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Asymptotic rates of response from forest tree breeding strategies using best linear unbiased prediction

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Abstract Genetic gain equations are developed for selection on multiple traits using either multi- or univariate best linear unbiased predictors (BLUP) and for selection under controlled and open pollination and polymix mating schemes. The equations assume an infinite population and account for the effects of selection. A comparison with simulated populations under the same mating schemes show that the gain equations predict selection response well, with the predictions having some upward bias. The gain equations are used to compare across mating schemes, to compare univariate to multivariate analyses, and to measure the reduction in the rate of genetic gain due to selection disequilibrium. Results show controlled pollination schemes can offer as much as a 56% advantage in genetic gain relative to open pollination. The reduction in the rate of genetic gain due to selection disequilibrium is approximately 27% under controlled pollination for the breeding goals studied. The results show a limited benefit in using multivariate analyses for predicting breeding values.

Key words BLUP-Multivariate analysis · Breeding strategy · Genetic gain

Introduction

Design of the breeding strategy is an important component of forest tree breeding. What criteria are avail-

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able to compare alternatives? Prediction of genetic gain is certainly important, while maintaining effective population size and minimizing inbreeding are often other considerations. Cotterill (1986) and more recently Shelbourne (1991) developed expressions for predicting genetic gain in a number of strategies. These strategies included combinations of controlled pollination (CP), open pollination (OP) and polycross mating with between-family, within-family and combined index selection methods. Cotterill in particular noted the clear advantage of combined index selection, independent of which type of mating was used.

The classical selection index, first used in plant and animal breeding by Smith (1936) and Hazel (1943), respectively, assumes equal amounts and quality of data available for all candidates. In addition, the classical selection index can realistically only incorporate information from direct relatives, and the fixed effects are predetermined often using only ordinary least-squares methodology. In field populations data are often unbalanced; individuals will have differing levels and sources of data. As a method of combined index selection, selection on best linear unbiased predictors (BLUP) is optimal (Goffinet 1983) because in effect a customized index is created for each individual. Because all relationships between individuals are included, any bias due to genetic trend is removed. Bias due to any known environmental trend is removed because solutions to environmental effects are computed simultaneously with the genetic effects. More optimal is selection on multiple traits using multivariate BLUP, as bias due to selection on a correlated trait can be avoided. BLUP is an integral component of national genetic evaluation strategies for animal breeding industries and more recently for the Eucalypt tree breeding industry within Australia (Jarvis et al. 1995; Borralho 1995).

However, deterministic prediction of genetic gain from selection on breeding values derived using BLUP is not straightforward because the amounts and types

of information used to predict breeding values will differ between individuals. Wray and Hill (1989) were able to formulate an index that was reasonably able to predict rates of response from single trait BLUP selection. In the same manner Villanueva et al. (1993) formulated equations for the multivariate case. These indices were able to predict asymptotic rates of response, an important feature, if for example, a long-term economic assessment of the strategy was being undertaken. If a prediction based on one round of selection was used, then most likely, projections of genetic gain and capital return, would be inflated. This is because there is considerable reduction in between-family additive genetic variance in the initial generations due to linkage disequilibrium, often referred to as the "Bulmer effect" (Bulmer 1971). An asymptotic rate of response is achieved when recombination offsets any new disequilibrium induced by continuing selection.

The aim of the study presented here was to formulate selection indices that could adequately predict asymptotic rates of response from BLUP selection in common tree breeding strategies. Once formulated these indices can then be used to compare alternative tree breeding strategies without resorting to time-consuming simulation studies. The loss in reduction of selection response due to linkage disequilibrium can also be quantified.

Theory

Selection indices, sometimes referred to as deterministic BLUP equations, were formulated separately for four breeding strategies. These strategies were: controlled pollination with both multiple- and single-pair mating; open pollination with no thinning; open pollination with 80% thinning; and a complete polycross mating system where all parents are used as females as well as in the pollen mix. Predicted response from each index was checked against realized response from simulation of the breeding strategy. Once good agreement was found the indices were then used to further compare breeding strategies across a range of genetic and phenotypic parameters.

There are q measured traits. The objective is to improve the r traits in the breeding objective. Measured traits may be the same as those in the breeding objective, otherwise correlations will exist which link measured traits to traits in the breeding objective. Selection is on an aggregate breeding value, H , given by

$$H = v' A_{BM} A_{MM}^{-1} \hat{a} \quad (1)$$

where v is a $r \times 1$ vector of economic weights, A_{BM} is a $r \times q$ additive genetic covariance matrix between traits in the breeding objective and measured traits, A_{MM} is a $q \times q$ additive genetic variance-covariance matrix between measured traits and \hat{a} is a $q \times 1$ vector of estimated breeding values for the measured traits (EBV). Let

$$w' = v' A_{BM} A_{MM}^{-1}$$

Thus, in the case where measured traits are the same as those in the breeding objective $w' = v'$. Consider s pieces of information which are used to calculate an EBV for each measured trait. These are denoted index components. The selection index used to predict H is then

$$I_t = b_{(t)}' x$$

where b is a $sq \times 1$ vector of weighting factors and x is a $sq \times 1$ vector of index components. The subscript (t) is introduced to signify that weighting factors, and index values are calculated for each generation t . Weighting factors are calculated from the selection index equations:

