

Genetic Gains expected from alternative Breeding Strategies including simple low Cost Options

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Summary

Gain formulations are developed and used to calculate genetic gains expected in the breeding population each generation, and each decade, from 10 strategies for breeding trees. The breeding population is assumed to be subdivided into lines of 3000 offspring of 30 parents. Special reference is made to *Pinus radiata* improvement in Australia. The strategies include single-pair mating with (1) two-stage within-family/progeny test selection, (2) within-family selection, and (3) combined index selection; half-diallel mating with (4) two-stage family/within-family selection, and (5) combined index selection; polycross mating with (6) within-family selection, (7) combined index selection, and (8) mass selection; and open-pollinated mating with (9) combined index selection, and (10) mass selection.

Half-diallel mating with combined index selection can maximise expected genetic gain per generation. However, the simpler and less expensive strategy of single-pair mating with combined index selection had a shorter generation interval and produced substantially greater gains per decade than half-diallel mating with combined index selection. Another simple option of polycross mating with combined index selection also produced good expected gains per decade. Strategies which rely solely on within-family selection produced poor gains per generation and per decade.

Key words: mass, individual within-family, family progeny test, and combined index selection, mating designs.

Zusammenfassung

Für 10 Züchtungsstrategien bei Bäumen werden Formeln für den Züchtungsfortschritt entwickelt und dazu benutzt, um in der Züchtungspopulation deren zu erwartenden Wert für jede Generation bzw. jede Dekade abzuschätzen. Es wird dabei unterstellt, daß die Züchtungspopulation in Linien mit 3000 Nachkommen von 30 Eltern unterteilt ist. Besondere Berücksichtigung findet dabei die Züchtungsarbeit bei *Pinus radiata* in Australien. Die Züchtungsstrategien schließen mehrere verschiedene Paarungs- und Selektionsverfahren ein, wie: Einfach und paarweise Kreuzung mit (1) Zwei-Phasen-Selektion innerhalb von Familien- bzw. Nachkommenschaftsprüfungen, (2) Selektion innerhalb von Familien und (3) kombinierte Index-Selektion; Kreuzungen in der Art eines halben Diallels mit (4) Zwei-Phasen-Selektion zwischen bzw. innerhalb von Familien, sowie (5) kombinierte Index-Selektion; Polycross mit (6) Selektion innerhalb von Familien, (7) kombinierte Index-Selektion und (8) Massenselektion; Freie Abblüte mit (9) kombinierter Index-Selektion und (10) Massenselektion.

Der erwartete Züchtungsfortschritt kann per Generation durch Kreuzungen in der Art eines halben Diallels und kombinierte Index-Selektion maximiert werden. Das Verfahren der paarweisen Kreuzung mit kombinierter Index-Selektion, das als einfachere und kostengünstigere Strategie angesehen werden kann, hatte jedoch ein kürzeres Generationsintervall und ergab substantiell größere Züchtungsfortschritte per Jahrzehnt als das vorhin erwähnte Verfahren. Eine weitere Möglichkeit, das Polycross mit kombinierter Index-Selektion, ergab ebenfalls gute zu erwartende Züchtungsfortschritte per Jahrzehnt. Strategien,

die nur auf Selektion innerhalb von Familien aufbauen, ergaben niedrige Züchtungsfortschritte per Generation und Jahrzehnt.

Introduction

A number of different strategies are available for long-term genetic improvement of trees, and the more practical advantages and disadvantages of each approach have been widely discussed (e.g. NAMKOONG *et al.*, 1966; SHELBOURNE, 1969; BURDON and SHELBOURNE, 1971; FRANKLIN and MESKIMEN, 1973; LIBBY 1973; WEIR, 1974; BURDON *et al.*, 1977; NAMKOONG, 1979; TALBERT, 1979; McKEAND and BEINEKE 1980; NAMKOONG *et al.*, 1980; SKRØPPA, 1982; MATHESON, 1983; COTTERILL, 1984). However, of the above studies only those of NAMKOONG *et al.* (1966) and SHELBOURNE (1969) extend the comparison of options to include the decisive factor of genetic gains expected from selection. Both these early papers present expected gains from seed orchards (clonal and seedling) under strategies which involve different combinations of mating patterns and individual, progeny, or clonal selection.

The aim of this study is to present further gain calculations for 10 different strategies that are of current importance, or potential (future) importance, for breeding trees but which do not appear to have been compared previously in terms of expected genetic gain. The calculations concentrate on gains per generation and per decade from selection in the breeding population, and special reference is made to *Pinus radiata* in Australia. The strategies represent various combinations of mating pattern and selection scheme, including single-pair mating with (1) two-stage within-family/progeny test selection, (2) within-family selection, and (3) combined index selection; half-diallel mating with (4) two-stage family/within-family selection, and (5) combined index selection; polycross mating with (6) within-family selection, (7) combined index selection, and (8) mass selection; and open-pollinated mating with (9) combined index selection, and (10) mass selection. There are considerable differences between strategies in generation interval, operational complexity, and demand for labour and financial resources.

Assumptions and Theory

Breeding Population

The 10 strategies have been compared for a hypothetical breeding population which is subdivided into lines of 3000 offspring derived from matings among a constant 30 parents each generation. Matings are permitted within, but not between, sublines. Selection within each subline would be for the same trait and general adaptation to the same breeding region.

The assumption of sublining has been used here because it allows calculations of genetic gain to be presented and discussed without too much concern about the effects of inbreeding. Under sublining the opportunity exists to 'release' inbreeding by allowing outcrossing in seed orchards established using unrelated clones from different sublines.

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(It is obviously important to have enough sublimes in the overall breeding population, say 10 sublimes or more, to supply adequate quantities of unrelated material for orchards). Of course, where seed orchards are replaced by mass vegetative propagation the opportunity exists to utilize (by cloning) either outcrossed individuals, or families, derived from controlled-crosses among unrelated parents from different sublimes; or any superior inbred individuals which happen to occur within a subline.

Genetic Gain Calculations

The following gain equations are based on additive genetic models which should provide reasonably reliable estimates of genetic gain in the breeding population (and seed orchards involving more than say four or five clones). The gain equations presented here are not intended for predicting responses from either mass propagation, or two or three clone orchards which may exploit substantial amounts of non-additive genetic variation.

(1) Single-pair mating with two-stage within-family/progeny test selection

Under this strategy the 30 parents in each subline are mated in single pairs to produce 15 full-sib families with 200 offspring per family (total 3000 offspring per subline). Each full-sib family is planted at one or more sites using replicated field designs. A two-stage selection process (detailed by COTTERILL, 1984) is employed to retain superior individuals for future breeding. At stage 1 of selection, four phenotypically superior trees are chosen from each full-sib family of 200 offspring. These four individuals from each family are then examined more closely in a stage-2 progeny test (using open-pollinated offspring) where the best two individuals are finally retained on the basis of the performance of their offspring. In other words, the stage-2 progeny test is conducted within families and, therefore, does not lead to the substantial reduction in effective population size usually associated with progeny testing (COTTERILL, 1982, 1984). The 30 individuals finally retained from the 15 full-sib families in each subline are mated in single pairs to regenerate the subline for the following generation of selection, and so on. For *P. radiata* in Australia this strategy may have a generation interval of 17 years (see flow diagram in COTTERILL, 1984).

Suppose that the selection at both stages is to improve a trait U which may be a single trait or alternatively, a multiple-trait index value representing a combination of traits. Let stage-1 selection be on a variable X which is the deviation of an individual's phenotypic value (P) for trait U from the mean of its full-sib family (\bar{P}). In other words, X is the within-family deviation ($X = P - \bar{P}$) for trait U. Stage-2 selection is on another variable Y which is the absolute mean performance of the offspring of an individual (parent) for the same trait U (i.e. \bar{Y} is the progeny test mean of a parent for U). Finally, let the variable G be the 'true' breeding value of an individual for the trait U. Genetic gain may be measured as the change (denoted $\Delta \bar{G}$) in the mean of G for the breeding population before and after two-stage selection.

