

Study of Early Selection in Tree Breeding

3. A Case Study Using Early Information to Enhance Selection Efficiency in Late Trait in Lodgepole Pine (*Pinus contorta* spp. *latifolia*)

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Abstract

We present a selection procedure that combines early performance from retrospective study and late performance from field testing into an index designed for enhancing the selection efficiency of the late performance. The prerequisite is that early performance from retrospective study and late performance from field testing must correlate genetically. This selection index procedure is particularly applicable when practical considerations make seedling selection of early traits preferable. An example is the study of biomass partitioning where young trees could offer a solution for large scale evaluation and serve as a useful first approximation to what might be expected in older trees. To numerically illustrate this selection procedure, we present a case study of retrospective early selection in 110 open-pollinated families from Alberta lodgepole pine (*Pinus contorta* spp. *latifolia*). Twenty-eight glasshouse traits in seedlings and the 9-year tree height of their siblings on four sites were conceived as the early and late traits, respectively. Five greenhouse traits having highest genetic correlations with overall field performance were selected and indices of one and two traits from these five glasshouse traits with 9-year tree height averaged 3.0% and 6% more efficient, respectively, relative to selection based on 9-year tree height alone. 24 seedling traits which had highest correlations with the field site height were selected for combination with 9-year tree height of one site. Their efficiencies, relative to selection based on 9-year tree height alone, for indices of one and two of glasshouse traits averaged 40% and 55% greater, respectively, than selection based on 9-year tree height alone. This demonstrates the potential of early retrospective genetic study to enhance later mature selection.

Key words: Early selection, index selection, genetic correlation, lodgepole pine.

Introduction

Time is one of the most important considerations in selective breeding of long-lived tree species (ZOBEL, 1978). Consequently, selection for economic traits of growth, form, pest resistance and wood quality is commonly made at or before 1/3 or 1/2 the rotation age (LAMBETH, 1980; ZOBEL and TALBERT, 1984). The expected response in a trait at rotation age due to early selection constitutes an indirect genetic gain. For mass selection, from the theoretical perspective, indirect early selection for late trait can be as effective as direct selection with the same selection intensity when $r_G h_j = h_m$, where h_j and h_m are, respectively, square root of the heritability of early and late

traits and r_G is their genetic correlation (SEARLE, 1965; FALCONER, 1981).

Considerable research in the last two decades was devoted to indirect early selection for late performance to increase genetic gain per unit time. A preponderance of this research was on age-age correlation of the same trees in progeny tests to determine the optimal age and criteria for family selection (e.g., LAMBETH *et al.*, 1983; COTTERILL, and DEAN, 1988; MCKEAND, 1988; BENTZER *et al.*, 1989; BASTIEN and ROMAN-AMAT, 1990; DANJON, 1994; MATHESON *et al.*, 1994). When examined on a short period, say before age 25, age-age correlations were generally high (e.g., YING and MORGENSTERN, 1979; REHFELDT, 1992). However, estimates varied widely when examined at or more than half the rotation age. They ranged from low or moderate in *Pinus elliotii* (HODGE and WHITE, 1992), *Picea glauca* (MAGNUSSEN, 1993) and *Pinus pinaster* (DANJON, 1994) to high in *Pinus taeda* and *Pinus radiata* (LAMBETH, *et al.*, 1983; COTTERILL and DEAN, 1988; MATHESON *et al.*, 1994), *Pseudotsuga menziesii* (BASTIEN and ROMAN-AMAT, 1990), and several other *Pinaceae* species (LAMBETH, 1980). The variable results were probably related to species and sample size differences, diverse test environments, designs, different time intervals, and other silvicultural treatments or factors.