$$b_{(t)} = P_{(t)}^{-1} G_{(t)} w$$

where P is a $sq \times sq$ phenotypic variance-covariance matrix for the index components, and G is a $sq \times q$ matrix of additive genetic covariances between the index components and the measured traits. Following Villanueva et al. (1993) it is helpful to partition P and G :

$$P_{(t)} = \begin{pmatrix} P_{11(t)} & P_{12(t)} & \cdots & P_{1q(t)} \\ P_{21(t)} & P_{22(t)} & \cdots & P_{2q(t)} \\ \vdots & \vdots & & \vdots \\ P_{q1(t)} & P_{q2(t)} & \cdots & P_{qq(t)} \end{pmatrix}$$

$$G_{(t)} = \begin{pmatrix} g_{11(t)} & g_{12(t)} & \cdots & g_{1q(t)} \\ g_{21(t)} & g_{22(t)} & \cdots & g_{2q(t)} \\ \vdots & \vdots & & \vdots \\ g_{q1(t)} & g_{q2(t)} & \cdots & g_{qq(t)} \end{pmatrix}$$

$$= (g_{1(t)} \ g_{1(t)} \ \cdots \ g_{q(t)})$$

where $P_{jk(t)}$ is a matrix containing the phenotypic variances of index components for trait j if $j = k$, or the phenotypic covariances of index components between trait j and trait k at time t , and where $g_{jk(t)}$ is a vector containing additive genetic covariances between index components for trait j and the breeding value of trait k . Individual index components, values for $P_{jk(t)}$ and $g_{jk(t)}$ are described below for each breeding strategy. The response to selection in aggregate breeding value at generation t is

$$R_{(t)} = i \sigma_{I(t-1)} \quad (2)$$

where i is the average selection intensity and $\sigma_{I(t-1)}$ is the standard deviation of the index at generation $t - 1$ and is calculated using the equation

$$\sigma_{I(t)}^2 = b_{(t)}' P_{(t)} b_{(t)}$$

For each breeding strategy it is assumed that a constant breeding population of 200 parents is maintained. The number of progeny able to be field tested is held constant at 8000. It is assumed that for all progeny field tested, a phenotypic record for each trait becomes available prior to selection of parents of the next generation's progeny. Generations are discrete. It is assumed that a phenotypic record for trait j (X_j) is the summation of additive gene effects (A_j) and individual environmental effects (E_j), that is

$$X_j = A_j + E_j$$

The phenotypic variance covariance matrix between measured traits at generation t is given by

$$X_{(t)} = A_{MM(t)} + E \quad (3)$$

where E is the environmental variance covariance matrix between measured traits. The matrix A_{MM} is as above (see Eq. 1) except that it no longer refers to an unselected population but to a selected population at time t .

Controlled pollination with multiple-paired mating

Under this strategy the 200 parents selected each generation are each involved in four matings. It is assumed that for any cross the 3 other trees crossed to the male parent and the 3 other trees crossed

to the female parent are mutually exclusive. The number of full-sib families created is 400, and 20 individuals per family are tested each generation. Let

n_f = number of full-sib families created per parent

n_c = number of individuals per full-sib family

Then the index components for trait j are as follows: a record on the individual (X_j); the mean of n_c full-sib records (F_j) (the individual's record is included in the mean); the mean of $n_f \times n_c$ half-sib records through the female parent ($H1_j$); the mean of $n_f \times n_c$ half-sib records through the male parent ($H2_j$) (half-sib records through each parent include the individual's and its full-sibs' records); the estimated breeding value of the female parent ($A1_j$); and finally the estimated breeding value of the male parent ($A2_j$). Sub-matrices $\mathbf{P}_{jk(t)}$ and vectors $\mathbf{g}_{jk(t)}$ are as follows:

$$\mathbf{P}_{jk(t)} = \begin{matrix} & \begin{matrix} X_k & F_k & H1_k \\ X_j & \begin{pmatrix} COV(X_j, X_k) & P_1(j, k)_t & P_2(j, k)_t \\ F_j & \begin{pmatrix} P_1(j, k)_t & P_1(j, k)_t & P_2(j, k)_t \\ H1_j & \begin{pmatrix} P_2(j, k)_t & P_2(j, k)_t & P_2(j, k)_t \\ H2_j & \begin{pmatrix} P_2(j, k)_t & P_2(j, k)_t & P_3(j, k)_t \\ A1_j & \begin{pmatrix} P_4(j, k)_t/2 & P_4(j, k)_t/2 & P_4(j, k)_t/2 \\ A2_j & \begin{pmatrix} P_4(j, k)_t/2 & P_4(j, k)_t/2 & P_4(j, k)_t/2n_f \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{pmatrix} \end{matrix} \\ \mathbf{g}_{jk(t)} = \begin{pmatrix} COV(A_j, A_k) \\ G_1(j, k)_t \\ G_2(j, k)_t \\ G_2(j, k)_t \\ P_4(j, k)_t/2 \\ P_4(j, k)_t/2 \end{pmatrix} \end{matrix}$$

where $COV(X_j, X_k)_t$ and $COV(A_j, A_k)_t$ are the phenotypic and additive genetic covariances between traits j and k at generation t , and

$$G_1(j, k)_t = COV_B(A_j, A_k) + COV_W(A_j, A_k)/n_c,$$

$$G_2(j, k)_t = 1/2COV_B(A_j, A_k) + 1/2COV_B(A_j, A_k)/n_f + COV_W(A_j, A_k)/n_f n_c$$

