stigmas of other subgenera that have few papillae such as *Monocalyptus*. The timing of control pollination would be more crucial in such species.

There would be commercial benefit in being able to pollinate flowers at the time of emasculation. It would cut down on the cost of labour and travel. From this study it is apparent that a considerable amount of seed can be produced from *E. camaldulensis* flowers pollinated at the time of emasculation. The benefits of such action compared to the increased seed produced when flowers are pollinated at peak receptivity would have to be analysed. Further studies on different genotypes in various environments are also required. HODGSON (1976) and GRIFFIN and HAND (1979) have shown a cool change in the weather can delay peak receptivity by up to two days. Such a delay in *E. camaldulensis* may significantly reduce the amount of seed produced when flowers are pollinated at emasculation.

This study indicates the optimal time to pollinate *E. camaldulensis* is just as the style turns red and the stigma becomes enlarged, yellow and sticky (three days following emasculation). However receptivity falls dramatically after this time without displaying any visual changes. Therefore pollination should be carried out before, or at peak receptivity rather than following it. Results indicate that there is potential to emasculate and pollinate *E. camaldulensis* flowers on the same day with only relatively small losses in seed production. This factor combined with relatively high seed production and the rapid maturation of capsules (14 to 16 weeks under conditions at Kwinana, Western Australia) makes *E. camaldulensis* highly amenable to controlled pollination techniques.

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Study of Early Selection in Tree Breeding

1. Advantage of Early Selection through Increase of Selection Intensity and Reduction of Field Test Size

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Summary

There are three main advantages for early selection in tree breeding: 1.) increased selection intensity or reduced field-testing size; 2.) a shortened generation interval; and 3.) genetic information from early testing can be used to enhance selection efficiency at mature age. The first advantage is realized when early testing results can be used for culling families with the poorest performance prior to field testing. The expected genetic gain formula is derived for early plus mature two-stage successive selection. This formula is used to study the first advantage of early selection, which results in an increase in total selection intensity or reduction of field-testing size. The gain increase from early selection for a larger base population and gain decrease from early culling of the poorest families is a function of heritabilities, selection intensities on early and mature traits and their phenotypic and genetic correlation. Both early-mature genetic correlation and heritability of the early trait affect the magnitude of genetic gain increase for the mature trait from early selection. The formula is also used to answer the following three questions: (1) is it possible that early selection can be used to reduce the size of field testing without any loss in ultimate gain for the mature trait? (2) are there any conditions where more gain can be obtained when both early and mature selection are practiced than when selection is only practiced at the mature stage? (3) what is the condition where any selection at the early stage will result in less gain than if all selection is postponed to the mature stage? Depending on genetic parameters, all above three conditions are possible. The relationships of genetic parameters for satisfying one of the three conditions were derived from the formula and the theory is applied to a lodgepole pine retrospective early selection study.

Key words: Early selection, indirect selection, two-stage successive selection, genetic gain, lodgepole pine.

FDC: 165.62; 165.3; 232.13; 174.7 *Pinus contorta;* (712.3).

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Introduction

Early selection has been a major issue in most tree improvement programs, particularly for longlived coniferous species. This is primarily due to the unique biology of tree breeding, e.g. final products (wood and paper) usually can only be realized for decades after trees were planted. Since the usual targets for tree breeding are traits at harvest-age (such as biomass and stem volume), the ideal age for selection should be at rotation age (genetic correlation is one). But this delay on genetic evaluation and selection at rotation age would dramatically slow generation turnover. There are other reasons that selection at rotation age should be avoided. Since regimes of stand competition are usually altered from early to rotation stage due to natural or artificial thinning and there would be more uneven among-family and within-family competition at later ages, the environmental variation at rotation age is expected to increase greatly. The larger environmental variation would reduce heritability and thus, effectiveness of selection. A common recommendation is that final evaluation and selection in progeny tests be delayed until trees reach approximately half of the projected rotation age (ZOBEL and TALBERT, 1984; LOWE and VAN BUIJTENEN, 1989). For most conifers, the attainment of half rotation age still takes 15 years or more, and waiting for such a long period to select breeding material is unacceptable for most operational tree breeding programs.

This long cycle of tree breeding has at least two constraints for the rapid advance of tree improvement. First, establishment and maintenance of large progeny testing in field environments for an extended period will be expensive and risky. Second, genetic gain per unit time (per year) will be dramatically reduced (LAMBETH, 1980). Thus, tree breeders are in constant pursuit of new approaches to predict mature tree performance on the basis of performance of younger trees, e.g. early selection (NANSON, 1970; JIANG, 1985; BURDON, 1989).

Numerous results of early testing and selection have been reported in forest trees (see reviews such as NANSON, 1968; SZIKLAI, 1974; WAXLER and VAN BUIJTENEN, 1981; LAMBETH *et al.,* 1982; JIANG, 1985; GILL, 1987). There are two approaches to study the effectiveness of early selection. The first are comparative studies, in which seedlings are grouped into fast-growing and slow-growing groups (or groups based on other distinguishing factors) to observe the effectiveness of this classification in later stages or in which super-seedlings are selected and comparisons with average (or check) seedlings are made in later stages to evaluate the effectiveness of early selection (KING *et al.,* 1965; OVERTON and CHING, 1978; NIENSTAEDT, 1981). The second approach is through quantitative genetic study in which early testing and selection are carried out in a population and the effectiveness of early selection can be quantified in terms of genetic gain.

