

# Family $\times$ Site Interactions in *Pinus radiata* in Victoria, Australia, and Implications for Breeding Strategy

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## Abstract

The question of whether the *Pinus radiata* breeding program for the State of Victoria should be designed with one statewide breeding zone or be divided into a number of regional breeding zones was considered with data from seven progeny trials. These trials included 18 families at each of four different sites and 19 different families at three of the same sites planted one year later. Three traits, diameter, stem straightness and branch thickness were assessed at age 12 to 14 years.

Family  $\times$  site interactions for diameter were highly significant ( $P < 0.01$ ) in both series of trials, but those for the other two traits were found to be much smaller and of little importance.

Two methods were used to compare gains in growth rate. Firstly, by selection of the parents of the best 50% of families from each trial on a regional or statewide basis (for "1.5 generation" seed orchards), and secondly, by comparison of heritability estimates for regional and statewide breeding (for second generation seed orchards). An initial apparent advantage of regional breeding calculated by both methods was found to be over-estimated when the effect of variation between sites within regions was considered. It was concluded that regional breeding zones would only yield higher gains if sites within regions were relatively uniform. As site variability within regions increased to the level existing between regions the advantage of regional over statewide breeding zones decreased.

**Key words:** *Pinus radiata*, interactions, family  $\times$  site interactions, genotype  $\times$  environment interactions, gains, breeding strategy.

## Introduction

Radiata pine (*Pinus radiata* D. Don) has proved to be a successful plantation species over a wide range of environmental conditions in southern Australia including different soil types, fertility levels and climates. For some time Australian tree breeders have been interested in the degree to which individual genotypes are adaptable to the range of sites and if it is possible to breed for general adaptation (MATHESON and RAYMOND, 1984).

In the south-eastern State of Victoria, State plantations (about 100,000 ha) are serviced by the breeding program of the Department of Conservation, Forests and Lands in which the whole State is considered to be one breeding zone. However, the plantations are distributed in a number of regions with quite different soils and climates and the question has often been asked — would it be better if the State was subdivided into a number of separate breeding zones?

The answer to this question of breeding zones depends, of course, on the magnitude and extent of genotype (family)  $\times$  site interactions. MATHESON and RAYMOND (1984) reported on one series of trials of radiata pine on eleven sites across southern Australia, measured when aged 8 to 11 years. In the present paper, data from two series of

progeny trials in the State of Victoria, replicated at four and three sites respectively, and assessed at 12 to 15 years of age, are analysed to determine the magnitude of family  $\times$  site interactions and to compare estimates of gains expected from breeding under one statewide breeding zone with those obtainable if the breeding program was reorganised into a number of regional breeding zones. The results have been examined for the case of family selection (establishment of "1.5 generation" orchards) and also for individual tree selection (establishment of second generation orchards).

## Method

In 1970 *P. radiata* progeny trials were established on four different sites in Victoria, spanning a distance of 450 km, and involving a range of physiographic, climatic and edaphic conditions, as follows:

- Rennick — southwest, deep sandy soils, rainfall 740 mm, altitude 30 m
- Daylesford — west-central, yellow-grey clays, 990 mm, alt. 620 m
- Narbethong — central northeast, red clay loam, 1150 mm, alt. 430 m
- Warrenbayne — northeast, red-brown loams on granite, 950 mm, alt. 630 m

Eighteen families were fully represented at all four sites. Fifteen of the families were grown from seeds collected in 1968 in an unculled first-generation clonal seed orchard which had been established in 1961. The other three families were derived from controlled pollination of three clones (not in the seed orchard at that time) with a mix of ten pollens (which included some of the clones in the orchard).

In 1971, a second series of progeny trials with a different set of families was planted at three locations, Rennick, Warrenbayne and Narbethong, on similar sites and within a short distance of the respective 1970 trials. Of sixteen families and three controls included in these trials, nine families were derived from seeds collected from three different unculled first-generation clonal seed orchards in southern Australia and another three families were from controlled pollination with a pollen mix. Thus, twelve families were of polycross origin with "improved" pollen parentage. The four other families were of open-pollinated origin, with seeds collected from the ortets. One of the three control lots represented a bulk seed orchard collection (the same 16-clone orchard that yielded the families planted in 1970) and the other two were routine unimproved seed collections.

At their respective sites in 1970 and 1971 the trials were set out in a randomised complete block design, replicated 12 times, with 5 trees per family plot. Survival in all trials was very high. The present paper reports results of assessment of the trials at ages 12 to 14 years for three

traits — stem diameter (DBHOB, cm), stem straightness and branch thickness. The latter two traits were scored on a 1 to 6 scale, 6 being best (straight-stemmed or thin-branched respectively), with the frequency of 1 to 6 scores approaching normality. The data were subjected to analysis of variance for each site separately and then with data pooled across sites according to the model shown in *table 1*. The mean values of each trait for each family at each site were also converted to a percentage of the mean for the site (see *Table 2*) to simplify comparisons of family data.