$$P_1(j, k)_t = G_1(j, k)_t + COV(E_j, E_k)/n_c$$

$$P_2(j, k)_t = G_2(j, k)_t + COV(E_j, E_k)/n_f n_c$$

$$P_3(j, k)_t = \frac{COV_B(A_j, A_k)}{n_f} + \frac{COV_W(A_j, A_k) + COV(E_j, E_k)}{n_c n_f^2}$$

where $COV_B(A_j, A_k)_t$ and $COV_W(A_j, A_k)_t$ are the between- and within-family additive genetic covariances, respectively, between traits

j and k . The within-family covariance is not affected by selection and remains at $1/2COV(A_j, A_k)_t=0$. However, the between-family covariance is reduced each round of selection and at generation t is given by

$$COV_B(A_j, A_k)_t = 1/2 \left(COV(A_j, A_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(A_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k \right)$$

where

$$COV(A_j, I)_t = \mathbf{b}'_{(t)} \mathbf{g}_{j(t)}$$

and is the additive genetic covariance between trait j and the index used to predict H in generation t . This formula follows directly from Wray and Hill (1989) and Villanueva et al. (1993), who partitioned the between-family (co)variance into between-sire and between-dam family (co)variances. The scalar k is equal to $i(i-x)$ where i is the selection intensity and x is the standardized deviation of the truncation point from the mean for all parents. For the example given, retaining the best 200 from a total of 8000 yields $i = 2.338$. The component $P_3(j, k)_t$ refers to the covariance between the means of the two half-sib families. Finally

$$P_4(j, k)_t = COV(A_j, I_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(I_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k,$$

where firstly

$$COV(A_j, I_k)_t = \mathbf{b}'_{k(t)} \mathbf{g}_{j(t)}$$

and is the additive genetic covariance between trait j and the index used to predict breeding values for trait k , the latter obtained from

$$I_{k(t)} = \mathbf{b}'_{k(t)} \mathbf{x}$$

where

$$\mathbf{b}_{k(t)} = \mathbf{P}_{(t)}^{-1} \mathbf{g}_{k(t)}.$$

Secondly,

$$COV(I_k, I)_t = \mathbf{b}'_{(t)} \mathbf{G}_{(t)} \mathbf{w}$$

and is the covariance between the index used to predict breeding values for trait k and the index used to predict breeding values for H . An index for controlled pollination with single-pair mating was obtained by using similar equations as shown above but deleting records for the mean of half sibs through both parents ($H1$ and $H2$).

An asymptotic rate of response was achieved when response calculated from Eq. (2) did not vary significantly from one generation to the next. Generally this did not occur within six generations.

Open-pollination strategies

Under open-pollinated strategies it is assumed that 40 open pollinated plantable seedlings are obtained from each of the 200 female parents. It is assumed the 8000 progeny are planted at a site isolated from other breeding and/or deployment populations to avoid cross pollination. Cotteril (1986) suggests single-tree plots should be used to encourage outcrossing among individuals of different families. For the following it is assumed all pollen is sourced from within the population, that is, there is no outside pollen contamination.

If n_0 is the number of open-pollinated progeny per female parent, the index components for trait j are: a record on the individual (X_j); the mean of n_0 half-sib records through the female parent ($H1_j$); and the estimated breeding value of the female parent ($A1_j$). Sub-matrices

$\mathbf{P}_{jk(t)}$ and vectors $\mathbf{g}_{jk(t)}$ are as follows:

$$\mathbf{P}_{jk(t)} = \begin{pmatrix} X_k & H1_k & A1_k \\ COV(X_j, X_k) & P_2(j, k)_t & P_4(j, k)_t/2 \\ P_2(j, k)_t & P_2(j, k)_t & P_4(j, k)_t/2 \\ P_4(j, k)_t/2 & P_4(j, k)_t/2 & P_4(j, k)_t \end{pmatrix} \quad (4)$$

$$\mathbf{g}_{jk(t)} = \begin{pmatrix} COV(A_j, A_k) \\ G_2(j, k)_t \\ P_4(j, k)_t/2 \end{pmatrix} \quad (5)$$

where $G_2(j, k)_t = COV_F(A_j, A_k)_t$ and $P_2(j, k)_t = G_2(j, k)_t + COV(E_j, E_k)_t/n_p$. The between-female parent family additive genetic covariance for traits j and k , $COV_F(A_j, A_k)_t$, is given by

$$COV_F(A_j, A_k)_t = 1/4 \left(COV(A_j, A_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(A_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k_f \right). \quad (6)$$

The between-male parent family additive genetic covariances are also computed each generation and are given by

$$COV_M(A_j, A_k)_t = 1/4 \left(COV(A_j, A_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(A_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k_m \right). \quad (7)$$

Additive genetic covariances are then updated each generation from summation of all components, that is

$$COV(A_j, A_k)_t = COV_F(A_j, A_k)_{t-1} + COV_M(A_j, A_k)_{t-1} + COV_W(A_j, A_k). \quad (8)$$

For the example given, selection intensity in the female parents (i_f) is 2.338 (selecting 200 of 8000 female parents), while the selection intensity in the male parents is 0.0 (selecting 8000 of 8000 male parents). Values for k_f and k_m are derived accordingly. A selection intensity in the male parents could be achieved by culling a percentage of the 8000 stems prior to collection of open-pollinated cones. Cotterill (1986) gives figures for the increase in genetic gain resulting from improvement in the genetic quality of the pollen cloud. He argued that an 80% thinning of stems was optimal for genetic gain whilst leaving adequate stems. If 80% thinning is applied to our example and culling is on the basis of index values for the breeding objective, then $i_m = 1.4$ (selecting 1600 of 8000 male parents). This value can then be applied to Eq. 7. Finally

$$P_4(j, k)_t = COV(A_j, A_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(A_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k_f.$$

Polycross mating

Under this strategy all the parents (200 in our example) are used as female parents as well as being used in the pollen mix. From each female parent 40 plantable seedlings are obtained and field-tested.