Assume X, Y and G are trinormally distributed in the base population with variances σ_X^2 , σ_Y^2 and σ_G^2 ; covariances $\text{cov}(X\bar{Y})$, $\text{cov}(XG)$ and $\text{cov}(\bar{Y}G)$; and correlations $R_{X\bar{Y}}$, R_{XG} and $R_{\bar{Y}G}$. Taking Equation 6 from COTTERILL and JAMES (1981) and adapting it to the present notation, it can be shown that genetic gain in each generation of two-stage within-family/progeny test selection is —

$$\Delta \bar{G} = i_1 h R_{XG} \sigma_P + i_2 h \sigma_P [(R_{\bar{Y}G} - R_{X\bar{Y}} R_{XG} H) / (1 - R_{X\bar{Y}}^2 H^2)] \quad (1)$$

where i_1 represents the standardised selection differential at stage-1 ($i_1 = 2.37$ for within-family selection of four individuals in every 200), i_2 the selection differential at stage-2 ($i_2 = 0.66$ for progeny test selection of two individuals in every four), h the square root of the individual heritability for trait U, and σ_P the phenotypic standard deviation for the same trait. The multiplier H is calculated as $H = i_1(i_1 - x)$ where stage-1 selection is by independent culling at a point (or culling level) x standard deviations from the mean of X (COTTERILL, 1984). The actual values assigned to i_1 and i_2 above, and elsewhere in this article, are taken from tables of standardised selection differentials for finite population size calculated by Drs D. LINDGREN and JAN-ERIK NILSSON (Swedish Univ. Agric. Sci., pers. comm.). Similar, but less extensive tables are given in BECKER (1975).

The phenotypic correlation $R_{X\bar{Y}}$ between the within-family deviation X and progeny mean Y is given by —

$$R_{X\bar{Y}} = \text{cov}(X\bar{Y}) / (\sigma_X \sigma_{\bar{Y}}) \quad (2)$$

It can be shown from first principles (described generally in TURNER and YOUNG 1969, Chapter 10; and to a lesser extent in FALCONER 1976, Table 13.2) that —

$$\text{cov}(X\bar{Y}) = \frac{1}{2} \sigma_A^2 [(q-1)(1-r)/q] \quad (3)$$

$$\sigma_X^2 = \sigma_P^2 [(q-1)(1-t)/q] \quad (4)$$

where σ_A^2 is the additive genetic variance for the trait U, q is the number of offspring in each full-sib family derived from the single-pair mating (i.e. $q = 200$), r is the coefficient of genetic relationship among these offspring, and t the intraclass correlation (for full-sibs $r = 1/2$ and $t = 1/2h^2$; where $h^2 = \sigma_A^2 / \sigma_P^2$). The variance of the progeny means \bar{Y} from the stage-2 progeny test may be estimated as (FALCONER, 1976; Table 13.2) —

$$\sigma_{\bar{Y}}^2 = \sigma_P^2 [(1 + (n-1)t)/n] \quad (5)$$

where n is the number of offspring of each parent progeny tested. COTTERILL (1984) specified a stage-2 progeny test based on 20 open-pollinated offspring per parent (i.e. $n = 20$ and, assuming half-sib relationships, $t = 1/4h^2$).

Substituting Equations 3, 4 and 5 in Equation 2 —

$$R_{X\bar{Y}} = \frac{1}{2} h^2 Q / (SK)^{1/2} \quad (6)$$

where Q represents the factor $(q-1)(1-r)/q$, S represents $(q-1)(1-t)/q$, and K represents $[1 + (n-1)t]/n$. (TURNER and YOUNG, 1969 define K as the inverse of the relationship used here, but the present definition is more convenient for the purposes of this article). Note that the coefficients r and t in Q and S refer to full-sib offspring, while the t in K refers to the open-pollinated offspring involved in stage-2 progeny test.

Other covariance and variance components can similarly be estimated from first principles —

$$\text{cov}(XG) = \sigma_A^2 Q \quad (7)$$

$$\text{cov}(\bar{Y}G) = \frac{1}{2} \sigma_A^2 \quad (8)$$

$$\sigma_G^2 = \sigma_A^2 \quad (9)$$

and used to obtain the correlations —

$$R_{XG} = hQ/S^{1/2} \quad (10)$$

$$R_{YG} = \frac{1}{2}h/K^{1/2}. \quad (11)$$

Substituting Equation 6, 10 and 11 in Equation 1 —

$$\Delta\bar{G}_1 = i_1 h^2 Q/S^{1/2} + i_2 h^2 \left[\frac{s-h^2 Q^2 H}{[S(4SK - h^4 Q^2 H)]^{1/2}} \right] \quad (12)$$

where the genetic gain $\Delta\bar{G}_1$ is measured in units of phenotypic standard deviations σ_P of the trait being selected for. Strictly speaking, Equation 12, and the gain equations given later that involve selection within families, apply only to circumstances where there is no restriction requiring selection of equal numbers of offspring from each family. Consequently, expected gains may be overestimated for circumstances where a constant number of breeding individuals are chosen per family. However, the bias should be slight.

Expected genetic gain per decade from single-pair mating with within-family/progeny test selection has been calculated by dividing gain per generation estimated from Equation 12 by the generation interval of 1.7 decades (i.e. gain per decade equals $\Delta\bar{G}_1/1.7$).

(2) Single-pair mating with within-family selection

As for the previous strategy, the 30 parents in each subline are mated in single pairs to produce 15 full-sib families with 200 offspring per family. However, there is only one stage of selection in which two phenotypically superior individuals are selected from each family, and these individuals are then mated in single pairs to regenerate the subline. In other words, there is stage-1 selection on the within-family deviations X , but no stage-2 progeny test.

The expected gain per generation (in units of σ_P) for this strategy may be obtained by setting $i_2 = 0$ in Equation 12 —

$$\Delta\bar{G}_2 = i_1 h^2 Q/S^{1/2} \quad (13)$$

The within-family selection differential for retaining two individuals in every 200 is $i_1 = 2.58$. For *P. radiata* this strategy may have a fairly short generation interval of about 11 years (assuming controlled-pollinations are carried out on ortets; see flow diagram Appendix 1). Gain per decade has therefore been calculated as $\Delta\bar{G}_2/1.1$.

Equation 13 reduces to the equation given by FALCONER (1976; Table 13.3) for predicting gain from selection within families.

(3) Single-pair mating with combined index selection

The 30 parents in each subline are again mated in single pairs to produce 15 full-sib families with 200 offspring per family. However, rather than restrict selection to within-family deviations only, the 30 best individuals from the total of 3000 in each subline are selected at one-stage using a combined index which integrates both individual and family information.

This case of combined index selection is the classical example considered by LUSH (1947). The index (denoted I) may be written —

$$I = b_1 P + b_2 \bar{P} \quad (14)$$

where P is the individual's phenotypic value for trait U , and \bar{P} the mean of its full-sib family (i.e. sib relatives) for the same trait (with the individual's phenotypic value included in the mean). The weighting factors b_1 and b_2 are determined as partial regression coefficients which maximise the correlation between the individual's index value I and its true breeding value G (LERNER, 1958; TURNER and YOUNG, 1969). TURNER and YOUNG (1969) provide details of the methodology for calculating b values for different types of combined indices using the correlation coefficients among the variables being integrated in the index. Determination of the b values in the above index requires knowledge of the correlations between the individual value and family mean ($R_{P\bar{P}}$), individual and breeding value (R_{PG}), and family mean and breeding value ($R_{\bar{P}G}$). The appropriate variance and covariance components (which have not already been given) for calculating these correlations can be shown to equal —

$$\text{cov}(P\bar{P}) = \sigma_{\bar{P}}^2 = \sigma_P^2 N \quad (15)$$

$$\text{cov}(PG) = \sigma_A^2 \quad (16)$$

$$\text{cov}(\bar{P}G) = \sigma_A^2 M \quad (17)$$

where $N = [1 + (q-1)t]/q$ and $M = [1 + (q-1)r]/q$. (TURNER and YOUNG 1969 again define N and M as the inverse of the relationships used here). Combining Equations 9, 15, 16 and 17 gives the correlations —