Within the quantitative genetic approach, there are two different ways to study effectiveness of early testing and selection: retrospective study and age-age correlation study. In retrospective studies, the seedlings are raised in controlled environments from seeds which are related to genotypes already being grown in field trials, to test genetic correlation and selection efficiency at very early ages (usually between three months to two years, LAMBETH, 1980; LAMBETH *et al.,* 1982). Age-age correlation studies utilize existing field trial data to observe relationships of growth at early and later ages on the same trees. From the age curve of heritability and genetic correlation, the optimal selection age can be calculated (MCKEAND, 1988; BURDON, 1989; MATHESON *et al.,* 1996). Early selection has been studied on different genetic entities: provenance (STEINHOFF, 1974; YING *et al.,* 1989), half-sib family (WILLIAMS, 1987, 1988; RIITER and PERRY, 1987; WU *et al.,* 1997), full-sib family (LAMBETH *et al.,* 1982; JIANG, 1988; JONSSON *et al.,* 1990) and clone (BENTZER *et al.,* 1989; ROULUND, 1987; HUEHN *et al.,* 1987). The results of reported early selection studies vary widely and are often controversial due primarily to differences among species, sample size, time interval considered, test environments, design, and silvicultural treatments. In addition, the indiscriminate use of phenotypic and genetic correlations in these studies has added to the confusion. There are three main conclusions to be drawn from early selection studies. First is that early selection should be delayed until the first few years of establishment are reached (usually first 3 years). LAMBETH's study in the early 1980 was the main support for this recommendation, and he analyzed juvenile-mature correlations of height in several conifer species (Douglas-fir, ponderosa pine, western white pine, red pine, loblolly pine, longleaf pine, shortleaf pine, and slash pine) and found age-age correlations (r), except when the early ages were between one to three years, could be estimated with reasonable accuracy, and selection after very early ages (first three years of establishing period) would be effective. FRANKLIN (1979) proposed a hypothetical growth model to explain long-term trends in genetic variance and heritability, based on data from four conifers (slash pine, loblolly pine, Douglas-fir and ponderosa pine). In his model, stand development was divided into juvenile-genotype, mature-genotype and codominance-suppression phases. The model suggests a trend of strongly positive age-age correlations within phases and generally weak or negative correlations between phases. Hence, little or no genetic gain would be produced from juvenile selection in these populations, and under typical stand conditions selection should be deferred until about half of rotation age. On the other hand, many very early (first two years) testing study in controlled environments (retrospective studies) indicate that very early selection is effective if appropriate early traits and testing environments are selected (LAMBETH *et al.,* 1982; WILLIAMS, 1987; JONSSON *et al.,* 1990; WU *et al.,* 1997).

The main purpose of early selection in tree breeding is to shorten the generation interval. In addition, two other major advantages from early testing have been advocated by tree breeders. Early selection can increase selection intensity or reduce field-testing size (ADAMS *et al.,* 1992) and genetic information from early testing can be used to enhance selection efficiency at mature age. The first advantage is realized when early testing results are used for culling families with the poorest performance prior to field testing. This either will result in an increase of selection intensity and possible expected genetic gain since more individuals can be screened before long-term progeny testing, or result in smaller, more environmentally homogeneous, and cost-effective field testing (LAMBETH, 1980; KANG, 1985; RIITER and PERRY, 1987). Information from early testing can be used to enhance the accuracy of mature selection and increase expected genetic gain. This can be achieved by including information from early testing, along with information on the mature trait, into selection indices designed for improvement of mature traits. This aspect of early testing is particularly useful when the efficiency of mature selection is low due to environmental heterogeneity on the long-term field testing. Therefore, in situations when there is low reliability in predicting the breeding value of mature traits, combining early and mature traits into a selection index can increase the accuracy of selection.

Shortening of the breeding cycle through early selection should bring more genetic gain per year either by quicker realization of genetic gain or by breeding several generations within a conventional breeding cycle. To evaluate this

advantage of early selection, a quantitative genetic method to estimate genetic gain from several generations of indirect early selection is required. To quantitatively evaluate the second advantage from early selection, e.g. increase of selection intensity or reduction of testing size, a quantitative genetic method is also required to quantify the expected genetic gain when a larger base population is early tested and culled down to the size of field testing with subsequent mature culling. This method should also address how reduction of field-testing size through early culling affects mature genetic gain. To evaluate third advantages of early testing, e.g. use of early genetic information, theory of index selection to include early genetic information should be examined. The relevant theories to deal with the three usages of early selection have been addressed in a comprehensive study. In this paper, a method to evaluate the effect of early selection on genetic parameters and gain due to increase of selection intensity or reduction of field-testing size was developed and applied to a lodgepole pine early selection case. The methods to evaluate multiple generations of early selection and use of early testing information to enhance efficiency of mature selection will be studied in subsequent papers. For convenience, conventional selection age (half-rotation age) or reference age (any age older than the age of early testing and selection) will be referred to as the mature age and ages younger than this will be referred to as the early age in the paper.

Theory

With mature tree selection only, a breeding cycle has one selection stage while with early selection, a breeding cycle has two selection stages (early and mature selection). This early and subsequent mature selection can be viewed as a two-stage successive selection process. Thus, to show the advantage of early selection (particularly very early selection in the nursery), we only need to compare genetic gain from early plus mature two-stage successive selection with genetic gain from mature selection only. Therefore, the method to estimate genetic gain from two-stage successive selection is needed. The selection theory of individual culling on two traits or traits at two stages has been well documented. In summary, the theory assumes traits at two stages to be bivariate normally distributed. The moments of two traits after independent culling have been derived by WEILER (1959) and WILLIAMS and WEILER (1964). These results have been used to determine optimum combination of culling levels for proportions of selection finally retained in animals (YOUNG and WEILER, 1961; YOUNG, 1964; COTTERILL and JAMES, 1981) and in trees (NAMKOONG, 1970; COTTERILL and JAMES, 1981). Two-stage independent culling theory also has been extended to multistage individual traits and index selection (YOUNG, 1964; CUNNINGHAM, 1975). However, two-stage independent culling theory can not be directly applied to early plus mature two-stage successive selection process since mature selection in the two-stage successive selection is not independent from early selection. Thus, selection intensity in a mature stage from early plus mature successive culling would be different from the selection intensity in two-stage independent culling process. In this paper, a method to calculate genetic gain for two-stage successive culling process is developed and is used to study the advantages of early selection.

