(88 to 105 percent as effective as direct selection for volume). Combined selection for one-year height was only 67 percent as effective as direct selection for seven-year volume. However, average volume gains per year were greater for one-year selection (1.61 dm³ vs. 1.20 dm³ per year), because of the reduced breeding cycle.

(4) Selecting for one, three, or five-year growth traits would have slight positive effects on wood specific gravity (from 5 to 13 percent as much gain as direct selection) and a negligible effect on branch angle ($-0.3°$ to $-1.4°$).

Acknowledgements

Literature Cited

BARR, A. J., J. H. GOODNIGHT, J. P. SALL, W. H. BLAIN and D. M. CHILKO: SAS Users Guide, 1979 edition. SAS Institute, Inc, Raleigh, N. C., 494 pp. (1979). — BRISCOE, C. B.: Establishment and early care of sycamore plantation. USFS Res. Pap. SO-50, 18 p. (1969). — FERGUSON, R. B., S. B. LAND and D. T. COOPER: Inheritance of growth and crown characters of American sycamore. Silvae Genetica 26: 180—182 (1977). — JOURDAIN, C. J. and J. R. OLSON: Variation and heritability of branching and growth characteristics among sycamore progeny. Proc. 17th. South. For. Tree Imp. Conf. pp. 203—208 (1983). — LAND, S.: Genetic variation, heritabilities, and selection strategies for early growth of sycamore in the Gulf South. Proc. 16th South. For. Tree Imp. Conf. pp 123—135 (1981). — McCUTCHAN, B.: Estimation of gain in form, quality, volumetric traits of American sycamore in response to selection of tree dry weight. Proc. 17th South. For. Tree Imp. Conf. pp 209—219 (1983). — NAMKOONG, G.: Inbreeding effects on estimation of genetic additive variance. For. Sci. 12: 8—13 (1966). — NAMKOONG, G. and E. B. SNYDER: Accurate values for selection and intensities. Silvae Genetica 17: 172—173 (1968). — NEBGEN, R. J. and W. J. LOWE: Inheritance of growth, branch angle, and specific gravity in three American sycamore populations. Silvae Genetica 31: 86—89 (1982). — SCHMITT, D. and J. R. WILCOX: Sycamore variation in the lower Mississippi Valley. USFS Res. Note SO-91, b p. (1969). — WEBB, C. D., R. P. BELANGER and R. G. McALPINE: Family differences in early growth and wood specific gravity of American sycamore (Platanus occidentalis L.). Proc. 12th South. For. Tree Imp. Conf. pp 213—217 (1973).

Juvenile Selection in Tree Breeding: Some Mathematical Models

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Abstract

Four different juvenile selection models are developed and evaluated. When the heritability is assumed to be constant for all ages and the coefficient of juvenile mature correlation function is set at .308 (LAMBETH, 1980), the optimum selection age varied between 1.3 and 21.5 for the rotation age of 25 years.

The large differences in the optimum selection age was due to the differences in the models and the evaluation criteria used. Important findings of the models are as follows. 1) Basic model: When linear functions are used to represent the heritability ratio ($g = h_t/h_T$) and the genetic juvenile mature correlation (r), the intercept of g must be equal or greater than that of r to guarantee that the early selections are always beneficial. When a linear function and a log function were used to represent g and r (= $1 + B \ln x$), respectively, g did not influence the time of maximum annual genetic gain (x_{max}) significantly up to B values around 0.3. 2) Extended time models: These models delayed the x_{max} of the basic model. 3) Maximum future net worth model: The early selection t_{max} is independent of the rotation age (T), and an economic criterion k was the prime factor which influenced x_{max}. 4) Multiple cycle model: Under many simplifying assumptions this model reduced to the basic model.

It was concluded that extremely early selection time such as earlier than 1/3 of rotation age should be used with caution. Other shortcomings of the models were discussed.

Key words: Accelerated tree breeding, juvenile selection, heritability ratio, juvenile-mature correlation, tree breeding.

Zusammenfassung

Es wurden vier verschiedene Methoden zur Frühselektion entwickelt und ausgewertet. Unter gewissen Voraussetzungen konnte gezeigt werden, daß das optimale Selektionsalter zwischen 1,3 und 21,5 Jahren variiert. Jedoch ist eine Selektion, die vor dem Ende des ersten Drittels der Umtriebszeit erfolgt mit Vorsicht durchzuführen. Andere Unzulänglichkeiten der Selektionsmodelle werden diskutiert.

Introduction

Accelerated tree breeding is receiving a new emphasis with success in early flower induction and potential early selection. The concept is based on the premises that an early return on investment is desirable, and that there is an optimum juvenile selection age at which the early return on investment will overcome the shortcomings of misclassifying good trees because of imperfect juvenile-mature correlation. Therefore, the central question has been: What is the optimum selection age? Recent reports show there is no single answer to the question. For example, FRANKLIN (1979) and LAMBETH (1980) addressed this question for several conifers and, although sharing some common data base (from NAMKOONG and CONKLE 1976. NAMKOONG et al. 1972, SQUILLACE and GANSEL 1974), suggested different selection ages. FRANKLIN concluded that accurate selections might be made after half the rotation length, while LAMBETH suggested that selection much earlier was feasible.

Such discrepancies indicate that either the premises of accelerated breeding are not sufficient to address the issue properly, or that there is more than one answer to the question of optimum selection age, depending on the model and the parameters used. A corollary to this point is that any answer obtained from a model in isolation should not be used for making generalized inferences.

In this paper, I will develop and evaluate various models of early selection. The objectives are 1) to define some elementary models which can be of further use, 2) to demonstrate that an array of selection ages can be obtained from different models but the answers do not converge to a narrow range of ages, and 3) to discuss the effects which influence optimum selection ages within and between the models.

The models to be discussed are not prediction models. They are rather simple, and assumptions used are unrealistic. The models are primarily useful for learning the dynamics of optimum selection age under various conditions. It ispossible that the models can be further improved and used for predictions in the future. Such application will however, require substatially more information on the changing nature of the parameters of the models. I will limit the discussion to a basic model and three modifications of the basic model.

Basic Model

One popular way to examine the question of optimum selection age has been to use genetic gain per year (annual genetic gain) as the measure for comparing selection at different ages (DICKERSON and HAZEL, 1944). Let the annual genetic gain be $G*_t$, then

$$\Delta G^*_t = \Delta G_t/t$$
$$= ih_t h_T r(t)\sigma_T/t \quad \text{------------------------------} \quad (1)$$

where   i is the standardized selection intensity.

h^2_t, h^2_T are heritabilities at age t and maturity (T),

respectively.

r(t) is the genetic correlation between t and T, and

σ_T is the phenotypic standard deviation at T.