Research in early selection also focused on retrospective studies where the performance of young seedlings in controlled environments was related to the late performance of their siblings in plantations. Contrary to age-age correlation studies of the same trees, retrospective studies are replications of family performance in space and time. Accordingly, they can be regarded as new initiatives, often designed to uncover indicator early traits (e.g., WILLIAMS, 1988; LOWE and BULTJENEN, 1989; PHARIS *et al.*, 1991) and optimal early test-environments (e.g., LI *et al.*, 1991; ERIKSSON *et al.*, 1993) that would maximise the early-late genetic correlations. Results reported in the literature, however, give a somewhat conflicting message. In studies where environmental factors limiting in the field have been mimicked, the early-late genetic correlations were improved (e.g., ERIKSSON *et al.*, 1993). Other studies have suggested that ontogenetic developments of the seedlings was crucial (e.g., WILLIAMS, 1987). Interpretations of the results have also been complicated by the small number of families, between 10 and 50 in most studies. Yet, precise estimation of genetic correlation between early and late stages in retrospective studies would probably require 100 or more families, and 15 to 20 seedlings per family, assuming an early-mature genetic correlation of 0.3 with heritability of 0.2 and 0.4 for the mature and early traits, respectively (ROBERTSON, 1959a, b; VAN VLECK and HENDERSON, 1961).

The deployment of retrospective studies in tree improvement has been a subject of interest. LOWE and VAN BULTJENEN (1989) revealed that use of the retrospective study could guide assortative mating to increase genetic gains and reduce cost in a two-step selection program where poor performing families in early tests were omitted from testing in the field. WHITE and

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HODGE (1991) showed that, relative to selection based on an individual early trait, efficiency of indirect early selection for late performance could be increased by using an index of early traits. Among three advantages of early testing and selection identified in tree breeding: e.g. increase of selection intensity, shortening of breeding cycle and the use of early information to enhance mature selection, theoretical bases on the first two have been presented (WU, 1998, 1999). The third application of retrospective early testing in tree improvement that we present herein is the integration of early and late performance to increase the selection precision of late performance. This is because genetic information from different sources can be combined for final selection (FALCONER, 1981).

We present the theoretical framework of a selection procedure that combines early performance from retrospective study and late performance from field testing into an index designed to enhance the selection efficiency of the late performance. The prerequisite of this selection is that early performance from retrospective study and late performance from field testing must correlate genetically. This index selection procedure is particularly useful when practical considerations make seedling selection of early traits preferable. An example is the study of biomass partitioning where young trees could offer a solution for large scale evaluation and serve as an useful first approximation to what might be expected in older trees (ST. CLAIR, 1989; WU and YEH, 1997). To numerically illustrate this index selection procedure we present a case study of retrospective early selection in 110 open-pollinated families from lodgepole pine (*Pinus contorta* spp. *latifolia*) in Alberta. Twenty-eight glasshouse traits in seedlings and the 9-year tree height of their siblings on four field sites were conceived as the early and late traits, respectively. Specifically, we estimated the predicted efficiencies of selection indices that combined single and multiple glasshouse traits with 9-year tree height relative to selection based on 9-year tree height alone.

Materials and Methods

The detailed description for the field and glasshouse experiments were presented in previous papers (WU *et al.*, 1995,

1997). In summary, a subset of 110 phenotypically superior trees from 33 stands used by Alberta Land and Forest Service as parents for collection of open-pollinated seeds in one breeding region in the range of latitude 53°58' to 55°12', longitude 115°11' to 116°50' and elevation 885 m to 1160 m was used in this study. For the field testing, trial seeds were sown in Spencer-Lemaire Hillson (150 cc) containers in a glasshouse in March 1981. The seedlings were grown in the glasshouse for 20 weeks and hardened outdoors. They were then outplanted in field trials at four sites in the spring of 1982 in a randomised complete block design with 5-tree row plots. Spacing between trees was 2.5 m x 2.5 m. All entries were replicated five times at each site. Total height was measured to the nearest cm in October 1990 for 9-year height, at which time 7% of the trees were missing due primarily to post planting mortality.

For the glasshouse retrospective evaluation, seeds from the same 110 families were imbibed in tap water for one day before spot sowing without stratification in plastic tube containers filled with peat moss in February of 1989. Seed germination was completed after 46 days with an average rate across families of 56.5%. Seedlings were transplanted in June into 20 cm x 20 cm x 18 cm plastic pots containing a mixture of peat, sand and sterilised soil. A completely randomised block design with single-tree plots in each of 20 replications was used. Seedlings were studied for two growth periods, totalling 36 weeks, using daylight-length manipulation to induce dormancy of seedlings between growth periods. Twenty-eight growth, branch and biomass traits were assessed (WU *et al.*, 1997). The seedling population in retrospective early study was slightly larger (116 families) than the 110 families measured on four sites. However, heritabilities and genetic correlations for glasshouse and 9-year tree height across four sites were calculated using only the 110 common families (Table 1).