$$R_{P\bar{P}} = N^{1/2} \quad (18)$$

$$R_{PG} = h \quad (19)$$

$$R_{\bar{P}G} = hM/N^{1/2}. \quad (20)$$

Substituting Equations 18, 19 and 20 in the partial regression equations given in TURNER and YOUNG (1969; Equation 10.24) provides the following standardised partial regression coefficients —

$$b'_1 = h(1-M)/(1-N) \quad (21)$$

$$b'_2 = h(M-N)/[N^{1/2}(1-N)]. \quad (22)$$

The standardised coefficients b'_1 and b'_2 are easily converted to the weighting factors b_1 and b_2 required in Equation 14 (see TURNER and YOUNG, 1969). Equally importantly, at least for the purposes of this study, the b values may be used to determine the gain ($\Delta\bar{G}_3$) expected from selection on the combined index given in Equation 14. The expected gain may be given as (TURNER and YOUNG, 1969) —

$$\Delta\bar{G}_3 = i_1 h R^{\frac{1}{2}} \sigma_P \quad (23)$$

where R , the multiple correlation between G as the dependent variable and P and \bar{P} as the independent variables, is equal to —

$$R = b'_1 R_{PG} + b'_2 R_{\bar{P}G} \\ = [h^2(1-M)/(1-N)] + [h^2 M(M-N)/(N(1-N))]. \quad (24)$$

Substituting Equation 24 in Equation 23 —

$$\Delta\bar{G}_3 = i_1 h^2 \sqrt{\frac{(1-M)}{(1-N)} + \frac{M(M-N)}{N(1-N)}} \quad (25)$$

in units of σ_p . The selection differential for retaining 30 individuals in every 3000 is $i_1 = 2.66$. The strategy is assumed to have a generation interval of 11 years, and gain per decade has been calculated as $\Delta \bar{G}_3/1.1$.

Equation 25 reduces to the same gain equation for this classical case of combined index selection given in LUSH (1947), OSBORNE (1957), LERNER (1958), FALCONER (1976), and others. LUSH (1947) and LERNER (1958) derive the equation using path diagrams while OSBORNE (1957) uses variances and covariances of the dependent and independent variables. (Note that if the trait U is itself a multiple-trait index combining phenotypic values for different characteristics the situation exists of having an index value combined in another index; see theory presented in CUNNINGHAM 1975).

(4) Half-diallel mating with two-stage family/within-family selection

The 30 parents in each subline are mated in five 6×6 disconnected half-diallels to produce a total of 75 full-sib families (i.e. 15 families in each half-diallel) with 40 offspring per family (3000 offspring per subline). Each family is planted at one or more sites using replicated field designs. Two-stage selection follows, but on this occasion stage-1 is to select the best three full-sib families in each group of 15 half-diallel crosses, and at stage-2 two phenotypically superior individuals are selected from each of these three best families. The total of 30 parents selected in each subline (i.e. six selections from each half-diallel) are mated in five 6×6 disconnected half-diallels to regenerate the subline, and so on.

Let \bar{P} again represent the full-sib family mean for trait U (stage-1 selection) and X the within-family deviation for the same trait (stage-2 selection). The covariance, and therefore the correlation, between the family mean \bar{P} and deviations X from the mean is —

$$R_{\bar{P}X} = \text{zero.} \quad (26)$$

Other correlations (R_{XG} and $R_{\bar{P}G}$) required for estimating expected gain from half-diallel mating with family/within-family selection have been given previously in Equations 10 and 20. Substituting Equations 10, 20 and 26 in Equation 1 (with, of course, \bar{P} replacing X and X replacing \bar{Y} in the correlations in Equation 1) gives —

$$\Delta \bar{G}_4 = i_1 h^2 M/N^{1/2} + i_2 h^2 Q/S^{1/2} \quad (27)$$

in units of σ_p . The stage-1 selection differential for retaining three families in every 15 is $i_1 = 1.31$ and the stage 2 selection differential for retaining two individuals in every 40 offspring is $i_2 = 1.96$.

Other combinations of two-stage selection might be used, such as selecting six families from each half-diallel at stage-1 and then, at stage-2, selecting one individual from each of these six best families. However, by solving Equation 27 it can be shown that this option usually provides less expected gain. Other types of diallel (e.g. disconnected 4×4 or 5×5 half-diallels) or even North Carolina Design II crosses (e.g. disconnected 4×4 or 5×5 Design II's) are sometimes used in tree breeding (BURDON *et al.*, 1977; TALBERT, 1979), but these alternatives have not been considered here partly because the 6×6 half-diallels are used for breeding *P. radiata* in Australia (GRIFFIN, 1976; MATHESON, 1978). Partly, also, because it can be shown using Equation 27 that expected gains from 6×6 half-diallel matings should never be less than the gains from 4×4 or 5×5

Winter, year 1	ESTABLISH 2nd GENERATION BREEDING POPULATION
Jan, year 7	MEASURE ALL TREES IN THE BREEDING POPULATION
	* Data analysed quickly and used to identify superior trees.
April, year 7	SELECT SUPERIOR INDIVIDUALS FOR FUTURE BREEDING
Winter, year 7	} CONTROLLED-CROSSES CARRIED OUT ON ORTETS
Winter, year 8	
Winter, year 9	
	* Neighbouring trees should be removed from around selected ortets to encourage flowering and development of cones.
Spring, year 11	COLLECT SEED FROM CONTROLLED-CROSSES AND SOW IN NURSERY
Winter, year 12	ESTABLISH 3rd GENERATION BREEDING POPULATION

Appendix 1. — Time-table of operations for second and subsequent generations of selection of *Pinus radiata* in Australia under circumstances where controlled-crosses are carried out on ortets in the field. Selection is carried out at 5½ years after planting when the tallest trees may be around eight to 10m, depending on site quality. The controlled-crosses are assumed to require three flowering seasons to complete; and a 2 year period is required for cones to develop on *P. radiata*. The generation interval is 11 years.

half-diallels or Design II's. A similar finding is reported by Drs J. P. VAN BUIJTENEN and R. D. BURDON (pers. comm.).

For *P. radiata* the strategy of half-diallel mating with family/within-family selection has been assumed to have a generation interval of 14 years. The controlled-pollinations are considered too complicated and numerous to complete on the ortets and would require establishment of a clone bank (Appendix 2). For instance, a breeding population comprising a total of 300 parents (which is arguably a minimal size for long-term breeding; BURDON *et al.* 1977; COTTERILL, 1984) would require 750 crosses (or fifty 6×6 half diallels) to regenerate each generation. Expected gain per decade has been calculated as $\Delta \bar{G}_4/1.4$.

Winter, year 1	ESTABLISH 2nd GENERATION BREEDING POPULATION
Jan, year 7	MEASURE ALL TREES IN THE BREEDING POPULATION
April, year 7	SELECT SUPERIOR INDIVIDUALS FOR FUTURE BREEDING
Winter, year 7	COLLECT SCIONS AND ESTABLISH CLONE BANKS
Winter, year 10	} CONTROLLED-CROSSES CARRIED OUT IN CLONE BANKS
Winter, year 11	
Winter, year 12	
Spring, year 14	COLLECT SEED FROM CONTROLLED-CROSSES AND SOW IN NURSERY
Winter, year 15	ESTABLISH 3rd GENERATION BREEDING POPULATION

Appendix 2. — Time-table of operations for second and subsequent generations of selection of *Pinus radiata* in Australia using disconnected half-diallel matings. It is assumed that the controlled-pollinations are too numerous and intricate to be manageable on the ortets, and clone banks are therefore established to simplify the task. The generation interval is 14 years.