By comparing the annual genetic gain ($\triangle G^*_t$) at different times, t, one can empirically determine the selection age at which $\triangle G^*_t$ is maximum. If the information on the genetic juvenile mature correlation r(t) and heritability (h^2_t) for all different time was available, then finding an accurate selection age with maximum $\triangle G^*_t$ would be a relatively simple matter. Currently, only limited information on such parameters is available.

Even if sufficient information is available learning the dynamic behavior of the optimum selection age under different models can be enhanced if the genetic correlation and heritability are expressed as functions of time. If we assume that such time dependent expressions exist and let

$$g = g(x) = h_t/h_T \ , \ \text{and}$$

$$r = r(x) \text{ represent r(t) at time } x = t/T. \text{ then (1) can be}$$

rewritten as

$$\Delta G^*_x = ih^2_T g(x)r(x)\sigma_T/xT$$
$$= Qgr/x, \ 0 < x \leq 1 \quad \text{------------------------------} \quad (2)$$

where $Q = ih^2_T\sigma_T/T$. Equation 2 will be referred to as the basic model in this paper. Note that $\triangle G^*_t$ is replaced by $\triangle G^*_x$. The assumptions of the model are as follows. Selections made at different ages are drawn from standard normal populations at different time, and the population size will remain constant over different selection periods. If the breeder uses a fixed proportion of individuals for all the selections the selection intensity i will remain constant. Only a single cycle of selection will be applied such that h^2_T will remain a constant. These assumptions assure that $Q = ih^2_T\sigma_T/T$ is a positive constant, and $\triangle G^*_x$ is maximum at x which maximizes the function $y = gr/x$. Clearly, y is a critical parameter indicating the relative

merits of selecting at $t < T$. $y < 1$ implies no advantage to early selection. Since y is a variable function of g, r and x, its behavior reveals the effects of those parameters on the efficiency of early selection.

The first and second derivatives of y are:

$$y' = \frac{(xg'-g)r + xgr'}{x^2} \ , \ \text{and} \quad \text{----------------------------} \quad (3)$$

$$y'' = \frac{(x^2g''-2xg'+2g)r + 2x(xg'-g)r' + x^2gr''}{x^3}. \quad \text{-----------} \quad (4)$$

If we let $y' = 0$, then

$$(xg' - g)r + xgr' = 0 \quad \text{------------------------------------} \quad (5)$$

One of the roots of (5) will be the maximum provided that y″ at the x is less than zero. The root will be referred to as x_{max}. The x_{max} will vary depending on the nature of the population which governs g and r.

Although g and r depend on the populations, efforts were made to describe some general behavior of the heritability and genetic juvenile mature correlation as time related functions. NAMKOONG and CONKLE (1976) and FRANKLIN (1979) indicated that the heritability can change substantially among three different phases of tree growing processes (i.e. juvenile genotypic phase, mature phase, and codominance suppression phase). Although the classification did not generate any explicit time related heritability function, their idea could be viewed as a step toward learning such functions.

LAMBETH (1980) suggested to use,

$$r(x) = B_0 + B_1lnx$$

where x = t/T.

r(x) = genetic juvenile mature correlation between t and T, and B_0, B_1 are constants representing intercept with x = 1 and regression coefficients of r(x) on lnx, respectively. The log function by LAMBETH seems to apply to many pine species and will be used extensively in this paper with the following modification.

$$r(x) = 1 + B1nx, \ \exp(-1/B) \leq x \leq 1 \quad \text{----------------------} \quad (6)$$

$B_0 = 1$ is used because B_0 values other than 1 will result in discontinuity of r at x = 1. The domain of x, exp(-1/B) $\leq$ x $\leq$ 1 will apply to all the pertinent equations in this paper unless specified differently.

In the remainder of this section I will use two sets of arbitrary functions to represent g and r, and discuss some properties of x_{max}.
Case 1. Both g and r are linear functions:

If we assume that both heritability ratio (g) and genetic juvenile-mature correlation (r) are linear functions of time, we may write,
g = A + (1-A)x, and
r = D + (1-D)x, with the restrictions that g = r = 1 at x = 1, and 0 < x $\leq$ 1. A and D are parameters that have to be estimated from actual data. Some of the data collected by FRANKLIN (1979), such as from SUILLACE and GANSEL (1974), indicate that it is possible to approximate g by a linear function depending on the definition of the rotation age. A linear function of r seems to be a fairly good approximation of (6) when 0.5 $\leq$ x $\leq$ 1 (Figure 1). Using the linear functions.

$$y = [A + (1-A)x][D + (1-D)x]/x.$$

By replacing proper expressions of g, g', r, and r' in Equation 5 we get.

$$(1-A)(1-D)x^2 - AD = 0, \text{ and}$$

$$x = \sqrt{\frac{A}{1-A}}\sqrt{\frac{D}{1-D}} \quad \text{--- (7)}$$

$y" = 2AD/x^3 > 0$ for all x, $0 < x \leq 1$. Therefore (7) represents minimum points rather than maxima. This implies that y tends to be reverse-J shaped (Figure 1). The equation

$$A = \frac{(1-D)x^2}{D + (1-D)x^2} \quad \text{--------------------------------------- (8)}$$

shows the value of A necessary to cause minima at the specified values of x and D. The most important special case of (8) is when x = 1. In this case any early selection will be guaranteed to generate y values greater or equal to 1. Then (8) reduces to
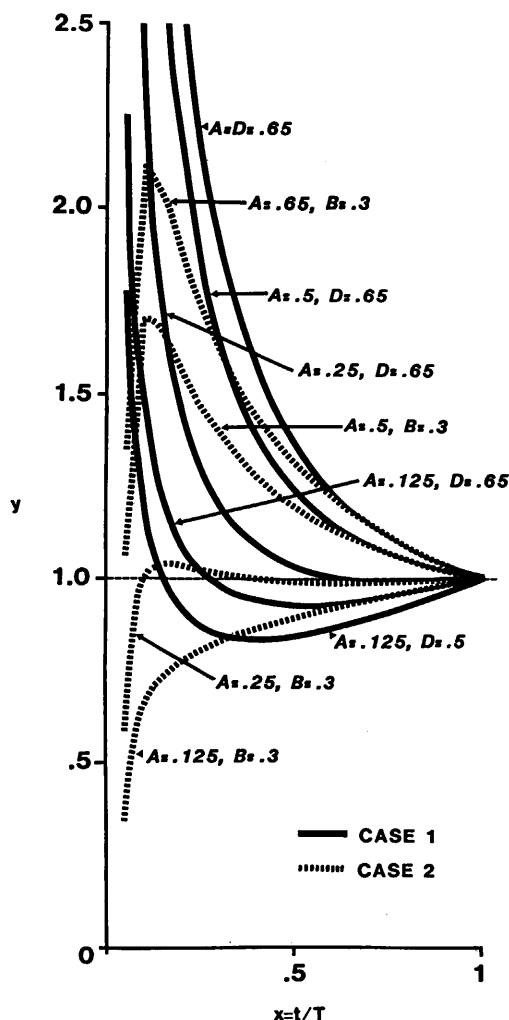
$$A = 1 - D.$$

Figure 1. — Values of i) $y = [A + (1 - A) x] [D + (1- D) x]/x$, and
ii) $y = [A + (1 - A) x] (1 + B\ln x)/x$ at various x.
i) and ii) represents Cases 1 and 2 Basic model, respectively.

