Study of Early Selection in Tree Breeding

2. Advantage of Early Selection Through Shortening the Breeding Cycle

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Summary

Three main advantages from early selection in tree breeding have been recognized: 1.) increased selection intensity or reduced field-testing size; 2.) shorter generation interval; and 3.) genetic information from early testing can be used to enhance selection efficiency at later ages. The second advantage is obtained through quicker realisation of genetic gain or by breeding several generations within a conventional breeding cycle from mature selection. To quantify the second advantage from early selection it is necessary to estimate genetic gain from indirect selection over several generations. In this paper, a method is derived to estimate genetic gain from several generations of early indirect selection and is used to study the advantage of early selection through shortening the tree breeding cycle relative to mature selection. The results show that genetic variance, heritability and selection response for the correlated (mature) trait as well as genetic correlation between directly selected (early) and correlated (mature) traits will decline after each generation of selection. When the number of generations approaches infinity, genetic variance, heritability and selection response for the correlated trait and the genetic correlation between directly selected and correlated traits each approach corresponding limiting values under FISHER's infinite genetic loci model. The reduction in genetic variance, heritability and selection response for the correlated trait is slower than the reduction of genetic variance for the trait under direct selection. The method is applied to a lodgepole pine early selection study.

Key words: early selection, multiple-generation indirect selection, genetic parameter, correlated genetic gain.

Introduction

Three main advantages from early selection in tree breeding have been identified: 1.) early selection could increase overall selection intensity or reduce field-testing size; 2.) it could shorten generation interval; and 3.) genetic information from early testing could be used to enhance selection efficiency at mature age (WU, 1998). Theory to study the first advantage has been developed (WU, 1998). However, the most frequently cited advantage of early selection in tree breeding is reduction in the length of the breeding cycle (NANSON, 1970; LAMBETH, 1980; ADAMS et al., 1989; ADAMS and AITKEN, 1992; MCKEAND, 1988; MATHESON et al., 1994). Shortening a tree breeding cycle through early selection could produce more genetic gain per unit time (year) if there is sizable genetic correlation between early and mature traits. Genetic gain per unit time through early selection could be obtained either by quicker realisation of genetic gain or by breeding several generations within a conventional breeding cycle of mature selection (say, at half-rotation age). Traditionally, tree breeders used the correlated genetic gain from indirect selection to study efficiency of early selection relative to direct mature selection (NANSON, 1970, 1988; LAMBETH, 1980; NEBGEN and LOWE, 1985; BURDON, 1989; JIANG, 1988; MCKEAND, 1988). The efficiency of indirect early selection relative to mature selection was calculated as

$$R_{x,y} = \frac{E_x(G_y)}{E_y(G_y)} \frac{T_y}{T_x} = \frac{i_x}{i_y} \frac{h_x}{h_y} r \frac{T_y}{T_x} \qquad (1)$$

where $E_x(G_y)$ and $E_y(G_y)$ are expected genetic gains for mature trait Y from selection at early and mature ages, respectively; i_x and i_y are selection intensities for early trait X and mature trait Y, respectively; h_x and h_y are square roots of the heritabilities of early and mature traits, respectively; r is the genetic correlation between early and mature traits; T_y and T_x are number of years (or unit time) required to complete a breeding cycle with mature and early selection, respectively (NANSON, 1970, 1988; LAMBETH, 1980). Both T_y and T_x consist of the ages for selection (mature or early) and the years required for breeding. This equation is often used in the literature to quantify efficiency of early selection through quicker realisation of genetic gain. Thus, if selection intensities at early and mature ages are the same, early selection will be more efficient as long as $h_x r T_y > h_y T_x$.