For convenience, Y is designated as the mature trait and X as the early trait. We assume in a large base population that Y and X are bivariate normally distributed with additive genetic values G_y and G_x, and environmental variation E_y and E_x, respectively. Before early selection, G_y and G_x has genetic correlation of r and corresponding variances of $\sigma_{G_y}^2$ and $\sigma_{G_x}^2$, respectively. The bivariate normal distribution is justified if one assumes the early and mature traits are each controlled by many loci with additive effects and environmental variation is normally distributed (BULMER, 1980). The phenotypic variances and heritabilities of X and Y are denoted as σ_x^2, h_x^2 and σ_y^2, h_y^2, respectively, with their phenotypic correlation ρ in the base population.

For a progeny testing with early, plus later on mature selection, the first stage selection is practiced in an early stage, followed by second selection at a mature stage in the early truncated population. We assume a proportion p(a) is selected with truncation point, a, on early trait X, and another proportion p(b|a) with truncation point, b, is selected for mature trait Y in the early truncated repopulation. Thus, the total proportion selected is p(a)•p(b|a), which can be expressed mathematically as

$$p(a)\cdot p(b \mid a) = p(a\ b{:}\rho) = \int_a^\infty \int_b^\infty \frac{1}{2\pi\sqrt{1-\rho^2}} \exp\left[-\frac{1}{2(1-\rho)^2}(x^2 - 2\rho xy + y^2)\right] dx\ dy \qquad (1)$$

The expected phenotypic mean of mature trait Y (denoted as E_{xy} (y)) after early plus mature two-stage selection can be estimated from this proportion (WEILER, 1959):

$$E_{xy}(y) = \frac{\frac{1}{\sqrt{2\pi}} e^{-\frac{b^2}{2}} \int_{\frac{(a-\rho b)}{\sqrt{1-\rho^2}}}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{x^2}{2}} dx + \rho \frac{1}{\sqrt{2\pi}} e^{-\frac{a^2}{2}} \int_{\frac{(b-\rho a)}{\sqrt{1-\rho^2}}}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{y^2}{2}}}{p(a\ b{:}\rho)} \qquad (2)$$

This expected phenotypic mean is a function of the allocation of selection intensities at the early and mature stages.

The genetic gain after early plus mature two-stage selection can be developed by similar consideration. At the early stage, we select a proportion p(a) with corresponding selection intensity i_x and correlated genetic response $E_x(G_y)$ for mature trait Y. This expected genetic gain in Y due to selection on X can be estimated by standard formula (FALCONER, 1981)

$$E_x(G_y) = i_x\ h_x\ h_y\ r\ \sigma_y \quad . \qquad (3)$$

After early selection based on X, phenotypic and genetic variances and heritabilities of X and Y are altered. If the base population is large enough and intensity of early selection is not so strong, the early selected population still approximately has a normal distribution (COCHRAN, 1952). If we further assume that both early and mature traits are controlled by infinite number of unlinked loci with additive gene effect (FISHER's infinitesimal model), the possible change of gene frequency and genetic correlation between early and mature traits could be ignored. Assuming the altered phenotypic and genetic variances and heritability of Y are $\sigma_y^{2'}$, $\sigma_{G_y}^{2'}$, and $h_y^{2'}$, respectively, the genetic gain from early plus mature two-stage successive selection ($E_{xy}(G_y)$), after a second-stage of mature selection with proportion p(b|a), and corresponding selection intensity i_y', can be estimated as

$$E_{xy}(G_y) = i_x\ h_x\ h_y\ r\ \sigma_y + i_y'\ h_y^{2'}\ \sigma_y' \quad . \qquad (4)$$

To estimate the genetic gain $E_{xy}(G_y)$, we must first estimate $\sigma_y^{2'}$ and $h_y^{2'}$. The phenotypic variance of Y ($\sigma_y^{2'}$) after selection on X can be obtained from bivariate normal distribution theory (COCHRAN, 1951; WEILER, 1959):

$$\sigma_y^{2'} = (1 - \rho^2\ k)\ \sigma_y^2 \ , \qquad (5)$$

where $k = i_x(i_x - a)$ and a is the value at truncate point of standard normal distribution curve corresponding to selection intensity i_x. To estimate $h_y^{2'}$, the genetic variance $\sigma_{G_y}^{2'}$ in the early truncated population can be derived as

$$\sigma_{G_y}^{2'} = (1 - r^2\ h_x^2\ k)\ \sigma_{G_y}^2 \quad . \qquad (6)$$

Thus, $h_y^{2'}$ can be estimated as

$$h_y^{2'} = h_y^2 \left(\frac{1 - r^2\ h_x^2\ k}{1 - \rho^2\ k}\right) \quad . \qquad (7)$$

Therefore, genetic gain from two-stage successive selection can be expressed as

$$E_{xy}(G_y) = \left(i_x\ h_x\ h_y\ r + i_y' \cdot \frac{1 - r^2\ h_x^2\ k}{\sqrt{1 - \rho^2 k}} h_y^2\right)\sigma_y \quad . \qquad (8)$$

This genetic gain $E_{xy}(G_y)$ from early plus mature two-stage successive selection can and will be used to evaluate the advantages of early selection in terms of increasing selection intensity and reduction of field testing size.

The above two-stage successive selection theory was derived based on assumption of FISHER's infinitesimal genetic model. Under this assumption, early selection will not affect gene frequency and genetic correlation between the early and mature traits. There are two main factors which would affect our assumption in the practical breeding population: population size and number of loci. If gene number controlling early and mature traits is very limited and there is large gene effect, or population is small, early selection would affect gene frequency and genetic correlation between early and mature traits. However, with large population size and weak early selection, the change of gene frequency and genetic correlation would be small and may be ignored. If we further assume there are many loci with small effect on both early and mature traits (plus weak early selection and large base population), effect of early selection on gene frequency and genetic correlation could be ignored.