CASE 1: Only when $A \geq D$, the minimum occur at x = 1, Otherwise minimum y will occur at an earlier stage. When D is smaller the minimum of y decreases for given A. For example, compare the two curves with the same A but with different Ds. Case 1 approximates Case 2 well for $x \geq$ .5. The intercept D of r (x) was taken by connecting two points. (.75, 1 + B\ln x) and (1.1) of the log function, y = 1 + \ln x.

CASE 2: The x_{max} falls at similar places regardless of A values for $A \geq$ .25. When A = .125, no intermediate maximum exists.

Table 1. — x_{max} at various values of A and B[1].

A	.1	.2	.3	.35	.4	.5
.1	.0001	.0224				
.2	.0001	.0198				
.3	.0001	.0192	.1319	.3712		
.4	.0001	.0188	.0053	.2158	.4172	
.5	.0001	.0187	.1080	.1885	.3018	.9999
.6	.0001	.0185	.1039	.1775	.2665	.5205
.7	.0001	.0185	.1013	.1678	.2482	.4452
.8	.0001	.0184	.0994	.1626	.2367	.4073
.9	.0001	.0184	.0980	.1589	.2289	.3839
1	.0001	.0183	.0970	.1561	.2230	.3678

1) Values below dotted lines represent x_{max} which differ by less than .05. Difference in x_{max} by .05 means 1 year difference in 20 years rotation age and 5 years difference in 100 years rotation age.

Therefore $A \geq 1 - D$ will meet the desired requirement. This implies that A = 1, or g(x) = 1, will certainly guarantee that any early selection will be favored.

Case 2. g is linear and r is logarithmic:
The necessary equation are:

$$y = [A + (1-A)x][1 + B\ln x]/x. \quad \text{------------------------- (9)}$$

$$y' = \frac{1}{x}\left[x - \frac{A}{1-A}\ln x - \frac{A(1-B)}{B(1-A)}\right], \text{ and } \quad \text{--------------------- (10)}$$

$$y" = [-B(1-A)x + 2AB\ln x + A(2-3B)]/x^3. \quad \text{----------------- (11)}$$

The roots of y = 0 were numerically obtained for some specified values of B and A *(Table 1)*. Up to values around .3, the change of A has little importance in changing the x_{max}. Therefore, The use of the assumption g = h_t/h_T = 1, such as applied by Lambeth (1980), can be justified up to B values around 0.3. As B increases (i.e. the genetic juvenile mature correlations become weaker) the change in the intercept of g becomes more important.

To determine the A value that will guarantee x_{max} for given x and B, Equation 10 is solved for A resulting in,

$$A = \frac{Bx}{1 + B(x+\ln x - 1)} \quad \text{------------------------------------- (12)}$$

The values of A obtained from Equation 12 represent the intercept of the linear g which might cause either maximum or minimum value of y *(Table 2)*. Table 2 shows that the difference between the first number and the second number of each row is much greater than those between other numbers not involving the first number in the same row. To obtain the earliest possible x_{max} for given B, A must increase greatly, although the actual changes in x_{max} is relatively small *(Figures 2)*. Note, however, that the actual values of y changes substantially. The increase in y is primarily due to the increase in A.

Another useful question for Case 2 is: how large should A be to guarantee y $\geq$ 1 at different values of x and B? Let A = B + m, where m is a constant, then from (9),

$$y = [B + (1-B)x][1+B\ln x]/x + m(1-x)(1+B\ln x)/x > 1. \quad \text{------ (13)}$$

First consider the case of m = 0, i.e. A = B, so that the second term of (13) can be ignored. We then ask what range of B values will guarantee the presence of y = 1, for given x? Equation 13 can be solved for B and,

$$A = B < \frac{x\ln x - (x-1)}{(x-1)\ln x} \cdot \exp(-1/B) \leq x < 1. \quad \text{-------------- (14)}$$

Table 2. — Values of A which will guarantee the extreme values of y at given X and B[1].

B	.05	.1	.15	.2	.25	.3	.35	.4	.45	.5	.55	.6	.65	.7	.8	.9	1	B
.1	.008	.014	.021	.027	.032	.037	.042	.047	.052	.058	.061	.066	.071	.075	.084	.092		.1
.2	.048	.056	.067	.077	.087	.097	.106	.115	.123	.131	.139	.147	.154	.161	.175	.188		.2
.3		.765	.256	.217	.209	.210	.214	.220	.227	.234	.241	.248	.255	.262	.275	.289		.3
.4				2.208	.688	.503	.437	.407	.391	.383	.379	.378	.378	.380	.385	.392		.4
.5						3.124	1.167	.828	.691	.620	.578	.551	.533	.521	.507	.501		.5
.6								2.66	1.414	1.056	.889	.744	.734	.693	.643	.616		.6
.7									5.621	2.124	1.445	1.159	1.003	.907	.796	.736		.7
.8										8.795	2.721	1.769	1.385	1.180	.968	.861		.8
.9											8.692	2.996	1.968	1.540	1.163	.993		.9
1												6.728	2.965	2.039	1.387	1.133		1

(Negative values in the lower-left region, rows .7 and below.)

1) Boxed in values represent A which will guarantee maximum y. Values above the box represent A which will guarantee minimum y.
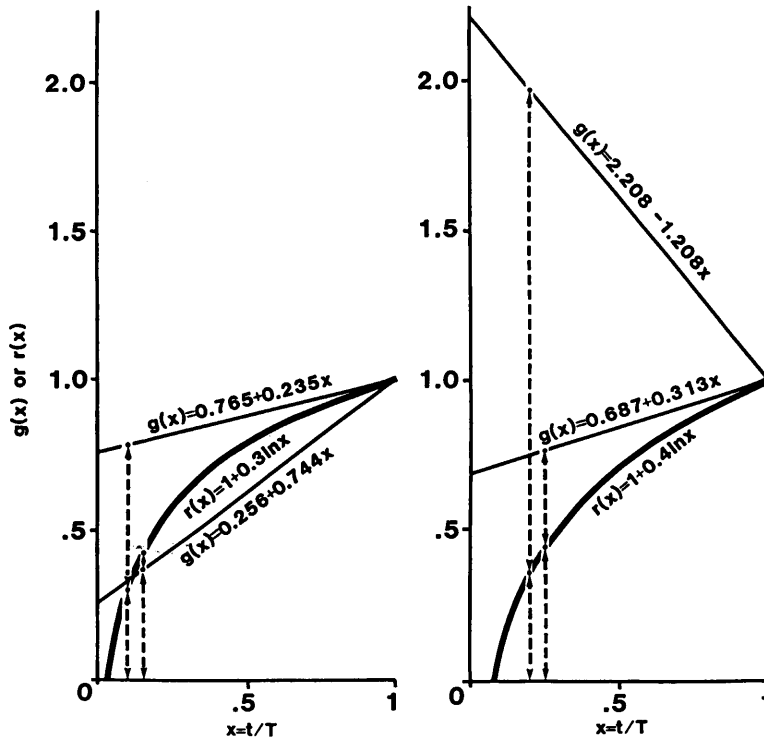

Figure 2. — Linear function $g = h_t/h_T$ necessary to guarantee the presence of maximum y at specified x_{max} values. Note the drastic changes in A Values to accomplish the change of x_{max} by 0.05.