But there are two disadvantages of using this equation to study the efficiency of early selection. First, in forward selection, genetic gain of the mature trait in one generation of early selection can be realised only after $T_x + T_m$ years (not T_x, due to selection age (T_x) plus production age (T_m, e.g. age required to reach mature age)). Similarly gain from mature age selection can only be realized after $T_y + T_m$ years (not T_y). Thus, more precise comparison of genetic gain from one generation of early selection relative to mature selection should be

$$R_{x,y} = \frac{E_x(G_y)}{E_y(G_y)} \frac{T_y}{T_x} = \frac{i_x}{i_y} \frac{h_x}{h_y} r \frac{2T_y}{T_x+T_y} \qquad (2)$$

assuming $T_m = T_y$ for convenience and for the reason that years of a breeding cycle from mature seletion (T_y) is relatively close to the age of reaching mature trait (T_m). The new equation indicates efficiency of early selection will be smaller than the estimate from equation 1 since $\frac{2T_y}{T_x+T_y} < \frac{T_y}{T_x}$. Moreover, this efficiency comparison (equation 1 or 2) is valid only for the first generation of early selection. A more effective way to compare efficiency between early and mature selection is to estimate genetic gain from several cycles of early selection within the time frame of a conventional breeding cycle of mature selection since breeders usually can have more than one (may be a few) generation of selection within time frame of a generation of mature selection. The total genetic gain in mature traits following several generations of early indirect selection is not a simple multiple of the gain estimated for a single generation of early indirect selection since selection, whether it is conducted directly or indirectly, alters genetic parameters. Thus, a

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method to estimate total genetic gain from several generations of early indirect selection is required before efficiency of early selection relative to mature selection can be more effectively studied.

BULMER (1971) studied the effect of direct selection on genetic variances and gains for multiple-generations. Assuming an infinite number of unlinked loci with additive gene effects, direct selection leads to a reduction in genetic variance. Correspondingly, genetic gain would be reduced in the next generation due to reduced genetic variance. The simulation results of BULMER (1976) indicated that changes in genetic variance due to selection with finite numbers of gene loci were in good agreement with those predicted on theoretical grounds with an infinite number of gene loci for the first few generations.

Selection affects not only phenotypic and genetic variances of traits under direct selection (for an early trait in the early selection case), but also phenotypic and genetic variances of correlated traits (the mature trait) and their phenotypic and genetic covariances and correlations (BOHREN et al., 1965; SHERIDAN and BARKER, 1974a and b). In this paper, we will derive the variance of a correlated trait and covariance between direct and correlated traits after indirect early selection and use these results to predict genetic gain in mature traits following several generations of early selection. The gain equation can be used to study the efficiency of indirect early selection relative to direct mature selection through shortening of the breeding cycle.

Theory

We assume, in a large base population, that Y and X represent mature and early traits with additive genetic values ${}^0G_y$ and ${}^0G_x$, and variances ${}^0\sigma_{Gy}^2$ and ${}^0\sigma_{Gx}^2$, respectively (0 denotes base population). The additive genetic values ${}^0G_y$ and ${}^0G_x$ are assumed to follow a bivariate normal distribution with a density function f{${}^0G_y$, ${}^0G_x$}, and a genetic correlation ${}^0r$. The bivariate normal distribution is justified when only additive genetic variance and covariance are considered for a random mating population and early and mature traits are controlled by numerous unlinked loci with pleiotropic effects (BULMER, 1980). As usual, phenotypic values of Y and X are composed of genetic values ${}^0G_y$, ${}^0G_x$ and environmental effects ${}^0E_y$, ${}^0E_x$ according to additive relationships. Thus, if environmental values are normally distributed, phenotypic values Y, X are also bivariate normally distributed. The following additional parameters are assumed for the base population: phenotypic variances ${}^0\sigma_y^2$ and ${}^0\sigma_x^2$; phenotypic correlations ${}^0\rho$; and heritabilities ${}^0h_y^2$ and ${}^0h_x^2$.

