trials were established, a study was made of the patterns of genotype-site interaction among those sites (Johnson 1992). No published study, however, has been made of the wider patterns of interaction that would be represented among a larger sample of plantings. This paper covers such a study, based on usable data from as many of the sites as possible.

The interactions were not studied in the form of genotype-site interaction variances, in relation to the main effects of genotypes and sites. Instead, they were studied in terms of departures from perfect positive genetic correlation ($r_g = 1$) between performance at the various pairwise combinations of sites (Burdon 1977). This approach was adopted partly to cope with the highly disparate and sometimes awkward properties of the data coming in from different trials, and partly because the results it can provide are in important respects much more informative.

MATERIALS AND METHODS

Seedlots

In total, 319 seedlots were involved in the exchange of genetic material (Table 1). While most of them represented open-pollinated families from seed parents, there were 31 pair-crosses, 26 polycrosses, and two bulked seed-orchard or clonal-archive lots. The expected within-lot genotypic variances differ among these categories but, with the typically low to moderate heritabilities of the traits concerned, it was assumed that these differences could be safely ignored.

The sources and the anticipated levels of genetic improvement varied widely among the groups of seedlots, but for purposes of this study it was generally deemed appropriate to treat them as a single composite population. The only exceptions that were made, as suspected outliers, were the progenies from the native Californian populations, which were expected to show effects of neighbourhood inbreeding, and the two progenies from Cedros trees.

Planting Sites

Particulars of the nine sites, under the control of six agencies in three countries, where the trials provided usable data are shown in Table 2. They represent a considerable range of

TABLE 1—List of seedlots (original workplan numbering)

| Group | Serial No. of seedlots | Number of seedlots | Particulars |
|-------|------------------------|--------------------|---|
| 1 | 1 | 1 | Tasmanian OP seed orchard lot |
| 2 | 2–13 | 12* | OP families from Cambria natural stands |
| 3 | 14–20 | 7* | OP families from Año Nuevo natural stands |
| 4 | 21–84 | 64 | New South Wales, mainly seed-orchard OP families |
| 5 | 85–112 | 28 | Australian Capital Territory (ACT), Tallaganda Seed Orchard, OP families |
| 6 | 113 | 1 | Western Australia, bulk of collections from select clone bank |
| 7 | 114–120 | 7 | South Africa, Plus-tree polycrosses |
| 8 | 121–139 | 19 | Victoria State, mainly seed-orchard OP families |
| 9 | 140–168 | 29 | France, select OP progenies from four stands |
| 10 | 169–79 | 11 | Traralgon, Victoria, plus-tree pair-crosses |
| 11 | 180 | 1 | Kenya, Dothistroma-resistant parent, OP progeny |
| 12 | 181–190 | 10 | Queensland, OP families from select trees |
| 12 | 191–192 | 2* | ACT, OP seed from two Cedros parents |
| 14 | 193–198 | 6 | ACT, OP seed from six Guadalupe parents |
| 15 | 199–210 | 12 | ACT, OP seed from 12 Cambria parents |
| 16 | 211–250 | 40 | South Australia, seed-orchard OP families |
| 17 | 251–292 | 42 | New Zealand, 13 CP plus-tree pair-crosses, balance seed orchard OP families |
| 18 | 293–297 | 5 | New Zealand, OP seed from five Cambria parents |
| 19 | 298–304 | 7 | New Zealand, OP seed from seven Guadalupe parents |
| 20 | 305–319 | 15 | South Africa, plus-tree polycrosses. |

OP and CP denotes open-pollinated and control-pollinated respectively.

* Treated as a separate category from the remaining lots, being potential outliers for some variables.

climates, soil textures, and soil fertility. In addition to the range of precipitation there is wide variation in the seasonal distribution of rainfall.

Experimental

Experimental protocols varied widely, largely according to variations among the collaborators in the emphasis placed on research and evaluation in addition to just having the material available as a background resource.

Nursery layouts were reportedly unreplicated throughout.

Field layouts (Table 3) varied in the type of field design, degree of replication, plot size, and the approach to coping with the wide variations among lots in the numbers of plantable seedlings. Four collaborators—New Zealand, South Africa, Western Australia, and a combination of Australian Paper Plantations Pty Ltd (then APM) and CSIRO in Victoria—opted for sets-in-replicates designs (cf. Schutz & Cockerham 1966) of one form or another; in some designs, some lots were repeated across more than one set. In New South Wales and South Africa the general approach was to represent all lots in the first replicate(s), with later replicates becoming progressively smaller as available stock ran out for more lots. Elsewhere, the tendency was to group the scarce seedlots into unreplicated plantings aside from the main experiment. In some places local control seedlots were included, typically with augmented replication.

TABLE 2—Summary of planting site characteristics

| Site | Lat. (°) | Alt. (m) | Precipitation (mm) | Soil characteristics, etc. |
|--------------------|-------------|-------------|-----------------------|--|
| New Zealand | 38 | 400 | 1600 | Deep rhyolitic pumice capped by 30 cm basaltic scoria, undulating, fertile |
| South Africa | 34 | 350 | 1000 | Phosphorus-deficient clay, some imperfect drainage. Slight slope, southerly exposure |
| New South Wales: | | | | |
| Nundle | 31½ | 1160 | 1500(S*) | Basaltic, 0–5° slope |
| Gurnang | 34 | 1140 | 900 | Siltstone-sandstone, slightly metamorphosed, low soil phosphorus, generally flat |
| Wee Jasper | 35 | 890 | 1300(W) | Parent material metabasic (granodiorite + gabbro), slope generally 0–5° |
| South Australia | 38 | 50 | 700(W) | Deep sand, overlying limestone with accessible water table |
| Western Australia: | | | | |
| Kirup | 33 | 160 | 865(W) | Fertile red loam, ex-pasture site, steep slope, northerly aspect |
| Grimwade | 33 | 240 | 797(W) | Loamy sand, ex-bush site, moderate slope, westerly aspect |
| Victoria † | 38 | 80 | 700 | Ex-pasture, loamy sand over heavy clay |

* S or W denote summer or winter rainfall maximum where a strong seasonal maximum is evident

† Australian Paper Plantations Pty Ltd

TABLE 3—Summary of experimental layout parameters (for recorded data)

| Country/State | Layout particulars |
|--------------------------------|---|
| New Zealand | Sets-in-reps, RCB*, 5 sets × 6 reps |
| South Africa | Sets-in-reps, RCB, 7 sets × 30–46 lots, 2–12 plots/lot |
| New South Wales (three trials) | RCB, 4 reps assessed, some imbalance |
| South Australia | RCB, 12 blocks, some imbalance |
| Western Australia: Kirup | Sets-in-reps RCB, 5 reps × 4 sets, 3-tree row plots. |
| Grimwade | Sets-in-reps RCB, 7 reps × 4 sets, 3-tree row plots. |
| Victoria | (a) RCB, 6 reps 45 lots |
| | (b) Sets-in-reps, RCB, 3 reps × 3 sets, 86 lots in 3 sets } 18 lots in common |

Note: Five-tree row-plots planted, unless otherwise stated

* RCB denotes randomised complete block

Representation of the groups of lots (Table 1) in the data used for analysis from the various trials is shown in Appendix 1.