If n_p is the number of progeny per female parent, the index components for trait j are: a record on the individual (X_j); the mean of n_p half-sib records through the female parent ($H1_j$); and the estimated breeding value of the female parent ($A1_j$). Sub-matrices $\mathbf{P}_{jk(t)}$ and vectors $\mathbf{g}_{jk(t)}$ are identical to Eqs. 4 and 5. The component

$P_2(j, k)_t$ is equal to $COV_F(A_j, A_k)_t + COV(E_j, E_k)_t/n_p$, where

$$COV_F(A_j, A_k)_t = COV_M(A_j, A_k)_t = 1/4 \left(COV(A_j, A_k)_{t-1} - \frac{COV(A_j, I)_{t-1} COV(A_k, I)_{t-1}}{\sigma_{I(t-1)}^2} k \right).$$

The selection intensity is the same as in controlled pollination strategies (selecting 200 of 8000 parents) where $i = 2.338$.

Validation of indices

Predictions of genetic gain using the indices presented above were compared with results from simulation. For all strategies base parent additive genetic values or breeding values [$a(i)_j$, stated as the breeding value of the i th individual for the j th trait] were sampled from a multivariate normal distribution $MN(\boldsymbol{\mu}, \boldsymbol{\Sigma})$ where $\boldsymbol{\mu}$ is a $1 \times q$ vector of zeros and $\boldsymbol{\Sigma}$ is a $q \times q$ positive definite additive genetic variance covariance matrix, with elements $\Sigma_{jk} = COV(A_j, A_k)_{t=0}$. For descendents $\Sigma_{jk} = 1/2(1 - \bar{F})COV(A_j, A_k)_{t=0}$ where \bar{F} is the average inbreeding coefficient of the female parent, f , and the male parent, m , and $\boldsymbol{\mu} = [\mu_1, \dots, \mu_q]$ where $\mu_j = 1/2a(f)_j + 1/2a(m)_j$, which is the mid-parental breeding value for the j th trait. The record for the j th trait of an individual was simulated as the sum of its breeding value, an environmental effect common to all individuals located in the same site and an individual environmental effect. Both environmental effects were sampled from multivariate normal distributions, with mean vectors containing zeros and variance covariance matrices with elements $\Sigma_{jk} = COV(E_j, E_k)$.

Two traits were considered, with heritabilities and genetic and phenotypic correlations realistic for cross-sectional area and density traits in *Pinus radiata* (see Table 1). For the simulation phenotypic standard deviations were set at unity for both traits. By assuming that measured traits were the same as those in the breeding objective $\mathbf{w} = [2 \ 1]$; that is, the relative economic weights for cross-sectional area and wood density were 2:1. Estimated aggregate breeding values (\hat{H}) were calculated as $\mathbf{w}'\hat{\mathbf{a}}$, where $\hat{\mathbf{a}}$ are EBVs calculated using a multivariate BLUP. Under open-pollination and polycross-mating strategies identities of all male parents were assumed unknown when calculating EBVs.

Under controlled pollination each of the 200 parents was mated 4 times, with no restrictions on matings between close relatives, and there was no overlap between the mates of female and male parents. Under open pollination each of the 200 selected female parents was mated 40 times, with the male parent randomly chosen from among 8000 individuals of the same generation as the female parents. Under the 80% thinning regime, 6400 of the 8000 individuals were first culled on

aggregate breeding value before crossing took place. The 80% thinning is the same as that used by Cotterill (1986). No selfing was allowed. Under polycross mating each of the 200 female parents was mated 40 times, with the male parent randomly chosen from among the selected 200 individuals. No selfing was allowed. For each strategy six generations of selection was simulated and replicated 50 times.

Table 2 shows the results of the simulations. For each strategy considered, simulated and predicted rates of response are shown at each of the six generations, in addition to the mean inbreeding level. Predicted response has generally reached an asymptote by six generations, while simulated response is still quite variable, especially for the controlled-pollination strategy. Under this strategy rate of inbreeding ($\Delta F \approx 0.03$) is quite

high, reducing the within-family additive genetic variance. Thus, in later generations inbreeding will prevent an asymptote from being reached. In other strategies there is much less emphasis on relatives' records, with the result that there is only negligible inbreeding, and simulated rates of response are much more stable in later generations. Despite inbreeding having some effect, the predicted response, while an overestimate, gives a reasonable approximation to the simulated response in all cases. The predicted response assumes an infinite population and assumes all variance components remain normal after selection. The fact that these assumptions do not hold in actual breeding populations explains the simulated response being less. Costs in accuracy by estimating block/site effects also contribute to lower simulated gains in comparison with the predictions.