2a) B = .3: When x_{max} = .1, A = .765 and y = 2.428,
When x_{max} = .15, A = .256 and y = .744.

2b) B = .4: When x_{max} = .2, A = 2.208 and y = 3.503.
When x_{max} = .25, A = .687 and y = 1.364.

The necessary values of A = B for various values of x are shown in the following table.

x	$\geq$	.1	.2	.3	.4	.5	.6	.7	.8	.9	1
A = B	$\leq$	.323	.371	.402	.425	.443	.458	.47	.481	.491	.5

When x = 1, Equation 14 is undefined. However, it can be shown that $\lim_{t \to 1} B = 1/2$ by repeated application of l'Hôpital's rule.

When B is greater than .5 or the value specified in the above table, A = B + m must be greater than B, or m > 0. By solving (13) for A = B + m we obtain,

$$A = B + m = \frac{x}{1-x}\ \frac{B\ln x}{1 + B\ln x}, \quad \exp(-1/B) \leq x < 1.$$

Table 3 shows the values of A necessary to guarantee y = 1 for various values of x and B. By comparing Tables 2 and 3 we can see that y = 1 exists in the earlier regions of x although x_{max} does not exist in the same area. In general A needed for y = 1 is smaller than that for x_{max} except for the boxed-in values (Figure 3). At these points y values are less than 1 at x_{max}.

A special situation of Case 2 arises when A = 1. Table 1 showed that A has relatively little influence on x_{max} for B values up to around .3. In this case, assuming A = 1 simplifies the analysis substantially. Therefore,

$$y = r/x = (1 + B\ln x)/x, \text{ and}$$
$$y = (B - 1 - B\ln x)/x.$$

Table 3. — Values of A which will guarantee that y = 1 at given x and B[1].

B	.05	.1	.15	.2	.25	.3	.35	.4	.45	.5	.55	.6	.65	.7	.8	.9	1	B
.1	.023	.033	.041	.048	.054	.059	.063	.067	.071	.074	.078	.081	.084	.086	.091	.096		.1
.2	.079	.095	.108	.119	.128	.136	.143	.150	.155	.161	.166	.171	.175	.179	.187	.194		.2
.3	.467	.248	.233	‍.233	.237	.242	.248	.253	.258	.263	.267	.271	.276	.280	.287	.294		.3
.4	.318	1.296	.555	.452	.415	.398	.390	.286	.384	.384	.384	.385	.387	.388	.392	.396		.4
.5			3.254	1.030	.753	.648	.595	.564	.544	.530	.521	.515	.510	.506	.502	.5		.5
.6				7.031	1.648	1.115	.916	.814	.753	.712	.684	.663	.647	.635	.618	.607		.6
.7					10.930	2.297	1.493	1.192	1.037	.943	.890	.835	.802	.776	.740	.716		.7
.8		Negative values				11.211	2.824	1.831	1.447	1.245	1.120	1.037	.977	.932	.869	.828		.8
.9							9.223	3.136	2.090	1.658	1.424	1.276	1.176	1.103	1.005	.943		.9
1								7.297	3.242	2.259	1.817	1.566	1.405	1.294	1.149	1.060		1

(The boxed combinations in the table are at B=.3 / x=.2, x=.25 and at B=.4 / x=.5, x=.55, x=.6.)

1) The boxes represent the combinations of x and B at which y values at x_{max} is less than 1.

The x_{max} occurs when

$$x = \exp(1 - 1/B).$$

The values of x at B = .3 are shown in *Table 4* for different rotation ages, and that at various B are shown in *Table 1* on the bottom row with A = 1. An interesting feature of this special case is that the genetic juvenile-mature correlation (r) is identical to B at x_{max}. This can be shown by replacing x_{max} in (6) such that

$$r(x_{max}) = 1 + B\ln(x_{max})$$
$$= 1 + B\ln[\exp(1-1/B)]$$
$$= B.$$

Extended Time Model

In the basic model, g and r were either linear or logarithmic functions. In this section we will let $g = h_t/h_T = 1$, $r = 1 + B\ln x$, and the denominator of the basic model (Equation 2) to vary. The extended time model is expressed as

$$Q_y = Qr/(x + k^*)$$
$$= Q(1 + B\ln x)/(x + k^*)$$

where $k^* = K/T$, $Q = ih_T^2 \sigma_T/T$, and

k represents the actual amount of time added.

By differentiating y with respect to x and equating the derivative to zero we get,

$$\ln x - k^*/x = 1 - 1/B, \text{ or}$$
$$\ln x - k/xT = 1 - 1/B \quad \text{---------------------------------} \quad (15)$$

By changing the k values a wide variety of situation can be examined. Two cases of interest are as follows.

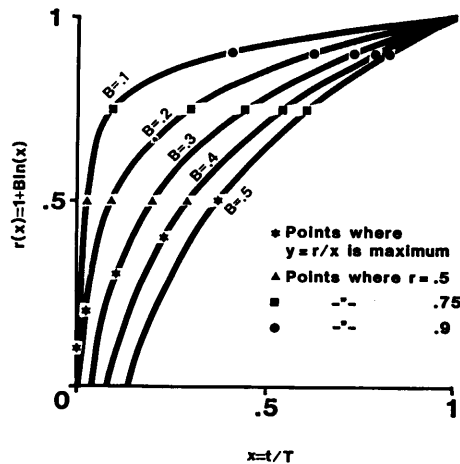*Case 1:* LAMBETH (1980) extended T and t to T + 3 and t + 5,

Figure 3. — Curves of r = 1 + Blnx with various values of B. The values of r at x_{max} (starred points) are: 0.1, 0.2, 0.3, 0.4, and 0.5 for points 1, 2, 3, 4, and 5, respectively.

respectively. Such extension was necessary to accomodate time needed to make the regeneration, such as flower induction. His scheme can be expressed as,

$$y = (1 + B\ln x)/(x + 5/T).$$

Note that T + 3 is a constant and can be incorporated into Q such that $Q^* = ih^2_T\sigma_T(T + 3)/T$. The replacement of k = 5 in Equation 15 will generate.

$$\ln x - 5/xT = 1 - 1/B.$$

The above equation is numerically evaluated for B = .3 *(Table 4)*.