The comparison of gains from statewide and regional breeding zones was first undertaken for the case of establishing new seed orchards ("1.5 generation" orchards) containing the best 50% of first generation clones, i.e. those yielding the best 9 out of 18 families in the 1970 trials and the best 6 out of 12 families in the 1971 trials. The families were selected on a multiple trait basis (with diameter converted to basal area) using the following index:

$$I = (\text{Basal area } \% \times 2) + (\text{Straightness } \% \times 1) + (\text{Branch } \% \times 1)$$

where phenotypic values for each trait are multiplied by economic coefficients reflecting the commercial importance of each trait (i.e. economic coefficient = 2 for basal area and 1 for form traits). This is the simple base index developed by WILLIAMS (1962) and proposed for use in forestry by COTTERILL (1985).

For the analysis, it was assumed that results of selection

on the data pooled across sites can be used to calculate the gains from a statewide breeding zone and that gains from regional breeding zones may be derived from results of selection at the individual sites, assuming that each zone is well represented by the trial located in it. This is not strictly correct because the effect of variation in environment within regional breeding zones is ignored as it could not be estimated, and the calculation is likely to yield an overestimate of gains from regional breeding zones. An attempt to correct for variation in regional sites is made later. Gains for combined sites and for separate sites, corresponding to statewide and regional breeding, were calculated from the average superiority of the selected families over all the families in the same trial multiplied by family heritability ( $h^2$ ), for each of the three traits and separately for each of the 1970 and 1971 trials.

Estimates of comparative gains were also made for the case of second generation breeding based on individual tree selection. In the case of statewide breeding it was assumed that the best individual trees were selected from all trials across the state giving an expected genetic gain (denoted  $\Delta G_{sw}$ ) of

$$\Delta G_{sw} = i_{sw} h^2_{sw} \sigma_{sw} \quad (1)$$

where  $i_{sw}$  is the intensity of selection,  $h^2_{sw}$  the statewide estimate of individual heritability, and  $\sigma_{sw}$  the phenotypic standard deviation. The  $\sigma_{sw}$  and  $h^2_{sw}$  were calculated as

*Table 1.* — Model for calculation of variance components from analysis of variance of progeny trials at a single location or for several locations combined.

| Source of variation               | d.f.         | Expected mean squares  |
|-----------------------------------|--------------|--|
| <b>(a) Single site analysis</b>   |              |  |
| Family                            | (f-1)        | $\sigma_e^2 + n \sigma_{fr}^2 + nr \sigma_f^2$                                     |
| Replication                       | (r-1)        | $\sigma_e^2 + n \sigma_{fr}^2 + nf \sigma_r^2$                                     |
| Family x replication              | (f-1)(r-1)   | $\sigma_e^2 + n \sigma_{fr}^2$   |
| Tree within plot (error)          | (n-1) fr     | $\sigma_e^2$   |
| <b>(b) Multiple site analysis</b> |              |  |
| Family                            | (f-1)        | $\sigma_e^2 + n \sigma_{fr}^2 + nr \sigma_{fs}^2 + nrs \sigma_f^2$                 |
| Site                              | (s-1)        | $\sigma_e^2 + n \sigma_{fr}^2 + nr \sigma_{fs}^2 + nf \sigma_r^2 + nrf \sigma_s^2$ |
| Family x site                     | (f-1)(s-1)   | $\sigma_e^2 + n \sigma_{fr}^2 + nr \sigma_{fs}^2$                                  |
| Rep. within sites                 | (r-1) s      | $\sigma_e^2 + n \sigma_{fr}^2 + nf \sigma_r^2$                                     |
| Family x rep. within sites        | (f-1)(r-1) s | $\sigma_e^2 + n \sigma_{fr}^2$   |
| Tree within plot (error)          | (n-1) fsr    | $\sigma_e^2$   |

where  $f$  = number of families

$s$  = number of sites

$r$  = number of replications per site

$n$  = number of trees per plot

and  $\sigma_e^2$  = variance due to differences between trees within plots

$\sigma_{fr}^2$  = variance due to interactions between families and replications within sites

$\sigma_r^2$  = variance due to differences between replications within sites

$\sigma_{fs}^2$  = variance due to interactions between families and sites

$\sigma_f^2$  = variance due to differences between families

$\sigma_s^2$  = variance due to differences between sites

Table 2. — Means for 18 families of *Pinus radiata* planted in 1970, assessed when 12 to 14 years old, at each of four sites and over all sites. Means are expressed as a percentage of the overall mean at each site.