Table 1 Heritabilities, phenotypic variances and genetic and phenotypic correlations for common traits in *Pinus radiata*. Genetic correlations above the diagonal and phenotypic correlations below the diagonal. (Values taken from Cotterill and Dean 1990, page 24)

Trait	Individual heritability (h^2)	Phenotypic variance	Correlations				
			Height ^a	Diameter ^b	Stem ^c	Branch ^d	Wood ^e
Height	0.20	1.0					
Diameter	0.20	250.0	0.65				
Stem	0.20	1.0	0.20	0.10			
Branch	0.25	1.0	-0.20	-0.30	0.20		
Density	0.45	90.0	0.0	-0.05	-0.05	0.05	

^a Measured in meters

^b Measured as cross sectional area (cm²)

^c Stem straightness (1-6 score)

^d Branch quality (1-6 score)

^e Wood density (kg m⁻³)

Table 2 Simulated^a and predicted rates of response in aggregate breeding value and mean inbreeding for six generations of selection under: controlled pollination; open pollination without thinning; open pollination with thinning; and polycross mating strategies

Breeding strategy	Generation					
	1	2	3	4	5	6
Controlled pollination						
Simulated response	1.491	1.150	1.104	1.062	1.075	1.071
Predicted response	1.518	1.165	1.128	1.125	1.125	1.125
Mean inbreeding	0.00	0.02	0.06	0.09	0.11	0.14
Polycross mating						
Simulated response	1.202	1.047	0.981	0.973	0.974	0.943
Predicted response	1.211	1.029	0.987	0.977	0.975	0.974
Mean inbreeding	0.00	0.01	0.02	0.03	0.04	0.05
Open pollination (thinning)						
Simulated response	0.862	0.743	0.783	0.788	0.786	0.796
Predicted response	0.968	0.826	0.796	0.787	0.785	0.784
Mean inbreeding	0.00	0.01	0.01	0.01	0.02	0.02
Open pollination (no thinning)						
Simulated response	0.545	0.489	0.509	0.531	0.527	0.528
Predicted response	0.605	0.538	0.529	0.524	0.522	0.522
Mean inbreeding	0.00	0.00	0.00	0.01	0.01	0.01

^a Standard errors of the simulated rates of responses ranged from 0.005 to 0.046 and were greatest under controlled pollination and least under open pollination

Comparison of breeding strategies

Villanueva et al. (1993) present a detailed summary of the behaviour of asymptotic response from multivariate and univariate BLUP selection over a wide range of genetic, phenotypic and economic parameters. Generally, the reduction in selection response due to the Bulmer effect increases with the absolute value of the correlations and with the magnitude of the difference between heritabilities. What is more important, in the present study, is to compare tree breeding strategies in terms of genetic response and to quantify the reduction in response when selecting for traits realistic for tree breeding. Because family sizes are larger than in animal breeding, there are two likely consequences: the reductions in response due to the Bulmer effect are likely to be more substantial; and for strategies which use more information from relatives (controlled pollination) the benefits in increased rates of response are likely to be greater.

For this section predicted rates of response were calculated for more complex breeding goals containing three, four and five component traits. In addition to predictions for multivariate BLUP selection, predictions were also calculated for univariate BLUP selection, where EBVs are computed ignoring information on correlated traits. For details on how this was done see Villanueva et al. (1993). Again it is assumed that selection criteria are the same as those traits in the breeding goal. Genetic and phenotypic parameters used were those described in Table 1. The three-trait breeding goal was for cross-sectional area (SA), stem straightness (SS) and branch quality (BQ); the four-trait breeding goal added height (HT); and the five-trait breeding goal added again wood density (WD). The economic weights used were the same as those used in Cotteril and Dean (1986), or if not explicitly described in that text, were derived using similar logic. On the assumption that the breeder wishes to place equal emphasis on each of the traits, Cotteril and Dean calculated w for cross-sectional area, straightness and branch quality containing $w_{SA} = 0.02$, $w_{SS} = 1.0$ and $w_{BQ} = 1.0$. These were obtained by assuming a one-point increase in straightness and branch quality being as important as a 50-cm² increase in sectional area, and in turn assuming that a one-point increase in form traits and the 50 cm² increase in sectional area equated to a 30% improvement in each case. Similarly, economic weights for height and wood density can be derived by assuming that a 30% improvement in these traits represents an increase of about 3 m and 102 kg m⁻³, respectively. A mean height of 10 m is assumed and a mean wood density of 340 kg m⁻³ was obtained from Dean et al. (1983). By inverting we obtain $w_{HT} = 0.3333$ and $w_{WD} = 0.0098$.

In this section a range of values are used for n_c , n_f , n_p , n_o and i , and no assumptions are made concerning

the numbers of parents. Table 3 shows the effect of n_c and n_f on selection response in aggregate breeding value at the first generation and at equilibrium under controlled pollination. For any given number of parents there are various combinations of n_c and n_f possible which will result in the same total number of progeny; that is, the product of $n_c/2$ and n_f is constant. For example, parents can be crossed 6 times each with 30 progeny collected from each cross, or alternatively, be arranged in single-pair matings with 180 progeny collected from each cross. The results show that multiple-pair matings have a 3–4% reduction in selection response relative to single-pair matings, with the reduction increasing with the number of crosses per parent. This relative reduction is approximately constant across the three values used for $n_c/2 \times n_f$ and the three breeding goals and for other selection intensities (results not shown). It may be noted that this increase in response due to single-pair matings has been shown for discrete generations only. It is possible that for overlapping generations or “rolling front” schemes as described by Borralho and Dutkowski (1996), multiple-pair matings are more optimal. Under these schemes parents are replaced only when there are candidates with higher EBVs and the accuracy of parental EBVs becomes important.