Field Assessments

Traits measured or scored and assessment ages are listed for the various trials in Table 4. Breast-height diameters over bark and stem straightness were assessed throughout, although at varying ages. Branching habit (either explicitly as branch habit quality or as branch cluster frequency) was visually scored on a range of bases. In most, the opposing ends of the scale were designated as light, regular, wide-angled *v.* heavy, irregular, steep-angled branching,

TABLE 4—Particulars of data used, by experiment(s)

| Country/state | Age(s) | Dbhob | Height | Str. | Br. qual. | Br. fr. | Clusters* | Malformation | |
|---------------------------|--------|-------|--------|------|-----------|---------|-----------|---------------|-----------|
| | | | | | | | | Forks | Ramicorns |
| New Zealand | 6.5 | ✓ | • | 1-9 | • | 1-9 | • |1-9..... | • |
| | 15 | ✓ | • | • | • | • | • | • | • |
| New South Wales (3 sites) | 8 | ✓ | • | 1-6 | 1-6 | • | • | ✓ | ✓ |
| South Africa | 8 | ✓ | ✓ | 1-8 | 1-8† | • | • | • | • |
| South Australia | 8 | ✓ | ✓ | 1-6 | 1-6 | • | ✓ | ✓ | ✓ |
| Western Australia | | | | | | | | | |
| Kirup | 6 | ✓ | • | 1-5 | 1-5 | • | • |1-3..... | • |
| Grimwade | 14 | ✓ | • | 1-5 | 1-4 | • | • |1-3..... | • |
| Victoria | 10 | ✓ | ✓ | 1-6 | 1-6 | • | ✓ | ✓ | • |

Str. = straightness score

Br. qual. = branch habit quality score (regularity and size of branches, generally in some relation to tree size)

Br. fr. = branch cluster frequency score

✓ = actual measurements made

* = count of branch clusters to 6 m from ground

† = branch thickness only, without allowing for tree size

or minor variations thereof. In Western Australia, however, trees were rated primarily for size of branching in relation to diameter of the individual stem, while in South Africa the rating was based on branch thickness. In New Zealand trees were rated for branch cluster frequency, which implied that a “multinodal” or “short-internode” type of branching was part of the ideotype that defined a breeding goal. Insofar as a high frequency of branch clusters tends to be associated with light, regular, wide-angled branching, the disparities between the scoring scales would be much reduced although long internodes would otherwise be attractive. The incidence of stem malformation was finally recorded for some sites by converting the combined incidence of forks and ramicorns on each tree to a combined score with a 2:1 weighting of the counts.

DATA ANALYSIS

Preliminary statistical analyses were conducted in order to explore the possible need for data transformation and to ascertain the appropriate analysis of variance models, at the respective sites. These analyses were also used to establish that plot means could be used as the basic data units with minimal bias. This left the statistical lots \times replicates interaction as the effective residual. Preliminary analyses were also used to decide the levels of replication of individual lots for acceptance of data for analysis. These were all six replicates (reps) for New Zealand; \geq five reps for South Africa, South Australia, and Grimwade (Western Australia); \geq four reps for Kirup (Western Australia); and \geq two reps elsewhere.

Analyses of variance at each site employed SAS Proc GLM/SS3 (SAS 1996) which tested for lot differences overall, gave least-squares means for the lots and average repeatabilities of lot means, and allowed estimation of variance components. The repeatabilities of lot means (h^2_g) were conveniently estimated as (King *et al.* 1993):

$$\hat{h}^2_g = (F - 1)/F \quad (1)$$

where F is the F ratio in the test for lot differences, which was made directly against the residual. The statistical significance of a repeatability is automatically given by the F ratio and the degrees of freedom.

Pairwise genetic correlations (r_g) between-sites were then estimated for each trait according to the availability of data (Table 5). (More correctly, r_g would denote an estimate of ρ_g). In one case, where appropriate data were available from a site at more than one age, age-age genetic correlations were also estimated. With respect to branch characteristics, between-site correlations were estimated despite the variations in criteria adopted for rating, on the basis that these variations could be taken into account in interpreting the estimated correlations.

From the results of analysis of variance a genetic correlation between sites x and y can be estimated from either of two formulae:

$$r_g = r_p / (\hat{h}^2_{gx} \cdot \hat{h}^2_{gy}) \quad (2)$$

$$\text{or} \quad r_g = c \hat{\sigma}_{V_{gxy}} / \sqrt{\hat{\sigma}^2_{gx} \cdot \hat{\sigma}^2_{gy}} \quad (3)$$

where r_p = correlation of lot means between the two sites,

\hat{h}^2_{gx} , \hat{h}^2_{gy} are the repeatabilities (“heritabilities”) of lot means at the respective sites,

TABLE 5—Numbers of lots in common (with acceptable representation) between pairs of sites. Above diagonal with native-population lots, below diagonal without.

| Country & site | New Zealand | South Africa | Australia | | | | | |
|-----------------------------|-------------|--------------|-----------------|---------|------------|-----------------|-----------------------------|----------|
| | | | New South Wales | | | South Australia | Western Australia (2 sites) | Victoria |
| | | | Nundle | Gurnang | Wee Jasper | | | |
| New Zealand | 126\147 | 133 | 108 | 112 | 125 | 138 | 105 | 36 |
| South Africa | 112 | 193\214 | 144 | 147 | 170 | 194 | 148 | 43 |
| New South Wales | | | | | | | | |
| Nundle | 88 | 124 | 142\162 | 160 | 166 | 153 | 113 | 45 |
| Gurnang | 92 | 127 | 140 | 148\168 | 160 | 148 | 116 | 45 |
| Wee Jasper | 105 | 150 | 140 | 146 | 215\235 | 183 | 143 | 44 |
| South Australia | 117 | 173 | 128 | 133 | 163 | 217\238 | 167 | 45 |
| Western Australia (2 sites) | 92 | 135 | 100 | 103 | 130 | 154 | 178\191 | 45 |
| Victoria | 26 | 33 | 35 | 35 | 34 | 34 | 35 | 35\45 |

cov_{gy} = genotypic covariance between performances at the respective sites which is estimated by the mean cross-product of lot means,
 $\hat{\sigma}_{\text{gx}}^2, \hat{\sigma}_{\text{gy}}^2$ are the among-lot variances at the respective sites.

