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Study of Early Selection in Tree Breeding

4. Efficiency of Marker-Aided Early Selection (MAES)

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Abstract

One of the main attractions of Marker-Aided Selection (MAS) in tree breeding is its potential for early selection through juvenile traits as Marker-Aided Early Selection (MAES). The theoretical advantages of incorporating molecular markers into early selection in tree breeding are examined. Equations were derived to answer the following questions: (1) how effective is the use of markers for early selection relative to conventional late (mature) selection? (2) what is the efficiency of using markers for early selection relative to early selection based on morphological traits? (3) how effective is incorporating markers into an early selection index relative to an early selection index based on morphological traits alone? (4) what are the efficiencies when MAS is used only for within-family selection in the combined family and within family selection approach, relative to selection using combined family and within family phenotypic information alone? and (5) how effective is selection when MAES is used for within-family selection only in the combined family and within family early selection approach, relative to early selection using combined family and within family phenotypic information alone? These equations could be used to compare relative efficiencies of MAES and QAES (QTL-Aided Early Selection) relative to traditional phenotypic selection in breeding programs. For Marker-Aided Early Selection or QTL-Aided Early Selection to be applicable in tree breeding populations, it may be necessary to demonstrate that efficiency from MAES or QAES is higher than efficiency of early selection using less expensive early phenotypic traits. Furthermore, the relative efficiency of MAES or QAES is higher when genetic correlation of early-mature trait and/or heritability of the early trait is lower and is less for full-sib family than for half-sib family selection.

Key words: Marker-Aided Selection, Marker-Aided Early Selection, Early Selection, Genetic Gain, Index Selection.

Introduction

The construction of genetic linkage maps using molecular markers and detection of quantitative trait loci (QTL) has been an exciting research area in forest genetics in recent years. Following the publication of restriction fragment length polymorphism (RFLP) linkage map in humans (Bostein *et al.,* 1980) and tomato (Bernatzky and Tanksley, 1986), genetic linkage maps based on RFLP markers were published for loblolly pine, *Pinus taeda* (Devey *et al.,* 1994), and based on random amplified polymorphism DNA (RAPD) markers in eucalypts (Grattapaglia and Sederoff, 1994). Since then, molecular (DNA) linkage maps have been constructed or are under construction for many important timber and pulping species (Neale and Sederoff, 1991; Neale and Harry, 1994; Sewell and Neale, 2000; Temesgen *et al.,* 2001). Major QTLs in crops have been identified using molecular markers, first in maize (Edwards *et al.,* 1987 and Stuber *et al.,* 1987) and tomato (Paterson *et al.,* 1988), followed by numerous other crop species (O'Brien, 1993; Tanksley, 1993) and for virtually all agronomically important traits (e.g. drought and salt resistance, seed hardness and size, plant biomass, size, and maturity, disease resistance, oil and protein content, fecundity, *et al.*) (Young, 1999). In forest tree species, significant QTLs have been detected in vegetative propagation traits (Grattapaglia *et al.,* 1995; Marques *et al.,* 1999), crown form (Harfouche *et al.,* 2000), early growth (Bradshaw and Stettler, 1995; Verhaegen *et al.,* 1997; Emebiri *et al.,* 1998), wood quality traits (Grover *et al.,* 1994; Grattapaglia *et al.,* 1996; Knott *et al.,* 1997; Neale *et al.,* 1997; Sewell *et al.,* 2000; Kuranmoto *et al.,* 2000), biotic and abiotic resistance (Kubisiak *et al.,* 2000; Skov and Wellendorf, 2000).

With potentially unlimited DNA markers available to tree species, forest geneticists soon began to believe that marker-aided selection (MAS) may become a reality (Strauss *et al.,* 1992). The possibility of selecting desirable trees based on genotypes rather than phenotypes and to select elite breeding trees in the seedling stage (very early selection) was extremely

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attractive to tree breeders. In the early 1990s, two special journal issues (Canadian Journal of Forest Research, 1992 and Forest Genetics, 1994) were dedicated to the potential of marker-aided selection in tree breeding.

With such possibility of increasing selection efficiency through marker-aided selection in tree species (KERR *et al.,* 1996; KERR and GODDARD, 1997; JOHNSON *et al.,* 2000; KUMAR and GARRICK, 2001; and WILCOX *et al.,* 2001) surprisingly, there is no report yet of actual application of MAS in tree species. Even in other crops, MAS was successfully used as a genetic tool for introgression of major genes into lines (BERNACCHI *et al.,* 1998; TOOJINDA *et al.,* 1998), yet there are few publications, if any, which actually describe the use of MAS leading to increased genetic gain (STROMBERG *et al.,* 1994; OPENSHAW and FRASCAROLI, 1997) or released germplasm or varieties (YOUNG, 1999; VAN BERLOO and STAM, 1999). There seem two obvious reasons why tree breeders are reluctant to adopt MAS in their breeding programs: MAS was still in its infancy in tree breeding and there could be technical limitations of MAS in tree breeding (STRAUSS *et al.,* 1992).

Most QTL mapping studies examine only one or a few pedigrees under limited environments. Few experiments have examined the issue of QTL stability over different sites, development stages and/or genetic background (GROOVER *et al.,* 1994; WILCOX *et al.,* 1997; KAYA *et al.,* 1999). However, the most serious technical obstacles in using MAS in tree breeding (for example, typified by conifer breeding program) are threefold:

1. In large conifer breeding populations, even if major QTLs have been detected, it will be impossible to predict whether a marker allele is in coupling or repulsion phase with the desired QTL alleles if the breeding population is at or near linkage equilibrium. Advanced conifer breeding populations usually consist of between 300-400 selected individuals (WHITE, 1993). They are usually selected from natural stands, plantations, or progeny trials. Most conifers are largely out-crossing and may be assumed to be random mating, thus the breeding populations are likely to be in linkage equilibrium (BROWN, 1990); therefore, correlation among QTL alleles and marker alleles must be determined separately for each pedigree of interest. This requires large resources and may limit the use of MAS in tree breeding. If markers are QTL themselves, this become a less problem.