| Family         | Over all sites |          |         | Rennick |      |      | Warrenbayne |      |      | Daylesford |      |      | Narbethong |      |      |
|----------------|----------------|----------|---------|---------|------|------|-------------|------|------|------------|------|------|------------|------|------|
|                | DBH (1)        | Str. (2) | Br. (3) | DBH     | Str. | Br.  | DBH         | Str. | Br.  | DBH        | Str. | Br.  | DBH        | Str. | Br.  |
| 30026          | 109            | 100      | 94      | 101     | 108  | 99   | 104         | 97   | 91   | 116        | 98   | 92   | 114        | 98   | 94   |
| 30055          | 106            | 92       | 97      | 108     | 87   | 84   | 111         | 87   | 94   | 101        | 95   | 101  | 105        | 96   | 106  |
| 50079 (4)      | 106            | 104      | 104     | 111     | 106  | 101  | 102         | 102  | 104  | 99         | 101  | 103  | 111        | 106  | 108  |
| 30028          | 104            | 101      | 103     | 93      | 101  | 106  | 106         | 97   | 103  | 113        | 107  | 103  | 105        | 97   | 98   |
| 30054          | 103            | 103      | 105     | 102     | 101  | 104  | 98          | 109  | 109  | 100        | 102  | 105  | 113        | 100  | 101  |
| 30041 (4)      | 103            | 114      | 99      | 105     | 120  | 99   | 99          | 118  | 104  | 101        | 109  | 95   | 108        | 112  | 98   |
| 30002          | 100            | 100      | 107     | 107     | 93   | 102  | 104         | 103  | 109  | 97         | 100  | 109  | 94         | 104  | 106  |
| 30043          | 100            | 91       | 89      | 102     | 89   | 89   | 98          | 97   | 89   | 102        | 89   | 90   | 99         | 91   | 88   |
| 30007          | 100            | 103      | 111     | 95      | 101  | 114  | 108         | 99   | 108  | 93         | 105  | 109  | 101        | 108  | 115  |
| 30036          | 99             | 112      | 102     | 99      | 117  | 107  | 100         | 113  | 99   | 101        | 109  | 103  | 97         | 107  | 98   |
| 30004          | 99             | 95       | 96      | 102     | 91   | 86   | 102         | 96   | 96   | 96         | 98   | 103  | 95         | 97   | 101  |
| 30016          | 98             | 106      | 104     | 97      | 114  | 107  | 99          | 106  | 101  | 95         | 101  | 106  | 100        | 103  | 104  |
| 50039 (4)      | 97             | 107      | 114     | 96      | 104  | 118  | 96          | 104  | 114  | 100        | 110  | 110  | 97         | 108  | 114  |
| 30048          | 97             | 93       | 88      | 106     | 94   | 82   | 97          | 97   | 90   | 93         | 89   | 90   | 92         | 93   | 91   |
| 30040          | 97             | 102      | 98      | 99      | 105  | 99   | 96          | 100  | 95   | 98         | 106  | 100  | 90         | 97   | 99   |
| 30022          | 95             | 94       | 100     | 94      | 97   | 109  | 100         | 101  | 98   | 97         | 92   | 96   | 89         | 88   | 98   |
| 30006          | 94             | 90       | 89      | 95      | 81   | 89   | 92          | 95   | 95   | 95         | 92   | 88   | 93         | 93   | 84   |
| 30017          | 93             | 90       | 99      | 87      | 89   | 103  | 88          | 78   | 99   | 100        | 96   | 97   | 95         | 95   | 98   |
| Mean (5)       | 17.6           | 3.63     | 3.65    | 17.5    | 3.48 | 3.55 | 19.0        | 3.51 | 3.58 | 17.5       | 3.84 | 3.76 | 16.5       | 3.68 | 3.70 |
| Unimproved (6) | 92.4           | 95.4     | 96.2    |         |      |      |             |      |      |            |      |      |            |      |      |

(1) DBH = Stem diameter at breast height over bark (cm).

(2) Str. = Stem straightness (scored 1 to 6, 6 = straight).

(3) Br. = Branch thickness (scored 1 to 6, 6 = thin branched, relative to vigour of tree).

(4) Families derived from controlled pollination with a pollen mix. The other 15 families derived from seeds collected by clone in the Korweinguboora seed orchard.

(5) Actual mean on which the percentage data above are based.

(6) Assessment of trees grown from unimproved seed sources, also expressed in percentage terms, calculated from controls in these and other trials.

$$\sigma_{sw} = \sqrt{(\sigma_f^2 + \sigma_{fs}^2 + \sigma_{fr}^2 + \sigma_c^2)} \quad (2)$$

$$h_{sw}^2 = \frac{\sigma_A^2}{\sigma_{sw}^2} \quad (3)$$

where  $\sigma_A^2$  is the additive genetic variance (or  $4\sigma_f^2$  for half-sib progeny trials) and the other symbols are defined in table 1.