In the event of very incomplete overlap between a pair of sites in the representation of lots the following formula has advantages (Burdon 1991):

$$r_g = \hat{\text{cov}}_{\text{gxy}} / [[\text{SS}_{\text{gx}} / (k - 1) - \hat{\sigma}_{\text{ex}}^2][\text{SS}_{\text{gy}} / (k - 1) - \hat{\sigma}_{\text{ey}}^2]]^{0.5} \quad (4)$$

where k = number of seedlots common to the two sites

SS_{gx} and SS_{gy} are the corrected sums of squares for the inputted means of the k seedlots at the respective sites.

$\sigma_{\text{ex}}^2, \sigma_{\text{ey}}^2$ are the error variances of estimated lot means at the respective sites (which were estimated using data from all available lots at each site rather than just the k lots, with expected gains in precision).

With a fully balanced classification, all three equations for r_g give identical estimates. These equations assume that the means for all lots were estimated with equal precision, which would be automatically violated by imbalance in the within-site classifications. For this reason, and the differing subsets of lots that were adequately represented in various pairs of sites, most of the r_g values were approximations in some degree. The extent of these approximations was limited by eliminating, from the processes of estimating h_g^2 and cov_g , those seedlots that were below a prescribed threshold of representation at either site, rather than by attempting any elaborate weighting procedure. Trade-offs, however, arose between obtaining relatively high and uniform precision of lot means within sites and the values of k between pairs of sites.

The inputted least-squares means used for estimating cov_g were not necessarily the most precise available. Rather, the emphasis was on using sets of means of well-characterised average precision in order to avoid bias in r_g .

The statistical significance of r_g ($H_0 : r_g = 0$) is automatically that of r_p in Eq. 2 (Burdon 1977). Tests for genotype-site interaction in the form of departures from $r_g = +1$ were not attempted; they have been suggested but they are problematic (Burdon 1977). Rather, the emphasis was on the general trends shown by the between-site correlations, knowing that the confidence limits for any such pairwise correlation are likely to be quite wide. In any case, the precision of r_g will tend to be low if either of h_{gx}^2 or h_{gy}^2 is low, or both of them are.

Two alternative equations (2 and 4) were often used for corroboration where sites with problematic data sets were involved, the results for Eq. 4 being presented. In fact, results from these equations almost always agreed very closely.

Since the rating scales used by some agencies for tree-form traits were inverse relative to those used by the others, all between-site genetic correlations were adjusted for sign. Details of the procedures adopted to cope with problems posed by the properties of data from particular sites are covered in Appendix 2. On one site, within-site genetic correlations (age-age for dbhob in New Zealand) were estimated using Eq. 3. The denominator variances were estimated from mean-squares in analyses of variance, and cov_g estimated analogously from analysis of between-trait mean cross-products which were obtained by using the MANOVA

statement in Proc GLM (SAS 1996). No specific test of statistical significance was attempted, such tests being suspect.

The 19 lots from the native Californian stands and the two Cedros hybrid lots, being potential outliers with respect to at least some traits, were liable to generate inflated r_g values. Accordingly, repeatabilities of lot means and between-site correlations were estimated both including them and excluding them from the data analysis, as a cross-check.

For dbhob, in which imperfect age-age genetic correlations can generate significant rank changes with time, a tentative adjustment was made to r_g between sites that were assessed at different ages (Appendix 3).

RESULTS

Repeatabilities of Lot Means

For dbhob there was almost universally strong resolution of lot differences overall (Table 6), which is reflected in repeatabilities that were all at least 0.5, with $p < 0.0001$ in all but one instance. However, the repeatabilities were always lower when the native-population lots were omitted from consideration, although this difference was least marked in Western Australia and South Africa.

Height, for which data were available for three sites, showed much more variable resolution of lot differences, \hat{h}_g^2 being 0.47, 0.81, and 0.26 for South Africa, South Australia, and Victoria respectively for all lots, compared with 0.45, 0.64, and 0.15 respectively with native-population lots omitted.

Stem straightness scores generally showed similar resolution of lot differences to dbhob. However, the repeatabilities of lot means (Table 7) were more variable among sites and showed no clear tendency to differ according to whether or not the native-population lots were considered. The highest value was shown in South Australia, where the replication was greatest, but the lowest values, in South Africa and at Kirup in Western Australia, were also associated with fairly high replication.

The various branch habit scores generally showed similar repeatabilities again (Table 8). However, there were some low values in Victoria where there were many fewer lots represented in the data and the statistical resolution of differences was weak. The values for South Africa were also fairly low. Lot-mean repeatabilities for branch cluster counts were higher, being around 0.84 in South Australia, and 0.59 and 0.49 with and without native-population lots respectively in Victoria. A relatively high value was also observed in New Zealand where the rating was directed at branch cluster frequency. As with dbhob, the values tended to be lower when the native-population lots were omitted from consideration. Branch angle scores in the Western Australian sites (details not shown) showed similar repeatabilities to the branch thickness scores.

The malformation scores showed highly variable lot-mean repeatabilities among the various sites (Table 9), being low or non-significant ($p > 0.05$) in the South African, Western Australian, and Victorian sites, although moderate to high elsewhere. Malformation scores sometimes showed marked skewness, and the components (counts of forks and ramicornis (results not generally shown)) sometimes showed even greater skewness. Use of normalising transformations, however, generally had very little effect on the results of analyses of variance, and so the results presented apply to untransformed variables.