Case 2. Two-cycle model:

Another special case of interest is when k = T. This represents the situation where the realized genetic gain in the subsequent production population is divided by the entire period of breeding and production. In this model the regeneration time, such as in Case 1, is ignored. Then the model becomes

$$y = (1 + B\ln x)/(x + 1), \text{ and}$$

the roots of

$$\ln x - 1/x = 1 - 1/B \quad \text{------------------------------------} \quad (16)$$

will generate the desired x_{max}. By using the first three terms of Taylor's series expansion about x = .5, (16) may be approximated as

$$20x^2 - 32x + 18.386 - 2/B = 0, B \leq .358$$

with the solution $x = .8 - .025 \sqrt{160/B\text{-}446.88}$. However, the approximation has a narrow range of application, say $.2 \leq B \leq .31$. For B values outside the above range the root of (16) was numerically evaluated *(Table 4)*.

When B = .5, (16) becomes

$$x\ln(x) + x - 1 = 0,$$

with the solution x = 1. Such evaluations show that, when compared to the basic model, the two-cycle model length-

Table 4. — Comparison of the basic model [g(x) = 1] and extended models when B = .3[1].

		T							
		20	25	30	35	40	45	50	100
Basic Model	x_{max}	.097	.097	.097	.097	.097	.097	.097	.097
	t_{max}	1.94	2.92	2.91	3.39	3.88	4.36	4.85	9.7
Lambeth model	x_{max}	.256	.231	.212	.199	.188	.180	.173	.139
	t_{max}	5.12	5.78	6.36	6.97	7.52	8.1	8.65	13.4
Two cycle model	x_{max}	.568	.568	.568	.568	.568	.568	.568	.568
	t_{max}	11.36	14.2	17.04	19.88	22.72	25.56	28.4	56.8

1) x_{max} values of the two cycle model at different B values are .142, .33, .791, and 1 for B values of .1, .2, .4, and .5, respectively.

ens the x_{max} substantially *(Table 4)*. When B = .3, the x_{max} is longer than 1/2 of the rotation. Furthermore, when B ≥ .5, juvenile selection loses its advantage completely. The coefficient B for the loblolly pine example of FRANK-LIN (1979, *Table 3)* is .432. At this B value, t_{max} = 0.86T.

Unless the juvenile-mature correlations are so high that B is less than .2, the early selection age suggested in the basic model will not be realized in the two-cycle model. Conceptually, it is possible to shorten the age when the annual genetic gain is maximum by reducing the rotation length (T). Such reduction in rotation length would tend to increase the genetic correlation between an earlier juvenile age and the rotation time. The reduction in rotation time, however, may not change B (LAMBETH, 1980). Therefore the impact of reducing the rotation length is to reduce t_{max}, but not x_{max}.

Maximum Future Net Worth Model (MFN)

The basic model and extended time models use different time parameters as the denominator for determining the annual genetic gain ($\triangle G^*_t$ or $\triangle G^*_x$). The annual genetic gain, however, does not always generate practically meaningful answers. Consider, for example, the basic model with g(x) = 1. As was discussed before r(x) at x_{max} equals B *(Figure 3)*, which means that the expected genetic gain at x_{max} ($\triangle G_{max}$) is only B fraction of that obtainable at the rotation age (i.e. $\triangle G_{max} = B\triangle G_T$). For small B, $\triangle G^*_x$ is maximum at x_{max} mainly because of the extremely small x used as the denominator. An extreme situation can be seen in *Figure 3*, when B = .1 The x_{max} = .0001 and $r(x_{max})$ = .1, meaning $\triangle G_{max}$ = $\triangle G_T/10$. However, the x at which $\triangle G_x$ = $.5\triangle G_T$ is .007 and that at which $\triangle G_x$ = $.75\triangle G_T$ is .083. All the x values are very small, and selecting at x = .0001 to maximize $\triangle G^*_x$ is a nonsense. The situation improves as B increases. When B = .3. the x values are 0.097 (x_{max}), 0.189, and 0.435 for $(3/10)\triangle G_T$, $0.5\triangle G_T$, and $0.75\triangle G_T$, respectively. Nevertheless, the example demonstrates the need to use the concept of annual genetic gain with caution.

One way of avoiding such potential complication is to use the expected genetic gain at different time ($\triangle G_t$ or $\triangle G_x$) directly, by incorporating it into an economic model. In this section the future net worth equation is utilized for that purpose.

Future net worth (FNW) is defined as follows (LUNDGREN, 1973):

$$FNW = P_tV_t - c(1 + R)^t,$$

where P_t and V_t represent the price and quantity (or volume) of the products at time t,

    R represents the interest rate, and

    c represents the initial cost.

The FNW equation can be modified to incorporate the genetic gain at different period as follows.

```
FNW = [1 + f(ΔG )]qV  - c(1+R)  ------------------------ (17)
               x    t
where P  is replaced by [1 + f(ΔG )]q.
       t                        x
   q represents the price of unimproved seeds, and
f(ΔG ) is an unknown function of expected genetic gain ΔG .
    x                                                    x
```

The assumption are: 1) The time between the selection and seed production is ignored. 2) $f(\triangle G_x) = \triangle G_x$ which implies that the price of the improved seeds is proportional to the expected genetic gain at different time. 3) all the seeds produced are utilized, and the quantity of seed production is constant for the different selection ages. Then we can

assume $V_t = V_T$. 4) The subsequent operation cost (including the seed production) is constant for all different selection times.

```
By replacing ΔG  = ih²g(x)r(x)σ  in (17) we get.
               x     T         T
    FNW = [(1 + ih²g(x)r(x)σ )qV  - c(1+R)^xT
                  T        T   T
where x = t/T, and 0 < x ≤ 1.
The above equation can be modified such that
    FNW - qV
          T      = g(x)r(x) - k(1+R)^xT
    (ih²σ )qV
       T T   T
              = H(x) = H
                     c
    where k = ----------.
              (ih²σ )qV
                 T T   T
If we assume that g(x) = 1, and r(x) = 1 + Blnx
    H(x) = (1+Blnx)-k(1+R)^xT
Differentiating H with respect to x, and equating the resulting
derivative to zero yields
    xT(1+R)^xT = B/kln(1+R) --------------------------------- (18)
Since x=t/T, (18) may be rewritten as
    t(1+R)^t = B/kln(1+R), 0 < t ≤ T ------------------------ (19)
From (19), we can see that t    no longer depends on T, the
                            max
rotation age. Approximate solutions to (19) may be obtained by
using the first two or three terms of Taylor's series expansion
of (1+R)^t about t=0. The use of the first three terms of the
Taylor's series expansion yields.
    t    = [(³√u+v + ³√u-v ) - 2] / 3ln(1+R)--------------- (20)
     max
where u = (54B/k + 20)/2, and
    v = [√(54B/k + 20)² + 32] / 2
```

Equation 20 tends to overestimate t_{max}, but is fairly useful for k ≥ .1. From *Table 5*, we can see that there are certain combinations of B, R, and k under which juvenile selection is not beneficial (for example, B = .3, R = .05, k = .1, and T = 20), where k represents the ratio between the initial cost and the return at the regular rotation age T.

