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AGE TRENDS IN GENETIC PARAMETERS AND EARLY SELECTION OF LODGEPOLE PINE PROVENANCES WITH PARTICULAR REFERENCE TO THE LAMBETH MODEL

Xiaoyang Chen[1], Barbara Hawkins[2], Chang-Yi Xie[3], & Cheng C. Ying[3]

1) Faculty of Forest Resources, Beijing Forestry University, Beijing 100083, China
2) Centre for Forest Biology, University of Victoria, P.O. Box 3020, STN CSC, Victoria, BC, V8W 3N5
3) Research Branch, BC Ministry of Forests, P.O. Box 9519, STN. PROV. GOVT., Victoria, BC, V8W 1L4
Corresponding Author: Cheng C. Ying, Phone: (250) 387-3976, Fax: (250) 387-0046, Email:cheng.ying@gems9.gov.bc.ca

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ABSTRACT

This study of time trends in genetic parameters is based on height growth from 50 provenance test plantations involving 140 provenances. Total heights were measured at plantation ages 1, 3, 6, 10, 15 and 20. We used correlative heritability (h_{jm}^2) to measure the response of early selection; h_{jm}^2 is the product of age-age genetic correlation (r_{Gjm}), and square root of provenance heritability at early (h_j^2) and target (h_m^2) age of selection ($h_{jm}^2 = h_j h_m r_{Gjm}$). We expect h_{jm}^2 to be a realistic measure of early selection since it reflects the collective effect of all determinant parameters. We estimated efficiency of early selection (E_{jm}) as the ratio of h_{jm}^2 and provenance heritability at target age of selection. We employed the logarithm of early-target age ratio ($\log(t_j/t_m)$) as predictor to extrapolate E_{jm} to different target ages of selection beyond age 20 (LAMBETH 1980).

Cumulative growth indicated that provenance variation in mean height became stable after age 6 and experienced only minor shifting in rankings after age 10. Heritability remained high throughout the testing period ($h^2 = 0.70$ to 0.85) and increased with age except for a slight decline from ages 1 to 3. Both age–age phenotypic and genetic correlations increased steadily with age, and coefficients of the latter were higher than those of the former. Genetic correlation reached 0.95 between age 6 and 20 on average. h_{jm}^2 showed an age trend similar to that of genetic correlation suggesting the latter drove early selection. E_{jm} increased exponentially and reached over 80% at age 6 and 90% at age 10 if target age of selection was 20. We found high predictability of $\log(t_j/t_m)$ to project E_{jm} ($r^2 = 0.92$), indicating high robustness of $\log(t_j/t_m)$ as a proxy for age-age correlation as expounded in the Lambeth model. However, we have some reservations about the soundness of gain per unit time as a measure of optimum age of selection. Instead we propose E_{jm} as an alternative to assess optimum age of selection. We discuss its advantages in both genetic and non-genetic considerations.

Key words: *Pinus contorta*, heritability, correlative heritability, genetic and phenotypic correlation, efficiency of early selection.

INTRODUCTION

Early selection is a major issue in most tree improvement programs. Early selection shortens the breeding cycle, but can cost genetic gain at harvest because the genetic correlation of even the same trait at different ages may not be perfect. Effectiveness of early selection depends also on heritability, which varies at different ages and thus adds further uncertainty (FALCONER 1981). Much research effort has been spent on developing quantitative models that can find the earliest age of selection with minimum cost of genetic gain at harvest (OVERTON & CHING 1978; LAMBETH 1980; KANG 1985; KANG 1991; MAGNUSSEN & KREMER 1993; MANGUSSEN & YANCHUK 1994; WU 1998). In essence, it is a process to find the optimal trade-off between minimum selection age and maximum genetic gain. Apparently, accurate information on age trends of genetic correlation and heritability is key to the success of such a process. The process would be much simpler only if the age trends of these genetic parameters followed some predictive mode mathematically. However, these genetic parameters change over time in complex ways and are difficult to abstract mathematically (NAMKOONG *et al.* 1972; NAMKOONG & CONKLE 1976; FRANKLIN 1979; FOSTER 1986).

LAMBETH (1980) proposed a model that employs the logarithm of the ratio of selection age over harvest age ($\log(t_j/t_m)$) as the proxy for age trends of the genetic parameters. The elegance of the Lambeth model lies in its simplicity and ingenuity, which well captures the biological norm of age-age correlation, that is, the closer the selection and the target (harvest) age, the higher the correlation, and vice versa. His model has found broad applicability (*e.g.* KING & BURDON 1991; JOHNSON *et al.* 1997; GREAVES *et al.* 1997; HAAPANEN 2001; GWAZE & BRIDGEWATER 2002). The Lambeth model remains the most practical for extrapolation of age trends for early selection (BURDON 1989).