TABLE 6—Estimates of within-site repeatability of lot means (h_g^2) and genetic correlations (r_g) for dbhob. Above diagonal with native-population lots, below without.

| | New Zealand | | South Africa | New South Wales | | | South Australia | Western Australia | | Victoria |
|-------------------|-------------|-------------|--------------|-----------------|-------------|-------------|-----------------|-------------------|-------------|-------------|
| | 6.5 years | 15 years | | Nundle | Gurnang | Wee Jasper | | Kirup | Grimwade | |
| \hat{h}_g^2 | 0.61 | 0.74 | 0.61 | 0.68 | 0.61 | 0.65 | 0.71 | 0.64 | 0.53 | 0.62 |
| New Zealand | | | | | | | | | | |
| 6.5 yr | 1 | 0.76 | 0.26 | 0.61 | 0.67 | 0.56 | 0.69 | 0.72 | 0.84 | 0.96** |
| 15 yr | 0.63† | 1 | 0.31 | 0.72 | 0.61 | 0.62 | 0.69 | 0.39** | 0.62 | 0.67** |
| South Africa | 0.23 | 0.29* | 1 | 0.50 | 0.33 * | 0.15 | 0.16 | 0.05 | 0.30 | 1.02 |
| New South Wales | | | | | | | | | | |
| Nundle | 0.44 ** | 0.63 | 0.44 ** | 1 | 0.98 | 0.80 | 0.60 | 0.44 *** | 0.51 | 0.86 |
| Gurnang | 0.55 ** | 0.49** | 0.23 | 1.02 | 1 | 0.74 | 0.50 | 0.35 * | 0.49 *** | 0.96 |
| Wee Jasper | 0.40 * | 0.38* | -0.11 | 0.63 | 0.70 | 1 | 0.65 | 0.51 | 0.70 | 0.93 |
| South Australia | 0.63 *** | 0.56 | 0.15 | 0.45 ** | 0.35 * | 0.59 | 1 | 0.43 | 0.44 | 0.80 |
| Western Australia | | | | | | | | | | |
| Kirup | 0.64 | 0.28* | -0.00 | 0.30 | 0.28 | 0.53 | 0.39 *** | 1 | 0.68 | 0.55 * |
| Grimwade | 0.76 | 0.43** | 0.20 | 0.28 | 0.36 * | 0.64 | 0.36 ** | 0.67 | 1 | 1.02 |
| Victoria | 0.63 | -0.08 | 0.63 * | 0.60 | 0.76 * | 0.51 | 0.80 | 0.42 | 0.61 | 1 |
| \hat{h}_g^2 | 0.53 | 0.68 | 0.60 | 0.59 | 0.54 | 0.54 | 0.66 | 0.60 | 0.50 | 0.53** |

Bold type $p < 0.0001$ *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$

† no reliable test for statistical significance

TABLE 7—Estimates of within-site repeatability of lot means (\hat{h}_g^2) and between-site genetic correlations (r_g) for stem straightness scores. Above diagonal with native-population lots, below diagonal without.

| | New Zealand | South Africa | New South Wales | | | South Australia | Western Australia | | Victoria |
|-------------------|-------------|--------------|-----------------|-------------|-------------|-----------------|-------------------|-------------|-------------|
| | | | Nundle | Gurnang | Wee Jasper | | Kirup | Grimwade | |
| \hat{h}_g^2 | 0.64 | 0.47 | 0.59 | 0.57 | 0.64 | 0.77 | 0.40 | 0.55 | 0.53 ** |
| New Zealand | 1 | 0.53 ** | 0.56 | 0.31 | 0.58 | 0.78 | 0.19 | 0.60 | 1.26 * |
| South Africa | 0.68 | 1 | 0.59 | 0.82 | 0.72 | 0.71 | 0.29 | 0.90 | 1.18 ** |
| New South Wales | | | | | | | | | |
| Nundle | 0.49 ** | 0.59 *** | 1 | 0.70 | 0.74 | 0.78 | 0.39 * | 0.58 | 0.92 *** |
| Gurnang | 0.34 | 0.82 | 0.68 | 1 | 0.73 | 0.69 | 0.17 | 0.52 | 0.88 ** |
| Wee Jasper | 0.82 | 0.67 | 0.71 | 0.67 | 1 | 0.83 | 0.59 | 0.64 | 0.59 * |
| South Australia | 0.83 | 0.72 | 0.74 | 0.66 | 0.83 | 1 | 0.29 | 0.65 | 0.66 ** |
| Western Australia | | | | | | | | | |
| Kirup | 0.22 | 0.26 | 0.40 * | 0.11 | 0.58 ** | 0.26 | 1 | 0.46 ** | 1.02 *** |
| Grimwade | 0.65 | 0.90 | 0.51 *** | 0.44 ** | 0.53 ** | 0.63 | 0.40 * | 1 | 0.75 ** |
| Victoria | 1.74 ** | 0.84 * | 0.93 ** | 0.83 * | 0.52 | 0.62 * | 0.97 ** | 0.75 * | 1 |
| \hat{h}_g^2 | 0.64 | 0.46 | 0.60 | 0.55 | 0.63 | 0.74 | 0.40 | 0.53 | 0.59 |

Bold type $p < 0.0001$

*** $p < 0.001$

** $p < 0.01$

* $p < 0.05$

TABLE 8—Estimates of within-site repeatability of lot means (h^2_g) and between-site genetic correlations (r_g) for branch habit scores. Above diagonal with native-population lots, below diagonal without.

| | New Zealand† | South Africa | New South Wales | | | South Australia | Western Australia | | Victoria |
|-------------------|--------------|--------------|-----------------|-------------|-------------|-----------------|-------------------|-------------|----------|
| | | | Nundle | Gurnang | Wee Jasper | | Kirup | Grimwade | |
| \hat{h}^2_g | 0.73 | 0.39 | 0.72 | 0.70 | 0.67 | 0.77 | 0.51 | 0.52 | 0.36* |
| New Zealand | 1 | 0.29 | 0.65 | 0.71 | 0.65 | 0.60 | 0.70 | 0.46 *** | 0.60 |
| South Africa | 0.36 | 1 | 0.09 | 0.51 ** | 0.36 | 0.35 ** | 0.17 | 0.28 | 0.58 |
| New South Wales | | | | | | | | | |
| Nundle | 0.60 | 0.04 | 1 | 0.74 | 0.87 | 0.74 | 0.54 | 0.70 | 0.73 * |
| Gurnang | 0.71 | 0.50 * | 0.64 | 1 | 0.93 | 0.83 | 0.55 | 0.90 | 0.97 *** |
| Wee Jasper | 0.72 | 0.24 | 0.85 | 0.90 | 1 | 0.94 | 0.71 | 0.80 | 1.01 *** |
| South Australia | 0.64 | 0.22 | 0.72 | 0.78 | 0.92 | 1 | 0.71 | 0.74 | 0.93 *** |
| Western Australia | | | | | | | | | |
| Kirup | 0.67 | 0.08 | 0.50 ** | 0.58 | 0.78 | 0.76 | 1 | 0.64 | 0.49 |
| Grimwade | 0.39 ** | 0.17 | 0.56 | 0.93 | 0.74 | 0.63 | 0.62 | 1 | 0.89** |
| Victoria | -0.54 | 0.14 | 0.72 | 0.75 | 1.07 | 1.01 | 0.19 | 0.71 | 1 |
| \hat{h}^2_g | 0.72 | 0.34 | 0.65 | 0.60 | 0.59 | 0.71 | 0.47 | 0.47 | 0.11 |