2. There are usually multiple alleles for each marker and QTL within a breeding population, particularly for microsatellite and AFLP markers (POWELL *et al.,* 1996). This, coupled with complex patterns of heterozygozity, indicates that important QTLs, their alleles and the marker alleles will frequently differ among genetic backgrounds and families. Therefore, the advantageous marker allele (or QTL allele) in one pedigree may not be advantageous in another pedigree. This creates a practical problem in using markers for selection in a breeding population. To circumvent the problem of multiple alleles in a breeding program, it would be useful to rank all alleles in the breeding population. Even markers are QTL themselves, it requires to rank all QTL alleles before correct alleles can be selected in a breeding population.

3. Low heritability of most important quantitative traits in conifers (ZOBEL and TALBERT, 1984; COTTERILL and DEAN, 1990) means that QTL detection has low power and so requires very large samples (STRAUSS *et al.,* 1992).

Several suggestions have been made to overcome these problems (O'MALLEY and MCKEAND, 1994). One is to construct maps for each genotype (individual) in a small elite breeding population. Since within-family phenotypic selection is an important component of advanced generation breeding in tree species, marker-aided within-family selection has been strongly advocated. Extremely high value families could be used for within-family selection and for clonal propagation in the deployment population to capture additional gain (STRAUSS *et al.,* 1992).

If linkage phase is known for all families and the effects of all marker alleles associated with QTLs are ranked, it is possible that MAS may result in higher genetic gain than conventional breeding in breeding populations. The efficiency of MAS relative to phenotypic selection has received considerable attention in the recent past. The efficiency of MAS in plant and animal breeding has been investigated by analytical (deterministic) and simulation approaches. LANDE and THOMPSON (1990) pioneered deterministic analysis in evaluating efficiency of MAS. They proposed a method of marker-assisted selection using linkage disequilibrium created by hybridisation between inbred lines. Selection is performed on an index combining phenotypic and marker information, the latter being derived from multiple regression of phenotype on the marker genotype. Recently, MOREAU *et al.,* (1998) extended this approach to finite population size and OLIVIER (1998) considered full-sib families nested within half-sib families. In animal breeding, BLUP (Best Linear Unbiased Prediction) was adopted to examine the efficiency of MAS (FERNANDO and GROSSMAN, 1989; MEUWISSEN and ARENDONK, 1992; GODARD, 1992). The main conclusions are that MAS could be more efficient than purely phenotypic selection in a fairly large population and for traits showing relatively low heritabilities.

One of main attractions of MAS in tree breeding is its potential for early selection so that breeders can use markers as juvenile traits. Since markers for mature traits (preferably rotation age) can be detected at an early age, Marker-Aided Early Selection (MAES) is extremely attractive to tree breeders for reducing the generation interval. This is because genetic correlation of the same markers between early and mature ages is unity and heritability of the markers is also unity (e.g. selection on genotypes). Early selection has been consistently pursued by tree breeders since the inception of conifer breeding programs in the 1950s (MCKINLEY and LOWE, 1986; NEALE and WILLIAMS, 1991). The main advantage of early selection in conifers was recognised as shortening the long interval between generations thus maximizing genetic gain per unit time (WU, 1999). In the 1970s and 1980s, breeders collected enough empirical evidence to support the value of selection for growth at half-rotation age (LAMBETH, 1980). Selection before half-rotation or even quarter-rotation age is now commonplace in recurrent breeding programs for many conifers (MCKEAND, 1988; COTTERILL and DEAN, 1988; JOHNSON *et al.,* 1997). In recent years, the focus of early selection research has shifted to seedling-stage selection on morphological traits in an effort to reduce expensive and time-consuming genetic testing. Early selection is now recognised not only for shortening the breeding cycle, but also for increasing selection intensity (WU, 1998) and enhancing the efficiency of mature selection (WU *et al.,* 2000). Tree breeders are particularly interested in examining the effectiveness of MAES, theoretically and experimentally. Several simulations studies in forest trees have indicated that MAS was more efficient than phenotypic selection in most cases, depending on genetic and economic assumptions (KERR *et al.,* 1996; KERR and GODDARD, 1997; JOHNSON *et al.,* 2000; KUMAR and GARRICK, 2001). In this paper, theoretical results to compare the efficiency of conventional phenotypic early selection and MAES are developed. The following questions are explored: (1) how effective is the use of markers for early selection relative to conventional late (mature) selection? (2) what are the efficiencies of using markers for early selection relative to early selection based on phenotypic traits? (3) how effective is it to incorporate markers into an early selection index relative to an early selection index based on phenotypic traits alone? (4) what are the efficiencies when MAS is used only for within-family selection in the combined family and within family mature selection approach relative to selection using combined family and within family phenotypic information alone? and (5) how effective is the selection when MAES is used only for within-family selection in the combined family and within family early selection approach relative to early selection using combined family and within-family phenotypic information alone? We assume that a molecular score m as proposed by LANDE and THOMSON (1990) could be derived from multiple regression of markers on phenotypes. We assume that phenotypes at mature age were available for all individuals when constructing the regression coefficient for the molecular score. But with MAES, the regression coefficient was used for early selection since there is unit (100 %) age-age correlation for the molecular score between early and mature ages. This molecular score will be used for Marker-Aided (Early) Selection (MAES) and QTL-Aided (Early) Selection (QAES).