First, we consider the result of selection on early trait X in the base population. The phenotypic and genetic variances for X and Y after selection on X have been shown to be (COCHRAN, 1951; WEILER, 1959; ROBERTSON, 1977):

$$ {}^0\sigma_x^{2\prime} = (1-k)\,{}^0\sigma_x^2 \ , \tag{3} $$

$$ {}^0\sigma_{G_x}^{2\prime} = (1-k\ {}^0h_x^2)\,{}^0\sigma_{G_x}^2 \ , \tag{4} $$

$$ {}^0\sigma_y^{2\prime} = (1-{}^0\rho^2 k)\,{}^0\sigma_y^2 \ , \tag{5} $$

$$ {}^0\sigma_{G_y}^{2\prime} = (1-{}^0h_x^2\, k\, {}^0r^2)\,{}^0\sigma_{G_y}^2 \ , \tag{6} $$

where k=i(i-α) with i and α representing respectively selection intensity and truncating point in a standard normal distribution curve and the prime on the variances indicates they are parameters in the truncated population after early selection. The genetic and phenotypic covariances between early and mature traits after early selection can be derived in the same manner as

$$ {}^0cov'(G_x\ G_y) = {}^0cov(G_X\ G_y)(1-{}^0h_x^2 k) \ , \tag{7} $$

$$ {}^0cov'(X\ Y) = {}^0cov(X\ Y)(1-k) \ . \tag{8} $$

If we assume that additive genetic values of early and mature traits are distributed as a bivariate normal distribution in the base population, there is a linear regression relationship between ${}^0G_y$ and ${}^0G_x$. This regression can be expressed as

$$ {}^0G_y = a\ {}^0G_x + {}^0E_y \ . \tag{9} $$

From this relationship, the correlated genetic variance for mature trait Y in the next generation after early selection can be derived (see Appendix 2.1, WU, 1993) as

$$ \begin{aligned} {}^1\sigma_{G_y}^2 &= \frac{1}{2}(1-{}^0h_x^2\ k\ {}^0r^2)\,{}^0\sigma_{G_y}^2 + \frac{1}{2}\,{}^0\sigma_{G_y}^2 \\ &= {}^0\sigma_{G_y}^2\left(1-\frac{1}{2}\,{}^0h_x^2\ k\ {}^0r^2\right) \ . \end{aligned} \tag{10} $$

If random mating and infinite unlinked loci are assumed, the same linear regression between early and mature genetic values holds in the next generation. Hence, the covariance of the two additive genetic values in the next generation (generation 1) can be predicted as

$$ {}^1cov(G_y\ G_x) = \frac{{}^0cov(G_y\ G_x)}{{}^0\sigma_{G_x}^2}\ {}^1\sigma_{G_x}^2 \ , \tag{11} $$

and accordingly, genetic correlation at the next generation is

$$ {}^1r = {}^0r\sqrt{\frac{1-\frac{1}{2}\,{}^0h_x^2\ k}{1-\frac{1}{2}\,{}^0h_x^2\ k\ {}^0r^2}} \ . \tag{12} $$

Under constant environmental variance (i.e. assuming the same environmental variances in different generations), the correlated phenotypic variation for mature trait Y, in the next generation (generation 1), can be deduced as

$$ \begin{aligned} {}^1\sigma_y^2 &= \frac{1}{2}(1-{}^0h_x^2\ {}^0h_y^2\ k\ {}^0r^2)\ {}^0\sigma_y^2 + \frac{1}{2}\,{}^0\sigma_y^2 \\ &= {}^0\sigma_y^2 - \frac{1}{2}\,{}^0h_x^2\ k\ {}^0r^2\ {}^0\sigma_{G_y}^2 \ . \end{aligned} \tag{13} $$

From these relationships, theoretical responses for both directly selected early and correlated mature traits, when selection is practised in the next generation (generation 1), can be predicted as:

(1) Response of early trait X under selection for X

$$ {}^1E_x(G_x)={}^1i_x\ {}^1h_x\ {}^1\sigma_{G_x} $$

$$ ={}^0E_x(G_x)\frac{1-\frac{1}{2}\,{}^0h_x^2\ k}{\sqrt{1-\frac{1}{2}\,{}^0h_x^4\ k}} \tag{14} $$

if selection intensity (${}^1i_x$) is assumed same as in the previous generation (${}^0i_x$).