The most important findings of MFN include, 1) the t_{max} is determined by both biological and non-biological factors, and 2) it might be easier to work with non-biological factors to adjust t_{max}. The combined influence of k and B on the t_{max} is in the form,

$$z = B/k$$

where z is a combined factor influencing the t_{max}. The explicit expression for z is,

```
z = (ih²σ )qV )³/c ----------------------------------- (21)
       T T  T
```

and all the components in the numerator influence the amount of return than the cost. Therefore larger z values mean larger return/cost rate, which will retard the t_{max}.

In equation (21), h^2_T, σ_T and B are biological variables, and i, q_t, V_t, and c are economic variables. In practice, it might be more practical to attempt to adjust the t_{max} by manipulating non-biological variables. For example, by increasing the selection intensity, the breeder can delay the t_{max}. If advanced propagation methods, such as tissue culture, become practical, the V_T, and h^2_T will increase, and the return on the selection could peak at rotation age. Low initial investment as well as high cost of unimproved seeds will also lengthen the t_{max}.

The t_{max} is also influenced by the interest rate (R). Equation 20 shows that higher interest rates will shorten the t_{max}. To obtain t_{max} values under different interest rates, one may multiple $\ln(1.05)/\ln(1+R)$ to the t_{max} shown in *Table 5*.

The MFN model also suggests that early selection for the sake of an early return on investment only may not be

K=.05

k	B				
	.1	.2	.3	.4	.5
.1	11.78	18.06	22.65	26.35	29.49
.25	6.11	10.14	13.25	15.83	18.06
.5	3.46	6.11	8.28	10.14	11.78
.75	2.43	4.41	6.11	7.60	8.93
.9	2.06	3.79	5.29	6.62	7.83
1	1.87	3.46	4.86	6.11	7.24

1) R = interest rate,
k = $c/(ih^2_T \sigma_T) qV_T$,
c = initial cost,
T = rotation age, and
B = the slope of r (x) in log scale.

always desirable. For example, assume that a breeder practiced selection at an early age to obtain an early return on investment. Also assume that he has to bear additional costs arising from early flower induction. In order to make up for the additional investment, MFN model suggests the selection be made sooner. The further shortened selection time will require even more investment for flower induction research and development. Obviously, this will not lead to a realistic maximum. In many tree breeding programs activities such as flower induction can be justified for reasons other than juvenile selection combined with mass propagation, and the investment may not be considered as an additional cost for making early selections.

Although MFN model avoids the problem of the basic model and extended time models, it has its own shortcomings. In addition to genetic assumptions such as g(x) = 1, and r(x) = 1 + Blnx, the model requires many economic simplifying assumptions. It is unlikely that assumptions such as no time lag between selection and seed production, $V_t = V_T$, $f(\triangle G_t) = \triangle G_t$, and no subsequent operational cost difference between different selection times can be justified in the real world. The model is, however, valuable because it demonstrates the need for balancing economic factors and biological factors to determine the optimum

selection time. It also indicates a direction of future development in economically realistic prediction models.

Multiple Cycle Model

There are two approaches to juvenile selection in tree breeding (KANG, 1982). The first deals with improving the juvenile trait itself, and the performance of the individuals at a later stage is not important: Hence, juvenile-mature correlation is not a pertinent issue. This approach reflects the recent interest in short-rotation forestry, which tend to change the quality of the wood supply.

In the second approach, juvenile selection is considered as a technique that influences the tempo of overall breeding activities. For a given time, say 50 years, the tree breeder has a choice of different selection cycles. For example, jack pine flowers as early as 12 months (RUDOLPH, 1979), so the breeder may then ask how selection cycles, say 6, 4, 3, 2, and 1, will influence the total genetic gain at the end of 24 years (Figure 4).

Since most breeding techniques are applied to breeding stocks during selection and crossing time, the more generations occuring within a fixed period the more opportunities to apply breeding techniques will be. Therefore, many well established crop breeding techniques can be more readily applied to tree breeding if a short multi-cycle option is used. For example, in jack pine (or other species with the possibility of early flower induction) the development of inbred lines, with or without selection, can be achieved in less than 50 years, which is a typical single rotation time for many tree species.

In the multiple-cycle model h^2_T and σ_T can no longer be considered fixed, because population parameters change over different selection cycles. Furthermore the distribution of g(x) and r(x) will vary over different generations. therefore, two types of time have to be considered: time within a single generation (x), and the number of generations (n). The general expression of the accumulative genetic gain for the multiple cycle model is:

$$\triangle G^n_x = i \sum_{j=1}^{n} h^2_{T_j} g_j(x) r_j(x) \sigma_{T_j} \quad \text{---------------------- (22)}$$

where j indexes the generation. Because $g_j(x)$ and $r_j(x)$ vary, x_{max} will also vary over different generation. As will be
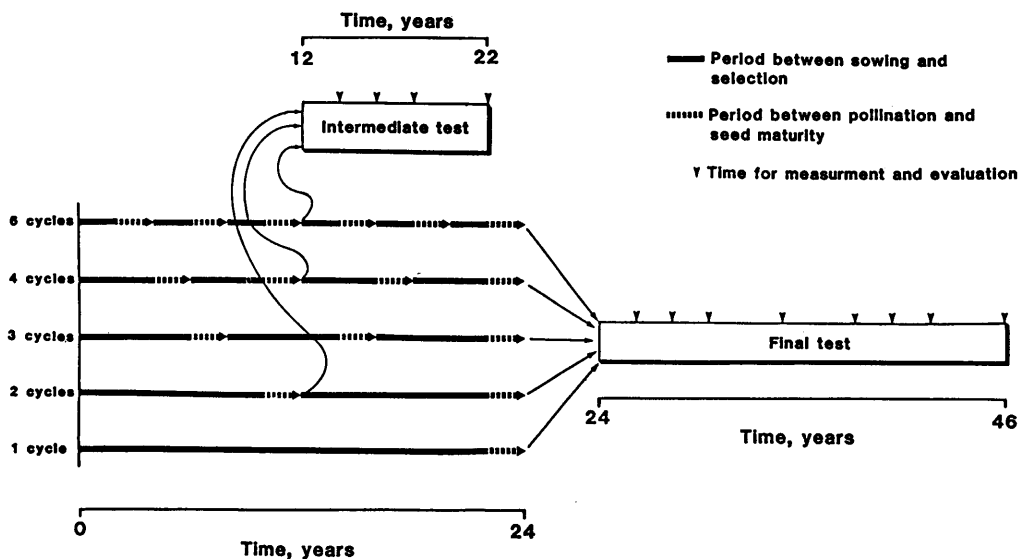

Figure 4. — A testing scheme for various generation turnover cycles under the multiple cycle selection model: An example that can be used for species such as jack pine.

assumed later, only when the distributions are considered fixed over generations the two different types of time, x and n, will have interchangeable meanings.