Method

To study how one or more early traits could combine with the late trait to enhance the selection precision of this Y late trait, we constructed the following selection index (I):

$$I = a y + b_1 \bar{x}_1 + b_2 \bar{x}_2 + \dots + b_p \bar{x}_p, \quad [1]$$

Table 1. – Estimates of individual heritabilities (h^2) and their standard errors for seedling traits and 9-year tree height across four sites (HT), and genetic correlation (r_G) between seedling traits and 9-year tree height for the population of 110 lodgepole pine families^{a)}.

Trait	H1	H2	H3	H4	H5	H6	H7	D3	D7	D8
h^2	0.97±0.16	0.75±0.15	0.67±0.14	0.58±0.13	0.54±0.14	0.57±0.13	0.50±0.13	0.47±0.11	0.40±0.10	0.40±0.09
r_G	0.02	0.01	0.06	0.07	0.09	0.08	0.11	0.14	0.09	0.08
Trait	HG1	HG2	HG3	DG	SB	BB	NB	RB	GB	TB
h^2	0.20±0.09	0.15±0.07	0.24±0.09	0.19±0.07	0.39±0.10	0.43±0.11	0.44±0.12	0.30±0.08	0.45±0.11	0.42±0.09
r_G	-0.05	0.25	0.21	0.06	0.07	0.01	0.07	0.06	0.07	0.07
Trait	HI	SR	HD	BUDN	BUDS	BRN1	BRS	BRN2	HT	
h^2	0.34±0.10	0.22±0.08	0.22±0.09	0.13±0.10	0.32±0.10	0.29±0.11	0.24±0.10	0.49±0.12	0.13±0.03	
r_G	0.07	0.27	0.08	0.05	0.21	0.18	0.04	0.11		

^{a)} H1, H2 – Seedling height after transplanting and at the start of first dormancy induction (11 weeks after transplanting). H3, D3, BUDN, BRN1, BUDS, BRS – Stem height, basal diameter, bud number on main stem, total number of branches, bud size and branch strength at the end of first growing period (11 weeks after the first dormancy induction). H4, H5, H6, H7, H8 – Seedling height at three weeks, six weeks, nine weeks, the end of second growth period, and at harvest. D7, D8 – Seedling basal diameter at the start of second dormancy induction and at harvest (three weeks after the second dormancy induction). BRN2 – Branch number at harvest. SB, BB, NB, RB – Dry weight for stem, branches, needles and roots. GB, TB – above-ground biomass (SB+BB+NB) and total biomass (GB+RB). HG1, HG2, HG3 – Growth increment of height in the first growth period, in the first dormancy induction period and in the second growth period. DG – Growth increment of diameter in the second growth period. HI, SR, HD – Harvest index (SB/GB), the ratio of above-ground biomass to root biomass (GB/RB) and the ratio of height to basal diameter at the end of second growth period.

where y is an individual observation on the late trait, $\mathbf{b}' = [a \ b_1 \ \dots \ b_p]$ is a vector of index coefficients, which are partial regression coefficients of I on the elementary predictions (COCHRAN, 1951) and $(\bar{x}_p, \bar{x}_2, \dots, \bar{x}_p)$ is a family-mean vector of early traits. This index is a single predictor of genetic value (or breeding value) for the late trait. The expected response to selection based on this index (I) is predicted by the equation (FALCONER, 1981; HENDERSON, 1984):

$$R_I = i_I \sigma_{G_y} r_{(I, G_y)} \quad [2]$$

where i_I is the standardised selection differential on I , σ_{G_y} is the standard deviation of genetic value for Y and $r_{(I, G_y)}$ is the correlation between the genetic value for Y and the index value. To present the efficiency of selection by combining early and late information relative to late selection only, the following genetic gain ratio was used to compare the selection efficiency for late trait under the same selection intensity

$$R_{I,y} = \frac{r_{(I, G_y)}}{h_y} = \frac{[\mathbf{b}'\mathbf{G}]\sigma_y}{\sqrt{[\mathbf{b}'\mathbf{P}\mathbf{b}]}\sigma_{G_y}^2} = \frac{\sigma_I \sigma_y}{\sigma_{G_y}^2} = \frac{\sqrt{[\mathbf{b}'\mathbf{G}]}}{\sigma_{G_y} h_y} \quad [3]$$

where \mathbf{G} and \mathbf{P} are genetic and phenotypic variance and covariance matrices and σ_I is standard deviation of index I .