Method and Results

1. Efficiency of using molecular markers associated with a mature trait for early selection

A major advantage of MAES in tree species is to reduce the generation interval by shortening the testing cycle substantially compared with that already possible with short- to intermediate-term phenotypic testing (half to one quarter of rotation age). This advantage can be evaluated as the relative gain of selection based on the phenotypic trait alone or based on molecular markers alone. The genetic gain per unit time based on selection for a mature phenotypic trait is

$$R_C = i\, h_y\, \sigma_{yA} \;/\; T_C$$

where i is the selection intensity, h^2_y is the heritability of the targeted mature trait, σ_{yA} is the standard deviation of additive genetic variance for the mature trait, and T_C is the number of years to complete a cycle of breeding from conventional mature selection.

The genetic gain per unit time based on selection of molecular markers is

$$R_E = i\, r_{MA}\, \sigma_{yA} \;/\; T_E$$

where r_{MA} is correlation between molecular score m and additive genetic values of targeted mature trait and is equal to the square root of p (where p is the proportion of the additive genetic variance that has been accounted for by the molecular marker score m). T_E is the number of years to complete a cycle of breeding when selection is based only on molecular markers at early age (early selection). In tree breeding, since the genetic correlation of molecular markers is 1 between early and mature ages, selection can be conducted at a very early (e.g. seedling) age. The relative gain per unit time from selection based on molecular score and conventional or mature selection can be expressed as

$$R_1 = \sqrt{\frac{p}{h_y^2}}\,\frac{T_C}{T_E}$$

This equation demonstrates that when $p*T^2_C > h_y^2 *T^2_E$, selection using molecular markers alone will be more efficient than phenotypic selection at a mature age.

Selection based on molecular score m can be conducted during the first year if molecular markers can be identified in one-year-old seedlings (enough tissue for DNA extraction). However, mating can only be conducted when selected seedlings start to reproduce. For most conifers, three years of growth are the absolute minimum for producing female and male strobili. Another two years are needed for cone maturation after controlled pollination for most conifers, then the minimum time period to complete a breeding cycle is at least 5 years. For many conifers, early selection is usually effective at age 6–7 (LAMBETH, 1980; FOSTER, 1986; MCKEAND, 1988; COTTERILL and DEAN, 1990; LI *et al.,* 1992). Therefore, tree breeders can have two breeding cycles using markers for selection within one breeding cycle of conventional early selection. Relative to selection at half-rotation age or later, tree breeders may have three or four breeding cycles with early molecular selection. For the first case (e.g. $T_C/T_E = 2$), if heritability for mature trait $h_y^2 = 0.4$, or $h_y^2 = 0.2$, then selection based on a molecular marker score m, accounting for 10 % and 5 % of additive genetic variance, would have the same efficiency as selection based on morphological traits. The thresholds for the required proportion of additive genetic variance by marker score, to obtain the same efficiency as selection based on phenotype are plotted in *Figure 1* for three scenarios; $T_C/T_E = 1$, $T_C/T_E = 2$ (two breeding cycles relative to one conventional breeding cycle), and $T_C/T_E = 4$ (four cycles within one breeding cycle of conventional phenotypic selection).

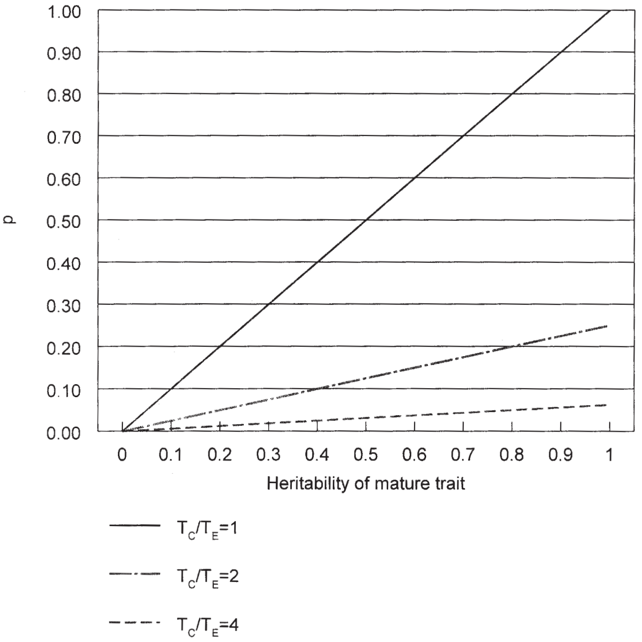

Figure 1. – Threshold for p (the proportion of additive genetic variance accounted for by markers) so that selection based on markers for a breeding cycle of T_E years being same efficiency as selection based on a mature trait for a breeding cycle of T_C years.