In the case of regional breeding it was assumed that the best individual trees were selected from the trials in each of the regions giving an expected gain from regional breeding ( $\Delta G_{reg}$ ) of

$$\Delta G_{reg} = i_{reg} h_{reg}^2 \sigma_{reg} \quad (4)$$

where  $i_{reg}$  is the intensity of selection, and  $h_{reg}^2$  and  $\sigma_{reg}$  the regional estimates of individual heritability and phenotypic standard deviation calculated as

$$\sigma_{reg} = \sqrt{(\sigma_f^2 + \sigma_{fr}^2 + \sigma_c^2)} \quad (5)$$

$$h_{reg}^2 = \frac{\sigma_A^2}{\sigma_{reg}^2} \quad (6)$$

The  $h^2$  and  $\sigma$  are calculated by ignoring family  $\times$  site (region) interactions (cf equations 5 and 2) because regional

breeding should overcome this source of interaction variance.

The relative efficiency of regional versus statewide breeding is therefore

$$\frac{\Delta G_{reg}}{\Delta G_{sw}} = \frac{i_{reg} h_{reg}^2 \sigma_{reg}}{i_{sw} h_{sw}^2 \sigma_{sw}} \quad (7)$$

or assuming selection intensity at the statewide and regional level is the same (i.e.  $i_{reg} = i_{sw}$ )

$$= \frac{h_{reg}^2 \sigma_{reg}}{h_{sw}^2 \sigma_{sw}} \quad (8)$$

The individual tree heritability estimates were calculated as follows:

$$h_{sw}^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fs}^2 + \sigma_{fr}^2 + \sigma_c^2} \quad (9)$$

$$h_{reg}^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fr}^2 + \sigma_c^2} \quad (10)$$

on the assumption that progeny raised by family from open-pollinated orchard seed are half-sibs, with coefficient of relationship  $r = 1/4$  (FALCONER, 1960) and there are no selfs.

In order to take into account variation in environments within regions,  $h_{reg}^2$  was modified by including a compo-

Table 3. — Variance components due to families ( $\sigma_f^2$ ), family  $\times$  site ( $\sigma_{fs}^2$ ), family  $\times$  replication ( $\sigma_{fr}^2$ ), trees within plots ( $\sigma_e^2$ ) and total phenotypic variance ( $\sigma_p^2$ ) for three traits of *Pinus radiata* calculated from analyses of variance of a series of progeny trials planted in 1970 (18 families aged 12 to 14 years at four sites), and another series in 1971 (19 families, 12 to 15 years old at three sites), together with estimates of individual ( $h_i^2$ ) and family ( $h_f^2$ ) heritability.

| Location            |                 | Diameter |        | Straightness |       | Branch thickness |       |
|---------------------|-----------------|----------|--------|--------------|-------|------------------|-------|
|                     |                 | 1970     | 1971   | 1970         | 1971  | 1970             | 1971  |
| Rennick             | $\sigma_e^2$    | 12.123   | 9.125  | 1.001        | 0.762 | 0.712            | 0.650 |
|                     | $\sigma_{fr}^2$ | 0.072    | 0.186  | 0.013        | 0.064 | 0.021            | 0.045 |
|                     | $\sigma_f^2$    | 0.904    | 0.585  | 0.123        | 0.132 | 0.119            | 0.063 |
|                     | $h_i^2$         | 0.27     | 0.24   | 0.43         | 0.55  | 0.56             | 0.33  |
|                     | $h_f^2$         | 0.83     | 0.81   | 0.91         | 0.94  | 0.94             | 0.87  |
|                     |                 |          |        |              |       |                  |       |
| Daylesford          | $\sigma_e^2$    | 20.739   | —      | 0.615        | —     | 0.577            | —     |
|                     | $\sigma_{fr}^2$ | 0.017    |        | 0.038        |       | 0.036            |       |
|                     | $\sigma_f^2$    | 0.755    |        | 0.055        |       | 0.053            |       |
|                     | $h_i^2$         | 0.14     |        | 0.31         |       | 0.32             |       |
|                     | $h_f^2$         | 0.69     |        | 0.86         |       | 0.86             |       |
|                     |                 |          |        |              |       |                  |       |
| Narbethong          | $\sigma_e^2$    | 18.677   | 19.142 | 0.700        | 0.833 | 0.550            | 0.712 |
|                     | $\sigma_{fr}^2$ | 0        | 0      | 0.041        | 0.056 | 0                | 0     |
|                     | $\sigma_f^2$    | 1.280    | 0.941  | 0.045        | 0.092 | 0.079            | 0.073 |
|                     | $h_i^2$         | 0.26     | 0.19   | 0.23         | 0.37  | 0.57             | 0.37  |
|                     | $h_f^2$         | 0.83     | 0.76   | 0.80         | 0.89  | 0.95             | 0.89  |
|                     |                 |          |        |              |       |                  |       |
| Warrenbayne         | $\sigma_e^2$    | 15.801   | 13.889 | 1.028        | 0.897 | 0.740            | 0.741 |
|                     | $\sigma_{fr}^2$ | 0        | 1.412  | 0.027        | 0.057 | 0                | 0.023 |
|                     | $\sigma_f^2$    | 0.705    | 0.677  | 0.069        | 0.061 | 0.050            | 0.077 |
|                     | $h_i^2$         | 0.17     | 0.17   | 0.24         | 0.24  | 0.25             | 0.37  |
|                     | $h_f^2$         | 0.73     | 0.73   | 0.81         | 0.81  | 0.82             | 0.89  |
|                     |                 |          |        |              |       |                  |       |
| Pooled across sites | $\sigma_e^2$    | 16.775   | 13.749 | 0.835        | 0.826 | 0.644            | 0.698 |
|                     | $\sigma_{fr}^2$ | 0        | 0.530  | 0.030        | 0.245 | 0.013            | 0.024 |
|                     | $\sigma_{fs}^2$ | 0.511    | 0.385  | 0.013        | 0.003 | 0.015            | 0.008 |
|                     | $\sigma_f^2$    | 0.406    | 0.339  | 0.062        | 0.093 | 0.062            | 0.063 |
|                     | $\sigma_p^2$    | 17.692   | 15.003 | 0.940        | 1.167 | 0.734            | 0.793 |
|                     | $h_i^2$         | 0.09     | 0.09   | 0.26         | 0.32  | 0.34             | 0.32  |
|                     | $h_f^2$         | 0.83     | 0.79   | 0.88         | 0.95  | 0.96             | 0.95  |
|                     |                 |          |        |              |       |                  |       |