From Table 3 it can be seen that halving the number of progeny per cross results in an approximately 1–2% reduction in selection response. The balance between selection response and the number of progeny per cross was further explored by testing a much wider range of values for n_c under single-pair mating. The results are shown in Fig. 1. Under controlled pollination and single-pair mating the selection response increases dramatically with the number of progeny per cross until there is between 20 and 40 progeny per cross. Beyond this point only marginal increases in selection response can be achieved with further increases in the number of progeny per cross. For open pollination (Fig. 2) a much reduced increase in selection response is achieved when the number of progeny per parent is increased beyond 60.

Table 4 shows the ratio of asymptotic response in aggregate breeding value to response at the first generation from multivariate BLUP selection for the different breeding strategies and for different levels of selection intensity and numbers of progeny per parent or cross. Results were similar for each breeding goal so ratios are shown only for the three-trait breeding goal. Reduction in response was greatest under controlled pollination with the loss in response from the first generation to the equilibrium ranging between 26% and 28%. Under polycross mating and open pollination the reductions are approximately 21% and 15%, respectively. Selection intensity and numbers of progeny per cross have only a slight effect on the reduction.

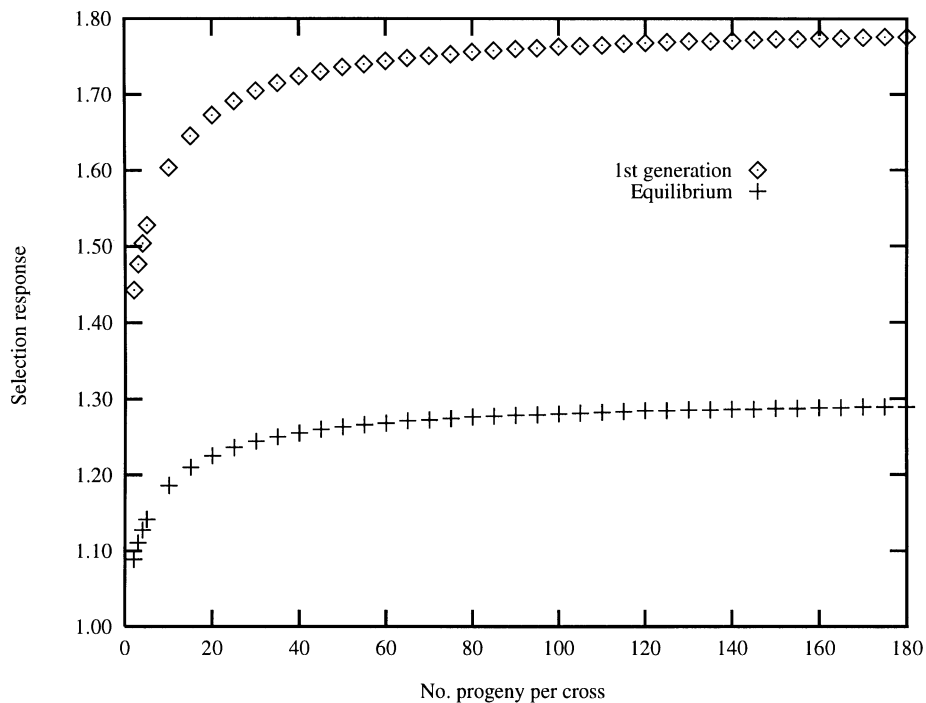
Table 5 shows the efficiency of strategies relative to controlled pollination for multivariate BLUP selection.

Table 3 Selection response^a at the initial generation (R_I) and at equilibrium (R_E) from multivariate BLUP selection and controlled pollination for different numbers of crosses per parent (n_f), numbers of progeny per cross (n_c) and for different breeding goals

Number of crosses per parent (n_f)	Number of progeny per cross (n_c)	Number of traits in breeding goal					
		3		4		5	
		R_I	R_E	R_I	R_E	R_I	R_E
1	180	1.776	1.289	1.980	1.438	1.934	1.404
2	90	1.761	1.280	1.965	1.428	1.918	1.395
4	45	1.744	1.272	1.947	1.420	1.900	1.886
6	30	1.730	1.270	1.941	1.418	1.893	1.384
1	90	1.760	1.278	1.964	1.426	1.916	1.392
2	45	1.736	1.265	1.939	1.412	1.890	1.378
4	22.5	1.714	1.256	1.917	1.403	1.867	1.368
6	15	1.709	1.254	1.911	1.401	1.862	1.366
1	45	1.730	1.260	1.933	1.407	1.884	1.372
2	22.5	1.696	1.242	1.898	1.389	1.847	1.353
4	11.25	1.673	1.232	1.874	1.378	1.822	1.342
6	7.5	1.669	1.230	1.869	1.376	1.818	1.340

^aSelection intensity was 2.59

Fig. 1 The effect of numbers of progeny per cross on response to selection at the first generation and at equilibrium using multivariate and controlled pollination with single-pair mating



Because efficiencies are similar for the four- and five-trait breeding goals efficiencies are shown only for the three-trait breeding goal. Controlled pollination assumed single-pair matings with 50 progeny per cross. For a given number of parents, polymix-mating, open-pollination and controlled-pollination strategies produce equal numbers of total progeny when $n_p = n_o = n_c/2$. The advantage of controlled pollination over polycross mating, when considering equal numbers of total progeny, is 19% at the initial generation and 12% at equilibrium. The advantage of controlled pollination over open pollination is 59% at the initial generation and 52% at equilibrium. Thinning significantly im-

proves the rate of response achieved by open pollination. The advantage of controlled over open pollination with thinning applied is 37% at the initial generation and 31% at equilibrium. Doubling the number of progeny per parent to improve the performance of polymix mating and open pollination, relative to controlled pollination, thus increasing twofold the total number of progeny to be field tested, had only a small effect in reducing the advantage of controlled pollination.