2. Selection efficiency using molecular markers relative to early selection based on a morphological trait

Using molecular markers is not the only means of very early selection for mature traits. Early selection can also be conducted by seedling morphological traits. An interesting question is whether very early selection based on molecular score is more efficient than early selection based on early seedling traits at a similar age. The relative efficiency between early selection using molecular marker scores and using early quantitative traits can be compared as

$$R_2 = \sqrt{\frac{p}{h_x^2 r_A^2}}$$

where h_x^2 is the heritability of early trait and r_A is genetic correlation between early and mature traits. Therefore, if genetic variance accounted for by molecular markers is larger than the product of h_x^2 and r_A^2, selection based on molecular markers will be more efficient than selection based on early morphological traits. Thresholds for the proportion (p) of genetic variance accounted for by molecular score m are depicted in *Figure 2* for the cases of $r_A = 0.25, 0.5, 0.75$, and 1 and in *Figure 3* for $h_x^2 = 0.25, 0.5, 0.75$, and 1. *Figures 2* and *3* show that if p lies above these thresholds, MAES is more efficient than early selection. For example, if early seedling height has a genetic correlation $r_A = 0.5$ with mature trait and a heritability of $h_x^2 = 0.2$, then selection using any molecular marker or markers accounting for more than 12 % of additive genetic variance will be more efficient than selection based on the early height.

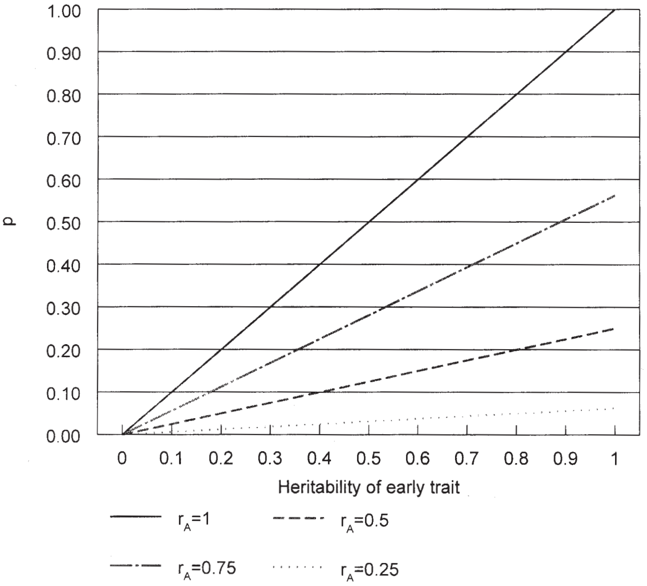

Figure 2. – Threshold for p (the proportion of additive genetic variance accounted for by markers) so that selection based on markers alone is more efficient that selection based on a single early trait under four early-mature genetic correlations.

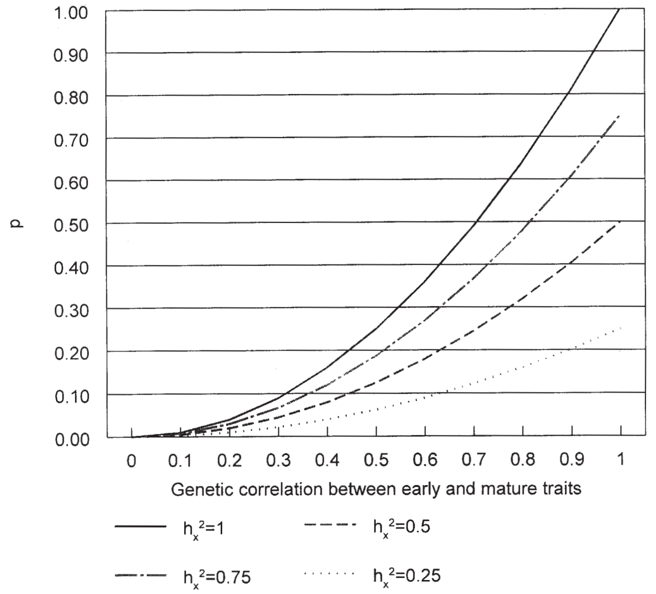

Figure 3. – Threshold for p (the proportion of additive genetic variance accounted for by markers) so that selection based on markers alone is more efficient that selection based on a single early trait under four heritabilities.

3. Efficiency of incorporating molecular markers for mature traits into early selection index

Molecular markers can be used for early selection alone as well as assisting in early morphological selection. This method of incorporating molecular markers in a selection index is preferable for increasing genetic gain. Incorporating molecular markers for mature traits into an early selection index may not only increase genetic gain, but also has the advantage of shortening generation time. This can be done through an index seletion approach as

$$I = ax + bm$$

where x is an early morphological trait, m represents the molecular score, and a and b are the estimated index coefficients for early trait x and molecular score m. Selection will be based on the index I. Now, the question we want to answer is what is the gain from incorporating molecular information into an early selection index relative to early selection based on the early morphological trait alone? Genetic gain from this index selection relative to selection based on early trait x alone can be derived as

$$R_3 = \sqrt{\frac{1-2\sqrt{p}+\dfrac{p}{h_x^2 r_A^2}}{1-h_x^2 r_A^2}}$$

The relationship between gain and genetic parameters in equation R_3 is more complex than previously one. *Figures 4* and *5* illustrate the thresholds for the proportion of genetic variance accounted for by markers in order for MAES to be more efficient than selection based on a single early trait alone under four early-mature genetic correlations ($r_A = 0.25, 0.5, 0.75$, and 1 and four early trait heritabilities ($h_x^2 = 0.25. 0.5. 0.75$, and 1). *Figures 4* and *5* show that genetic correlation has more influence than heritability on the proportion of genetic variance needed for the thresholds.