ment of variance for family  $\times$  site interactions within regions. This could not be estimated directly but was considered to be greater than that for family  $\times$  replications within sites ( $\sigma_{fr}^2$ ) and less than that for family  $\times$  sites ( $\sigma_{fs}^2$ ). This is detailed later in the paper.

The family heritability ( $h_f^2$ ) estimates were calculated as:

$$h_f^2 = h^2 \frac{1 + (n - 1)r}{1 + (n + 1)t} \quad (\text{Falconer 1960}) \quad (11)$$

where  $n$  = number of offspring per family ( $n = 50$  per site in this study)

$r = 1/4$  for half-sibs

$t$  = correlation of phenotypic values of members of the families ( $t = 1/4 h^2$ ).

### Results and Discussion

Family means for each trait and site in the 1970 series of trials, converted to a percentage of the overall mean for each site for convenient comparison are shown in table 2. Results from the 1971 trials have similar variation.

The heritability estimates for each trait derived from the two series of trials were quite similar (Table 3), which has given confidence to the use of these data.

The heritability ( $h_{sw}^2$ ) estimates for diameter across sites in this study (0.09 in both series of trials, Table 3)

Table 4. — Gains (%) from new "1.5 generation" seed orchards of radiata pine composed of the best 50% of first generation clones (or by culling half the clones from a first generation orchard) additional to the gains from uncultured first generation orchards, calculated for one statewide breeding zone and regional breeding zones.

| Region                  | Statewide breeding   |                     |                    | Regional breeding |      |     |
|-------------------------|----------------------|---------------------|--------------------|-------------------|------|-----|
|                         | Diam. <sup>(1)</sup> | Str. <sup>(2)</sup> | Br. <sup>(3)</sup> | Diam.             | Str. | Br. |
| <b>Rennick</b>          |                      |                     |                    |                   |      |     |
| 1970 trial              | 1.9                  | 3.3                 | 1.6                | 2.3               | 4.8  | 2.0 |
| 1971 trial              | 1.9                  | 3.8                 | 1.4                | 1.9               | 3.8  | 1.4 |
| <b>Daylesford</b>       |                      |                     |                    |                   |      |     |
| 1970 trial              | 1.6                  | 2.3                 | 1.8                | 2.2               | 3.3  | 1.1 |
| <b>Narbethong</b>       |                      |                     |                    |                   |      |     |
| 1970 trial              | 4.2                  | 2.3                 | 2.4                | 4.7               | 2.3  | 3.7 |
| 1971 trial              | 4.6                  | 2.0                 | 0.6                | 4.9               | 2.5  | 0.1 |
| <b>Warrenbayne</b>      |                      |                     |                    |                   |      |     |
| 1970 trial              | 2.5                  | 2.1                 | 1.8                | 2.1               | 2.8  | 2.7 |
| 1971 trial              | 0.6                  | 2.0                 | 2.8                | 3.0               | 1.8  | 0.8 |
| <b>Average of above</b> |                      |                     |                    |                   |      |     |
| 1970 trials             | 2.6                  | 2.5                 | 1.9                | 2.9               | 3.3  | 2.4 |
| 1971 trials             | 2.4                  | 2.6                 | 1.2                | 3.3               | 2.7  | 0.8 |
| Mean                    | 2.5                  | 2.6                 | 1.6                | 3.1               | 3.0  | 1.6 |