(2) Response of mature trait Y under selection for Y

$$ {}^1E_y(G_y)={}^1i_y\ {}^1h_y\ {}^1\sigma_{G_y} $$

$$ ={}^0E_y(G_y)\frac{1-\frac{1}{2}\,{}^0h_x^2\ k\ {}^0r^2}{\sqrt{1-\frac{1}{2}\,{}^0h_x^2\ {}^0h_y^2\ k\ {}^0r^2}}\ . \tag{15} $$

(3) Correlated response of mature trait Y under selection for X

$$ {}^1E_x(G_y)={}^1i_x\ {}^1h_x\ {}^1h_y\ {}^1r\ {}^1\sigma_y $$

$$ ={}^0E_x(G_y)\frac{1-\frac{1}{2}\,{}^0h_x^2\ k}{\sqrt{1-\frac{1}{2}\,{}^0h_x^4\ k}}\ . \tag{16} $$

From equation 16, it is apparent that ${}^1E_x(G_y) < {}^0E_x(G_y)$ for ${}^0h_x^2 \leq 1$. This suggests that the correlated response of mature trait Y due to selection on early trait X will decline after each generation of indirect selection.

For several generations of early indirect selection, the correlated genetic variance and the phenotypic variance of Y and the genetic correlation between X and Y can be derived in the same manner if it is assumed that selection does not change the regression relationship of additive values between early and mature traits. This assumption can be justified only if the following three conditions are satisfied: (1) the number of loci controlling early and mature traits is effectively infinite; (2) only additive gene effects are considered; (3) mating is random. With these conditions, genetic variance of the correlated trait Y after n generations of selection on X should be

$$ {}^n\sigma_{G_y}^2={}^0\sigma_{G_y}^2-{}^nD_y\ , \tag{17} $$

where ${}^nD_y$ is the reduction of genetic variance of correlated mature trait Y and is derived as

$$ \begin{aligned} {}^nD_y &= {}^{n-1}r^2\ \frac{k}{2}\ {}^{n-1}h_x^2\ {}^{n-1}\sigma_{G_y}^2+{}^{n-2}r^2\ \frac{k}{4}\ {}^{n-2}h_x^2\ {}^{n-2}\sigma_{G_y}^2 \\ &\quad +\dots+{}^0r^2\frac{k}{2^n}\ {}^0h_x^2\ {}^0\sigma_{G_y}^2 \\ &= \sum_{i=0}^{n-1}{}^ir^2\frac{k}{2^{n-i}}\ {}^ih_x^2\ {}^i\sigma_{G_y}^2\ . \end{aligned} \tag{18} $$

Similarly, the genetic correlation after nth generations of early indirect selection is

$$ {}^nr={}^0r\sqrt{\frac{1-\dfrac{{}^nD_x}{{}^0\sigma_{G_x}^2}}{1-\dfrac{{}^nD_y}{{}^0\sigma_{G_y}^2}}} \tag{19} $$

and the phenotypic variance of trait Y at generation n should be

$$ {}^n\sigma_y^2={}^0\sigma_y^2-{}^nD_y\ . \tag{20} $$

if environmental variance is assumed constant among generations. Therefore, the correlated gain in the mature trait Y after n generations of early indirect selection can be estimated by

$$ {}^nE_x(G_y)={}^0E_x(G_y)\frac{1-\dfrac{{}^nD_x}{{}^0\sigma_{G_x}^2}}{\sqrt{1-\dfrac{{}^nD_x}{{}^0\sigma_x^2}}}\ . \tag{21} $$

Equation 21 indicates that the correlated selection response in Y after n generations of early indirect selection is a function of the reduced genetic variance in the directly selected trait X. It is also noted that the correlated response in the next generation is always less than in the present generation since the denominator of equation 21 is always greater than the numerator. This is similar to the response developed for direct selection (BULMER, 1971). After several generations of early indirect selection, the correlated response will reach some limiting value. Using the full ancestral covariance structure from TALLIS (1987), the reduction in genetic variance of the correlated mature trait Y after n-generations of early indirect selection can be shown by the equation:

$$ {}^nD_y\doteq\frac{{}^0cov^2(G_x\ G_y)}{{}^0\sigma_{G_x}^4}\ {}^nD_x\ . \tag{22} $$