Table 6 shows the relative efficiencies of univariate BLUP selection to multivariate selection for each combination of breeding goal and strategy. Ratios of

Fig. 2 The effect of numbers of progeny per parent on response to selection at the first generation and at equilibrium using multivariate BLUP and open pollination

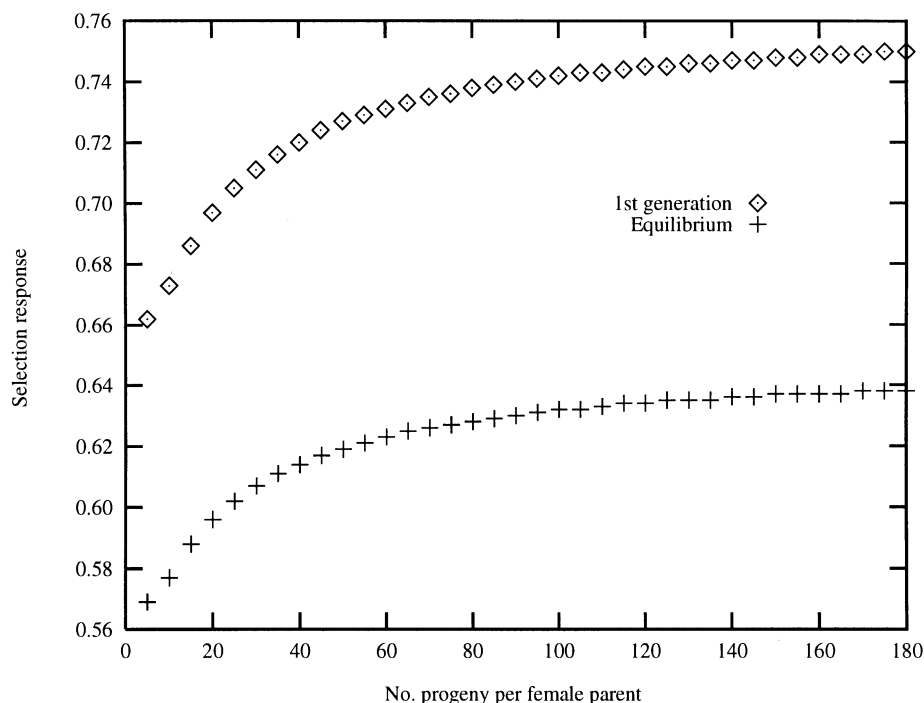


Table 4 Ratio of asymptotic response in aggregate breeding value to response at the initial generation from multivariate BLUP selection for controlled pollination (CP), polycross mating (PM), open pollination (OP) with and without thinning, for different numbers of progeny per cross or parent (n), and for different selection intensities (i)

n^a	i^b	Breeding strategy			
		CP	PM	OP (thinning)	OP (no thinning)
10	2.34	0.741	0.797	0.804	0.860
	2.59	0.738	0.795	0.802	0.858
	2.82	0.736	0.793	0.801	0.856
50	2.34	0.731	0.790	0.797	0.855
	2.59	0.728	0.788	0.795	0.853
	2.82	0.725	0.786	0.794	0.851
90	2.34	0.729	0.789	0.796	0.854
	2.59	0.726	0.786	0.794	0.852
	2.82	0.724	0.784	0.793	0.850

^a For controlled pollination this value is number of progeny per cross (n_c); for polymix mating the value is number of progeny per parent (n_p); for open pollination the value is number of progeny per female parent (n_o)

^b For open pollination with thinning the value for i is with respect to selection intensity in the females only

aggregate breeding value are given for the first generation and then at equilibrium. For all the breeding strategies described it is apparent there is only negligible gain from using a multivariate analysis. There is some evidence that only when the number of traits used as selection criteria is increased is there any substantial

Table 5 Ratio of response in aggregate breeding value relative to response under controlled pollination^a, in the first generation (RE_1) and at equilibrium (RE_∞), for: polycross mating (PM) and open pollination (OP) with and without thinning

Number of progeny per parent	PM		OP (thinning)		OP (no thinning)	
	RE_1	RE_∞	RE_1	RE_∞	RE_1	RE_∞
25	0.812	0.882	0.626	0.686	0.406	0.477
50	0.834	0.907	0.645	0.705	0.419	0.490

^a Single pair mating and 50 progeny per cross was considered for controlled pollination

advantage in using a multivariate analysis. When the number of traits used as selection criteria is three the gain in using a multivariate analysis is under 1% for all strategies. However, when the number of traits is five the gain in using a multivariate analysis increases to 3% under open pollination and to 1.3% under controlled pollination.