One special case is when only one early trait is included in the index I . Then, the estimator of the index coefficient vector $\mathbf{b}' = [a \ b]$ is

$$\begin{bmatrix} a \\ b \end{bmatrix} = \frac{1}{\sigma_x^2 \sigma_y^2 - \sigma_{xy}^2} \begin{bmatrix} (\sigma_x^2 \sigma_{G_y}^2 - \sigma_{xy}) & \sigma_{(G_x, G_y)} \\ (\sigma_y^2 \sigma_{(G_x, G_y)} - \sigma_{xy}) & \sigma_{G_y}^2 \end{bmatrix} \quad [4]$$

where $\sigma_{(G_x, G_y)}$ is the covariance between the genetic values of early and late traits. Thus, the efficiency ratio between this special index selection and late-trait selection alone is

$$R_{I,y} = \sqrt{\frac{\sigma_x^2 \sigma_{G_y}^2 - \sigma_{xy} \sigma_{(G_x, G_y)} + \frac{(\sigma_y^2 \sigma_{(G_x, G_y)}^2 - \sigma_{(x,y)} \sigma_{G_y}^2 \sigma_{(G_x, G_y)})}{\sigma_{G_y}^2}}{(\sigma_x^2 \sigma_y^2 - \sigma_{(x,y)}^2) h_y^2}} \quad [5]$$

which could be simplified as

$$R_{I,y} = \sqrt{\frac{1 - 2\rho r \frac{h_x}{h_y} + r^2 \frac{h_x^2}{h_y^2}}{1 - \rho^2}} \quad [6]$$

$$= \sqrt{1 + \frac{(\rho - r \frac{h_x}{h_y})^2}{1 - \rho^2}}$$

where ρ is phenotypic correlation between early trait x and late trait y (in the retrospective early study, ρ is the family mean

phenotypic correlation). Since $-1 \leq \rho \leq 1$, the second term in the square root of equation 5 will always be positive. Thus, $R_{I,y}$ is always greater or equal to unity. This suggests that the inclusion of information on early and late traits will result in greater genetic gain, relative to selection based on the late trait alone.

Results

The narrow-sense heritability (h_i^2) for 28 glasshouse traits and 9-year tree height across the four field sites, and the genetic correlations between glasshouse traits and 9-year tree height based on 110 lodgepole pine families are listed in *Table 1*. The h_i^2 for absolute heights at 0.50 to 0.97 were highest among the seedling growth traits and considerably larger than 0.12, the h_i^2 for 9-year tree height, across four sites. Five of 28 glasshouse traits had genetic correlations with 9-year tree height equal or larger than 0.18. These five traits were number of branches at end of first growing period (BRN1), bud size at end of first growing period (BUDS), height growth increment to the first dormancy induction period (HG2), height growth increment to the second growth period (HG3), and ratio of above-ground biomass to root biomass (SR). These five traits were used to numerically demonstrate the integration of early glasshouse seedling traits with 9-year tree height (late performance) into an index designed to enhance the selection efficiency based on late performance of this Alberta lodgepole pine population.

An example of the combined selection index with one glasshouse trait, BRN1, and 9-year tree height Y is:

$$I = 0.123 Y + 4.090 \bar{X}_{BRN1} \quad [7]$$

where \bar{X}_{BRN1} is the family mean of BRN1. The predicted relative efficiency of this selection index ($R_{I,y}$) is 1.03. This suggests that selection based on this index was 3% more efficient than selection based on 9-year tree height alone. Likewise, we computed the index coefficients and predicted relative selection efficiencies for each of the remaining four glasshouse traits (*Table 2*). The predicted efficiency of selection for 9-year tree height based on combining 9-year tree height with any one of five glasshouse trait was always greater than selection based only on 9-year tree height, with the average increase being 3.0%. SR was the best glasshouse trait to enhance the selection of 9-year tree height ($R_{I,y}=1.06$) across all four sites.