(5) Half-diallel mating with combined index selection

In this case the 30 parents in each subline are again mated in five 6×6 disconnected half-diallels with 40 offspring per full-sib family, and the best 30 individuals out of the 3000 offspring in each subline are selected using a combined index. The index previously defined in Equation 14 which combines individual and full-sib family information may be used under half-diallel matings. However, a more efficient index (i.e. an index I having a higher correlation with true breeding value G) should be one which also utilizes information on the half-sib classifications that occur among full-sib families generated by diallel matings. Such a combined index has been considered for half-diallel matings in this study —

$$I = b_1P + b_2\bar{P}_2 + b_3\bar{P}_3 \quad (28)$$

where P is the individual's phenotypic value for the trait U , \bar{P}_2 the mean of the full-sib family, and \bar{P}_3 the mean of the half-sib classification to which the individual belongs (i.e. \bar{P}_3 is the mean of all offspring which have at least one parent in common). In fact, the average relationship among offspring in the "half-sib" classification is somewhat less than $r = 1/4$ (discussed later). In the case of both \bar{P}_2 and \bar{P}_3 the individuals' phenotypic value is assumed to be included in the mean.

Correlations required for solving the standard partial regression coefficients b_1 , b_2 and b_3 include R_{PG} , given previously by Equation 19, and $R_{\bar{P}_2G}$ and $R_{\bar{P}_3G}$ which are both given by Equation 20. The correlation $R_{\bar{P}_2G}$ has been calculated using values of N_2 and M_2 determined for $q_2 = 40$ full-sib offspring. While $R_{\bar{P}_3G}$ has been calculated using values of N_3 and M_3 for $q_3 = 360$ offspring (i.e. under 6×6 half-diallel matings there are nine full-sib families in each half-sib classification) with an average coefficient of relationship of approximately $\bar{r} = 0.2$ (i.e. marginally less than a true half-sib relationship). This average coefficient \bar{r} has been determined using the general methodology described in SQUILLACE (1974; see Table 4). The correlations $R_{P\bar{P}_2}$ and $R_{P\bar{P}_3}$, given by Equation 18, have been calculated using the previous values of N_2 and N_3 , respectively. Assuming the parents involved in each half-diallel are unrelated, the correlation between \bar{P}_2 and \bar{P}_3 is zero —

$$R_{\bar{P}_2\bar{P}_3} = \text{zero.} \quad (29)$$

Combining the above correlations in the appropriate partial regression equations for three independent variables (e.g. TURNER and YOUNG, 1969; Equations 10.36) gives —

$$b_1' = h(1-M_2-M_3)/(1-N_2-N_3) \quad (30)$$

$$b_2' = h(M_2-N_2-M_2N_3+M_3N_2)/[N_2^{1/2}(1-N_2-N_3)] \quad (31)$$

$$b_3' = h(M_3-N_3-M_3N_2+M_2N_3)/[N_3^{1/2}(1-N_2-N_3)]. \quad (32)$$

Genetic gain ($\Delta\bar{G}_5$) expected from selection on the combined index given in Equation 28 is —

$$\begin{aligned} \Delta\bar{G}_5 &= i_1 h R^{1/2} \\ &= i_1 h (b_1' R_{PG} + b_2' R_{\bar{P}_2G} + b_3' R_{\bar{P}_3G})^{1/2} \\ &= i_1 h^2 \sqrt{\frac{(1-M_2-M_3)}{(1-N_2-N_3)} + \frac{M_2(M_2-N_2-M_2N_3+M_3N_2)}{N_2(1-N_2-N_3)} + \frac{M_3(M_3-N_3-M_3N_2+M_2N_3)}{N_3(1-N_2-N_3)}} \\ &\dots (33) \end{aligned}$$

in units σ_P . Note that when N_3 and M_3 equal zero (i.e. when there are no half-sib family groupings) Equation 33 reduces to Equation 25. The selection differential for retaining 30 individuals in every 3000 is of course $i_1 = 2.66$. Gain per decade has been calculated as $\Delta\bar{G}_5/1.4$.

The above approach to constructing combined indices is cumbersome where information from more than two types of relatives, as well as the individual's own record, are involved. For instance, in the case of half-diallel matings another (perhaps more efficient) index would be one which combines the individual's performance, the mean of the full-sib family, the mean of the maternal half-sib classification (i.e. female parent general combining ability; gca) and the mean of the paternal half-sib classification (male gca). (The index given by Equation 28 utilizes the maternal and paternal gca information as a single mid-parent value \bar{P}_3 .) The method of best linear unbiased prediction (BLUP) provides a more general approach to utilizing information from many different types of relatives to improve the accuracy of breeding value prediction (HENDERSON and QUAAAS, 1976; HENDERSON, 1985). Dr N. JACKSON (CSIRO, pers. comm.) is presently attempting to build a modified BLUP approach into the selection index program RESI (described in COTTERILL and JACKSON, 1985). The problems with BLUP are that it requires a complete relationship matrix (determined from pedigree information on each individual), and the method is iterative, and therefore costly on computer time.

(6) Polycross mating with within-family selection

Each subline is represented by 3000 polycross offspring from matings among 30 parents. The matings may be carried out as either a "complete" polycross where each of the 30 parents are used both as female (seed) parents and in the pollen mix, or as an "incomplete" polycross where half of the parents (i.e. 15 parents) are used as females and the other half as males in the pollen mix (BURDON and SHELBORNE, 1971). There would be 100 offspring per female parent for the complete polycross (giving 3000 offspring per subline) and 200 offspring per female parent for the incomplete design. Each family is planted at one or more sites using replicated field lay-outs. The best one (in the case of the complete polycross) or two individuals per family (in the case of the incomplete polycross) are chosen on the basis of within-family deviations (i.e. on the basis of X) to give a total of 30 selections per subline. These selections are then mated in the appropriate polycross design to regenerate the subline.

Genetic gain from each generation of selection within polycross families (denoted $\Delta\bar{G}_g$) has been calculated from Equation 13; setting $r = 1/4$ and $t = 1/4h^2$ (for half-sib offspring). In the case of the complete polycross the selection differential for retaining the best one out of 100 offspring in each family is $i_1 = 2.51$. In the case of the incomplete polycross the selection differential (and hence genetic gain)

for retaining two out of 200 offspring is marginally higher at $i_1 = 2.58$. The incomplete polycross would usually be preferred in practice, not only because of its slight gain advantage, but also because the incomplete polycross requires only half as many controlled-crosses as the complete polycross. Hence, the gain calculations presented in this article are for the incomplete polycross only.

Polycross mating with within-family selection should have the same generation interval as single-pair mating with within-family selection (i.e. 11 years; Appendix 1), and gain per decade has been calculated as $\Delta\bar{G}_q/1.1$.

(7) Polycross mating with combined index selection

The 30 parents in each subline are mated in an incomplete polycross with 200 half-sib offspring per family. A combined index integrating individual phenotype (P) and the mean of the half-sib (polycross) family (\bar{P}) is used to select the 30 best individuals from the total of 3000 offspring in each subline.

Genetic gain ($\Delta\bar{G}_7$) expected from this particular combined index has been calculated by solving Equation 25 for an intensity of selection $i_1 = 2.66$ and assuming $q = 200$ half-sib offspring. Gain per decade is $\Delta\bar{G}_7/1.1$.

(8) Polycross mating with mass selection

Each subline is again represented by 3000 offspring from incomplete polycross matings among 30 parents. However, on this occasion the offspring are bulk planted with no identification of pedigree, and the 30 individuals having the highest phenotypic value P for trait U are selected *en masse* from each subline. These 30 individuals are crossed in an incomplete polycross, the seed sown in a nursery, and in due course the seedlings are lifted, bulked and planted out to regenerate the subline. The female pedigree may be identified at the nursery stage to ensure that equal

numbers of seedlings of each family are bulked before planting out in the field.