Bold type $p < 0.0001$ *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$

† branch cluster frequency score

TABLE 9—Estimates of within-site repeatability of lot means (\hat{h}_{g}^2) and between-site genetic correlations (r_{g}) for malformation. Above diagonal with native-population lots, below diagonal without.

| | New Zealand | New South Wales | | | South Australia | Western Australia | | Victoria† |
|------------------------|-------------|-----------------|-------------|-------------|-----------------|-------------------|-------------|-----------|
| | | Nundle | Gurnang | W. Jasper | | Kirup | Grimwade | |
| \hat{h}_{g}^2 | 0.58 | 0.13 | 0.44 | 0.45 | 0.67 | 0.07 | 0.19* | 0.29 |
| New Zealand | 1 | 1.00 *** | 0.77 | 0.86 | 1.07 | 1.21 ** | 0.82 *** | -0.27 |
| New South Wales | | | | | | | | |
| Nundle | 0.89 * | 1 | 0.81 ** | 1.01 | 0.96 | 1.50 | 0.64 | 0.89 |
| Gurnang | 0.88 | 0.69 * | 1 | 0.87 | 0.74 | 0.97 * | 1.36 | -0.17 |
| Wee Jasper | 1.02 | 0.98 *** | 0.99 | 1 | 0.77 | 1.68 *** | 1.15 | 0.05 |
| South Australia | 1.08 | 0.84 *** | 0.70 | 0.68 | 1 | 1.24 *** | 1.47 | -0.03 |
| Western Australia | | | | | | | | |
| Kirup | 1.49 *** | 1.26 | 0.80 | 1.99 | 1.54 | 1 | 1.78 | -0.39 |
| Grimwade | 0.72 ** | 0.59 | 1.02 | 1.16 | 1.41 | 2.08 | 1 | 0.68 |
| Victoria | -0.51 | 0.74 | -0.11 | -0.26 | 0.13 | -0.39 | 0.34 | 1 |
| \hat{h}_{g}^2 | 0.58 | 0.12 | 0.42 | 0.41 | 0.63 | 0.06 | 0.21* | 0.23 |

Bold type $p < 0.0001$

*** $p < 0.001$

** $p < 0.01$

* $p < 0.05$

† forks only

Genetic Correlations

Estimates of between-site genetic correlations for dbhob are shown in Table 6. Values were extremely variable, ranging from close to unity to small negative values, although the lower confidence limits of all estimates were clearly well within the upper theoretical bounds, while the two negative estimates were very close to zero. Among the sites, New Zealand, the three New South Wales sites, South Australia, and Victoria were generally associated with moderate to high inter-correlations. However, some of the correlations involving the Victorian site, where far fewer data were available, were statistically non-significant ($p > 0.05$). The two Western Australian sites, especially Kirup, tended to show lower intercorrelations, and the South African site the lowest inter-correlations of all, except with the poorly represented Victorian site. As with the repeatabilities of site means, the estimated correlations tended to be lower when the native-population lots were disregarded. This was more marked for correlations involving New Zealand, the three New South Wales sites (where the trees were older), and Victoria.

After the adjustment for differences in sites in age of measurement, many of the r_g values were raised (Table 10) but never radically even through some relative age differences were large.

Height (assessed at only two sites—details not shown) showed almost zero genetic correlations between South Australia and South Africa, but estimated genetic correlations exceeded unity between these sites and Victoria, where the calculated repeatability of lot means was low.

Stem straightness scores (Table 7) showed much more consistently high estimates of between-site correlations than did dbhob, although this difference was minor overall after adjusting r_g for measurement-age differences in the case of dbhob (Table 10). Only one site, Kirup, tended to be involved in weak correlations for straightness (Table 7). All correlations were in fact positive. Inclusion or exclusion of the native-population lots was generally immaterial.

Branch habit scores, on the whole, tended to show even higher positive between-site correlation estimates (Table 8), the one clear exception being the South African site where the ratings focused specifically on branch thickness. The fact that the New Zealand ratings were specifically on branch cluster frequency did not appear to affect the pattern. As with stem straightness, inclusion or exclusion of native population lots generally had little effect on the results, allowing that the figures for the Victorian site were very imprecise, particularly when the native-population lots were excluded (Table 8).

Malformation scores (Table 9) generally showed very high positive between-site correlation estimates, except for some obviously imprecise values involving Victoria. Many of the values exceeded the theoretical upper bound of unity, particularly those involving the Western Australian sites where the calculated repeatabilities of lot means were very low. While none of the estimates would significantly exceed the upper theoretical bound (which in fact is equivalent to obtaining $F < 1$ in testing for genotype-site interaction in analysis of variance involving genotypes and sites as main effects), the number of very high values suggests that lot means in the Western Australian sites were actually estimated better than the apparent repeatabilities indicated, which can easily happen through random errors, especially with a variable showing such severe non-normality of distribution. In fact,

TABLE 10—Estimates of genetic correlations for dbhob, after adjusting for assessment-age difference between sites (Appendix 3) (cf. Table 6). Above diagonal with native-population lots, below without. Dashed lines enclose correlations where no adjustment was needed.