Table 2. – Index coefficients (a , b_1) of selection indices for improving the late trait (9-year tree height) across four sites when the individual value for the late trait and the family mean for a single seedling trait are included in the index. Efficiencies relative to selection based on 9-year tree height alone ($R_{I,y}$) for these indices are also given^a.

Seedling trait	Index coefficient		$R_{I,y}^b$
	a	b_1	
HG2	0.124	0.301	1.02
HG3	0.124	0.105	1.02
SR	0.123	4.090	1.06
BUDS	0.124	7.036	1.02
BRN1	0.124	10.277	1.03

^a see *table 1* for detailed description of seedling traits.

^b $R_{I,y}$ is the ratio of genetic gain due to index selection relative to selection of 9-year tree height alone.

Table 3. – Index coefficients (a , b_1 , b_2) of selection indices for improving the late trait (9-year tree height) across four sites when the individual value for the late trait and family means for two seedling traits are included in the index. Efficiencies relative to selection based on 9-year height alone ($R_{I,y}$) for these indices are also given^{a)}.

Seedling trait		Index coefficient				Seedling trait		Index coefficient			
x_1	x_2	a	b_1	b_2	$R_{I,y}^b$	x_1	x_2	a	b_1	b_2	$R_{I,y}$
HG2	HG3	0.124	0.200	0.067	1.03	HG3	BUDS	0.124	0.099	6.568	1.04
HG2	SR	0.122	0.289	4.030	1.08	HG3	BRN1	0.123	0.092	9.474	1.05
HG2	BUDS	0.124	0.268	6.213	1.04	SR	BUDS	0.122	7.287	4.142	1.08
HG2	BRN1	0.123	0.278	9.764	1.05	SR	BRN1	0.122	9.373	3.899	1.08
HG3	SR	0.122	0.090	3.902	1.07	BUDS	BRN1	0.124	3.253	8.315	1.04

^{a)} see table 1 for detailed description of seedling traits.

^{b)} $R_{I,y}$ is the ratio of genetic gain due to index selection relative to selection of 9-year tree height alone.

There were 10 possible pairwise combinations of indices when two glasshouse traits were combined with 9-year tree height (Table 3). Using two glasshouse traits, for example, HG2 and BRN1, the selection index is

$$I = 0.123Y + 0.278\bar{X}_{HG2} + 9.764\bar{X}_{BRN1}. \quad [8]$$

The predicted relative efficiency of this index was 1.05 and it is more efficient than selection based on 9-year tree height alone, and more efficient than indices combining 9-year tree height with HG2 ($R_{I,y}=1.02$) or BRN1 ($R_{I,y}=1.03$). The average increase in predicted selection efficiency that combined two glasshouse traits with 9-year tree height was 6%, relative to selection based on 9-year tree height alone. This also represents a 3% average increase over the indices that combined only one glasshouse trait and 9-year tree height.

It is noteworthy that the size of genetic correlation between seedling traits and 9-year tree height varied greatly between

the field sites (WU *et al.*, 1997). 24 greenhouse traits which had highest genetic correlation with field site B, the most productive field site (Table 4) were used to compute the predicted relative selection efficiencies that combined one glasshouse traits with 9-year tree height. The average increase relative to selection based on 9-year tree height alone was 40% and this represent a 37% average increase over the selection indices across four sites. HG2 was the best glasshouse trait to enhance selection based on 9-year tree height ($R_{I,y}=1.76$) at field site B. Other valuable glasshouse traits were D8 ($R_{I,y}=1.63$), H7 ($R_{I,y}=1.54$) and H4 ($R_{I,y}=1.54$).

There were 276 pair-wise combinations of 24 glasshouse traits for site B, but only those with relative selection efficiencies greater than 1.85 are listed in table 5. The average increase in predicted selection efficiency where two glasshouse traits were combined with 9-year tree height was 55%, relative to selection based on 9-year tree height alone (Table 5). This is a 49% average increase over the indices that combined only one glasshouse trait and 9-year tree height across four sites.