It is important that the field design used in planting out the bulked offspring should include the same sort of blocking (i.e. the same block sizes and lay-out) that would be used in planting out controlled-pollinated offspring under the previous strategies. If environmental variance due to blocks is not taken into account under mass selection the realised heritability would, of course, be reduced. It is assumed that the block sizes are sufficiently large (say 50 or more trees) to ensure relative uniformity in average genetic value from one block to the next, thereby avoiding any serious confounding between environmental and genetic effects among blocks.

The correlation between an individual's phenotypic value P for trait U and its breeding value G for the same trait is given in Equation 19. Substituting Equation 19 into Equation 1 (with P replacing X and i_2 set at zero) gives the well known equation —

$$\Delta\bar{G}_8 = i_1 h^2 \quad (34)$$

in units of σ_P . The selection differential for retaining 30 individuals in every 3000 is $i_1 = 2.66$. The generation interval is 11 years and gain per decade has been calculated as $\Delta\bar{G}_8/1.1$.

(9) Open-pollinated mating with combined index selection

Each subline is represented by 3000 open-pollinated offspring of 30 female parents (100 offspring per female parent) planted at a site isolated from other sublines to avoid cross-pollination. The field design at each site should use single-tree plots (with the female pedigree identified) to encourage outcrossing among individuals of different families. A combined index integrating the individual's phenotype (P) and the mean of its open-pollinated family (\bar{P}) is used to select the 30 best individuals in each subline, and the population is regenerated using open-pollinated seed collected from each of these 30 superior seed parents.

A number of years prior to collecting the open-pollinated cones, the genetic quality of the local pollen cloud may be improved by culling say 80% of the offspring from each subline to leave only the best 600 out of 3000 trees. In practice, the culling may be carried out over a few years to help maintain the stability of the stand. A schedule is suggested in Appendix 3 where the poorest 50% of trees (judged visually) are removed at around four years after planting and, after final measurement at 5½ years, the worst 60% of the remaining trees (according to the combined index) are removed to give an overall thinning of 80% of trees planted. (Breeders may prefer to identify trees for removal at the first thinning on the basis of a combined index utilizing early measurements.)

Genetic gain ($\Delta\bar{G}_q$) has been calculated according to Equation 25 under the assumption that the open-pollinated offspring are half-sib. The overall intensity of selection i_1 has been calculated as the average of the intensities of selection on the female (i_F) and male parents (i_M) —

$$i_1 = (i_F + i_M)/2. \quad (35)$$

In this case $i_F = 2.66$ (selecting 30 in 3000 female parents) and $i_M = 1.40$ (selecting 600 in 3000 parents to contribute to the pollen cloud). This 80% thinning of trees contributing to the pollen cloud is a fairly arbitrary figure which

Winter, year 1	ESTABLISH 2nd GENERATION BREEDING POPULATION
Winter, year 5	PRELIMINARY THINNING TO REMOVE THE POOREST 50% OF TREES
Jan, year 7	MEASURE ALL REMAINING TREES
Feb, year 7	SELECT <u>EN MASSE</u> SUPERIOR FEMALE (SEED) PARENTS
March, year 7	FINAL THINNING TO REMOVE POOREST 60% OF REMAINING TREES
*	In two thinnings a total of 80% of trees planted have been removed to improve the genetic quality of the local pollen cloud.
Winter, year 9	COLLECT OPEN-POLLINATED CONES FROM THE SELECTED FEMALE PARENTS
Winter, year 10	
Spring, year 10	SOW OPEN-POLLINATED SEED IN NURSERY
Winter, year 11	ESTABLISH 3rd GENERATION BREEDING POPULATION

Appendix 3. — Time-table of operations for second and subsequent generations of selection of *Pinus radiata* in Australia using open-pollinated matings. The two-year period required for one development accounts for the delay between final thinning and collection of first open-pollinated cones. The generation interval is 10 years.

Table 1. — Total gain per generation ($\Delta\bar{G}_{10}$) from mass selection on female parents at a constant intensity of 30 trees in very 3000 ($i_F = 2.66$), and differing intensities of selection on the male (pollen) parent. Selection on the male parent is achieved by thinning trees to improve the genetic quality of the pollen cloud. Selection is assumed to be for a single trait of individual heritability $h^2 = 0.2$.

Percent trees thinned	Male selection intensity	Gain due to male selection	Percent gain due to male selection	Gain due to female selection	Total genetic gain
	i_M	$h^2 i_M / 2$		$h^2 i_F / 2$	$\Delta\bar{G}_{10}^\dagger$
0	0	0 [‡]	0	.27 [‡]	.27 [‡]
30	0.50	.05	16	.27	.32
40	0.64	.06	19	.27	.33
50	0.80	.08	23	.27	.35
60	0.97	.10	27	.27	.36
70	1.16	.12	30	.27	.38
80	1.40	.14	34	.27	.41
90	1.75	.18	40	.27	.44
99	2.66	.27	50	.27	.53

$$^\dagger \Delta\bar{G}_{10} = h^2 (i_M + i_F) / 2.$$

[‡] Genetic gain expressed in units of phenotypic standard deviation σ_p .

represents a compromise between maximising genetic gain (by removing as many trees as possible) and yet retaining sufficient stems per hectare, and reasonably evenly spaced, to achieve both a stable stand and a fairly dense cloud of local pollen.

Table 1 gives the percentage of gain per generation that may be expected under different intensities of thinning to improve the genetic quality of the pollen cloud (assuming a constant intensity of female selection $i_F = 2.66$, and $h^2 = 0.2$). The calculations have been made for open-pollinated mating with mass selection (discussed later) for the sake of simplicity, but the trends are the same for open-pollinated mating with combined index selection. It is apparent from Table 1 that the contribution of male (pollen) selection to total genetic gain increases almost linearly as the percentage of trees thinned is increased up to about 80%. At 80% thinning the selection on male parent contributes 34% of total genetic gain. Further increases in the level of thinning, to 90% and 99%, lead to a roughly exponential increase in the contribution of male selection to 40% and 50% of total gain respectively. However, thinning over 80% of trees may leave too few stems, too unevenly spaced. The 80% thinning is therefore used in the gain calculations presented here.

For *P. radiata* the strategy of open-pollinated mating with combined index selection is assumed to have a generation interval of 10 years (Appendix 3). Gain per decade is therefore equal to the gain per generation.

(10) Open-pollinated mating with mass selection

In this case each subline is represented by 3000 bulked open-pollinated offspring of 30 female parents planted (in a blocked lay-out) on a site isolated from other sublines. The 30 individuals having the highest phenotypic value P for trait U are selected *en masse* from each subline, and the population is regenerated using bulked seedlings grown from open-pollinated seed collected from each of the 30 selected trees. Before collecting the open-pollinated cones

the genetic quality of the local pollen cloud may be improved by culling 80% of the offspring planted at the site.

Total response from mass selection in this instance is given by Equation 34, but with the overall intensity of selection partitioned into the intensities of selection on the female and male parents —

$$\Delta\bar{G}_{10} = h^2 (i_F + i_M) / 2 \quad (36)$$

in units σ_p . As was the case for the previous option $i_F = 2.66$ and $i_M = 1.40$. The generation interval is 10 years and gain per decade equals $\Delta\bar{G}_{10}$.

The most basic form of open-pollinated mating with mass selection is, of course, the approach of select-tree seed collections from carefully thinned stands. However, this option is usually associated with much longer generation intervals.

Results

Solutions to Equations 12, 13, 25, 27, 33, 34 and 36 are presented in Table 2 for a range of individual heritabilities from $h^2 = 0.05$ to 0.4 (this range includes the heritabilities of almost all economic traits in forestry); under the general assumption of selection in a subline of 3000 offspring of 30 parents. The gains presented in Table 2 are expressed both as absolute values and, to simplify comparisons among different strategies, as percentage values relative to the gains produced by the option of single-pair mating with combined index selection.

Perhaps the most obvious feature of Table 2 is that expected gains increase fairly dramatically with increasing heritability, particularly in the lower range of heritabilities between $h^2 = 0.05$ and around $h^2 = 0.15$. Another striking feature of Table 2 is that for each mating design studied the technique of combined index selection produced substantially greater expected gains than any of the other methods of selection (including the two-stage selection techniques).