In lodgepole pine (*Pinus contorta* Dougl.) in British Columbia (B.C.), XIE and YING (1996) also found high predictability of the Lambeth model by fitting the genetic correlation to $\log(t/t_m)$ ($r^2 = 0.98$) based on a large family-structured provenance test. This feeds our further interest in examining its predictability of provenance selection of the same species in diverse site environments. Our report is based on extensive lodgepole pine provenance testing over 20 years, which involves 60 test plantations throughout interior B.C. and a range-wide sample of 140 provenanaces (ILLINGWORTH 1978; YING *et al.* 1985). Our objectives are twofold: 1) report age trends in provenance heritability and between-age phenotypic and genetic correlation in height growth, and 2) evaluate efficiency of early selection with specific focus on the applicability of the Lambeth model.

MATERIALS AND METHODS

Provenance Test Data

Seeds of 140 provenances were sown at B.C. Ministry of Forests' nursery at Red Rock, Prince George, central interior of B.C., and 3-year-old seedlings were planted at the 60 sites throughout the B.C. interior in the spring of 1974. The 60 test sites were distributed in 12 geoclimatic regions which were broadly delineated according to latitude and precipitation. The general pattern of increasing precipitation parallels longitude from coast to inland. At each of the five sites within a given region, a subset of 60 out of the 140 provenances were planted. The 60 provenances were planted in two replications of 9-tree square plots spaced 3 x 3m. Between sites in different regions, 20 to 40 provenances were overlapping. See ILLINGWORTH (1978) and YING *et al.* 1985 for details on test site selection and scheme of provenance collection.

Total heights of living trees were measured at plantation ages 1, 3, 6, 10, 15, and 20 years. Two tests in region 12 were lost to road construction, leaving data from 58 tests available for analysis.

Statistical Analysis

Analyses of variance and covariance were carried out using SAS PROC GLM based on plot means according to the following linear model for each measurement age at each site:

$$Y_{ij} = \mu + B_i + P_j + e_{ij}$$

Where Y_{ij} is the plot mean of the j^{th} provenance ($j = 68$) in the i^{th} block ($i = 2$), μ the general average, B the block effect, P the provenance effect, and e_{ij} the experiment error. Test plantations in which provenance effect was not statistically significant ($p > 0.05$) at more than one measurement age were excluded from further analyses.

Variance and covariance components were estimated using SAS VARCOMP procedure assuming random effect of provenances. Heritability (h^2) of provenance means was obtained as:

$$h^2 = \frac{(MS_p - MS_e)}{MS_p} = \frac{\sigma_p^2}{(\sigma_p^2 + \frac{\sigma_e^2}{b})}$$

where MS_p and MS_e are the mean squares of provenance and error variance, respectively, and σ_p^2 and σ_e^2 their variance components obtained from variance analysis; b is the number of blocks in each test plantation. h^2 as estimated above is equivalent to repeatability that sets an upper limit of heritability estimate (FALCONER 1981). For conventional purposes, we term h^2 as heritability or provenance heritability.

The standard measure of genetic gain from selection (G) is:

$$G = i\,h^2 s$$

where i is selection intensity, and s phenotypic standard deviation of provenance means. When selection is made before harvest age (indirect selection), the response (genetic gain in the mature trait, CG_m) can be expressed as:

$$CG_m = i_j\, h_j\, h_m\, r_{Gjm}\, s_m \qquad [1]$$

where r_{Gjm} is the genetic correlation (variance component correlation derived from covariance analysis) of height at different ages (FALCONER 1981), and the subscripts j and m are, respectively, the indicators of selection and harvest age. In order to conveniently show the age trend of the correlated response of early selection, selection intensity is assumed to be the same at different selection ages (i.e., $i_j = i_m = 1$). Selection intensity is usually not a significant differentiating factor in selection gain at different ages, unless increasing selection intensity simultaneously improves genetic correlation and heritability (WU 1998). In essence, projection of CG_m amounts to a discounting process for r_{Gjm} and h_j.

Efficiency of early selection (E_{jm}) is defined as:

$$E_{jm} = (CG_m / G_m) = i_j h_j h_m r_{Gjm} \sigma_m = h_j h_m r_{Gjm} / h_m^2 = h_{jm}^2 / h_m^2 \qquad [2]$$

We term h_{jm}^2 as correlative heritability. h_{jm}^2 expresses the joint discounting effect of both heritability and genetic correlation, and thus represents a collective measure involving all parameters that determine the gain from early selection. Age trend of E_{jm} provides a quantitative framework for decisions on age of early selection. The concept expounded in Equation 2 defines efficiency of early selection, in essence, as an optimisation (not necessarily maximisation) process. We will further elaborate on this in relation to the Lambeth model's optimum age of selection on gain per year basis.