Table 4. – Index coefficients (a , b_1) of selection indices for improving the late trait (9-year tree height) on site B when the individual value for the late trait and the family mean for a single seedling trait are included in the index. Efficiencies relative to selection based on 9-year height alone ($R_{I,y}$) for these indices are also given^{a)}.

Seedling trait	Index coefficient			Seedling trait	Index coefficient		
	a	b_1	$R_{I,y}^b$		a	b_1	$R_{I,y}$
H1	0.18	0.64	1.34	DG	0.18	0.21	1.48
H2	0.18	0.40	1.22	SB	0.18	0.10	1.34
H3	0.18	0.54	1.44	NB	0.18	0.02	1.20
H4	0.18	0.55	1.54	RB	0.18	0.04	1.18
H5	0.18	0.46	1.50	TB	0.18	0.01	1.28
H6	0.18	0.41	1.44	GB	0.18	0.02	1.29
H7	0.18	0.43	1.54	HI	0.19	344.59	1.18
D3	0.18	0.17	1.41	SR	0.18	19.70	1.43
D7	0.18	0.12	1.53	BUDN	0.19	63.89	1.16
D8	0.17	0.13	1.63	BUDS	0.18	44.49	1.27
HG2	0.17	3.42	1.76	BRN1	0.18	74.15	1.51
HG3	0.18	0.86	1.43	BRN2	0.18	32.18	1.35

^{a)} see table 1 for detailed description of seedling traits.

^{b)} $R_{I,y}$ is the ratio of genetic gain due to index selection relative to selection of 9-year tree height alone.

Table 5. – Index coefficients (a , b_1 , b_2) of selection indices for improving the late trait (9-year tree height) on site B when the individual value for the late trait and family means for two seedling traits are included in the index. Efficiencies relative to selection based on 9-year height alone (R_{ly}) for these indices are also given (only combinations of traits where $R_{ly} > 1.85$ are listed out of possible 276 combinations^a).

Seedling trait		Index coefficient				R_{ly}^b	Seedling trait		Index coefficient			
x_1	x_2	a	b_1	b_2	x_1		x_2	a	b_1	b_2	R_{ly}	
H1	HG2	0.16	0.52	3.21	1.90	H2	H3	0.16	-3.77	3.94	2.01	
H2	H4	0.16	-2.24	2.29	1.98	H4	HG2	0.16	0.28	2.74	1.82	
D8	RB	0.17	0.27	-0.09	1.86	D8	TB	0.16	0.40	-0.04	1.97	
D8	GB	0.16	0.35	-0.04	1.89	D8	HG2	0.16	0.08	2.55	1.88	
HG2	SR	0.16	19.17	3.39	2.02	HG2	BU DS	0.17	3.26	34.91	1.86	
HG2	BRN1	0.16	3.28	68.67	2.05	HG2	BRN2	0.15	3.22	26.30	1.99	

^a) see table 1 for detailed description of seedling traits.

^b) R_{ly} is the ratio of genetic gain due to index selection relative to selection of 9-year tree height alone.

This also represents a 15% average increase over the indices that combined only one glasshouse trait and 9-year tree height on site B. The best combination of early traits was HG2 + BRN1, with a predicted selection efficiency of 2.05.

Discussion and Conclusion

Genetic information from different sources can be combined to increase the precision of selection (FALCONER, 1981). This selection concept is particularly important for traits with low heritability, such as tree growth in plantations. We now extend this selection concept to combine early performance from retrospective study and late performance from field testing into an index designed for enhancing the selection efficiency of the later field performance. We have thus shown in equation [5] that the inclusion of information from retrospective study on one or more early traits with the late trait for siblings in the field will result in expected greater genetic gain, relative to selection based on the late trait alone. This is because ρ , the family mean phenotypic correlation between early trait and late trait in retrospective early study has a value between -1 and 1 (see equation [5]). Consequently, the second term of equation [5] is always positive. Hence, the efficiency ratio between this combined selection index, relative to the late-trait selection alone, must be greater or equal to unity. Nevertheless, early and late traits must have a significant genetic correlation. In our judgement such index will become increasingly important in tree improvement, in addition to use of selection efficiency for the late trait, as breeders incorporate biomass (ST. CLAIR, 1989; WU and YEH, 1997) and physiological traits (e.g., MONSON and GRANT, 1989; ABRAMS *et al.*, 1990; LEMCOFF *et al.*, 1994; TAN *et al.*, 1995) into their analyses in order to better understand the genetic determinants of tree growth. Biomass and physiological traits are difficult and laborious to measure, and under field conditions are almost impossible to assess. Thus, use of glasshouse-grown seedlings could offer a practical solution to the large scale evaluation of families and serve as a useful first approximation to what might be expected in older stands for those families.