Advantages of Early Selection

1. Effect of increasing base population size on genetic gain

This is the situation where early selection enables more individuals to be screened at an early age before field testing. For example, if the size of long-term testing is set to M individuals and n final individuals will be selected, the size of base population N can be increased with an early screening and the increased base population could be $100 \cdot M/p$ with an early selection proportion of p%, without increasing field-testing size. Thus, under early plus mature two-stage selection, the final selection proportion can be divided into two parts

$$p_{xy} = \frac{n}{N} = \frac{M}{N} \times \frac{n}{M} = p(a)\ P(b \mid a) \quad , \qquad (9)$$

with corresponding selection intensities denoted as i_x and i_y'. If early screening was not implemented, only M individuals in the base population can be tested. Thus, selection proportion will be

$$p_y = \frac{n}{M} = p(b') = p(b \mid a) \quad , \qquad (10)$$

with $i_y = i_y'$.

Using the genetic gain equation for two-stage successive selection, the ratio of genetic gain of two-stage early plus mature selection relative to mature one-stage selection only is the form

$$R_{xy,y} = \frac{E_{xy}(G_y)}{E_y(G_y)} = \frac{i_x}{i_y}\ \frac{h_x}{h_y}\ r + \frac{1 - r^2\ h_x^2\ k}{\sqrt{1 - \rho^2 k}} \quad . \qquad (11)$$

The first part of the equation is the ratio of indirect genetic gain achievable from early selection at two-stage selection approach relative to gain from direct selection under one-stage mature selection. The advantage of early plus mature stage selection relative to mature selection only can be evaluated under various genetic parameters and selection intensities. In the following, genetic effect from the increase of overall selection intensity when early selection is implemented will be considered under several special cases:

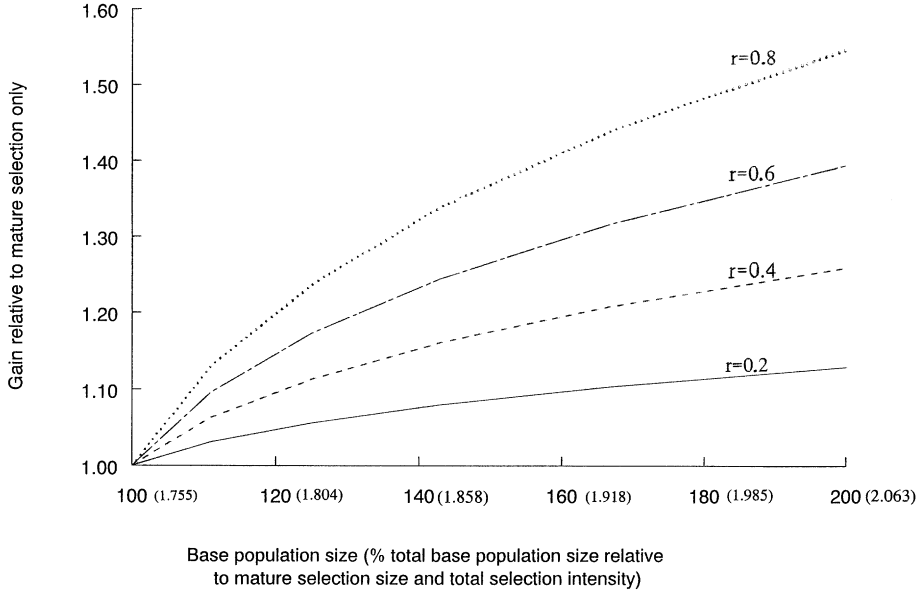

Figure 1. – Effect of increasing selection intensity on genetic gain of mature trait when early selection is used to increase population size for selection (Trends for four-mature genetic correlations when $r = \rho$, $h^2 = 0.5$ and $h_y^2 = 0.25$ with 90% mature culling level are shown).

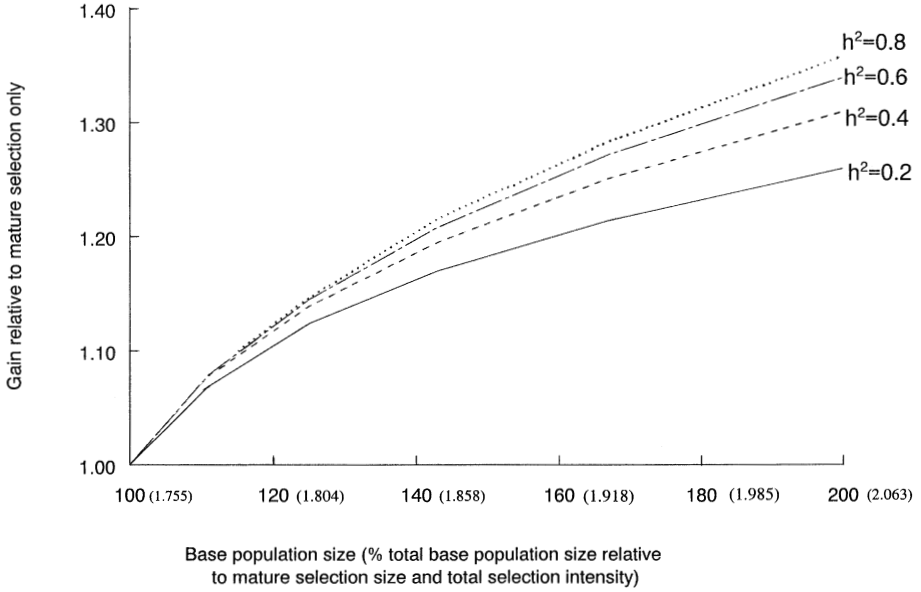

Figure 2. – Effect of increasing selection intensity on genetic gain of mature trait when early selection is used to increase population size for selection (Trends for four heritabilities of early trait when $r = \rho = 0.5$, $h_y^2 = 0.25$ with 90% mature culling level are shown).