(1) Diameter (DBHOB)

(2) Stem straightness (scored 1 to 6, 6 = straight)

(3) Branch thickness (scored 1 to 6, 6 = thin branched, relative to vigour of tree)

were lower than those reported from other studies of the species across sites, i.e. SHELBOURNE and Low (1980) reported a value of 0.12 (for 3 sites, trees 7 years old), MATHESON and RAYMOND (1984) reported 0.18 (11 sites, 8 to 11 years) and DEAN *et al.* (1983) 0.23 (2 sites, 5 to 6 years). The heritability estimates for straightness in this study (0.26 and 0.32) were intermediate between those of MATHESON and RAYMOND (0.39) and DEAN *et al.* (0.21), while the value reported by SHELBOURNE and Low (0.06) seems unusually low for this trait. Branch thickness was not assessed as a separate trait in the other studies.

#### Gains from 1.5 generation orchards

The estimate of gain in diameter growth to be obtained from 1.5 generation seed orchards, in this case composed of the best half of the first generation clones in each series of trials, designed for a statewide breeding zone was less than that for regional breeding zones. The estimates were about 2.5% and 3.1% respectively (Table 4).

For stem straightness, statewide breeding was also associated with less potential gain than calculated for regional breeding, in this case about 2.6% compared with 3.0%. For branch thickness there was no difference, but there were conflicting results from the two series of trials. The response of this trait (and also straightness) to the selection process seemed to be more sensitive to sampling error than was diameter, due to the greater weight used for diameter in the selection index.

The difference in gains from statewide and regional breeding are attributed to family  $\times$  site interactions. In

the 1970 trials this interaction component was significant for diameter and branch thickness ( $P < 0.01$ ) and also for straightness ( $P < 0.05$ ). In the 1971 trials the interaction was also highly significant for diameter but was not significant for the other two traits.

SHELBOURNE (1972) proposed, as a rule of thumb, that genotype  $\times$  site effects should only be troublesome in breeding programs if the ratio of the variance component for family by site interactions over that for variation among families ( $\sigma_{fs}^2/\sigma_f^2$ ) exceeded 0.5. For the 1970 and 1971 trials this ratio was calculated to be 1.25 and 1.17 respectively for diameter, 0.21 and 0.03 for straightness and 0.24 and 0.13 for branch thickness. These figures suggest that for *P. radiata* the interactions should be of concern for growth rate but not for the form traits. The ratios for diameter and straightness were smaller than those reported by MATHESON and RAYMOND (1984), 1.96 and 0.64 respectively, though their relative magnitude was similar.

When the relative diameter growth (percent) for each family at each site was compared, some families were found to be consistent while others varied from site to site. For example, in the 1970 trials family 30028 grew relatively more slowly at Rennick than at the other sites, and family 30048 was relatively faster growing at Rennick (Table 2). These families obviously contributed to the significant interactions in the analyses of variance across sites.

#### Second generation breeding

Substantial numbers of second generation selections have been made in the Victorian breeding program. It is therefore desirable to compare gains from second generation orchards designed for statewide and for regional breeding zones. Since no direct experimental data are available on the response to second generation selection, the gains must be calculated from a theoretical basis.

If trees were selected at the same intensity in both types of breeding zone, the relative gain from regional versus statewide breeding, from equation 8, is

$$\frac{\Delta G_{reg}}{\Delta G_{sw}} = \frac{h_{reg}^2 \sigma_{reg}}{h_{sw}^2 \sigma_{sw}} \quad (12)$$

The average individual tree heritability estimate for diameter at separate sites in the 1970 and 1971 trials was 0.20 while the average heritability across sites was 0.09 (Table 3). Comparison of the average phenotype variances at each site and pooled across sites (Table 3) indicates that  $\sigma_{reg}/\sigma_{sw}$  was very small compared to  $h_{reg}^2/h_{sw}^2$ , and that relative gain from regional over statewide breeding approximates  $h_{reg}^2/h_{sw}^2$ . From these figures it therefore appears that regional breeding would give over twice the gains obtained from statewide breeding.

However, in this case the estimate of 0.20 for regional breeding applies strictly to trees grown under exactly the same site conditions as at one of the trials, and does not include any component representative of the effect on family performance of variation in site conditions that would be expected in a breeding region, i.e. an estimate of  $\sigma_{fs(reg)}^2$ .