Currently, little knowledge on the genetic causal components, such as the number of loci, linkage structure, and interaction among alleles etc., of quantitative traits of trees is available. Therefore, developing a prediction model of multiple-cycle selection is even more difficult than that in the previous models. It is, however, possible to develop theoretical models which can be used to understand the changes of the parameters over generations. These questions will be discussed further in another paper.

In this section the assumption that h^2_T, σ_T, $g(x)$, and $r(x)$ do not vary over generations is made. The assumption will make it possible to connect x and n in an explicit form. Under the assumption Equation 22 can be rewritten as:

$$\triangle G^n_x = nih^2_T g(x)r(x)\sigma_T.$$

If we further impose the restriction that different selection schemes will be evaluated at time T, then the number of cycles (of length t) one can have during time T is n = T/t = 1/x, and

$$\triangle G^n_x = (1/x)ih^2_T g(x)r(x)\sigma_T$$
$$= TQgr/x$$

where $Q = ih^2_T \sigma_T/ T$ as was the case in Equation 2. Because both T and Q are constants, x_{max} can be obtained by finding x which maximizes y = gr/x. Once x_{max} is found, the number of generations which maximizes $\triangle G^n_x$ can be determined by the relation,

$$n_{max} = 1/x_{max}.$$

The changing nature of x_{max} has been discussed in the basic model and extended time models.

Another worthwhile question is: how many short cycles are necessary to obtain a level of genetic gain equivalent to that achieved with a single long cycle? This question is equivalent to asking for the x which guarantees y =1 in

Table 6. — B^*_{min} at various values of x.

Time for seed maturation	x								
	.1	.2	.3	.4	.5	.6	.7	.8	.9
1 year	.367	.466	.545	.614	.677	.734	.789	.841	.890
2 years	.345	.438	.513	.578	.636	.691	.742	.791	.837

Table 7. — Genetic correlation, r(t), n, and n* for loblolly pine height at various ages (data from FRANKLING, 1979). Underlines represent situations where n* > n.

t		T					
		5	7	10	15	20	25
3	r(t)	.93	.84	.66	.41	.07	.17
	n*	1.08	1.19	1.52	2.44	14.29	5.88
	n	1.4	1.8	2.4	3.4	4.4	5.4
5	r(t)		.93	.76	.50	.19	.34
	n*		1.08	1.32	2.00	5.26	2.94
	n		1.29	1.71	2.43	3.14	3.86
7	r(t)			.86	.60	.34	.40
	n*			1.16	1.67	2.94	2.50
	n			1.33	1.89	2.44	3.00
10	r(t)				.62	.49	.41
	n*				1.61	2.04	2.44
	n				1.42	1.83	2.25
15	r(t)					.88	.88
	n*					1.14	1.14
	n					1.29	1.59
20	r(t)						.87
	n*						1.15
	n						1.23

the basic model. This question is useful if early selection is viewed as an activity that influences the tempo of overall tree breeding efforts. Because the question does not seek for x_{max}, the answer is likely to point towards smaller x and larger n. Larger n will generate more chances to apply different breeding techniques. In a qualitative sense, larger n might generate more overall gain from breeding than smaller n which maximizes $\triangle G^n_x$. To obtain the answer we equate $\triangle G^n_x$ with $\triangle G_T$, and solve for n:

$$\triangle G^n_x = nih^2_T g(x)r(x)\sigma_T = ih^2_T \sigma_T = \triangle G_T$$
$$ng(x)r(x) = 1$$
$$n = \frac{1}{g(x)r(x)}.$$

If we assume as before that g(x) = 1, and r(x) = 1 + Blnx

$$n = 1/(1+Blnx) \quad \text{------------------------------------} \quad (23)$$

To determine n it is necessary to find the intermediate root of

$$T(1-x) + (T+s)Blnx = 0,$$

where s represents an arbitrary constant such as the time required for seed maturation. Note that x = 1 is a trivial solution. The replacement of the intermediate root in (23) will yield the desired n.

Let n* = (T+s)/(t+s), for species that require s years for seed maturation. If n* > n, repeated juvenile selection at age t will yield a greater genetic gain than selection at T.

It is also possible to use B to compare different selection cycles. Let r* = 1/n*, then n* > n is equivalent to saying that r > r*, or

$$1+Blnx > (t+2)/(T+2), \quad \text{------------------------------------} \quad (24)$$

for species with 2 years for seed maturation. By solving equation (24) for B we get

$$B < \frac{T}{T+2} \frac{x-1}{lnx} = B^*, x \neq 1.$$

Since B* is an increasing function of T, any B that is smaller than B* with a small T will certainly be smaller than B* with a larger T. If we let T = 15 as the shortest rotation time, then we can write

$$B < B^*_{min}$$

where $B^*_{min} = .882(x-1)/lnx$.
For species with 1 year for seed maturation, we get

$$B^*_{min} = .938(x-1)/lnx.$$

Table 6 shows B^*_{min} for various values of x. By comparing the actual B values and the table values, we can determine at what age juvenile selection begins to be acceptable.

Table 7 shows r(x), n, and n* for various values of t and T of loblolly pine (from FRANKLIN, 1979). It is difficult to explain why r(t*, 20), r(10, 15), and r(10, 25) are not large enough to justify juvenile selection, where t* represents ages 3, 5, 7, and 10. But the disadvantage of the selection at age 3 when T = 25 is not unexpected. The B = .432, in the loblolly pine data leads to the conclusion that juvenile selection is advantageous at x > .2, or 1/5 of the rotation time (T) (Table 6). At age 3 with T = 25, x = .12, B* = .384, and B > B*.

LAMBETH (1980) used B = .308 for several Pinaceae species. At B = .308 juvenile selection at any time greater than or equal to 1/10 of the rotation time will be advantageous (Table 6). Therefore, in most practical situations, repeated juvenile selection will lead to genetic gains equivalent to single generation turnover at maturity. This finding, together with the increase in the number of opportunities to apply breeding techniques in multiple short cycles, make juvenile selection an attractive option.

Table 8. — Selection time (in years) suggested under various models when the rotation age is 25.