Of the breeding strategies themselves, half-diallel mating with combined index selection produced the greatest ex-

Table 2. — Genetic gains expected per generation from ten different strategies for improving a single trait (or index) having an individual heritability between 0.05 and 0.40. Figures in brackets give the percent efficiency of each breeding strategy relative to single-pair mating with combined index selection.

Breeding strategy	Individual heritability (h^2)						
	.05	.10	.15	.20	.25	.30	.40
Single-pair mating with -							
(1) within-family/progeny test	.13 [†] (32)	.24(41)	.35(47)	.45(52)	.56(56)	.66(59)	.85(64)
(2) within-family selection	.07(17)	.13(22)	.20(27)	.27(31)	.34(35)	.42(38)	.58(43)
(3) combined index selection	.39(100)	.59(100)	.74(100)	.87(100)	.99(100)	1.11(100)	1.32(100)
Half-diallel mating with -							
(4) family/within-family	.20(51)	.35(59)	.47(64)	.59(67)	.70(70)	.80(72)	1.01(76)
(5) combined index selection	.39(100)	.62(106)	.80(108)	.95(109)	1.09(109)	1.21(109)	1.43(108)
Polycross mating with -							
(6) within-family selection	.10(25)	.20(33)	.30(40)	.40(45)	.50(50)	.60(54)	.81(61)
(7) combined index selection	.27(70)	.44(75)	.58(78)	.71(81)	.83(83)	.95(86)	1.18(89)
(8) mass selection	.13(34)	.27(45)	.40(54)	.53(61)	.67(67)	.80(72)	1.06(80)
Open-pollinated mating with -							
(9) combined index selection	.19(49)	.32(54)	.43(58)	.53(61)	.62(63)	.72(65)	.90(68)
(10) mass selection	.10(26)	.20(35)	.30(41)	.41(47)	.51(51)	.61(55)	.81(61)

[†] Absolute gains given in units of phenotypic standard deviations σ_p of the trait being improved.

pected gains per generation except at very low heritabilities (Table 2). At the high heritability of $h^2 = 0.4$ half-diallel mating with combined index selection produced $1.43\sigma_p$ units of gain per generation (or 8% more than the next most successful strategy which was single-pair mating with combined index selection; i.e. relative efficiency of 108%). At the intermediate heritability $h^2 = 0.2$ (which happens to be fairly typical of the average individual heritability of many important economic traits for *P. radiata*; summarised in DEAN *et al.* 1983) half-diallel mating with combined index selection produced $0.95\sigma_p$ units of gain per generation (relative efficiency 109%; Table 2). At the low heritability $h^2 = 0.05$ half-diallel mating with combined index selection produced the same gain ($0.39\sigma_p$ units) as single-pair mating with combined index selection. The large full-sib families of 200 offspring generated under single-pair matings apparently provided similarly reliable information on breeding values for poorly inherited traits as the combined full-sib and half-sib family information obtained from half-diallel matings.

To express these gains per generation in some actual units of measurement consider say stem diameter of *P. radiata* at 6 years after planting which, in existing first generation breeding populations in Australia, may have a mean of around 11.5cm (depending of course on site quality) and a standard deviation $\sigma_p = 2.94$ cm (see values for test VRC105; DEAN *et al.* 1983). Genetic gains of $1.43\sigma_p$, $0.95\sigma_p$ and $0.39\sigma_p$ therefore represent improvements of around 4.2cm (or 1.43×2.94 cm), 2.8cm and 1.1cm, respectively, in diameter of *P. radiata* at 6 years.

Polycross mating with combined index selection proved to be another promising strategy producing 89% and 81% as much gain per generation as single-pair mating with combined index selection at $h^2 = 0.4$ and 0.2, respectively, but declining to 70% relative efficiency at the low heritability $h^2 = 0.05$ (Table 2). The half-sib family information utilized in combined indices under polycross mating is obviously a less reliable guide to breeding value compared with the full-sib family information from single-pair matings, particularly at low heritabilities. Of the other strate-

gies, half-diallel mating with family/within-family selection, polycross mating with mass selection and open-pollinated mating with combined index selection all produced relative efficiencies of between 67% and 61% at $h^2 = 0.2$ (Table 2). The polycross mating with mass selection was more promising at higher heritabilities, having a relative efficiency of 80% at $h^2 = 0.4$.

Single-pair mating with within-family/progeny test selection produced marginally greater gains per generation (52% relative efficiency at $h^2 = 0.2$; Table 2) than open-pollinated mating with mass selection or polycross mating with within-family selection (47% and 45% relative efficiencies, respectively, at $h^2 = 0.2$). Single-pair mating with within-family selection was the least successful strategy in terms of gains per generation having only 31% relative efficiency at $h^2 = 0.2$. The substantially greater gains from selection within half-sib families (i.e. polycross mating with within-family selection) compared with selection within full-sib families (single-pair mating with within-family selection) may surprise some readers, but is of course due to the fact that there is greater additive genetic variability within half-sib offspring. Given equal intensity of selection and equal individual heritability, selection within half-sib offspring should always yield greater responses than selection within full-sib offspring (FALCONER, 1976).

Table 3 presents absolute gains expected per decade for each strategy, calculated by dividing the gains per generation in Table 2 by the appropriate generation interval (in decades). Table 3 also gives the percent efficiency of each strategy relative to single-pair mating with combined index selection.

Expressing expected gain on a per unit time basis has clearly enhanced the relative merits of strategies that should require only 10 or 11 years to complete each generation of improvement for *P. radiata* in Australia. For instance, single-pair mating with combined index selection (11 year generation) produced greater gains per decade than the more elaborate approach of half-diallel mating with combined index selection (14 year generation). The absolute

Table 3. — Genetic gains expected per decade from ten different strategies for improving a single trait (or index) having an individual heritability between 0.05 and 0.40. Figures in brackets give the percent efficiency of each breeding strategy relative to single-pair mating with combined index selection.

Breeding strategy	Individual heritability (h^2)						
	.05	.10	.15	.20	.25	.30	.40
Single-pair mating with -							
(1) within-family/progeny test	.07 [†] (21)	.14(27)	.21(31)	.27(34)	.33(36)	.39(38)	.50(42)
(2) within-family selection	.06(17)	.12(22)	.18(27)	.25(31)	.31(35)	.38(38)	.52(43)
(3) combined index selection	.36(100)	.53(100)	.67(100)	.79(100)	.90(100)	1.01(100)	1.20(100)
Half-diallel mating with -							
(4) family/within-family	.14(40)	.25(46)	.34(50)	.42(53)	.50(55)	.57(57)	.72(60)
(5) combined index selection	.28(78)	.44(83)	.57(85)	.68(86)	.78(86)	.86(86)	1.02(85)
Polycross mating with -							
(6) within-family selection	.09(25)	.18(33)	.27(40)	.36(45)	.45(50)	.55(54)	.74(61)
(7) combined index selection	.25(70)	.40(75)	.53(78)	.64(81)	.75(83)	.86(86)	1.08(89)
(8) mass selection	.12(34)	.24(45)	.36(54)	.48(61)	.60(67)	.73(72)	.97(80)
Open-pollinated mating with -							
(9) combined index selection	.19(53)	.32(60)	.43(64)	.53(67)	.62(69)	.72(71)	.90(75)
(10) mass selection	.10(28)	.20(38)	.30(45)	.41(51)	.51(56)	.61(60)	.81(67)

[†] Absolute gains expressed in units of phenotypic standard deviations σ_p of the trait being improved.

gains expected per decade from single-pair mating with combined index selection for $h^2 = 0.4, 0.2$ and 0.05 were $1.20\sigma_p$ (or 3.5cm for diameter of *P. radiata* at 6 years), $0.79\sigma_p$ (2.3cm) and $0.36\sigma_p$ (1.1cm), respectively (Table 3). Corresponding gains from half-diallel mating with combined index selection were $1.02\sigma_p$ (3.0cm), $0.68\sigma_p$ (2.0cm) and $0.28\sigma_p$ (0.8cm). Polycross mating with combined index selection (11 year generation) also produced substantial gains per decade, and exceeded the gains per decade from half-diallel mating with combined index selection at higher heritabilities above $h^2 = 0.3$. In general the strategies of half-diallel mating with combined index selection and polycross mating with combined index selection had efficiencies of between 89% and 70% relative to single-pair mating with combined index selection (Table 3).