The effectiveness of increasing genetic gain by using molecular score can also be studied by the equation R_3. First, we observe that R_3 will be always larger than 1. Therefore, incorporating molecular markers in early selection will always increase genetic gain if these markers are real. Second, the

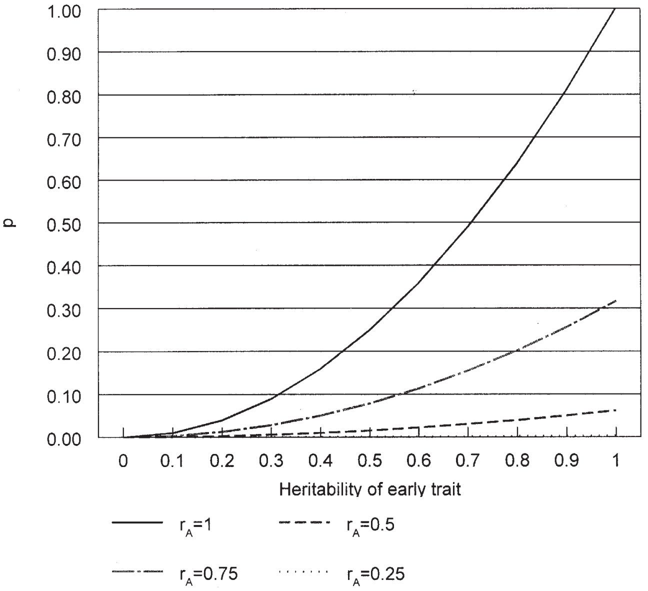

Figure 4. – Threshold for p (the proportion of additive genetic variance accounted for by markers) so that MAES is more efficient that selection based on a single early trait alone under four early-mature genetic correlations.

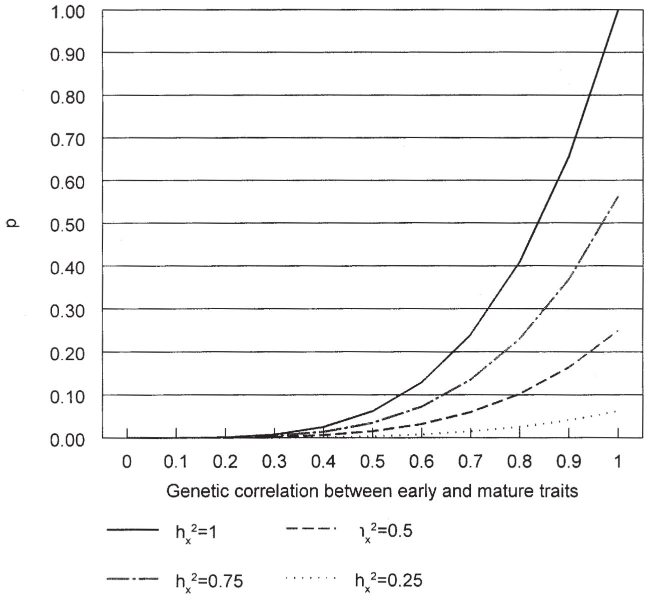

Figure 5. – Threshold for p (the proportion of additive genetic variance accounted for by markers) so that MAES is more efficient that selection based on a single early trait alone under four heritabilites.

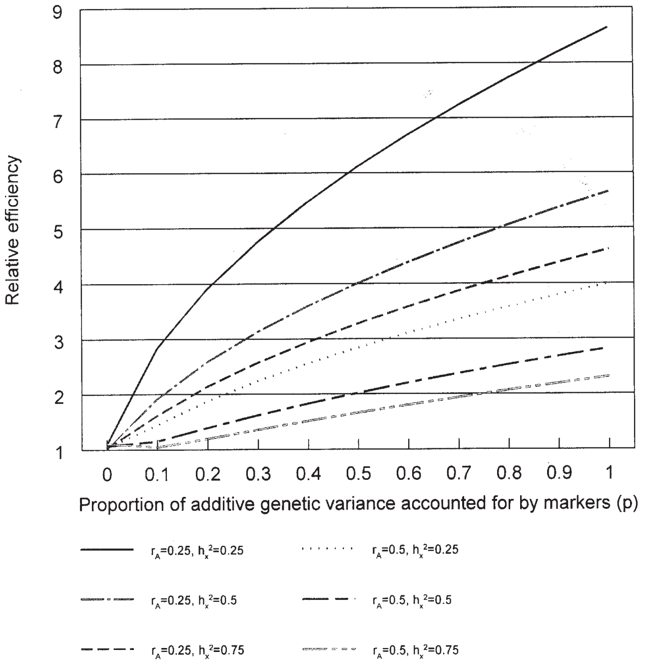

Figure 6. – Efficiency of MAES using population-wide markers information relative to early selection under six combinations of early-mature genetic correlations (r_A) and heritabilities of early trait (h_x^2).

relative efficiency is a function of the early-mature genetic correlation and the heritability of the early trait. The efficiency of MAES is plotted in *Figure 6* for six combinations of genetic parameters (r_A = = 0.25, 0.5, and h_x^2 = 0.25. 0.5. 0.75). These plots show that the efficiency of MAES increases as the percentage of genetic variance accounted for by markers increases. Furthermore, MAES is more effective when the genetic correlation between early and mature traits and the heritability of the early trait is relatively low. For example when r_A = 0.5 and h_x^2 = 0.5. the maximum efficiency when p =1 is only 2.8 times that of early phenotype selection. However, when r_A = 0.25 and h_x^2 = 0.25, the maximum efficiency is 5.6 times that of early phenotypic selection.

Genetic gain when using the above index relative to marker selection alone can also be studied. The equation for the relative efficiency is;

$$R_4 = \sqrt{\frac{1 - 2\sqrt{p} + \dfrac{p}{h_x^2 r_A^2}}{p(\dfrac{1}{h_x^2 r_A^2} - 1)}}$$

In addition, this early selection index can be extended to selection index incorporating multiple early traits and multiple molecular scores for multiple trait selection.