We analysed the growth data by site, but present the results with emphasis on overall time trends in parameter estimates as genetic parameter estimates were largely independent of site attributes. Survival of individual plantations was higher than 80%, most above 90%, and not a significant factor in computation of mean height.

RESULTS AND DISCUSSION

Age Trends in Genetic Parameters

Variance analyses indicated provenance effect was not statistically significant ($p > 0.05$) at eight test plantations, which were excluded from further analyses. These plantations suffered extensive snow press, severe pest damage or wildlife disturbance. Consequently, 50 test sites from 11 of the 12 geoclimatic regions were used in analyses.

Figure 1 illustrates the cumulative height growth among 10 representative provenances from the species' northern distribution (north of latitude 46°. The height was a mean over the 50 test plantations. All provenances were still at their active growth expansion phase (ZEIDE 1993) and showed the same general age trend, but varied significantly in rate of growth as indicated by the slope of their growth curves. Provenance rankings in total height varied only slightly after age 10.

Heritabilities of provenance means for the 50 plantations decreased slightly from age 1 to age 3, and then increased steadily (Table 1). Decreasing heritability during the early years shortly after planting is similar to that found in other lodgepole pine provenance tests in B.C. (YING *et al.* 1989; XIE & YING 1996) and seems to be a common phenomenon with conifers, e.g. *Pseudotsuga menziesii* (JOHNSON *et al.* 1997). Overall, heritability did not vary a great deal at different ages.

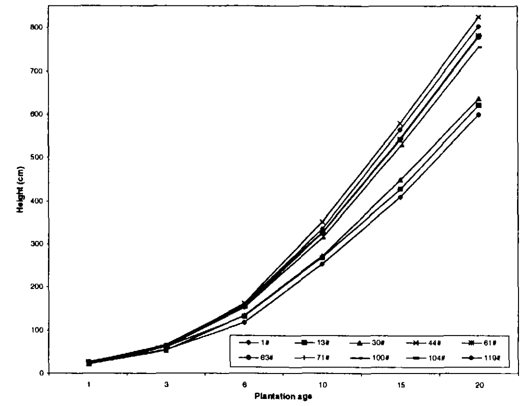

Figure 1. Cumulative mean height of 10 representative lodgepole pine provenances over 50 plantations.

The age-age phenotypic, genetic, and environmental correlations presented as an average by geoclimatic regions are given in Table 2. The closer the plantation ages the higher the correlation coefficients, a norm in growth traits at different ages in tree species (LAMBETH 1980). Age-age phenotypic and genetic correlations were positive at all sites and relatively strong except between ages 1 and 20. Genetic correlation coefficients were higher than those of phenotypic correlation at all sites with a few exceptions, and close to 1.0 at most sites after age 6 with age 20 as a reference mature age. Genetic correlations also showed a steeper age trend than those of heritabilities (Table 1), and thus carried more weight in their discounting effect on early selection. Age-age environmental correlation showed a somewhat different trend. Correlation coefficients 1–20 and 3–20 were significantly lower than those of phenotypic and genetic correlations, and negative correlations were observed at age 1 in a number of plantations. The environmental coefficients also rose more rapidly than the phenotypic and genetic coefficients. Environmental correlation carries both extrinsic and intrinsic components (KANG 1991). The age trend in size of the coefficients suggests the environment correlation at early ages was largely extrinsic in nature, and increasingly intrinsic as the trees aged. Otherwise, we should expect a less structured (or stochastic) age trend of environmental correlation.

Age trend of correlative heritability (h_{jm}^2, Equation 2) (Table 3) was very similar to that of age-age genetic correlation (Table 2) rather than that of heritability (Table 1). Both h_{jm}^2 and genetic correlation rose quickly

Table 1. Repeatability of lodgepole pine provenance mean height at different ages at 50 plantations over 11 geoclimatic regions.