(1) The general effect of increasing selection intensity (base population size) on total genetic gain of mature trait Y is illustrated in *figure 1* and *2* for a case of 90% culling level in mature selection with heritability of 0.25 for mature trait and $r = \rho$. It is observed that genetic gain increases almost linearly with increase of total selection intensity (base population size). However, the magnitude of genetic gain increase is affected by early-mature genetic correlation (*Figure 1*) and heritability of early trait (*Figure 2*) and genetic correlation has far more effect than heritability of early trait. At low genetic correlation, an increase of base population size has a limited effect on gain increase of Y while increase of base population size for selection based on a highly correlated early trait has a large effect on gain increase of Y, for, example, doubling population size only increases gain by 13% for $r = 0.2$ while gain increases by 55% for $r = 0.8$.

(2) $\rho = r \cdot h_x$ (early-mature phenotypic correlation is equal to the product of genetic correlation and square root of heritability of early trait). This is an example where the phenotypic correlation (ρ) is less than the genetic correlation (r) while heritability of early trait is less than unity. The condition of $\rho < r$ is common for correlations estimated between early and mature traits in trees (LAMBETH *et al.,* 1983; LOO *et al.,* 1984; COTTERILL and DEAN, 1988; RIEMENSCHNEIDER, 1988). At this case, the genetic gain ratio is

$$R_{xy,y} = \frac{i_x}{i_y}\,\frac{h_x}{h_y}\,r + \sqrt{1-\rho^2 k} \quad . \qquad (12)$$

By definition, k is always less than unity because $k = i_x(i_x - a)$. When ρ is small (say $\rho < 0.5$), the second term $Q = \sqrt{1-\rho^2 k}$ approximates unity such that the genetic gain ratio is approximately

$$R_{xy,y} \approx 1 + \frac{i_x}{i_y}\,\frac{h_x}{h_y}\,r \quad . \qquad (13)$$

Thus, the increase in genetic gain due to increasing base population size with two-stage selection over one-stage mature selection only can be approximated by the proportion, $(i_x \cdot h_x \cdot r)/(i_y \cdot h_y)$. The values of the second term $Q = \sqrt{1-\rho^2 k}$ when $\rho = 0.5$, for example, depend on the early selection proportion (intensity), but most of the values are above 0.90 (*Table 1*).

(3) $i_x = i_y$ and $h_x \cdot r = h_y$ (the intensity of early selection in early plus mature selection is equal to selection intensity for the procedure with mature selection only and the square root of heritability for mature trait is equal to the product of genetic correlation and square root of heritability for early trait). This is an example where heritability of the early trait is greater than heritability of the mature trait when the genetic correla-

Table 1. – The value of $Q = \sqrt{1-\rho^2 k}$ when phenotypic correlation $\rho = 0.5$, for different proportions selected at early stage (P%)*).

P%	10	20	30	40	50	60	70	80	90
a	1.282	0.842	0.524	0.253	0.000	-0.253	-0.524	-0.842	-1.282
i_x	1.755	1.400	1.159	0.966	0.798	0.644	0.497	0.350	0.195
k	0.830	0.78	0.736	0.689	0.637	0.578	0.507	0.417	0.288
Q	0.89	0.90	0.90	0.91	0.917	0.925	0.934	0.947	0.963

*) a – the truncation point of the normal curve when selection proportion is P%; i_x – selection intensity for early trait; $k = i_x(i_x - a)$.

tion is less than unity. These are the usual cases from many early testing studies (heritability of early trait is greater than heritability of the mature trait due to more controlled homogeneous environment in early testing). Under these conditions, the genetic gain ratio can be expressed as

$$R_{xy,y}=1+\frac{1-r^2\ h_x^2\ k}{\sqrt{1-\rho^2 k}}\ , \qquad \textbf{(14)}$$

Thus, the increase of genetic gain under two-stage early plus mature selection over one-stage mature selection is the proportion, $(1-r^2h_x^2k)/\sqrt{1-\rho^2k}$.

(4) Both conditions (2) and (3) above are met.

The genetic gain ratio is $R_{xy.y}=1+\sqrt{1-\rho^2k}$ and the genetic gain under two-stage early plus mature selection over one-stage mature selection is significantly greater than that in conditions (2) and (3) above. Some ratios are calculated in *table 2.* In most cases, genetic gain with two-stages of selection is almost twice that compared to genetic gain without early selection. But this usually requires a substantial increase of base population size for early selection.

2. Effect of reducing the size of field testing on genetic gain

Reduction of field-testing size through early selection has important implications for efficient progeny testing in forest trees since forest planting sites are often highly variable and larger than agricultural testing sites although there are efficient experimental designs to reduce environmental errors (WILLIAMS and MATHESON, 1994). An issue of concern for reduction of field-testing size is how much genetic gain would be lost by reducing long-term field-testing size through early selection. Related to this issue are the following three questions: (1) is it possible that early selection can be used to reduce the size of field testing without any loss in ultimate gain for the mature trait? (2) are there any conditions under which more gain can be obtained when both early and mature selection are practiced than when selection is only practiced at the mature stage? (3) what is the condition where any selection at the early stage will result in less gain than if all selection is postponed to the mature stage? All three situations are possible with early selection, but these are dictated by the early-mature genetic correlation, the proportion early-selected and the heritabilities. When the following parameter relationships hold, any early selection in order to reduce field-testing size will not have an impact on genetic gain of mature trait:

$$i_x\ h_x\ r + i_y'\cdot\frac{1-r^2\ h_x^2\ k}{\sqrt{1-\rho^2 k}}h_y\ =\ i_y\ h_y. \qquad \textbf{(15)}$$