4. Efficiency of incorporating within-family molecular marker information into combined family and within-family selection

As indicated earlier, one major technical hurdle for applying MAES in tree breeding is the unknown linkage phase for families not mapped. Therefore MAES may be valuable only for within-family selection of those mapped families. In addition, a typical QTL study involving more than two families usually reveals different QTLs and varying size of QTL effects in the different families (SEWELL and NEALE, 2000). In these cases, only within-family marker information can be used for selection. The efficiency of using within-family marker information relative to combined family and within-family selection without marker information can be compared. Within-family selection is particularly attractive in clonal forestry. Since only the best clones are selected for mass propagation and planting in clonal plantations, the extra gain from clonal selection within family may be well worthwhile, if the best clones can be reliably identified at a very early age and deployed in large number. However, identification of the best clones requires clonal testing and this may delay deployment of clones. In addition, reliable clonal testing usually takes many years and so when the best clones are identified, the material selected (ortets and ramets) may be too old for vegetative propagation. This is particularly true for conifers (AHUJA and LIBBY, 1982). STRAUSS *et al.,* (1992) studied the relative efficiency of two-stage selection (first-stage for among-family selection and second stage using within-family marker information) and observed that when within-family marker information is used only, the advantage of MAS is dramatically reduced relative to mass selection.

Within-family marker information can also be combined with between-family morphological traits in a one-stage selection approach. To accommodate different QTLs and varying sizes of their effects among families, a molecular marker score m_w can be established for each individual family. Then these molecular scores can be incorporated into the following combined selection index

$$I = a_1 y_f + a_2 y_w + b m_w$$

where y_f, y_w are measures of between-family and within-family morphological traits, a_1, a_2, and b are index coefficients for between-family, within-family and molecular scores. The advantage of selection based on this combined index using within-family marker information relative to combined family and within-family index selection can be investigated. Assuming molecular scores m_w accounted for same within-family genetic variances in different families, the relative gain is derived as

$$R_5 = \sqrt{\frac{\dfrac{C_A}{t} + \dfrac{C_B - 2(1-r)^2 p + (1-t)p}{(1-t) - (1-r)^2 p}}{\dfrac{C_A}{t} + \dfrac{C_B}{1-t}}}$$

where $C_A = r^2 h_y^2$, $C_B = (1-r)^2 h_y^2$, and r is the coefficient of relationship (correlation between breeding values within-family member), t represents intraclass correlation. Due to complexity of the equation for R_5, the advantage of selection using this combined index relative to selection based on combined index without molecular markers is presented in *Figures 7* and *8* for full-sib and half-sib within-family selection, respectively. Several observations can be made from comparisons between full-sib and half-sib families and from using within-family marker information and using population-wide marker information (LANDE and THOMPSON, 1990). First, the relative advantage of marker-aided selection is much reduced in combined family and within-family selection using within-family marker information alone relative to using population-wide marker information. Second, the relative efficiency of marker-aided selection for full-sibs is lower than for half-sibs. Therefore, molecular marker information is more useful in enhancing selection efficiency for half-sib families than for full-sib families. For most QTL detection experiments in conifers, only a few elite families were used. *Figures 7* and *8* can be used to calculate efficiency for combining markers within elite families with among family selection.

5. Incorporating within-family molecular marker information for mature traits into combined family and within-family early selection

In tree breeding, it is more practical to use within-family molecular marker information for mature traits in early selection since selection is rarely conducted at a mature age for mature traits. Therefore, examining the efficiency of incorporating molecular marker information into combined family and within-family early selection is more relevant to tree breeders. When within-family molecular marker information is used, early selection can be conducted by using the following selection index:

$$I = a_1 x_f + a_2 x_w + b m_w$$

where x_f, x_w are measures of between-family and within-family early phenotypic traits, a_1, a_2, and b are index coefficients for between-family, within-family early phenotypic trait and for molecular scores of mature trait. The advantage of selection based on this combined early selection index using within-family marker information associated with a mature trait relative to early selection based on combined family and within-family index alone can be examined. The relative gain is derived as

$$R_6 = \sqrt{\frac{\frac{D_A}{t} + \frac{D_B - 2D_B\sqrt{p} + (1-t)p}{(1-t) - D_B}}{\frac{D_A}{t} + \frac{D_B}{1-t}}}$$

where $D_A = r^2 * r_A^2\, h^2$, $D_B = (1-r)^2 * r_A^2\, h^2$, and r is the coefficient of genetic relationship, r_A is the genetic correlation between early trait X and mature trait Y. This equation even involves more genetic parameters than the previous one. To demonstrate the relative efficiency of combined family and within-family MAES relative to combined family and within-family early selection, the relative efficiencies of MAES are plotted in *Figures 9* and *10* as a function of p (the proportion of the genetic variance accounted for by markers) for various combinations of early and mature genetic correlations and heritabilities of early traits. Examining these figures reveals that the relative efficiency increases as p increases. Furthermore, the efficiency is higher when genetic correlation between early and mature traits and/or the heritability of the early trait is lower. As with within-family marker-aided mature selection, the relative efficiency is less for full-sib family than for half-sib family selection. For example, the maximum relative efficiency is only 3.8 times that of full-sib family selection, but it is 5.5 times that of half-sib family selection when the genetic correlation between early and mature traits is 0.25, the heritability of mature trait is 0.25, and p is 100 %.