Region	Plantation	Age					
		1	3	6	10	15	20
Kootenay	Wuho	0.711	0.791	0.848	0.876	0.903	0.908
	Lamb	0.726	0.760	0.765	0.863	0.916	0.913
	Elkc	0.775	0.660	0.732	0.816	0.848	0.877
	Luss	0.764	0.575	0.485	0.552	0.738	0.858
	Free	0.749	0.813	0.785	0.772	0.568	0.727
Monashee	Rody	0.761	0.577	0.728	0.766	0.813	0.881
	Bisn	0.373	0.594	0.531	0.735	0.810	0.900
	Lasi	0.610	0.697	0.740	0.830	0.900	0.936
	Mcla	0.740	0.739	0.721	0.802	0.903	0.929
Thompson Plateau	Chuw	0.781	0.719	0.817	0.893	0.953	0.955
	Comm	0.748	0.446	0.540	0.760	0.853	0.908
	Peti	0.695	0.310	0.369	0.754	0.867	0.897
	Hado	0.739	0.560	0.725	0.835	0.893	0.918
	Equi	0.844	0.215	0.619	0.785	0.904	0.932
Upper Columbia	Wigw	0.657	0.740	0.821	0.852	0.884	0.857
	Suef	0.669	0.576	0.430	0.663	0.832	0.895
	Suem	0.759	0.659	0.842	0.855	0.900	0.932
Cariboo	Niqu	0.592	0.605	0.679	0.852	0.855	0.913
	Timy	0.679	0.666	0.599	0.782	0.852	0.891
	Boss	0.758	0.630	0.653	0.771	0.840	0.807
	Bosk	0.708	0.779	0.656	0.730	0.803	0.843
	Tuya	0.778	0.304	0.396	0.645	0.777	0.862
Chilcotin	Hold	0.778	0.696	0.574	0.650	0.823	0.882
	Mons	0.640	0.616	0.837	0.789	0.869	0.908
	Klok	0.763	0.698	0.711	0.708	0.760	0.763
	Cuis	0.612	0.691	0.962	0.901	0.928	0.921
Upper Fraser	Bate	0.570	0.613	0.661	0.782	0.765	0.881
	Goat	0.749	0.780	0.750	0.841	0.874	0.891
	Holm	0.621	0.574	0.768	0.812	0.712	0.645
	Vale	0.652	0.392	0.724	0.809	0.888	0.879
	Dave	0.709	0.643	0.704	0.819	0.734	0.710
Willow	Atis	0.530	0.558	0.600	0.589	0.663	0.640
	Bakr	0.416	0.611	0.758	0.776	0.848	0.898
	Neck	0.532	0.802	0.838	0.860	0.919	0.921
	Whit	0.739	0.589	0.521	0.595	0.571	0.845
Nechako	Deck	0.796	0.712	0.635	0.815	0.880	0.912
	Fras	0.788	0.067	0.856	0.883	0.919	0.879
	Otsa	0.791	0.632	0.660	0.760	0.888	0.929
	Tzen	0.653	0.656	0.770	0.820	0.882	0.895
	Bart	0.708	0.499	0.693	0.766	0.809	0.819
Mackenzie	Blac	0.614	0.595	0.618	0.729	0.773	0.787
	Carp	0.660	0.731	0.769	0.835	0.891	0.857
	Dogc	0.839	0.841	0.796	0.845	0.867	0.864
	West	0.764	0.725	0.752	0.850	0.888	0.851
	Samn	0.574	0.684	0.651	0.700	0.704	0.760
Takla	Mcbr	0.786	0.662	0.507	0.619	0.738	0.850
	Chap	0.662	0.398	0.385	0.365	0.428	0.566
	Susk	0.846	0.800	0.675	0.452	0.456	0.540
	Nilk	0.897	0.760	0.611	0.600	0.742	0.762
	Telk	0.753	0.714	0.722	0.762	0.719	0.778
Mean		0.701	0.625	0.681	0.759	0.811	0.847

Table 2. Age-age phenotypic (r_p), genetic (r_g), and environmental correlation (r_e) of lodgepole pine provenances presented as regional averages.