It is cumbersome to derive relationships of genetic parameters under which early selection will not reduce any genetic gain from equation 17 since the equation is a function of 7 variables (three selection intensities, two heritabilities, and phenotypic and genetic correlations). To demonstrate an essential relationship among genetic parameters required to answer the above three questions, we could simplify the equation in order to derive the threshold of genetic parameters which will not result in any reduction of total genetic gain when early selection is implemented. If we assume that $\rho=r\cdot h_x$ (early-mature phenotypic correlation is equal to the product of genetic correlation and the square root of heritability of early trait) and final selection proportion is 10%, the threshold of early-mature genetic correlation and heritability of early trait was calculated for five levels of heritabilities for mature traits ($h_y^2=0.1$, 0.2, 0.3, 0.4 and 0.5) under five early culling levels each (*Figure 3* to *7*). Any early selection on populations having genetic correlation and heritability of early trait on these thresholds will not produce any loss of overall genetic gain relative to full-size testing and selection at mature stage if early selection was used to reduce field testing size. In contrast, early selection on populations having genetic parameters higher than the threshold would increase genetic gain. However, any early selection to reduce field testing size on populations having parameters below the threshold would reduce overall genetic gain of the mature trait.

Example of Lodgepole Pine

A retrospective study has been conducted for 110 lodgepole pine (*Pinus contorta* ssp. *latifolia*) families from Alberta, Canada. The 28 seedling traits assessed during the first two growing seasons in the greenhouse were jointly studied with four field plantations at age nine. Genetic correlation between basal diameter after two growing seasons and tree height at one field site (site B) will be used to illustrate the advantages of early selection through increase of selection intensity and reduction of field testing size. The heritabilities of basal diameter and nine-year tree height were 0.681 and 0.349, respectively, with greenhouse-field genetic correlation of 0.362 and family-mean correlation of 0.194 (WU *et al.,* 1995; WU and YEH, 1997).

(1) The effect of increasing base population (total selection intensity) through early selection based on two years basal diameter on genetic gain of nine-year height.

This is the situation where early testing is used to cull an initially larger population down to the planned field-testing size. Assuming field-testing size is set at 110 families, we can easily increase base population size by 10% to 100% in the greenhouse testing without substantially increasing cost. The increase of genetic gain for nine-year height was calculated for a 10% selection proportion in the final field selection (*Table 3*). When the base population in early testing is increased from 110 to 122, 138, 157, 183 and 220 families, the genetic gain in nine-year tree height from two-stage early plus mature selection is expected to be 5.1%, 9.6%, 13.5%, 18.5% and 23.9% greater than expected from field selection of 110 families only.

Table 2. – Genetic gain ratio of two stage selection (early selection plus mature selection with selection intensities i_x and i_y, respectively) to one stage mature selection only (with selection intensity i_y) when phenotypic correlation $\rho=r\cdot h_x=0.5$ and $i_x=i_y$, $h_x\cdot r=h_y$ [a]).

P%	10	20	30	40	50	60	70	80	90
i_x	1.755	1.400	1.159	0.966	0.798	0.644	0.497	0.350	0.195
$R_{xy.y}$	1.89	1.90	1.90	1.91	1.92	1.93	1.93	1.95	1.96

[a]) P% – selection proportion at early stage in two stage selection; r – genetic correlation between early and mature traits; h_x and h_y are heritabilities for early and mature traits, respectively; $R_{xy.y}$ – gain ratio of two stage selection to one stage mature selection.

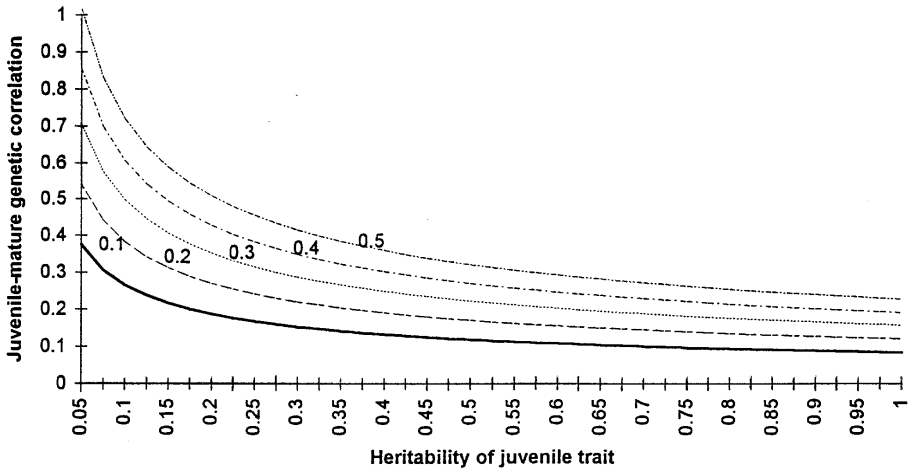

Figure 3. – Threshold of juvenile-mature genetic correlation and juvenile heritability for a 10% early culling level when early selection will not reduce genetic gain of mature trait (five curves representing five levels of mature trait heritability).

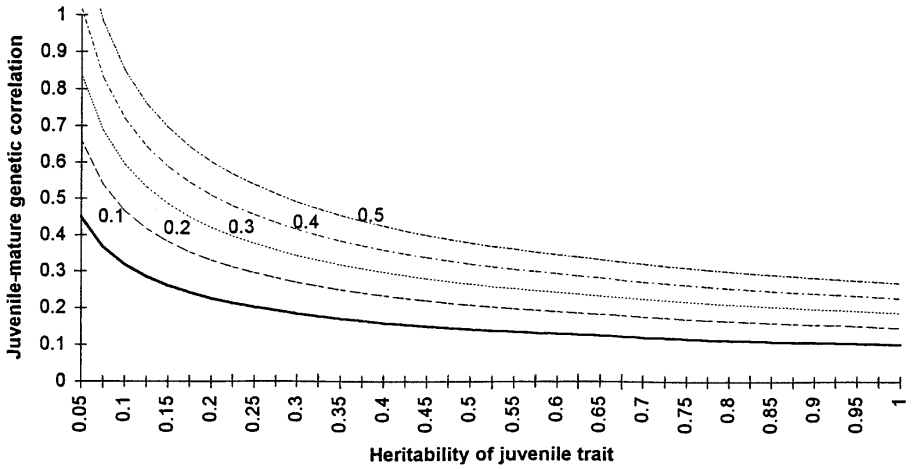

Figure 4. – Threshold of juvenile-mature genetic correlation and juvenile heritability for a 20% early culling level when early selection will not reduce genetic gain of mature trait (five curves representing five levels of mature trait heritability).