Polycross mating with mass selection (11 year generation) produced fairly high gains per decade at higher heritabilities, having a relative efficiency of 80% at $h^2 = 0.4$ (Table 3). Open-pollinated mating with combined index selection (10 year generation) produced greater gains per decade than polycross mating with mass selection at low and intermediate heritabilities, but less gain at heritabilities $h^2 \geq 0.3$.

Open-pollinated mating with mass selection (10 year generation), polycross mating with within-family selection (11 year generation) and half-diallel mating with family/within-family selection (14 year generation) produced approximately the same expected gains per decade at intermediate to high heritabilities (Table 3). (The half-diallel mating with family/within-family selection was somewhat more appealing at lower heritabilities due to the stage-1 family selection). It is interesting to note that breeders who invest the considerable time and effort required to complete elaborate diallel matings, but then employ the much recommended approach of two-stage family/within-family selection to choose individuals for future breeding, may achieve only about the same gains per decade that would be expected from a very simple and low cost option such as open-pollinated mating with mass selection. If sophisticated diallel (or Design II) matings are used to regenerate the breeding population they should clearly be supported by efficient selection techniques such as the combined index.

The main reason for the greater efficiency of combined index selection in this instance is the fact that the index allows superiority in say individual performance to compensate at least to some extent, for poorer family performance. Under the two-stage family/within-family selection individuals are automatically culled when their family mean falls below some arbitrary "culling level", regardless of their own phenotypic merit.

The poorest options in terms of gain per decade were single-pair mating with within-family/progeny test selection and single-pair mating with within-family selection (both strategies having relative efficiencies below 43%; Table 3). The long generation interval of 17 years for single-pair mating with within-family/progeny test selection reduced the gains per decade for this strategy to a level approaching the gains per decade for the more simple approach of single-pair mating with within-family selection (employing no stage-2 progeny test).

Gains from single-pair mating with within-family/progeny test selection may be considerably enhanced by not restricting the stage-1 selection to within-families, but simply selecting phenotypically superior individuals regardless of family (i.e. two-stage individual/progeny test selection). COTTERILL and JAMES (1981; Figure 3 for $p = 0.01$, $p_1 = 0.02$) report an expected gain per generation of around $0.75\sigma_p$ (or $1.68\sigma_A$) for single-pair mating with individual/progeny test selection at $h^2 = 0.2$. However, the long 17 year generation reduces this gain to only $0.44\sigma_p$ per decade (or 56% relative efficiency).

The differences between strategies in Table 2 and 3 hold for population sizes other than the 3000 offspring of constant 30 parents considered here. In calculations not reported, gains have been compared for each strategy under circumstances where the number of offspring per parent was set at a much higher level (e.g. 3000 offspring of only 12 parents per subline). Although the intensities of selection, and therefore the absolute gains, were higher under these circumstances of more offspring per parent, the relative differences between strategies remained about the same. The case of 30 parents and 3000 offspring per subline has been used in this study because it represents the size of sublimes actually employed in the breeding program for

P. radiata in South Australia. (A total of 10 sublimes will eventually be incorporated into this program giving 300 parents for the entire breeding population.)

In other calculations not reported here it was found that the relative differences between strategies in terms of gains per generation and per decade were also similar under the exceptionally high intensities of selection that may be used in choosing individuals for seed orchards (e.g. in choosing only the best one or two individuals from each subline). Options involving half-diallel, polycross and open-pollinated matings do, however, provide information on the breeding values of parents which may, over time, be used to further increase gains by culling orchards. No accurate estimates of breeding value can be obtained from single-pair matings. Results and discussion in this article concentrate on gains in the breeding population because this is the fundamental population of cumulative improvement.

Finally, the calculations of genetic gain represented in Table 2 and 3 ignore the effects of inbreeding since it is assumed that inbreeding which accumulates within each subline can be released by outcrossing, and therefore not carried through to the plantations. Calculations (which involve theoretical considerations together with results of experimentation by Dr A. R. GRIFFIN, CSIRO, on inbreeding in *P. radiata*) have been made of the expected rate of increase in inbreeding under some strategies, but are omitted to avoid further lengthening the present article. It is, however, worth mentioning that after say five generations of improvement of *P. radiata* under open-pollinated mating with mass selection the expected accumulation of inbreeding in each subline may only reduce diameter at 6 years about 6% below the mean predicted from the gains per generation in Table 2. (Details of these calculations can be obtained on request from the author.) Corresponding estimates of inbreeding depression for single-pair mating with individual (mass) selection and polycross mating with mass selection were around 2% and 4%, respectively.

Rates of increase in inbreeding can be much greater under combined index selection because of the potentially strong component of family selection involved. It is common for breeders applying combined indices to reduce the rate of inbreeding by setting some arbitrary limit on the number of individuals which may be selected from any one family. In breeding *P. radiata* in South Australia the limit has often been set at retaining no more than five individuals per family. This type of mild restriction will lead to some reduction in expected gain from the combined index, but the decrease may be moderately small. (In future studies the author intends to consider this option of imposing restrictions on combined index selection to reduce inbreeding, and examine the effect the restrictions have on reducing genetic gain).

General Discussion

The half-diallel mating designs which are presently employed in many pine breeding operations in Australia (GRIFFIN, 1976; MATHESON, 1978) and elsewhere (BURDON *et al.*, 1977; TALBERT, 1979) can clearly produce maximum genetic gains per generation when used in conjunction with combined index selection. However, under the generation intervals assumed here, half-diallel mating with combined index selection yielded less gain per decade (regardless of heritability) than the much simpler approach of single-pair mating with combined index selection. At heritabilities of above $h^2 = 0.3$, polycross mating with combined index

selection also produced more gain per decade than options involving half-diallel matings. These higher heritabilities are reasonably common in tree breeding. For instance, multi-trait selection indices reported by COTTERILL and JACKSON (1985) for *P. radiata* improvement in Australia had individual heritabilities of between $h^2 = 0.25$ and 0.36. (Although indices involving strongly adversely correlated traits may be much more poorly inherited.)

The main problem with elaborate diallel (or Design II) matings is that a very well managed and staffed breeding operation is required to complete the numerous and intricate controlled-crosses in a reasonably short period of time (say three pollination seasons; Appendix 2). Indeed, the 14 year generation assumed here for half-diallel mating is probably optimistic compared with the 10 or 11 year generations assumed for strategies involving simpler mating designs. Obviously the more simple the mating design the better the chance of completing the controlled-crosses, and therefore the generations, on schedule. (It was evident in carrying out gain calculations for this study that an increase of just one year in generation interval can have a marked influence in reducing gains per decade.) Another important problem with half-diallel matings is that in practice they are invariably used in conjunction with smaller population sizes (less than say 150 parents) and, while the fewer parents reduce the work load in controlled-pollinations, the longer-term consequences may be significantly reduced stability and flexibility of future breeding populations. An overall population size of at least 300 parents may be required to provide a reasonably broad genetic base to meet new selection criteria (e.g. resistance to new diseases) which can arise over time (BURDON *et al.*, 1977; COTTERILL, 1984). One advantage of half-diallels which should be noted is that the mating design does provide information on specific combining effects which may be utilized through mass vegetative propagation or even two-clone orchards.