This equation also demonstrates the relationship between reductions in genetic variance of directly selected and correlated traits. By this equation, the limiting value of genetic variance reduction in correlated trait Y can be derived as

$$ {}^\infty D_y\doteq\frac{{}^0r^2\ {}^0h_y^2\ {}^0\sigma_y^2}{{}^0h_x^2\ {}^0\sigma_x^2}\ {}^\infty D_x \tag{23} $$

and correspondingly, the limiting value of the correlated response for Y can be estimated by

$$ {}^\infty E_x(G_y)={}^0E_x(G_y)\frac{1-\dfrac{{}^\infty D_x}{{}^0\sigma_{G_x}^2}}{\sqrt{1-\dfrac{{}^\infty D_x}{{}^0\sigma_x^2}}}\ . \tag{24} $$

These mathematical derivations can be summarized as following:

(1) Genetic correlation between directly selected and correlated traits will decline after each generation of selection, but will never change sign. Under this infinite locus model, when generation number approaches infinity, genetic correlation approaches a limiting value.

(2) Genetic variances of directly selected and correlated traits also decline after each generation of selection. Comparing ^nD_x with ^nD_y, it is observed that the reduction in genetic variance of a correlated trait will be slower than the reduction of genetic variance for a trait under direct selection, because $r^2 \leq 1$.

(3) Selection responses for directly selected and correlated traits decline after each generation of selection and will quickly approach limiting values. The decline of selection response in the correlated trait will be relatively slower than the decline in directly selected trait.

Numerical Example

Bulmer's numerical example for effect of direct selection (1976) can be extended to correlated genetic gain. Assuming that 20% of the population is selected through early selection at each generation, the intensity of selection is equal to $f(\alpha)/p$, where $p = 20\%$, α is the standard normal deviate corresponding to p, and $f(\alpha)$ is the ordinate of the standard normal density function at α. For this example, the value of α is 0.8416 with $f(\alpha)=0.2800$, $i_x=1.400$ and $k=0.7818$. If we further assume in the base population that $^0h_x^2 = {}^0h_y^2 = 0.5$, $^0\sigma_{G_x}^2 = {}^0\sigma_{G_y}^2 = 50$, $^0\sigma_x^2 = {}^0\sigma_y^2 = 100$, and $^0r = 0.5$, then the reduction of genetic variance, phenotypic variance and heritability for the correlated mature trait Y, genetic correlation between early and mature traits, and correlated selection response in the first four generations are computed as in *table 1*. As illustrated in the table, selection response for the correlated trait declined from 2.500 in the base population, soon reaching a limiting value at 2.004 after five generations of indirect selection.

Table 1. – Effect of indirect early selection (based on trait X) on genetic parameters and genetic gain of correlated mature trait Y in different generations [a]).

	Generation (n)					
	0	1	2	3	4	∞
^nD_x [b])	0	9.8	11.9	12.4	12.5	12.5
$^n\sigma_{G_x}^2$	50	40.2	38.1	37.6	37.5	37.5
$^n\sigma_x^2$	100	90.2	88.1	87.6	87.5	87.5
$^nh_x^2$	0.5	0.446	0.432	0.429	0.428	0.428
$^nE_x(G_x)$	7.00	5.93	5.68	5.63	5.61	5.61
^nD_y	0	2.443	2.975	3.096	3.125	3.125
$^n\sigma_{G_y}^2$	50	47.557	47.025	46.904	46.875	46.875
$^n\sigma_y^2$	100	97.557	97.025	96.904	96.875	96.875
$^nh_y^2$	0.5	0.4875	0.4847	0.4840	0.4839	0.4839
^nr	0.5	0.4599	0.4501	0.4477	0.4399	0.4399
$^nE_x(G_y)$	2.50	2.116	2.030	2.009	2.004	2.004

[a]) Assuming 20% is selected each generation.