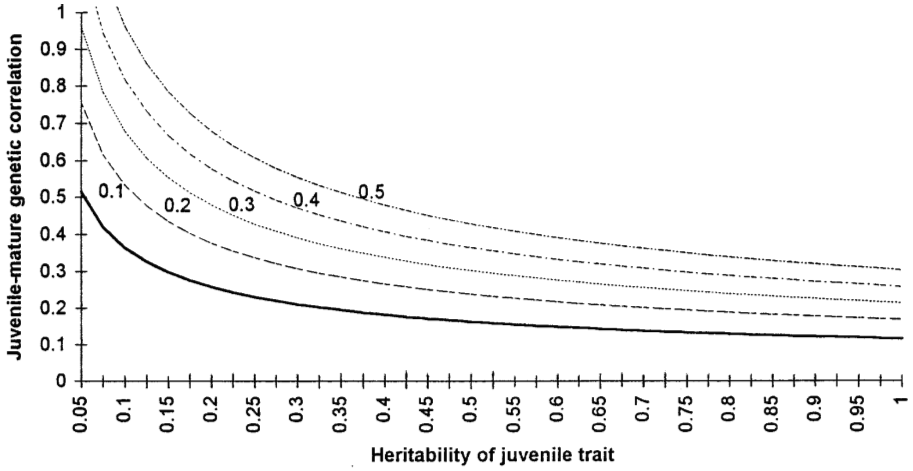

Figure 5. – Threshold of juvenile-mature genetic correlation and juvenile heritability for a 30% early culling level when early selection will not reduce genetic gain of mature trait (five curves representing five levels of mature trait heritability).

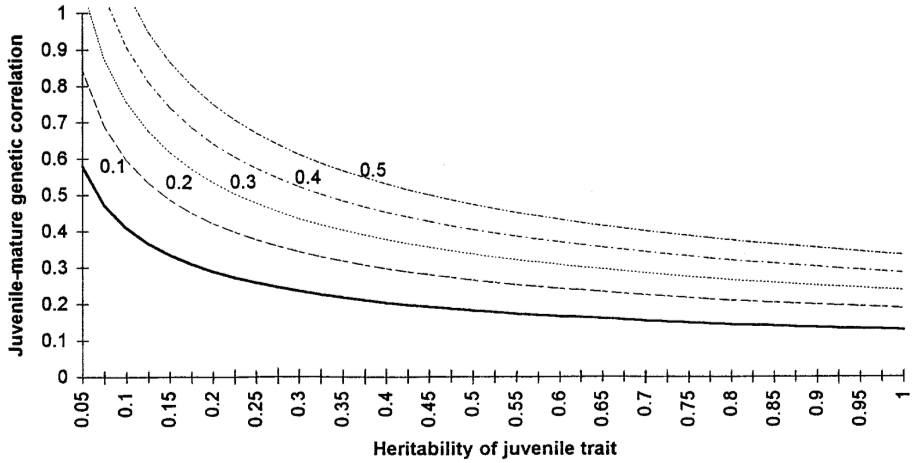

Figure 6. – Threshold of juvenile-mature genetic correlation and juvenile heritability for a 40% early culling level when early selection will not reduce genetic gain of mature trait (five curves representing five levels of mature trait heritability).

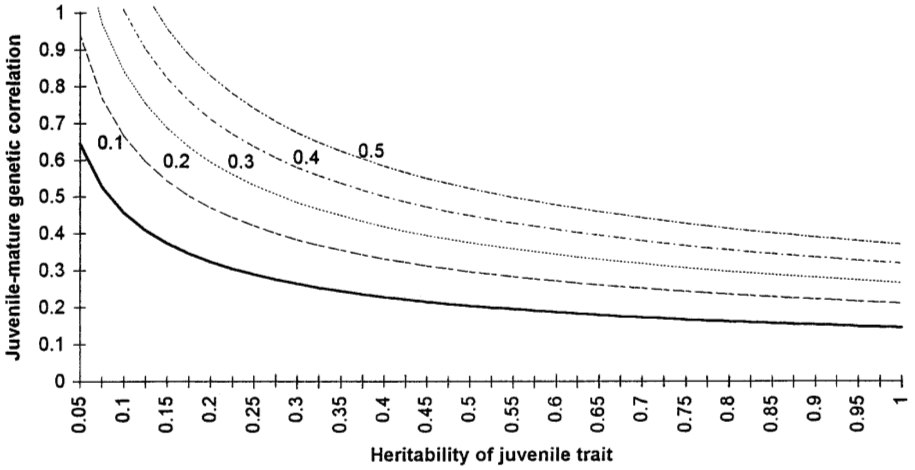

Figure 7. – Threshold of juvenile-mature genetic correlation and juvenile heritability for a 50% early culling level when early selection will not reduce genetic gain of mature trait (five curves representing five levels of mature trait heritability).

Table 3. – Effect of increase in overall selection intensity on total genetic gain due to early selection (estimated genetic gain in nine-year tree height after two-stages of family selection, when selection in the first stage is based on basal diameter after two growing seasons of seedlings in the greenhouse, selection in the second stage is one nine-year tree height at field, and the final 11 families are selected from 110 families field tested)[a]).