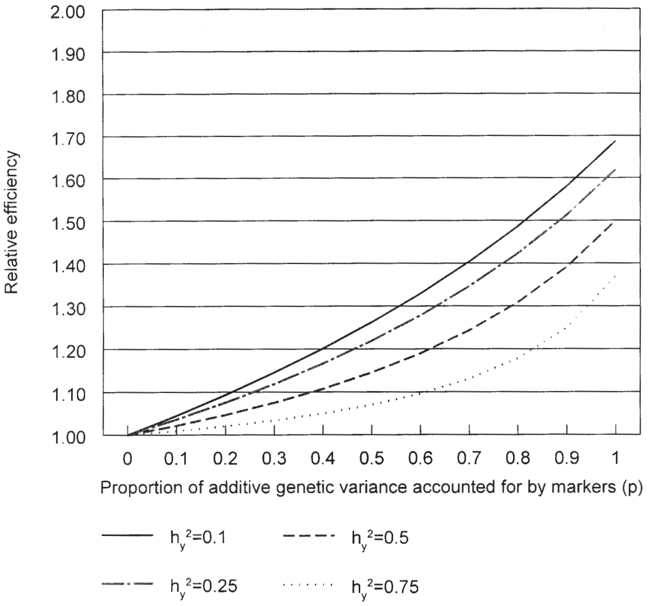

Figure 7. – Efficiency of MAS of using within-family marker information relative to phenotypic family and within-family combined index selection under four heritabilities for full-sib case.

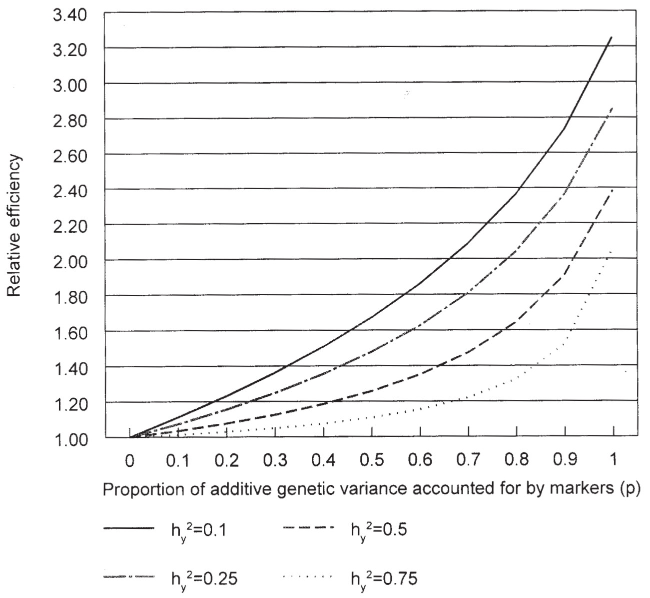

Figure 8. – Efficiency of MAS using within-family marker information relative to phenotypic family and within-family combined index selection under four heritabilities for half-sib case.

Discussion

Genetic efficiencies for marker aided mature selection (MAS) and marker aided early selection (MAES) have been examined in this study for tree breeding. Genetic efficiency for maker-based selection was considered in the Scenarios 1 and 2 and genetic efficiency for maker-aided selection was examined in the Scenarios 3, 4, and 5. The prerequisite for effective MAS or MAES within a breeding population is that the linkage phase between marker and QTL alleles must be known for all pedi-

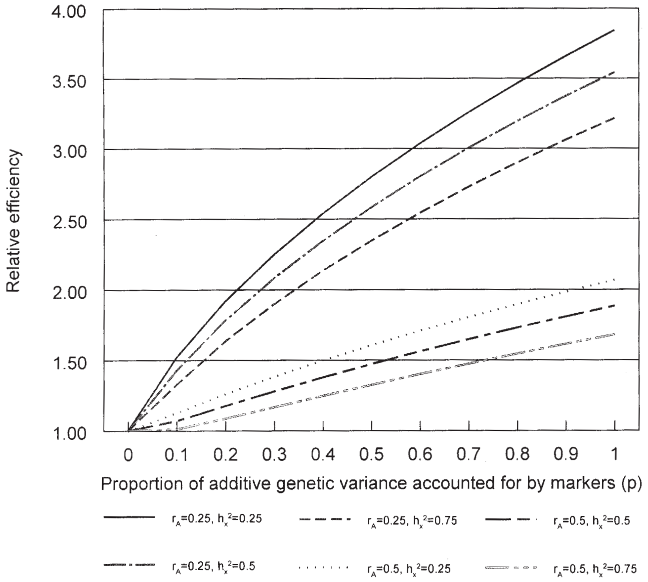

Figure 9. – Efficiency of MAES using within-family marker information relative to family and within-family combined index selection under six combinations of early-mature genetic correlations (r_A) and heritabilities for early trait (h_x^2) for full-sib family.

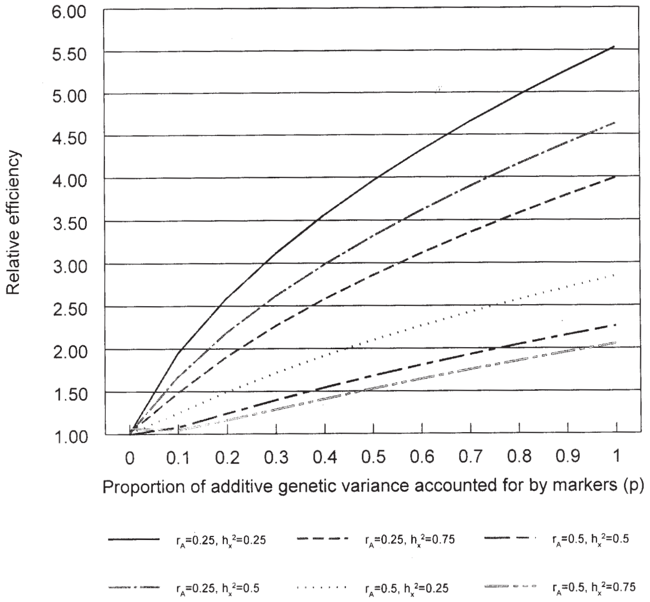

Figure 10. – Efficiency of MAES using within-family marker information relative to family and within-family combined early index selection under six combinations of early-mature genetic correlations (r_A) and heritabilities for early trait (h_x^2) for half-sib family.