[b]) $D_x(n)$ and $D_y(n)$ are the reductions of genetic variances of early trait X and mature trait Y at nth-generation; $E_x(G_y)(n)$ is genetic gain of mature trait Y after nth generation of early selection on trait X.

Example for Lodgepole Pine Early Selection and Discussion

A retrospective early selection study has been conducted for a population of 110 lodgepole pine (*Pinus contorta* ssp. *latifolia*) families from Alberta, Canada. The 28 seedling traits representing growth, biomass, branch and bud characteristics for the first two growing seasons in a greenhouse were jointly studied with four field plantations at age nine (Wu et al., 1995, 1997; Wu and Yeh, 1997). The comparison between early selection for three seedling traits (H, AGB, BRN-height, aboveground biomass, branch number at harvesting after two growing seasons in greenhouse) and conventional half-rotation field selection will be made by considering the expected genetic gain for several generations of early selection within a cycle of conventional breeding. The estimated heritabilities are 0.6806, 0.5776, and 0.4840 for H, AGB and BRN, respectively and genetic correlations with field height at age nine are 0.312, 0.225 and 0.244, respectively, and estimated heritability of nine-year height is 0.188.

Using conventional field progeny testing, the duration of one breeding cycle of lodgepole pine in Alberta is about thirty years (for a progeny test of 25 years – approximately half rotation, plus 5 years of breeding). An alternative breeding scheme would be to reduce the breeding cycle to ten years, based on results of early selection of seedling traits and subsequent mating (lodgepole pine can reproduce at age 5, Critchfield, 1980). Hence, there can be three breeding cycles using early selection within the thirty years of the conventional breeding cycle. Assuming that 20% of the population is selected each generation and that genetic parameters for tree height at age nine are applicable to age thirty, the expected genetic gains in tree height at age thirty across sites were computed for three generations of early mass selection *(Table 2)*. The expected correlated genetic gains in thirty-year height after three generations of early selection based on H, AGB, and BRN were 55%, 4% and 0% greater than the genetic gain (11.12 units) achievable from one generation of direct selection for height at age thirty. If the genetic correlation between early and mature was higher, the additional gain from early selection would be greater.

The theory and examples of early indirect selection are derived here under assumptions of infinite population size, an effectively infinite number of unlinked genetic loci, and with only additive gene effects. However, selection is usually conducted in a finite population and the traits under selection are usually controlled by a finite number of genetic loci. There are at least three possible violations of these assumptions. With limited population sizes in practical tree breeding programs, random drift may play a significant role in reducing genetic variance and hence reducing genetic gain. However, population sizes (similarly effective population sizes as one hopes) are usually relatively large in breeding populations (160 to 800 parents for *Pinus taeda,* 300 to 400 for *Pinus radiata,* and 800 to 900 for *Pinus elliottii)* (WHITE, 1993), and so random drift may be negligible for the first few generations. Although the expected number of loci controlling growth traits is usually large, it is certainly not infinite. In addition, some loci may have relatively large effects (DEVEY et al., 1995). With a finite number of genetic loci, directional selection will change allele frequency and so ultimately some will be fixed and some will be lost (ROBERTSON, 1960). This would accelerate the decline in genetic variance and possibly also that of genetic correlation. Moreover, with a finite number of loci, genetic correlation may also change greatly with indirect selection if the correlation is mainly due to pleiotropic genes. This is because the pleiotropic genes affecting both characters in the desired direction will be acted upon by selection and brought rapidly toward fixation. These genes will contribute little to the variances or to the covariance of the two traits under consideration. On the other hand, the pleiotropic genes affecting one trait favourably and the other adversely will be less strongly influenced by selection and will remain for longer at intermediate frequencies (FALCONER and MACKAY, 1997). Most of the remaining covariance of the two traits might therefore be due to these genes, possibly resulting genetic correlation being zero or negative. Third, random mating is seldom used in tree breeding populations and sublining or assortative mating is more popular. With assortative mating, the assumed similar regression relationship among generations between genetic values may not hold. Thus, if these assumptions are seriously violated, random drift due to finite population size and gene frequency changes due to a finite number of genetic loci may cause the actual observation to deviate from theoretical results. With finite population size

Table 2. – Estimated correlated response in tree height from three generations of early selection based on seedling height (H), above-ground biomass (AGB) and branch numbers (BRN), and changes in genetic parameters over several breeding generations in lodgepole pine [a]).