Base population size	110	122	138	157	183	220
Number of families culled at early stage	0	12	28	47	73	110
i_x	0	0.195	0.350	0.497	0.644	0.798
a		-1.282	-0.842	-0.524	-0.253	0
k	0	0.288	0.417	0.507	0.578	0.637
$R_{xy,y}$	1	1.051	1.096	1.135	1.185	1.239
Gain increase	0%	5.1%	9.6%	13.5%	18.5%	23.9%

[a]) i_x is selection intensity at the first stage (early selection); a – truncation point corresponding i_x; $k = i_x (1–i_x)$; i_y' – selection intensity at the second stage (mature selection); $R_{xy \cdot y}$ is ratio of genetic gain between two-stage early plus mature selection and mature selection alone.

Table 4. – Effect of reduction of field test size on total genetic gain due to early selection (estimated genetic gain in nine-year tree height after two-stages of family selection, when selection in the first stage is based on basal diameter after two growing seasons of seedlings in the greenhouse, selection in the second stage is on nine-year tree height at field, and the final selection proportion is 10%)[a]).

	Culling levels at the first stage									
	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%
i_x	0	0.195	0.350	0.497	0.644	0.798	0.966	1.159	1.40	1.755
a		-1.282	-0.842	-0.524	-0.253	0.000	0.253	0.524	0.842	1.282
k	0	0.288	0.417	0.507	0.578	0.637	0.689	0.736	0.780	0.830
i_y'	1.755	1.704	1.647	1.580	1.500	1.400	1.271	1.091	0.798	0
$R_{xy,y}$	1	1.01	1.01	1.01	1.00	0.99	0.96	0.93	0.83	0.57
%	0%	1%	1%	1%	0%	-1%	-4%	-7%	-17%	-43%

[a]) i_x – selection intensity at the first stage (early selection); a – truncation point corresponding to i_x; $k = i_x (i_x - a)$; i_y' – selection intensity at the second stage (mature selection); $R_{xy \cdot y}$ – ratio of genetic gain between two-stage early plus mature selection and mature selection alone; % – the percentage difference on genetic gain due to reduction of field testing size after early selection relative to mature selection alone.

(2) The effect of culling inherently poor families based on two years basal diameter prior to outplanting on overall genetic gain of nine-year height.

In this scenario, poor families are culled at the first stage based on family mean of basal diameter in the greenhouse, with subsequent selection of the remaining families based on family average of nine-year height in field site B.

Assuming 10% of the families will be selected after two stages of family selection, overall genetic gains in nine-year tree height for different early culling levels at the greenhouse stage (from 90% to 10%), were calculated and compared with genetic gain achievable when all family selection was postponed until nine-years of age (no early selection). The ratio of expected genetic gain between two-stage early plus mature selection and field selection only is listed in *table 4.* It is observed that early selection with less than 50% culling level would not reduce total genetic gain. But culling levels of 50%, 60%, 70% and 80% would reduce genetic gain by 1%, 4%, 7% and 17%, respectively. Were a 90% culling level to be implemented at early age, 43% of genetic gain would be lost.

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Mating System Variation in a Scots Pine Clonal Seed Orchard

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Summary

The mating system was investigated in a Scots pine (*Pinus sylvestris* L.) seed orchard consisting of 32 clones, using 10 isozyme loci as genetic markers. The multilocus outcrossing rate calculated for the data pooled over three years of observations was estimated to be 0.987 (0.005). The population multilocus estimates of three consecutive years exhibited a decreasing trend (0.976, 0.966 and 0.962 for the years 1988 to 1990, respectively), but this variation was not significant. Individual outcrossing rates were homogeneous across years for most sampled ramets. Individual tree estimates were heterogeneous across sampled ramets for the pooled data in the years 1988 and 1990 but not for 1989. Individual outcrossing rates were not significantly related to individual pollen production. Although no significant variation of outcrossing rates in time could be detected, estimates of variance effective population size in the three years suggest temporal variation in outcross mating patterns.

Key words: Pinus sylvestris, mating system, outcrossing, inbreeding, flowering, seed orchard.

FDC: 165.3; 165.41; 181.521; 232.311.3; 174.7 *Pinus sylvestris.*

Introduction

Mating systems in conifers were generally found to be variable (MITTON, 1992). Estimates of outcrossing rate vary among species, among populations within species, among individuals within populations, among different parts of the crown within individuals and among loci (see for reviews: ADAMS and BIRKES, 1991; MUONA, 1990; MITTON, 1992). These variations are due to both genetical and ecological influences, such as stand density and age and the availability of local or foreign pollen (FARRIS and MITTON, 1984; KNOWLES et al., 1987; BURCZYK et al., 1991).

Temporal variation of outcrossing rate resulting either from different pollination patterns or from the time elapsed since fertilization, despite its great practical and theoretical importance, arrested only limited attention in mating system studies (MITTON, 1992). While PERRY and DANCIK (1986) did not find significant variation, several authors found an increase in outcrossing rates with the time elapsed since fertilization (CHELIAK et al., 1985; SNYDER et al., 1985; HAMRICK, 1989). They suggested that selection acting against inbred progeny during the retention of seed in serotinous cones could be responsible for the observed increase, but this has never been proven.

Outcrossing rates estimated at the population level were found to be high in conifers, but individual tree estimates may vary widely from 0.5 to 1.0 (SHAW and ALLARD, 1982; EL-KASSABY et al., 1987; ERICKSON and ADAMS, 1990; BURCZYK et al., 1991). In Scots pine (*Pinus sylvestris* L.), the most important conifer species in Central and Northern Europe, the range of estimates seems to be narrower (KOSKI and MUONA, 1986; BURCZYK, 1991; KÄRKKÄINEN and SAVOLAINEN, 1993). Although selfing was generally found to be low, inbreeding depression is still considered an important factor in many genetic programs. It is still unclear, if there are any specific situations when selfing could

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