The New Zealand Forest Research Institute (NZFRI) was able to complete (in the late 1970's) some 16 disconnected 5×5 half-diallel matings among 80 parents of *P. radiata* in three seasons of controlled-pollinations on the ortets; thereby achieving a generation interval of 11 years (Dr M. D. WILCOX, NZFRI, pers. comm.). However, these 80 parents represent only a part of the overall NZFRI breeding population. It is unlikely that even an operation as well managed as *P. radiata* breeding in New Zealand could complete half-diallel matings among 300 parents in less than a 14 year generation. A national cooperative for breeding *P. radiata* in Australia has taken seven pollination seasons (between 1978 and 1984) to complete 21 disconnected 6×6 half-diallel matings among 126 parents in clone banks; giving a generation interval in excess of 18 years.

The most important finding of this study is undoubtedly that maximum or near-maximum gains per decade may be achieved from simple mating designs, such as single-pair or polycross matings, when they are used in conjunction with an efficient method of selection such as the combined index or even mass selection. Single-pair mating (as first proposed by LIBBY, 1968) is already widely employed in tree breeding, but often in conjunction with within-family selection. While single-pair mating with within-family selection may have advantages in minimising the rate of increase in inbreeding, it was among the worst of the strategies considered here in terms of genetic gain. Breeders would be foolish to rely entirely on selection

within families to improve trees. Polycross mating (proposed by BURDON and SHELBORNE, 1971) does not appear to have been used at all in tree breeding, at least in the programs reported in the literature. It is difficult to understand why the incomplete polycross mating design has not been better accepted by tree breeders because, like single-pair matings, the option involves a minimum of controlled-crosses. One potentially important advantage of incomplete polycross mating compared with single-pair mating is that under the former option the best half of the individuals selected each generation may be assigned as female parents and their breeding values determined (the other half of the individuals being used as male parents in the pollen mix). This information on breeding values of the best half of the previous-generation selections would be very useful for culling orchards. (Another important use of breeding values which is presently being considered in breeding eucalypts in southern Australia is to construct "best mate indices", described by COTTERILL, 1984, that should provide maximum probability of generating outstanding families in an elite "nucleus" population for mass vegetative propagation. It is intended to elaborate more on this approach in future publications).

The majority of *P. radiata* breeding operations in Australia should be sufficiently well managed and staffed to conduct single-pair or polycross matings with say combined index selection for a reasonably large breeding population (a total of around 300 parents) in a reasonably short generation time (around 11 years). However these same breeding operations (even when they are brought together in a cooperative) have not been able to complete half-diallel matings involving a relatively small number of parents (126 parents) in anywhere near the 14 year generation interval assumed here. This situation in Australia appears to be typical of the capacity of many breeding operations around the world. An important principle of tree breeding is clearly that it is far better to satisfactorily conduct a simple, less sophisticated breeding strategy than to make a poor job of an elaborate strategy. Another practical advantage of simpler strategies is that the labour saved in say controlled-pollinations may be used very profitably to establish more offspring in the breeding population, and therefore permit more intensive selection in the next generation.

In circumstances where breeders might lack the expertise or computing facilities to employ combined index selection, polycross mating with mass selection offers a very appealing alternative. This strategy represents one of the most simple and inexpensive options available for breeding trees. Breeding operations having only the most basic of resources, and few skilled staff, should be able to complete each generation of this strategy in a short time (11 years for *P. radiata*) and using a reasonably large population (300 parents). However, despite this simplicity and low cost, polycross mating with mass selection can produce substantial gains per decade, particularly for traits of moderate to high heritability. It is interesting to speculate that if polycross mating with mass selection had been used when *P. radiata* breeding began in Australia in the late 1940's the local operations may now have been into the fourth generation of improvement rather than just entering the second generation of more elaborate strategies. The cumulative genetic progress in *P. radiata* in Australia at present could have been three or four times greater under the mass selection option. (Another very simple strategy not considered here is single-pair mating with mass selection

which would, of course, produce the same expected gains as polycross mating with mass selection).

The main argument against mass selection has been that one or two parents may dominate the ancestry of individuals selected for future breeding, and thereby seriously increase the level of inbreeding and, of course, restrict the genetic base (WEIR and ZOBEL, 1972; WEIR, 1974; ROBERTS *et al.*, 1980). The problem is alleviated, at least to some extent, by sublining. In any case, the previously mentioned calculations of inbreeding under different strategies suggest that the expected levels of inbreeding after say five generations of polycross mating with mass selection would not be high.

Breeders who remain concerned about the possibility of one or two parents dominating a subline under mass selection might consider retaining the female pedigree of offspring in the field, and selecting individuals *en masse* but with the proviso of no more than say five selections per family. Such a mild restriction may not greatly reduce genetic gain and would act as insurance against serious levels of inbreeding.

Open-pollinated mating with combined index selection produced reasonable gains per decade, but the gains from open-pollinated mating with mass selection were lower. It is clear from Table 1 that the latter option cannot be expected to yield very substantial gains until there is over 10% selection (i.e. over 90% thinning) of pollen parents, but such drastic silviculture is often not practicable in young stands. The main problem with the open-pollination options may be their vulnerability to pollen contamination. Pollen from plantations of seed orchard origin could be particularly troublesome because of its effect in breaking down the genetic uniqueness of each subline.

Open-pollinated matings have, nevertheless, been employed with considerable success in eucalypt breeding. For instance, the well known improvement programs of *Eucalyptus robusta* and *E. grandis* in southern Florida both rely on open-pollinated mating with combined index selection (FRANKLIN and MESKIMEN, 1973, 1983). The two programs began in the early 1960's and the *E. robusta* operation has proceeded to the third generation of selection, while the *E. grandis* operation is in the fourth generation (FRANKLIN and MESKIMEN 1983). Another improvement program of *E. grandis* using open-pollinated mating with family/within-family selection was begun in South Africa in 1976 and has reached the third generation (Dr G. VAN WYK, FRI South Africa, pers. comm.). An improvement program of black walnut (*Juglans nigra*) in Indiana, USA, also employs open-pollinated matings (McKEAND and BEINEKE 1980).

The single-pair mating with within-family/progeny test selection suggested by COTTERILL (1984) does not produce adequate gains and will be replaced by either incomplete polycross or single-pair mating with combined index selection in the breeding program for *P. radiata* in South Australia. The original breeding plan outlined in COTTERILL (1984) was intended as a carefully considered "starting point", but never an ultimate plan. Many changes have been made to the plan, including the one above, as a direct consequence of having a well documented breeding policy which can be read, understood, criticised and therefore improved. However, most of the fundamental features of the plan, namely the breeding objectives, hierarchy of populations, low cost gene pool, best mate index, and so on, remain unaltered.

The breeding strategies considered in this study do not, of course, represent a complete list of all possible options.

For instance, double-pair and circular matings are sometimes mentioned in the tree breeding literature as possible alternatives (NAMKOONG, 1979). However, the gain equations presented in this article can be used to show that the responses per generation expected from say double-pair mating with combined index selection are about the same as the gains from single-pair mating with combined index selection, while the former option requires twice as many controlled-crosses. Dr PH. BARADAT (INRA France, pers. comm.) has mentioned nested (or Design I) matings with combined index selection. The strategy has been employed with some success in poultry breeding, and gain formulations given in OSBORNE (1957; Equation H) suggest that nested mating with combined index selection may produce only marginally lower gains than half-diallel mating with combined index selection. However, the nested matings again require at least twice as many controlled-crosses as single-pair matings and would be expected to lead to a longer generation interval. In other instances breeders may wish to employ more than one mating design in a breeding program (BURDON and SHELBORNE, 1971; Dr PH. BARADAT, Dr G. VAN WYK, pers. comm.) and the gain formulations for predicting response would need to be tailored to each particular case.

Conclusions

The strategies which are currently being used to improve pines in Australia are almost certainly not producing as much gain per decade as may be achieved from simpler and less expensive options involving single-pair or polycross matings with combined index selection or even mass selection. A similar situation is likely to be true in many tree breeding programs around the world. The results of this study suggest that tree breeders may be well advised to disregard elaborate mating designs, and concentrate their efforts on efficient selection and short generations.

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