The efficiency of this combined selection index of early and late traits, relative to selection based solely on the late trait, is a function of heritabilities of early and late traits and their genetic correlations. These genetic estimates are highly derivative statistics and are subject to large error when the sample size is small. A review of the literature suggests that retrospec-

tive studies rarely used more than 25 families (e.g., CANNELL *et al.*, 1978; WAXLER and BULJTENEN, 1981; LAMBETH, *et al.*, 1982; RIITERS and PERRY, 1987; WILLIAMS, 1987, 1988; JIANG, 1988; LOWE and BULJTENEN, 1989; BRIDGWATER, 1990; CARTER *et al.*, 1990; JONSSON *et al.*, 1990; LI *et al.*, 1991; LI 1992; ERIKSSON *et al.*, 1993; MATHESON *et al.*, 1996). In a simulation study of 25 families each with 25 trees, LAMBETH (1983) found that the average family rank correlation could be 0.6 when the actual underlying correlation was one. ROBERTSON (1959a, b) provided some useful formulae for predicting the sampling variance of the additive genetic correlation. Calculations from these formulae indicate that precise estimate of genetic correlation between early and late stages of tree growth in a retrospective study would require 100 or more families for an effective genetic correlation of 0.3. This assumes a relatively low heritability estimate for the late trait and medium heritability estimate for the early trait, as was the case in our study of 110 lodgepole pine families from Alberta.

The predicted increase in selection efficiency across four sites when 9-year tree height was combined with one and two glasshouse traits averaged 3% and 6%, respectively, relative to selection based on 9-year tree height alone (Table 2 and 3). This modest increase in selection efficiency across the four field sites might suggest that retrospective early selection was not effective for this lodgepole pine population. However, the size of genetic correlation between glasshouse seedling traits and 9-year tree height varied greatly between the sites. Genotype-by-environment interaction is a concern in this type of retrospective study and thus much research has been devoted to defining optimal early test-environments (e.g., LI *et al.*, 1991; ERIKSSON *et al.*, 1993), ones that can maximise the early-late genetic correlations. In this study of lodgepole pine the exact cause of family-by-site interaction was unknown, but site B was most productive and trees averaged 20% taller than the test average across all four sites. This led us to hypothesize that growth conditions at site B might be closer to the glasshouse growth environment which is presumed to be near-optimal (WU *et al.*, 1997).

In contrast to selection across four sites, the predicted selection efficiencies for each of 24 glasshouse traits that had highest correlation with 9-year tree height on site B increased on average by 37% than the average index that combined one glasshouse trait and 9-year tree height across four sites (Table 4). Also, the 276 pair-wise combination of 24 glasshouse

traits on site B increased an average of 55% in predicted selection efficiency when we combined two glasshouse traits with 9-year tree height, relative to selection based on 9-year tree height alone (Table 5). This is a 49% average increase across all four field sites over the indices where only one glasshouse trait was combined with 9-year tree height. Therefore, the benefit of integration of early and late performance to increase the selection precision of late performance from retrospective study in this lodgepole pine population could best be realized on site B and likely also on other sites with growth conditions similar to site B. This suggests that selection of sites and early test environments are of paramount importance when deploying retrospective early genetic selection.

The selection of glasshouse seedling traits in this study is also important for maximizing the selection efficiency of the late trait, as has been shown in other retrospective studies (e.g., WILLIAMS, 1988; LOWE and BULJTENEN, 1989; PHARIS *et al.*, 1991). For lodgepole pine at site B, the increase in selection efficiency for a single seedling trait with 9-year tree height ranged from 18% to 76% (Table 4). The best glasshouse trait to increase the selection efficiency of 9-year tree height, either individually or in pairwise combination with another glasshouse trait was HG2 (Tables 4 and 5). HG2 is the early trait with the highest genetic correlation (0.50) with 9-year tree height. Other glasshouse traits that substantially enhanced the selection of 9-year tree height were height and diameter measurements. They often had higher heritability estimates and were better correlated with 9-year tree height on site B than the other glasshouse traits.