Region	Number of plantation		Age-age				
			1-20	3-20	6-20	10-20	15-20
Kootenay	5	r_p	0.526	0.735	0.889	0.941	0.980
		r_g	0.637	0.836	0.996	1.006	1.007
		r_e	0.109	0.392	0.554	0.701	0.809
Monashee	4	r_p	0.406	0.672	0.859	0.942	0.984
		r_g	0.521	0.786	0.992	1.001	1.000
		r_e	-0.066	0.396	0.499	0.695	0.897
Thompson Plat.	5	r_p	0.335	0.589	0.843	0.944	0.984
		r_g	0.373	0.849	0.990	0.990	0.996
		r_e	0.128	0.321	0.599	0.738	0.865
Upper Columbia	3	r_p	0.368	0.802	0.867	0.947	0.979
		r_g	0.418	0.930	0.990	0.994	0.996
		r_e	0.229	0.492	0.603	0.799	0.873
Cariboo	5	r_p	0.459	0.679	0.787	0.903	0.972
		r_g	0.570	0.830	0.914	0.961	0.995
		r_e	0.099	0.419	0.590	0.701	0.862
Chilcotin	4	r_p	0.419	0.696	0.891	0.970	0.985
		r_g	0.523	0.813	0.951	1.003	0.994
		r_e	0.073	0.333	0.683	0.805	0.928
Upper Fraser	5	r_p	0.407	0.722	0.852	0.920	0.959
		r_g	0.564	0.903	0.886	0.891	0.884
		r_e	-0.079	0.307	0.440	0.657	0.826
Willow	4	r_p	0.392	0.632	0.794	0.880	0.962
		r_g	0.516	0.725	0.890	0.946	0.989
		r_e	0.419	0.377	0.535	0.703	0.853
Nechako	5	r_p	0.379	0.709	0.876	0.842	0.983
		r_g	0.478	0.893	0.998	0.998	1.000
		r_e	-0.032	0.228	0.472	0.682	0.871
Mackenzie	5	r_p	0.329	0.657	0.767	0.893	0.948
		r_g	0.432	0.800	0.898	0.896	1.003
		r_e	0.020	0.186	0.355	0.511	0.715
Takla	5	r_p	0.436	0.724	0.810	0.875	0.945
		r_g	0.524	0.808	0.901	0.938	0.975
		r_e	0.153	0.540	0.690	0.806	0.891

from ages 1 to 6, and then started to level off. This indicates that genetic correlation rather than heritability drove the gain in early selection carrying a higher discounting effect (Wu 1998).

Genetic gain at age 20 (CG_m, Equation 1) from selection at younger ages varied widely from region to region, but showed high similarity in age trend (Fig. 2). The amount of gain rose rapidly from ages 1 to 6, and then started to level off, perhaps with the exception of the sites in Thompson Plateau. Age trend in efficiency of early selection ($E_{jm,}$ Equation 2) showed a rapid convergence among regions (Fig. 3) despite their large differences in response to selection (Fig. 2).

Despite the large variation in genetic parameter estimates from plantation to plantation, the differences were not associated with site attributes, e.g. geographic location (latitude, longitude and elevation), climate (mean annual temperature and precipitation) or site

Table 3. Correlative repeatability (h^2_{jm}, Equation 2) of lodgepole pine provenance means averaged over each region.

Region	Number of plantations	Age-age				
		1-20	3-20	6-20	10-20	15-20
Kootenay	5	0.507	0.659	0.779	0.817	0.829
Monashee	4	0.417	0.604	0.779	0.846	0.883
Thompson Plat.	5	0.313	0.522	0.736	0.853	0.905
Upper Columbia	3	0.331	0.712	0.764	0.834	0.879
Cariboo	5	0.440	0.585	0.652	0.776	0.839
Chilcotin	4	0.403	0.624	0.764	0.814	0.852
Upper Fraser	5	0.433	0.668	0.772	0.812	0.824
Willow	4	0.349	0.535	0.670	0.726	0.802
Nechako	5	0.387	0.667	0.796	0.845	0.881
Mackenzie	5	0.330	0.615	0.690	0.793	0.825
Takla	5	0.400	0.554	0.572	0.585	0.643

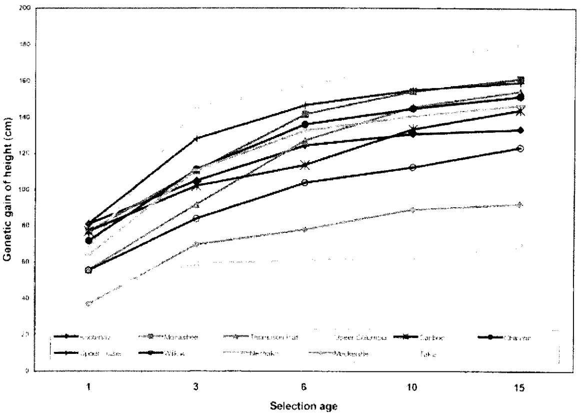

Figure 2. Genetic gain (Equation 1) in height at plantation age 20 from selection at younger ages for 11 geoclimatic regions for lodgepole pine provenances.