| | New Zealand | | South Africa | New South Wales | | | South Australia | Western Australia | | Victoria |
|---------------------------|-------------|----------|--------------|-----------------|---------|------------|-----------------|-------------------|----------|----------|
| | 6.5 years | 15 years | | Nundle | Gurnang | Wee Jasper | | Kirup | Grimwade | |
| New Zealand | | | | | | | | | | |
| 6.5 years | 1 | — | 0.28 | 0.65 | 0.71 | 0.60 | 0.73 | 0.73 | 1.08 | 1.10 |
| 15 years | — | 1 | 0.38 | 0.85 | 0.74 | 0.76 | 0.84 | 0.53 | 0.63 | 0.75 |
| South Africa (8 years) | 0.25 | 0.37 | 1 | 0.50 | 0.33 | 0.15 | 0.16 | 0.05 | 0.36 | 1.09 |
| New South Wales (8 years) | | | | | | | | | | |
| Nundle | 0.47 | 0.79 | 0.44 | 1 | 0.98 | 0.80 | 0.60 | 0.48 | 0.60 | 0.92 |
| Gurnang | 0.59 | 0.62 | 0.23 | 1.02 | 1 | 0.74 | 0.50 | 0.38 | 0.58 | 1.03 |
| Wee Jasper | 0.43 | 0.48 | −0.11 | 0.63 | 0.70 | 1 | 0.65 | 0.56 | 0.83 | 0.99 |
| South Australia (8 years) | 0.68 | 0.71 | 0.15 | 0.45 | 0.35 | 0.59 | 1 | 0.47 | 0.52 | 0.85 |
| Western Australia | | | | | | | | | | |
| Kirup (6 years) | 0.66 | 0.40 | −0.00 | 0.33 | 0.31 | 0.59 | 0.43 | 1 | 0.87 | 0.64 |
| Grimwade (14 years) | 1.02 | 0.44 | 0.25 | 0.34 | 0.44 | 0.79 | 0.44 | 0.93 | 1 | 1.15 |
| Victoria (10 years) | 0.73 | −0.08* | 0.68 | 0.65 | 0.83 | 0.55 | 0.86 | 0.51 | 0.70 | 1 |

* No adjustment made because $r_g < 0$.

estimated correlations involving the component traits, forking and to a lesser extent ramicorns, often fell even further out of bounds (details not shown).

For three of the variables the Victorian site gave a disproportionate number of very high correlation estimates. This could well reflect the inherently low statistical power of the data from that site, plus a possible interdependence of the errors in the genetic statistics for the different traits.

DISCUSSION

Statistical Aspects

It is necessary to consider the statistical limitations of the combined data set represented in all the trials considered, and their likely impacts on the estimation errors.

As already mentioned, coefficients of relationship were not identical among the various lots, which included both full-sib and half-sib progenies plus some bulked seedlots. There were also variations among some categories in the levels of expected genetic improvement. While these factors may be unimportant for estimating between-site genetic correlations they pose a problem for obtaining satisfactory estimates of individual heritabilities within sites which could help characterise the resolving power of various sites for selection for elsewhere.

Various approximations were deemed necessary, in the interest of obtaining sufficient linkages, in terms of common lots between pairs of sites. It was assumed that for any site, lot means were estimated with the same level of precision throughout, although the samples of lots that were common to other sites would show some variation in this respect. It was also assumed that the inherent variability among lots was similar among sites and among the subsets of lots that were common to various pairs of sites. Some departures from these assumptions were inevitable, particularly as collaborators varied in their use of their own lots in the field trials, and in the numbers of planting stock from the lots contributed by various other collaborators. These complications led to correlations being estimated using both the alternative equations 2 and 4 as a cross-check.

For the tree-form traits, differences among collaborators in rating scales or scoring criteria, and the different assessment crews, were obvious sources of potential interaction, particularly for the branching behaviour. Yet the generally high correlations often observed must reflect good concurrence among observers as well as little biological rank change interaction. For branch habit, it is noteworthy that in South Africa, which showed the lowest correlations with elsewhere, the scoring criterion was rather different from that in most other sites.

For the three New South Wales sites our results agreed very closely with those of Johnson (1992), despite our using different criteria for inclusion of data. The estimation errors for the various correlations in site arrays were far from independent, because they had common contributions from the errors involving the site concerned. In this connection, it is suspected that the correlations involving the Victorian site are generally inflated; this could reflect under-estimates of true h^2_g which in turn could reflect fortuitous overdispersal of errors which would depress the denominators' values in Eq. 2 and 3. While there is no specific reason to suspect underdispersal of errors on any particular site, some appreciable random

under-dispersal might well occur, with consequent under-estimation of genetic correlations with other sites.

Lack of nursery-bed replication, if accompanied by a carry-over of effects of nursery stock size, could inflate the variances of lot means for diameter during the first few years. This would inflate the variances and repeatabilities of lot means and thence estimated genetic correlations among sites that were served by the same nursery (as in New South Wales) but depress the estimated genetic correlations between sites served by different nurseries.

The adjustment of r_g values for differences between sites in measurement age was necessarily tentative, and so the adjusted values must be viewed with great caution. The assumption of a single function governing age-age correlations at all sites is simplistic, and there may have been over-adjustment because the parameter values were chosen from results from sites where needle cast can drive strong rank changes (King & Burdon 1991; cf. Burdon *et al.* 1992b).

Interpretation

The inclusion of data from the native Cambrian material and the Cedros hybrids, which grew relatively poorly at most sites, was thought likely to inflate between-site genetic correlations. This seems to have happened in most dbhob data (Table 6), such that the correlations disregarding these lots provide a more reliable guide to the practical importance of genotype-site interaction for growth rate. For other traits, however, inclusion or exclusion of that material appears to have had very little influence on the results (Tables 7–9).

The trial sites, while diverse, still represent a finite sample which cannot therefore be very representative. Given the difficulties that have been experienced by some workers in identifying coherent patterns of genotype-site interaction in *P. radiata* (Matheson & Raymond 1984; Carson 1991), this is a concern. On the other hand, some of the sites feature phosphorus deficiency, which has been associated with some very coherent patterns of interaction (Johnson & Burdon 1990). At the same time, most of the sites would appear to be at least representative of important site categories for selection, testing, and deployment of genetically improved stock among the collaborating agencies. The New Zealand trial was on a fertile and highly productive site type, although on it *Dothistroma* needle blight and *Cyclaneusma* needle cast can be severe in susceptible *P. radiata* material. This site type has been intensively used for both selection and testing, although the pattern of microsite variation made the row-plot layout inherently inefficient, and it evidently cross-correlates well for growth performance with a wide range of other New Zealand site types (Shelbourne & Low 1980; cf. Carson 1991). Moreover, it appears that on the volcanic plateau of the North Island, within which the New Zealand trial was located and where around 400 000 ha of *P. radiata* are grown, genotype-site interaction is very minor indeed (Shelbourne & Low 1980; Johnson & Burdon 1990) despite wide variation in both altitude and terrain.