Accordingly, the regional heritability ( $h_{reg}^2$ ) was recalculated to include this component. First, the mean values of the variance components obtained from the seven separate trials (Table 3) were calculated to be:

|                 |        |
|-----------------|--------|
| $\sigma_e^2$    | 15.644 |
| $\sigma_{fr}^2$ | 0.241  |
| $\sigma_f^2$    | 0.835  |
| $\sigma_p^2$    | 16.720 |

Since no direct evidence of the magnitude of the family  $\times$  site component of variance within regions is available, it is necessary to estimate a value. Two cases can be considered.

Case 1. It would seem that  $\sigma_{fs}^2$  should be at least as large as the family  $\times$  replication interaction within single trials, (i.e.  $\sigma_{fs(\text{reg})}^2 = \sigma_{fr}^2 = 0.241$ , as above). This could be considered a lower limit estimate of  $\sigma_{fs(\text{reg})}^2$ .

Case 2. The upper limit for  $\sigma_{fs(\text{reg})}^2$  would seem to be equal to the family  $\times$  site interaction statewide, i.e.  $\sigma_{fs(\text{reg})}^2 = \sigma_{fs(\text{sw})}^2 = 0.448$ , which is the average for the 1970 and 1971 trials (Table 3).

The variance components for the two cases, and the heritability estimates derived from them, will then be:

|                    | Case 1 | Case 2 |
|--------------------|--------|--------|
| $\sigma_e^2$       | 15.644 | 15.644 |
| $\sigma_{fr}^2$    | 0.241  | 0.241  |
| $\sigma_{fs}^2$    | 0.241  | 0.448  |
| $\sigma_f^2$       | 0.594  | 0.387  |
| $\sigma_p^2$       | 16.720 | 16.720 |
| $h_{\text{reg}}^2$ | 0.142  | 0.093  |

Note that the  $\sigma_f^2$  has been reduced by the amount of  $\sigma_{fs}^2$  used in calculating  $h_{\text{reg}}^2$  and that the total variance is the same in both cases.

The efficiency of regional breeding zones over statewide breeding zones may then be calculated as the ratio of heritability estimates, assuming that the intensity of selection practised in each is the same and that the phenotypic variation in regions and statewide is not very different. The efficiency of regional breeding would be 56% greater than statewide breeding in Case 1 but only 2% greater in Case 2.

In the areas surrounding the trial sites which might be considered as the regional breeding zones in Victoria, there are considerable variations in soil type, rainfall and other climatic factors. In fact, the variation within regions might be almost as large as that within the State as a whole. If this was so,  $h_{\text{reg}}^2$  would be closer to the estimate in Case 2 than that in Case 1, but if a breeding region was notable for similarity of sites then  $h_{\text{reg}}^2$  might be more similar to Case 1.

For straightness and branch thickness the gains with statewide breeding were not much different to those calculated for regional breeding even before family  $\times$  site effects were estimated because of the minor importance of family  $\times$  site effects with these traits. The relative magnitude of gains in straightness and branch diameter would be further reduced below that of diameter by reason of the lower selection intensity that is likely to be applied to these traits.

#### Over-estimation of gains from results of a single trial

The assumption on which the initial calculations of gain in a region were made in this paper, based on results of a single trial in a region, is not valid. Gains calculated from results at one site are attainable only when the future trees are grown on the same site and experience the same climatic conditions. Since the sites and conditions are unlikely to be repeated identically, the actual gains are likely to be less than the estimated values.

Regions are not homogeneous areas, and one should expect some interaction between genotypes and the variety of sites within each region. Examples of such interactions occurring in Australian studies have been reported by GRIFFIN (1977) and MATHESON and RAYMOND (1984).

In the analyses reported here for the three traits in the two series of statewide trials the component of variance due to interactions between families and replications within sites,  $\sigma_{fr}^2$ , was greater than that for interactions between families and sites,  $\sigma_{fs}^2$ , in 4 out of 6 cases (Table 4). This indicates that there can be as much variation in environment causing interactions within a site as there is variation in environment across sites.

For these reasons therefore, any calculation of gain from results of a single trial is likely to be an overestimate unless allowance is included in the calculation for the effect of family  $\times$  site interactions. Since the size of these interactions can not be determined from a single trial it should logically be estimated to be greater than the family  $\times$  replication interaction in the trial, but its size would probably be related to the degree of site variability in the region for which the estimate of gain is to be made.

#### Consideration of the practical effects of the interactions

The gains calculated in this paper for new 1.5 generation orchards will be additional to those already obtained from first generation seed orchards, because all the families tested in trials were derived from clones used in first generation orchards or were of equivalent merit. Gains from the State's first generation orchards in Victoria, prior to thinning, have been estimated at 7.4% in volume growth, based on many trials throughout the State (PETERICK, unpubl.).