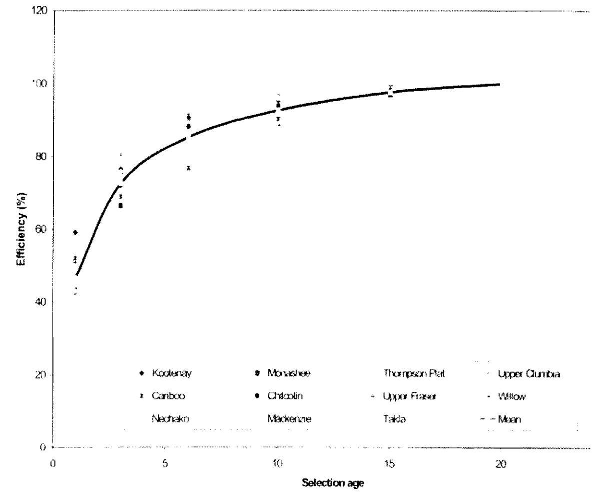

Figure 3. Mean efficiency of early selection (E_{jm}, Equation 2) in relation to target age 20 for lodgepole pine provenances. The mean efficiency is averaged from 11 geoclimatic regions.

productivity (20-year height). Only the correlation coefficients of age-age correlations 1–20 and 3–20 with mean annual temperature and 20-year height were statistically significant ($r \cong 0.5, p < 0.01$). This suggests genetic potential in height growth was expressed earlier on mild, productive sites, perhaps due to the fast recovery from planting shock at these sites (JANSSON *et al.* 2003). HAAPANEN (2001) found that time trends in age-age correlations were largely independent of site characteristics in an extensive progeny testing of Scots pine in Finland.

Early Selection with Specific Reference to the Lambeth Model

The consistency of provenance height rankings (Fig. 1) is consistent with other studies of lodgepole pine in B.C. (YING *et al.* 1989; YING 1991). Age trends in genetic parameters were similar to that of family means (XIE & YING 1996). This suggests a similar mode of responses to selection can be expected at both provenance and family means. The age trend of correlative heritability (h^2_{jm}) (Table 3), which represents the joint effect of the two determinant parameters (heritability and genetic correlation), ought to give a realistic overall indication of progress from selection at different ages. Indeed, age trend in efficiency of selection (E_{jm}, Equation 2) closely paralleled that of h^2_{jm}, which exhibited an exponential increase from ages 1 to 6; E_{jm} reached over 80 % at age 6 and 90 % at age 10 on average (Fig. 3). These results suggest early selection after age 6 can achieve most of the gain at target age 20.

Harvest age of plantation lodgepole pine in B.C., however, is around 60 to 70 years. It requires extrapolative projection in order to assess the efficiency of early (indirect) selection in relation to direct selection at various harvest ages beyond age 20. We emulated the analytical procedure expounded in Lambeth's (1980) model to extrapolate E_{jm}. The Lambeth model (Equation 3) is:

$$E = r_{Pjm}\, T_m / T_j =$$
$$= [1.02 + 0.308\log(t_j/t_m)](t_m + Tlag_m)/(t_j + Tlag_j) \qquad [3]$$

where, r_{Pjm} is phenotypic age-age correlation, and $T_m = t_m + Tlag_m$ and $T_j = t_j + Tlag_j$. t_j and t_m are, respectively, the selection and target ages. *Tlag* is the time lag in years between the selection and the start of the next cycle of breeding, and again the subscripts *m* and *j* refer to target and selection age, respectively. The model contains two components. The first component projects phenotypic age-age correlation (r_{Pjm}) from the logarithm of selection-target age ratio (t_j/t_m) as predictor, and the second is the ratio of the length of breeding cycles at target ($T_m = t_m + Tlag_m$) verses selection ($T_j = t_j + Tlag_j$) age. The model is simplified by assuming equal heritabilities at selection and target ages, and equal phenotypic and genetic age-age correlation to allow the former (r_{Pjm}) as proxy for selection efficiency (equivalent to E_{jm}, Equation 2). The second component of the model converts genetic gain to a per year basis as a measure of optimal age of selection.

Employing the first component procedure (by fitting the E_{jm} from our lodgepole pine results to $\log(t_j/t_m)$), the resulting regression equation is:

$$E_{jm} = 1.035 + 0.179\log(t_j/t_m) \quad (r^2 = 0.92) \qquad (4)$$

The high coefficient of determination (r^2) indicates a strong linear relationship between E_{jm} and the $\log(t_j/t_m)$. Our study is based on 50 provenance tests in diverse site environments, so we expect Equation 4 is highly representative. Xie & Ying (1996) found high predictability of genetic correlation from the same predictor in lodgepole pine ($r_A = 1.10 + 0.48\log(t_j/t_m)$, $r^2 = 0.98$). Their study was based on a large number of open-pollinated families (610) from 42 interior provenances from the subspecies *ssp. latifolia* (Critchfield 1957), and over a testing period of 20 years. The provenance samples were common to both studies. These results suggest high robustness of the logarithm of (t_j/t_m) ratio as the predictor of age-age correlation in growth behaviour in lodgepole pine. Similar results were also reported with other species (e.g. King & Burdon 1991; Johnson *et al.* 1997; Greaves *et al.* 1997; Gwaze & Bridgwater 2002). The log t_j/t_m ratio seems to have captured the biological essence of age trends in genetic parameters that govern the behaviour of tree growth, regardless of the underlying mechanisms.