The South Australian site was representative of large areas which comprise a high proportion of the State's plantation forest and a significant area in westernmost Victoria. The three New South Wales sites, while diverse, represented some important categories in the spectrum of site types. Of these sites, Wee Jasper would be the most typical, with relatively good fertility, but a minor problem with *Dothistroma* in the hollows. The Gurnang site was relatively dry and infertile, being somewhat phosphorus-deficient, and rates as being near the lower limit of acceptable quality for plantation forestry. The Nundle site, being in a summer-

rainfall area, posed severe adaptational problems for *P. radiata* which were clearly manifested in severe Dothistroma blight (Ades & Simpson 1991; Johnson *et al.* 1997; cf. Burdon *et al.* 1992a) despite inherent fertility and rainfall that are conducive to good productivity. The Victoria site was also representative of a substantial portion of the plantation forest estate there, although there were significant areas of quite different soil types. The two Western Australian sites were on contrasting soil types, of which both rated as fairly typical of their respective parts of the fertility spectrum.

The South African site, being markedly phosphorus-deficient, typified a widespread (although easily corrected) problem of growing *P. radiata* within the climatically suitable winter-rainfall zone of Cape Province.

Nevertheless, it was only for the New Zealand site that there was appreciable direct evidence that it was broadly representative of a large and definable unit within which rank-change interaction is very minor indeed.

In any event, the between-site genetic correlations for stem diameter growth were often very imperfect (Tables 6 and 10), even allowing for the spread of assessment ages and the virtual certainty that age-age genetic correlations would be by no means perfect. Some of the notably poor genetic correlations involved pairs of sites of which only one was phosphorus-deficient, although a coherent pattern in this respect was not evident. Susceptibility to Dothistroma needle blight was another factor that evidently influenced the correlations. When the highly susceptible Cambria material was included in the data analysis, the correlation between the two sites of highest Dothistroma hazard (New Zealand and Nundle) was markedly increased for dbhob. Apart from these examples, however, no very coherent pattern of genotype-site interaction has emerged for dbhob (cf. Matheson & Raymond 1984; Carson 1991), at least in respect of recognisable site factors. It may well be that certain lots contributed predominantly to the interactions, but with the very imperfect repeatabilities of lot means at individual sites (Table 6), and the numerous missing lot/site subclasses, not to mention some within-site imbalance, it would be difficult to arrive at any detailed interpretation. A much more detailed analysis of the dbhob results, however, may shed further light.

It is tempting to try to identify from Tables 6 and 10 groups of sites within which between-site genetic correlations are high and within which they are low. However, given the lack of a really clear pattern (which may stem largely from estimation errors) and doubts as to the representativeness of various sites, detailed inferences have not been drawn.

Straightness, by comparison with dbhob, showed consistently strong genetic correlations among almost all sites, despite likely variation in the site conditions that might influence stem straightness, and likely variations among assessment crews in the weightings given to different components of crookedness (lean, sweep, and sinuosity). This was despite a widespread perception (which could not be systematically verified because the visual scores were aimed at resolution of within-trial differences) that straightness differs so much among sites that it would rank high among the breeding-goal traits at some sites but not at others.

Branching likewise showed generally good between-site genetic correlation despite the obvious diversity of scoring scales that were used and the associated differences in emphasis on different aspects of branching. (The main exception among the sites was South Africa, where scoring was on the basis of branch size without any allowance for tree size). It would imply, though, that no collaborator was placing a high premium on internode length.

Malformation has also shown apparently high between-site genetic correlations; although it was not always assessed, the ratings or scoring varied markedly among sites, and the resolution of lot differences on four sites was so weak as to give correlation estimates that were at best very imprecise.

Overall, the behaviour of the various traits, involving both growth rate and tree form, in terms of their comparative levels of interaction, was well foreshadowed by Johnson's results (1992) for just the three New South Wales sites where dbhob was more interactive than the tree-form traits.

Application

The results for diameter, which shows generally strong but by no means perfect between-site genetic correlations, indicate that some very wide geographic transfer of genetic material can be made with modest sacrifice of genetic gain, even without local testing. The losses in genetic gain through imperfect genetic correlations will be markedly reduced if, after introduction, progenies are deployed for forwards selection with an acceptance that some progenies can be dropped altogether. Such losses of gain upon transfer might also be reduced by corrective measures such as fertiliser application, spraying against *Dothistroma*, or using tending regimes that otherwise reduce the *Dothistroma* hazard.

Rank-change interactions for the tree-form traits appear to be inherently minor. Nevertheless, certain exchanges of genetic material may be of limited immediate value, even where growth rate correlates well across sites, if selection criteria have differed strongly among breeding programmes. It has become evident (Shelbourne unpubl. data) that the New Zealand breeding programme, having been based on comparatively fertile sites, has tended to place greater emphasis on tree form than some of the other breeding programmes, since overseas lots generally performed worse in this respect on the New Zealand site than the local lots. With new plantings becoming concentrated on ex-pastoral sites rather than forest sites, some breeders outside New Zealand can be expected to select more stringently for tree form in the future.

Exchange of select "land-race" material, while it can broaden the base of a breeding population and boost short- to medium-term gains in production populations, is likely to be of secondary importance for boosting the diversity of the total genetic resource in a breeding programme.

ACKNOWLEDGEMENTS

We thank R. Boardman, Dr K. G. Eldridge, A. Franclet, Prof. W. J. Libby, Dr D. G. Nikles, Dr F. Owino, Dr L. A. Pederick, H. A. van der Syde, and A. Went for providing seedlots from South Australia, Australian Capital Territory, France, California, Queensland, Kenya, Victoria, South Africa, and New South Wales respectively; Dr A. R. Griffin for setting up the trial in Victoria; the numerous individuals who helped with the establishment, tending, and field assessments; V. Coetzee for arranging a field data check; L. Gea and C. B. Low for assistance in initial data processing; and Dr G. R. Hodge, Dr A. C. Matheson, and Dr T. L. White for helpful criticism of the manuscript.