Discussion

Interest in the statistical procedure known as BLUP by forest tree breeders has increased in recent years. This interest stems, in part, from the desire to analyse breeding populations which are presently moving into advanced generations. Interest has also been motivated by the expertise seen coming from animal breeding research. As new breeding programmes are initiated

Table 6 Ratio of response in aggregate breeding value relative to response from univariate to multivariate analyses in the first generation (RE_1) and at equilibrium (RE_∞) for: controlled pollination; polycross mating (PM); and open pollination (OP) with and without thinning

Number of traits in the breeding goal	CP		PM		OP (thinning)		OP (no thinning)	
	RE_1	RE_∞	RE_1	RE_∞	RE_1	RE_∞	RE_1	RE_∞
3	0.996	0.997	0.995	0.993	0.995	0.998	0.995	0.997
4	0.993	0.994	0.987	0.988	0.987	0.993	0.987	0.991
5	0.987	0.987	0.966	0.965	0.966	0.971	0.966	0.969

and old ones revised, certainly BLUP will be an integral component. Thus, it is important to be able to predict genetic gain using this technology. One alternative is to use simulation. However, tree breeding populations are very large by nature and soon number in the tens of thousands. Simulation then becomes cumbersome and time consuming. This study has shown that genetic gain predictions can be obtained with much less effort using deterministic equations. However, the one drawback is that the predictions tend to be biased upward, compared to the simulated values, because of assumptions concerning infinite population size.

In addition to predicting genetic gain, the index equations have added value in determining the most efficient numbers of progeny to be collected from parents or crosses. Interestingly, under controlled pollination and when considering discrete generations, it would appear that single-pair matings are most efficient with at least 20 progeny collected from each cross. Cotterill (1986) states that "No accurate estimates of breeding value can be obtained from single-pair mating". An important issue here is whether discrete or overlapping generations are used in the breeding programme. If discrete generations are considered then results in this study suggest it is more important to accurately estimate family means, and this is best achieved with single-pair matings with more progeny per cross rather than with multiple-pair matings with fewer progeny per cross. However, if overlapping generations are considered then accurate estimation of parental EBVs becomes important, and intuitively this is best achieved with more contrasts between parents; that is, each parent is involved in more than one cross.

Another significant finding is the degree to which response to BLUP selection is affected by selection disequilibrium. The deterministic equations correct for selection disequilibrium by correcting genetic parameters at each round of selection using Bulmer's theory (Bulmer 1971) and as demonstrated in the multivariate case by Villanueva et al. (1993). Tree breeding strategies which use multivariate BLUP selection can expect, at equilibrium, as much as a 28% loss in response compared to first-generation response. This will have significant implications for cost-benefit studies but will not alter significantly the rankings of alternative strategies as demonstrated by Wray and Hill (1989).

Strategies, all of which use some type of multivariate BLUP selection while differing in the amounts of

information available, can be compared. A controlled-pollination strategy can offer as much as a 56% greater gain than an open-pollination strategy, but the costs involved are far greater. It is recommended that genetic gain predictions be used in a cost-benefit study to establish if expensive controlled pollination schemes are economical. Generally, controlled-pollination schemes offer little advantage over polycross-mating strategies in terms of genetic gain. However, both strategies incur roughly the same costs in undertaking similar numbers of controlled crosses. Of note in controlled-pollination strategies and to a lesser degree in polycross strategies is the greater increase in inbreeding. After six generations the mean inbreeding level in the simulated population under controlled pollination was 0.14. If this level is unacceptable, some simple steps can be implemented to reduce the level of inbreeding whilst maintaining the same level of genetic gain. Restrictions on the co-selection of relatives and avoidance of matings of close relatives are two such steps which do not require further complex analytical methodology.

It should be noted that schemes in this study were compared on the basis of gain per generation. Comparison on the basis of gain per decade or year may prove more beneficial for practical breeders. This is easily achieved by dividing gain per generation by the generation interval relevant to each scheme. Cotterill (1986) used generation intervals of 11 and 10 years for controlled pollination and open-pollinated breeding strategies, respectively.

While the strategies outlined in this study and the gain equations developed for each may in some situations be oversimplistic, they provide a base from which to develop more complex models. For example, it is most likely that some import of foreign pollen is expected in open pollination strategies. This information could be incorporated into the gain equations by adjusting the between-male parent additive genetic variance and introducing a negative selection intensity to account for the genetically unimproved pollen. The indices could also be modified to account for some assumed level of selfing. Another aspect not considered in this study is the possibility of thinning male parents on the basis of different selection criteria to that of female parents. Further simulation studies are perhaps needed to ascertain how these modifications are best achieved.

A further aspect of this work has been the demonstration of the limited advantage in using a multivariate analysis. This research is in agreement with the findings of Villanueva et al. (1993) who found that with increasing family sizes (which is certainly the case in tree breeding) the benefit of multivariate analyses is reduced. Often high computational cost will weigh against consideration of multivariate analyses. It is far easier to estimate breeding values for each trait separately and then combine into an aggregate breeding value by weighting each one by its economic weight. In tree breeding this would be a safe and sensible course to take if multivariate analysis becomes too unwieldy.

In conclusion, the gain equations developed in this study offer a reliable and quick way of predicting genetic gain from multivariate BLUP selection in common tree breeding strategies. Breeders need to be aware of the loss of genetic gain due to linkage disequilibrium and account for this loss if undertaking an economic assessment of the strategy. The equations offer a convenient check to ensure the predicted gains match desired gains.

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