	Greenhouse traits								
	H			AGB			BRN		
Generation	0	1	2	0	1	2	0	1	2
D_x	0	387.90	449.16	0	128861	153263	0	0.0263	0.0322
$\sigma_{G_x}^2$	1458	1070.1	1008.8	570726	441865	417463	0.139	0.1127	0.1068
σ_x^2	2142	1754.1	1692.8	988059	859198	834796	0.287	0.2607	0.2548
h_x^2	0.6806	0.6101	0.5959	0.5776	0.5143	0.5001	0.484	0.432	0.4192
D_y	0	8.68	10.04	0	3.83	4.56	0	3.78	4.62
σ_{Gy}^2	335.4	326.7	325.4	335.4	331.6	330.8	335.4	331.6	330.8
σ_y^2	1785.9	1777.2	1775.9	1785.9	1782.1	1781.3	1785.9	1782.1	1781.3
h_y^2	0.188	0.184	0.183	0.188	0.186	0.185	0.188	0.186	0.185
r	0.312	0.271	0.263	0.225	0.199	0.194	0.244	0.221	0.215
$E_x(G_y)$	6.605	5.358	5.124	4.387	3.637	3.486	4.355	3.702	3.040
$\Sigma E_x(G_y)$	6.605	11.963	17.087	4.387	8.024	11.510	4.355	8.057	11.097

[a]) D_x – cumulative reduction of genetic variance in greenhouse trait; $\sigma_{G_x}^2$ – genetic variance in greenhouse trait; σ_x^2 – phenotypic variance in greenhouse trait; h_x^2 – heritability of greenhouse trait; D_y – cumulative reduction of genetic variance in field tree height; σ_{Gy}^2 – genetic variance of field tree height; σ_y^2 – phenotypic variance of field tree height; h_y^2 – heritability of field tree height; r – genetic correlation between greenhouse trait and field tree height; $E_x(G_y)$ – genetic gain in field tree height; $\Sigma E_x(G_y)$ – cumulative genetic gain in field tree height.

and limited number of loci, the best way to investigate genetic consequence of indirect early selection is through computer simulation. The infinite model presented here is only a first approximation for predicting expected genetic gain under several generations of indirect early selection. This expected response can be regarded only as an upper limit of possible genetic gain from several generations of indirect early selection.

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Stomatal Characteristics and Water Relations of *In Vitro* Grown *Quercus robur* NL 100 in Relation to Acclimatization

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Abstract

Experiments were carried out to study stomatal characteristics and the % of moisture loss of *in vitro* grown leaves of *Q. robur* NL 100 in relation to acclimatization. Microscopic observations on the abaxial leaf surfaces of acclimatized and greenhouse grown plants showed elliptical stomata (16 µm to 18 µm) with narrow apertures (3 µm to 4 µm). In comparison, the stomata of leaves from *in vitro* showed spherical stomata (20 µm to 30 µm) with widely opened apertures (6 µm to 8 µm). Leaves from shoot multiplication and the two stages of rooting *(in vitro)* had higher stomatal density and index values as compared to acclimatized and greenhouse-grown plants. The % of moisture loss of *in vitro* grown leaves was considerably greater than that of acclimatized and greenhouse grown plants. This study will help to explain the failure of *in vitro Q. robur* NL 100 plants after transplanting to the greenhouse.

Key words: Fagaceae, *Quercus robur,* stomata, water loss, weaning.

Abbreviations: AC: acclimatization, BA: N^6 benzyladenine, B_5: Gamborg *et al.* (1968), GD: Gresshoff and Doy (1972) medium, GH: greenhouse

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