With statewide breeding 1.5 generation orchards should yield extra gains of 2.5% in diameter (Table 4), which is equivalent to about 5% in basal area or volume growth when using the best 50% of clones. With a more intensive selection of clones, i.e. one in four (25%), this figure would increase to about 8.4% volume growth. This estimate was substantiated by other calculations with family data from 127 clones in which selection of the best 26 for use in 1.5 generation orchards was estimated to yield an extra gain in volume of 8.7% (PETERICK, unpubl.).

The total gains in volume growth from statewide 1.5 generation orchards should therefore range from about 12.4% for 50% clone selection to 15.8% for 25% clone selection. Gains from separate orchards for regional breeding zones may be higher, by up to 1.3 % and 2.5 % respectively.

These calculations did not take into account the effect of variation in site conditions within regions, which would reduce the advantage from regional breeding zones.

This aspect was, however, included in the consideration of second generation breeding, which was examined by an entirely different method. The result indicated that in areas with general uniformity of site and climate the advantage of regional breeding over statewide breeding may be greater than that calculated for 1.5 generation orchards, though in regions of considerable site variability there may be no advantage at all. Thus the final result will depend on the amount of site variability within regions.

It would be expected that the relative gains from regional or statewide breeding estimated from 1.5 gene-

ration or second generation orchards should be similar. Though calculated by different methods the results from each are compatible.

The case for regional breeding over that for one statewide breeding zone appears therefore to hinge on the importance of obtaining an extra gain in volume of up to 2% above that of 12% to 15% expected from a statewide breeding zone — if site variation within regions is small, but little extra gain at all if it is appreciable. The tree form traits need not be considered at all, since the interactions were of much smaller magnitude than those for growth.

However, costs of obtaining the extra gain for regional breeding could be much greater because separate programs of selection, controlled crossing, testing and seed orchards would be needed for each region. On balance, I believe that any extra gain is unlikely to be cost effective. There would also be the problem of actually defining the number and extent of the breeding zones.

### Conclusions

Highly significant family  $\times$  site interactions for diameter growth of *P. radiata* were recorded in two series of progeny trials. The interactions for stem straightness and branch thickness were found to be relatively small.

The effect of the variation in relative growth rate of families from site to site on potential gains was calculated for the case of 1.5 generation orchards established for statewide or regional breeding. However, due to the variation in sites that occurs within a region and the magnitude of interactions between families and replications within sites, an apparent advantage of regional breeding over statewide breeding may only partly be realised. When the effect of family  $\times$  site interactions within regional breeding zones was considered for the case

of gain from second generation orchards, it appeared that regional breeding would only be advantageous over statewide breeding when there was a general uniformity of sites in a region.

The sites for growing *P. radiata* within potential regional breeding zones in Victoria are not regarded as uniform. Therefore in view of the much higher costs and effort associated with regional breeding, it is concluded that a change from a statewide to regional breeding zones would not be cost effective.

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## Predictions of Genetic Gain from Various Selection Methods in Open Pollinated *Pinus banksiana* Progeny Trials

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### Abstract

Variance components and heritabilities of tree height and stem diameter on three sites at age 6 and 14 are presented for 100 open pollinated *Pinus banksiana* (LAMB.) progenies. The progenies were sampled from two stands within each of five distinct areas (populations) in the Ottawa Valley, Ontario. Combining information from several sources into an index promised to double the expected genetic gain from selections based on single trait values. Family selection followed by within-family selection was less effective than index selection but superior to simple mass selection. Mass selection did not lead to a rapid loss of variation or inbreeding. The lack of significant  $G \times E$  interactions and the absence of important stand and area effects in the Ottawa Valley will facilitate the breeding programs in this commercially important

species. Results at age 14 generally confirmed results obtained at age six.

**Key words:** *Pinus banksiana*, selection index, genetic gain, heritability, variance components, selection methods, genotype by environment interactions.

### Introduction

Jack pine (*Pinus banksiana*, LAMB) has emerged during the last two decades as a major commercial pulp and lumber species in the Lake States and in Canada's boreal forests (OMNR, 1986; RIEMENSCHNEIDER, 1982; SMYTH and RAMSAY, 1984). Further, easy sexual propagation, stand establishment, and management has made it an important reforestation species as well (BELLA and FRANCESCHI, 1974; BENZIE, 1977; MARTELL and FULLERTON, 1988; RALSTON, 1953). Consequently, efforts are now well underway to genetically improve growth and yield of jack pine (DOJACK, 1988; KLEIN, 1986; OMNR, 1987; YEATMAN, 1974). Reliable esti-

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