grees in a breeding population unless the markers themselves are QTL and the ranking of additive effect for all alleles of the QTL loci within the breeding population should also be known. The probability that a marker score generated with data from one set of families (or one family) will be applicable across genetic backgrounds depends on many factors: relatedness of families, tightness of linkage, status of linkage disequilibrium *et al.* Deterministic analyses from the five scenarios indicate that molecular marker loci for mature traits can be used to increase the rate of improvement in quantitative traits by early or conventional mature selection. The potential advantage of marker assisted early selection relative to standard early selection of phenotypic traits depends on the heritability of early traits and genetic correlations between early and mature traits. With mass selection, the relative efficiency of MAES is greatest for early traits that have low heritabilities and low early-mature genetic correlations.

LANDE and THOMPSON's analyses on the efficiency of MAS (1990) and this analysis on the efficiency of MAES indicate that MAS and MAES will increase genetic gain as long as markers account for significant genetic variance. However, these theoretical predictions of genetic gains assume QTLs are real and are detected without error, with infinite population size, and that the same QTLs detected in the reference population can be applied to the breeding population. The possibility of false QTL detection and the overestimation of the effects associated with markers are usually high, particularly with small sample size. In a Monte Carlo simulation study, BEAVIS (1995) found that in a population of 100 individuals and ten theoretical QTLs controlling a large proportion (63%) of the phenotypic variability, the power to identify QTL was only 0.117 (234 out of 2000 simulated QTL). Moreover, the size of the phenotypic effect was overestimated. For 10 QTLs, the estimated phenotypic effect was twice that of the actual simulated effect and ten times that for 40 QTLs. Even if MAS appears to be most interesting for low heritabilities, simulation for a finite population size using a cross between two homozygous lines indicates there is an optimal heritability (~ 0.2) below which the low power of quantitative trait loci detection and the bias caused by the selection of markers reduces efficiency greatly (MOREAU *et al.,* 1998). Therefore, very large sample sizes are needed for common tree growth traits with low heritability for more accurate estimates of QTLs and their effects. For example, STRAUSS *et al.* (1992) estimated approximately 2300 individuals are needed to detect half of the additive genetic variance at the 1% confidence level for a trait with heritability of 0.1 and 11 effective QTLs controlling the trait. The efficiencies of MAS in one generation and over several successive generations have also been studied using computer simulations (ZHANG and SMITH, 1992, 1993; EDWARDS and PAGE, 1994; GIMELFARB and LANDE, 1994a, 1994b, 1995; RUANE and COLLEAU, 1995; WITTAKER *et al.,* 1995; SPELMAN and BOVENHUIS, 1998; HOSPITAL *et al.,* 1997). Simulations showed that the additional genetic gain provided by MAS, compared with purely phenotypic selection, rapidly decreased when several successive cycles of selection were considered, and that MAS could become less efficient than phenotypic selection in the long term (HOSPITAL *et al.,* 1997).

For marker-aided early selection to be applicable in tree breeding, it must be demonstrated that efficiency from MAES is much higher than the efficiency of early selection from less expensive early phenotypic traits (e.g. $p > h_x^2\ r_A^2$). Otherwise, it would be difficult to convince breeding organizations to justify the extra costs of detecting QTLs, verification and individual genotyping for selection. In a conifer breeding program, MAES for deployment clones in the deployment population may be more attractive than use in the breeding population. The saving from long-term and expensive clonally testing might make MAES advantageous in using MAES to select best clones, although there are extra costs of detecting QTLs in these elite clones.

It may be that early selection, better methods of predicting breeding values, use of non-additive genetic variance in breeding programs, developing breeding objectives, managing and using inbreeding in an advanced breeding population, and genetic engineering can achieve more genetic gain in the short or medium term. However, there are exceptions. For some traits with simple inheritance mode, yet difficult and very expensive to measure, MAS and MAES might be a powerful tool for selection. Some disease resistance or wood quality traits might be candidates for MAS or MAES because for disease traits, establishing reliable inoculation and scoring methods is usually expensive and challenging. For wood quality traits, accurate measurement is rather expensive and can only be done after several years of plantation establishment (Neale and Williams, 1992). An example of the successful application of MAS in an agricultural crop is soybean cyst nematode (SCN) resistance (Mudge *et al.,* 1997; Mudge, 1999; Young, 1999). Breeders used gene mapping to locate a tightly linked SSR marker (Sat309) for the major SCN resistance gene *rhg1*, the gene primarily responsible for SCN resistance. Genotypic selection with Satt309 was 99 % accurate in predicting lines that were susceptible in subsequent greenhouse assays for two test populations and 80 % accurate for a third population. Selection for disease resistance in conifers may be similarly successful. A single major gene has been identified for resistance to western gall rust (van Der Kamp, 1991) and it is stable across environments (Wu and Ying, 1998). Using tightly linked markers, it may be possible to select for major gene resistance to white pine blister rust in sugar pine (Kinloch and Comstock, 1980; Devey *et al.,* 1995), and resistance to fusiform rust in loblolly pine (Kinloch and Walkinshaw, 1991; Wilcox *et al.,* 1996).

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