In theory, the predicted efficiency of selection indices would increase with each addition of a seedling trait that is genetically correlated with the late trait. In reality, however, each addition of a trait to an index may increase the standard error of predicted genetic gain (HARRIS, 1963, 1964). This is because selection indices are functions of heritabilities, genetic correlations, and phenotypic and genetic variances. These parameters alone are exposed to large estimation errors and large standard errors, thus making prediction of gain increase unreliable (WILLIAMS, 1962a, b; SALE and HILL, 1976), especially when many interrelated traits are involved. Consequently, the reliability on the increase in predicted selection efficiency when one or more seedling traits are included should be investigated, albeit a difficult subject.

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Mating System and Genetic Diversity in Natural Populations of European Larch (*Larix decidua*) and Stone Pine (*Pinus cembra*) Located at Higher Elevations

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Summary

Mating system and genetic diversity were investigated in natural populations of European larch (*Larix decidua* MILL.) and stone pine (*Pinus cembra* L.) located at the upper limits of the species ranges in the Italian Alps. Multilocus estimates of outcrossed progeny (t_m) were relatively low in both populations ($t_m = 0.675$ for larch and 0.808 for stone pine), indicating that self-fertilization is an important component of their mating system. Mean single-locus estimates of t differed only slightly from t_m suggesting that there was a little inbreeding other than selfing, despite expected clustering of family members in those stands. The genetic structure of adult trees was consistent with the high levels of genetic diversity typically observed within populations of conifer species.

Key words: *Larix decidua*, *Pinus cembra*, allozymes, outcrossing, mixed-mating model, genetic diversity.

Introduction

Coniferous forest tree species are wind-pollinated and typically have high proportions of outcrossed progeny ($t > 0.80$) (MUONA, 1990; ADAMS and BIRKES, 1991) and high levels of genetic diversity within populations (HAMRICK et al., 1992). However, population outcrossing rates lower than 0.80 are occasionally reported (PERRY and KNOWLES, 1990; XIE et al., 1991; EL-KASSABY et al., 1994), and the levels of outcrossing vary widely both among and within species (MITTON, 1992; BURCZYK, 1998).

Density of forest tree populations decreases at limits of distribution, i.e. at higher elevations or in the far north. This

may reduce the density and movement of the pollen cloud and cause a relatively large proportion of offspring resulting from self-fertilization. The trees are usually growing in pioneer conditions. The result is that trees often exist in clusters, probably of close relatives, since seed dispersal and pollen movement may be limited. If mating occurs primarily between near neighbors, the clustering of relatives is expected to result in high levels of inbreeding and reduced effective population size.

In this paper we investigated and compared levels of allozyme variation and mating systems parameters of a forest stand composed of two coniferous species: European larch (*Larix decidua* MILL.) and Swiss stone pine (*Pinus cembra* L.). These species differ in the extent and geographic localization of their natural ranges. Natural range of European larch is restricted to four distinct areas of Central Europe (Alps, Sudety, Tatras and central part of Poland) (RUBNER, 1953). It is especially widespread in the Alps, from about 800 m elevation up to the subalpine vegetation zone. Swiss stone pine is restricted to few high elevation areas in Europe and consists of relatively small and scattered populations (HOLZER, 1975).

Materials and Methods

The two natural populations investigated in this study are located in the Alps of northern Italy, at the Stelvio National Park. The sampled populations lie at about 2000 m elevation. The main plant community of the stand was *Larici-Cembra-tum*, and the trees were loosely distributed at a density of 100 to 150 trees/ha. The trees were over 100 years old. Seeds were collected from 35 trees of European larch and 28 trees of stone pine.

Analyses of the population genetic structure were performed using macrogametophyte tissue from seeds. The following 10 enzyme systems encoded by 16 loci were used to assess genetic

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