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APPENDIX 1**REPRESENTATION OF SEEDLOT GROUPS (TABLE 1) IN NUMBERS OF SEEDLOTS IN DATA USED FROM THE VARIOUS TRIALS**

| Group | New Zealand | South Africa | New South Wales | | | South Australia | Western Australia (2 sites) | Victoria |
|-------|-------------|--------------|-----------------|---------|------------|-----------------|-----------------------------|----------|
| | | | Nundle | Gurnang | Wee Jasper | | | |
| 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2 | 12 | 12 | 12 | 12 | 12 | 12 | 9 | 7 |
| 3 | 7 | 7 | 7 | 7 | 7 | 7 | 4 | 3 |
| 4 | 16 | 40 | 0 | 0 | 14 | 52 | 58 | 0 |
| 5 | 20 | 28 | 28 | 28 | 28 | 26 | 1 | 1 |
| 6 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 7 | 4 | 7 | 4 | 4 | 5 | 4 | 4 | 0 |
| 8 | 13 | 16 | 18 | 18 | 19 | 17 | 18 | 3 |
| 9 | 0 | 0 | 1 | 0 | 25 | 0 | 4 | 0 |
| 10 | 1 | 1 | 0 | 0 | 4 | 2 | 1 | 0 |
| 11 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 12 | 9 | 9 | 7 | 6 | 10 | 10 | 9 | 3 |
| 13 | 2 | 2 | 1 | 1 | 1 | 2 | 0 | 0 |
| 14 | 5 | 6 | 1 | 1 | 1 | 6 | 0 | 0 |
| 15 | 3 | 5 | 1 | 1 | 3 | 5 | 0 | 0 |
| 16 | 11 | 25 | 33 | 32 | 39 | 31 | 28 | 0 |
| 17 | 24 | 42 | 41 | 41 | 40 | 40 | 41 | 25 |
| 18 | 4 | 5 | 5 | 5 | 5 | 5 | 0 | 0 |
| 19 | 0 | 6 | 0 | 0 | 7 | 5 | 0 | 0 |
| 20 | 13 | 0 | 7 | 4 | 13 | 11 | 13 | 2 |

APPENDIX 2

NOTES ON SPECIFIC PROBLEMS FOR ANALYSING INDIVIDUAL DATA SETS

New Zealand

With the sets-in-replicates layout, neither set nor replicate effects approached statistical significance, so they were pooled with the error. The resulting error item was thus a composite of effects of set/rep block environments and row-plot environments. This gave an estimate of the average precision of the least-squares means, even though pairwise comparisons of lots could be more precise within sets than across them. Precision of least-squares lot means could have been improved slightly by a mixed-model adjustment for the set/rep effects which for that purpose could be deemed fixed, but the simpler procedure was adopted since it was already deemed to give a satisfactory estimate of the overall precision of means used.

South Africa

Some poorly represented lots were initially dropped from the data. Preliminary analyses indicated no need to take special account of set effects as such. Replicate effects were statistically significant and large, so were incorporated in the final GLM model, but rep \times set effects were pooled with the error item as with the New Zealand data.

New South Wales (three sites)

Plot means were available for four replicates at each of the three sites. Within each site, lots were accepted for the data analysis provided they were represented by plots in at least two replicates. These criteria differed from those of Johnson (1992), who considered only those lots with at least four trees each of at least the first three replicates at each of the three sites, because we were concerned with obtaining satisfactory pairwise connections with additional sites.

South Australia

The main problem was unequal representation of different lots arising mainly from shortages of nursery stock. Accordingly, lots were accepted for data analysis if they were represented in a minimum of five replicates.

Western Australia (two sites)

The three-tree plots combined with some imbalance made plot-mean data suspect, although it was easier to obtain least-squares means using such data. However, comparison of analyses of variance using both individual-tree and plot-mean data showed very little disparity in results, so plot means were used. There was a complication arising from the fact that some lots were common to several of the sets instead of the sets being fully disconnected, such that in each set only 50 of the 69 IGP lots were confined to that replicate. This was addressed by carrying out separate analyses of variance for each of the sets, both with and without the data from the lots that were represented in more than one set. The following

algorithm was adopted to obtain composite statistics (estimates of within-site variances, and of covariances of lot means with other sites):

$$Q = \frac{(A' + B' + C' + D') + 3(A + B + C + D)}{4}$$

where Q is the composite statistic

A, B, C, D are the statistics from each set with recurring seedlots omitted

A', B', C', D' are the statistics using data from all IGP lots.

The coefficients of 3 and 4 were used to weight information for representation of the respective lots.

Victoria

The variable availability of nursery stock had been addressed by grouping the lots into two adjoining experiments. One (Trial A) contained six replicates in a randomised complete block design representing 47 IGP lots. The other (Trial B) contained three replicates and represented 86 IGP lots, in a randomised complete block layout. The two experiments had 18 IGP lots in common. In the event, only 46 lots were assessed (being those that were represented at seven of the eight Australian sites)—29 in Trial A and 27 in Trial B, and thus 10 common to both trials.

Preliminary analyses of variance for Trial A indicated that the sets main effect and sets \times replicates interaction effect could be pooled with the error. Accordingly, the data were reanalysed, for the two trials combined with trials and lots as main effects, with replicates nested within trials. It was possible to test for the first-order trials \times lots interaction (expected to be a null effect), and to obtain thereby an estimate of the average precision of lot means. From the two trials it was possible to obtain joint estimates of statistics (Q) according to the formula:

$$Q = \frac{A \times 29 \times 6 + B \times 27 \times 3}{29 \times 6 + 27 \times 3}$$

where A and B denote statistics from the respective trials.

These estimates, however, were necessarily rough approximations given the very unequal representation of various lots.

APPENDIX 3

ADJUSTMENT OF r_g INVOLVING DBHOB FOR BETWEEN-SITE DIFFERENCES IN AGE AT ASSESSMENT

Adopting a path-coefficient approach we have:

$$r_g = r_g' r_t$$

where r_g' is the between-site genetic correlation at a given age (i.e., age-adjusted correlation), and r_t is the age-age genetic correlation within a site (assumed to be the same for both sites of a pair). Given r_g and r_t one can readily solve for r_g' .

Values for r_t were inferred assuming a modified form of the relationship of Lambeth (1980):

$$r_t = 1 + b \log_e (t_1/t_2)$$

and t_1 and t_2 are the respective assessment ages ($t_1 \leq t_2$)

where b is a regression coefficient.

On this basis, a value for b can, in principle, be inferred from a single within-site age-age correlation (Table 6). Including the native-population material, a value of 0.287 for b was inferred from r_t of 0.76 between ages 6.5 and 15 years. Omitting the native-population material, $r_t = 0.63$ indicated a considerably higher value of b . This was also higher than values indicated by King & Burdon (1991, accepting an intercept of zero) and Burdon *et al.* (1992b) for similar material on very similar sites. Accordingly a "consensus" value for b of 0.33 was chosen for calculations omitting native-population lots.