There are cases that found low fitting of $\log(t_j/t_m)$ (e.g. Matheson *et al.* 1994; Lambeth & Dill 2001). Individual cases of low fitting does not diminish the value of such a normative model that mathematically abstracts the biological phenomenon of age-age correlation. It is up to the practitioner to find a descriptive model with proper parameterisation and construction of response variable, that fits specific conditions of a local situation. For example, in our study, we found E_{jm}, instead of r_{Gjm} or r_{Pjm}, improved the fitting.

Use of $\log(t_j/t_m)$ as a predictor in finding the time trend of phenotypic age-age correlation as proxy for gain from selection as described in Lambeth (1980) is simple, but requires the assumptions of h_j^2 (selection age heritability) = h_m^2 (target age heritability) and r_{Pij} (phenotypic age-age correlation) = r_{Gij} (genetic age-age correlation). h_j^2 can be considerably different from h_m^2 (Riemenschneider 1988; Kang 1991); and r_{Pij} is commonly smaller than r_{Gij} (Sato 1994). Use of E_{jm} as in our analysis does not involve such assumptions. E_{jm} is the ratio of h_{jm}^2 / h_m^2, and h_{jm}^2 (correlative heritability) integrates all the genetic parameters that together determine the accuracy of early selection (see Equation 2). Arguably, projection based on the whole ought to be of higher reliability than that based on the parts individually, though the three elements are correlated (Kang 1985). Thus the use of E_{jm} to assess early selection may be of considerable advantage.

The first component of the Lambeth model represents a successful mathematical abstraction of the biological phenomenon in age-age correlation, and empirical evidence has shown a high universality of its applicability. However, we have some reservations about the Model's second component – the use of the $(t_m + Tlag_m) / (t_j + Tlag_m)$ ratio as the weighting factor and the logic of gain per year as the criterion in determining optimum age of early selection. Our discussion below focuses on its implications on operational tree improvement in general. Firstly, the Lambeth model assumed $Tlag_j = 5$, $Tlag_m = 3$ for any selection age. Precocity depends on the physiological age of the scion donors and inductive site environment, and varies among species (Dr. Joe Webber, personal communication, 2003).

Secondly, the ratio t_m/t_j has a steep inverse relationship with early selection at young ages (e.g. before age 10) (Fig. 4). This carries a significant bias towards favouring selection at a very young age when the length between selection and target ages is large (Fig. 4). For example, comparing the weighting effect of two selection ages $t_j = 6$ versus 15 for the same target age of harvesting $t_m = 60$, the t_m/t_j ratio for the former is 10 (= 60/6) and the latter 4 (= 60/15) (Fig. 4). This represents a 2.5 (= 10/4) times difference in weight when efficiency of early selection is converted to a per year

Table 4. Efficiency of early selection (E_{jm}, Equation 4) of lodgepole pine provenances for various selection and target ages.

Selection age	Target age (years)					
	20	30	40	50	60	70
1	0.500	0.427	0.376	0.336	0.303	0.276
2	0.624	0.551	0.500	0.460	0.427	0.400
3	0.696	0.624	0.572	0.532	0.500	0.472
4	0.747	0.675	0.624	0.584	0.551	0.524
5	0.787	0.715	0.663	0.624	0.591	0.563
6	0.820	0.747	0.696	0.656	0.624	0.596
7	0.848	0.775	0.724	0.684	0.651	0.624
8	0.871	0.799	0.747	0.708	0.675	0.647
9	0.892	0.820	0.769	0.729	0.696	0.668
10	0.911	0.839	0.787	0.747	0.715	0.687
12	0.944	0.871	0.820	0.780	0.747	0.720
14	0.971	0.899	0.848	0.808	0.775	0.747
16		0.923	0.871	0.831	0.799	0.771
18		0.944	0.892	0.853	0.820	0.792
20		0.963	0.911	0.871	0.839	0.811
22			0.928	0.888	0.856	0.828
24			0.944	0.904	0.871	0.844
26				0.918	0.886	0.858
28				0.932	0.899	0.871
30					0.911	0.884
32					0.923	0.895
34						0.906
36						0.916

basis. Such a large difference in weighting can render age-age correlation and other parameters virtually irrelevant. Figure 4, which illustrates differential weighting effect of the ratio t_m/t_j in relation to different selection and target ages, supports KANG's (1985) diagnosis that the Lambeth model has a built-in mathematical bias in favour of selection at a very young age. However, this differential weighting effect diminishes when selection age increases to 10 and older (Fig. 4).

Early selection is indirect selection, and gain from early selection should always be lower than selection at target age. There always exists a level of uncertainty, and the earlier the selection age, the higher this uncertainty. We believe age of selection should be a managerial decision taking into consideration all factors affecting a tree improvement program, genetic as well as non-genetic. For example, completion of a breeding cycle including progeny testing requires considerable resource investment. One has to balance the costs and benefits associated with gain per unit time. Urgency of seed requirements for reforestation and size of land base for such reforestation can have enormous impact on the cost-benefit ratio associated with unit time gain. Market demand for the type of wood product can play a determining role on trait selection and harvest age, and age-age correlation varies from trait to trait.

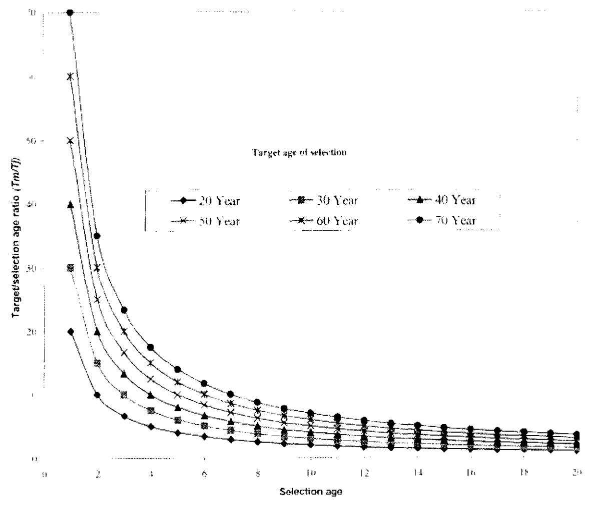

Figure 4. Distribution shape of the ratio of target/selection ages (t_m/t_j) for different target ages of selection.

From the above perspective, we believe early selection efficiency expressed as the ratio of gain at selection age in relation to the gain at harvest (E_{jm}) may provide an effective alternative guiding decisions on age of early selection. If high gain at harvest with high certainty is the goal, selection may need to be delayed till 1/3 to 1/2 the rotation age or even later. Otherwise, it can be much earlier. We prepared Table 4 (derived from Equation 4) which provides such a quantification scheme assisting decisions on selection age. For example, if 50% or lower gain of that at harvesting age 60 is acceptable, testing results after 3–5 years may be sufficient. If gain at 80% or higher is desirable, selection may need to be delayed till 1/3 of the harvesting age. Another advantage of E_{jm} (Table 4) is that it does not involve the assumptions of $h_j^2 = h_m^2$ and $r_{Pjm} = r_{Gjm}$ as already described.

Gain per unit time is no doubt an important consideration in decision-making on age of selection, but ought not to be the only one. Decision on age of selection ought to be a process of optimisation incorporating many relevant factors, rather than a process of maximisation based on a gain per unit time alone. FRANKLIN (1979) and KANG (1985) called for caution in selection at early age (i.e. before 1/3 of rotation ages) out of similar concerns after evaluating a number of early selection models.

Based on the above deliberation, we propose to treat the Lambeth model as two distinctive components in practical application. The first component – the use of the $\log(t_j/t_m)$ ratio in construction of a model predicting age trend of genetic parameters – should be considered as a normative procedure because of its mathematical abstraction in nature and its high universality across species and site environments. The second component – the use of $(t_m + Tlag_m)/(t_j + Tlag_m)$ to convert the gain to per year basis – should be considered as only one of potentially many factors affecting decision-making on age of selection.

CONCLUSIONS

Height growth among lodgepole pine provenances varied, but showed similar age trend over the testing period of 20 years (Fig. 1). Age trends in genetic parameters peaked after age 6. Genetic parameter estimates were largely not associated with site environment. Genetic correlation rather than heritability seems to be the significant factor driving early selection. We derived h^2_{jm} (correlative heritability, Equation 2) – a joint effect of both genetic correlation and heritabilities – to measure response to selection at different ages. Selection efficiency (E_{jm}) was expressed as the ratio of correlative heritability to heritability at target age (h^2_{jm}/h^2_m). E_{jm} fits well the $\log(t_j/t_m)$ ratio ($r^2 = 0.92$), indicating high robustness of the first component of the Lambeth model. E_{jm} (Table 4) can be considered as an alternative to gain per year (the second component of the Lambeth model) as a quantitative framework for decision on ages of early selection. We also propose to consider the Lambeth model as two distinctive components in practical application.

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