Model	g			
	.432	.4	.35	.308
Franklin (1979)	12.5	12.5	12.5	12.5
Basic model (x_{max})	6.7	5.6	3.9	2.6
Basic model (r'=1)	10.8	10	8.75	7.7
Lambeth (1980)	10.7	9.5	7.6	5.8
Two cycle	21.5	19.8	17.0	14.6
MFN k=.1	T[1]	T[2]	24.6	21.8
k=.5	10.7	10.1	9.2	8.4
k=1	6.5	6.1	5.5	5.0
Multiple cycle (s=2)	4.2	3.4	2.3	1.5
Multiple cycle (s=1)	3.8	3.0	2.0	1.3

1) The age suggested by the model is 27.4.
2) The age suggested by the model is 26.3.

Discussion

To determine a precise optimum selection age of a population one needs a rather detailed information on the performance of the population over a wide range of locations as well as time. When such information is present, it is not critical to develop models described in this paper to determine the optimum selection age. When such information is lacking, but general information for early selection is desired, the models could be useful, with the understanding that the models generate elementary information which could be of some value in decision making, but not prediction values. In this section I will discuss subjects which are useful for understanding the dynamics of t_{max}, and the components that influence optimal selection age. No efforts will be made to discuss any particular numbers generated from the models.

The models presented in this paper are by no means complete or realistic. To understand the validity of the models it is necessary to examine their shortcomings. We will use four different, but interdependent factors to examine the models. They are: 1) the available information on basic parameters, 2) the validity of approximating the parameters by using some time dependent functions, 3) the structure of the models, and 4) the nature of the evaluation criteria.

Information on Parameters: Two most important parameters are the heritability ratio. g, and the genetic juvenile-mature correlation, r. The information on both parameters are limited, but sufficient to develop simple models on single cycles of selection. Recent papers by FRANKLIN (1979) and LAMBETH (1980) summarized the available information. The information on g is not as well structured as that of r. Although the information on g and r come from similar sets of data base, the specific nature of r, which we will discuss later, makes it easier to incorporate it into models. The available information is not sufficient to make the early selection ages of different models to converge to a small range of numbers (Table 8). Note, however, that more information does not necessarily imply a convergence to early selection ages.

Further work on economics of early selection is necessary to generate information on economic parameters, such as k, as described in the MFN model. Such efforts will also generate economic models which are more realistic than MFN.

Little information on the nature of g, and r over different generations is available. It is unlikely that the information will be generated for a majority of conifer species in the near future. It is however, possible to obtain information from species such as jack pine and willows. Some information can be generated by theoretical means. This subject will be discussed in a separate paper.

Approximation of the Parameters: In this paper the heritability ratio, g, was approximated by a linear function of time. It is possible to use other functions to represent g and r. For example FRANKLIN's phase concept can be approximated by using a step function or a quadratic function of time. Such functions might influence the x_{max} to move toward the middle of x values rather than to the early part of x as was shown in the basic model. However, if x_{max} is the criterion of interest in the basic model, the nature of the function might not matter for r values up to somewhere around 0.3.

Furthermore Defining a function to approximate g also depends on the definition of the rotation age. If the mature stage in the sense of FRANKLIN (1979) is considered as the rotation age, a linear approximation might be acceptable. If the codominance suppression phase is considered as the rotation age, a quadratic function would be more useful. If the changes in the heritability is not too drastic among different phases, the assumption that g = 1 might be considered as a good approximation.

The choice of the function to approximate the genetic juvenile mature correlation, r, does not depend on the definition of the rotation age. The closer the time is to the reference point the higher the correlation will tend to be, regardless of the time chosen as the reference point. This is why the information on r is structured better than that on g although both come from the similar data base.

A number of different functions may be taken to represent r. Both a linear function and a log function were used here. The linear function is not as descriptive as the log function, but the simplicity makes it useful. The linear function of *Figure 1* was obtained by connecting two points, (.75, 1+Blnx) and (1, 1) of the log function, y = 1 + Blnx. In practice, however, data points between x = .5 and x = 1 may be used to fit a linear regression line which passes through (1, 1). It is possible to use a quadratic or cubic functions in place of the linear function. In that case the points between a smaller number, say x = .3, and x = 1 may be fitted, provided that the r tends to be high in general. The use of cubic function does not simplify the approximation. It carries too many parameters (i.e. coefficients). The log function as defined here carries only one parameter, B.

Of the functions that may be used to approximate r, the log function seems to offer the best results, but its usefulness for small x values is questionable. As x approaches zero the function drops quickly, and enters into the region of negative correlation (Figure 3). This problem is shared by other functions also, except that they migh overestimate the correlation. Regardless of the function used one should be careful about the interpretation of the values at small x. At this time it is not advisable to choose a small x as optimum selection age even if the model indicates to that direction. This is the area where the added information on r could make a difference. It can help to choose a function that is suitable for the approximation, and to determine how close to zero the function can be extended.

Structure of the Models and Evaluation Criteria: The two factors are treated together because they are very in-

terdependent. All the models address the optimum selection time, but the criteria used to evaluate the time vary. The basic model, extended time model and multiple cycle model use the expected annual genetic gain as the measure for determining the time for $\triangle G^*_{max}$, or when $\triangle G^*_x = \triangle G^*_T$. The MFN uses the expected genetic gain $\triangle G_{max}$. The expected genetic gain migh be a better measure than the annual genetic gain for economic analysis of early selection.

The annual genetic gain is a relative quantity, like heritability, and is useful for comparing different populations, but the relative nature itself makes it difficult to interpret the validity of x_{max} evaluated in the models. As discussed in the introduction to the MFN section, the division of the expected genetic gain by x could lead to a nonsense value for maximum point for cases with high genetic juvenile mature correlations. It was also shown in *Table 2* and *Figure 2* that the reduction in x to obtain smallest x_{max} requires an extremely large increase in the intercept (A) of the heritability ratio, g.

Obviously, there must be a point where the reduction in x is accompanied by fast decrease in the correlation, r. The log functions in *Figure 3* show that any of the curves may indeed be approximated by two linear functions of different slopes. The point where such division occurs might be the point where the loss of correlation does not justfy the reduction in x. For the log function, the point is where the slope of the curve (or $r = dr/dx$ is 1, or x = B. Any reduction of x below x = B will cause faster reduction in r than in x. Despite the faster reduction in r, the annual genetic gain will continue to increase as x decreases beyond B until it reaches x_{max}.

An alternate way of defining x_{max} with respect to annual genetic gain is to apply the restriction that x_{max} be defined between $B \leqq x \leqq 1$. When x_{max} does not exist within the range, then x = B is taken as x_{max}. If g(x) = 1, the basic model has no intermediate x_{max}, and y is maximum when x = B. In extended models the addition of

constants in the denominator delays the x_{max}, and increases the chance that the x_{max} will fall between B and 1.

The problems associated with interpreting the concept of annual genetic gain and defining the x_{max} suggest that it is not necessarily correct to equate the optimum selection age and x_{max}. In the basic model x = B could be the optimum selection age even though the annual genetic gain is not maximum at this point. In multiple cycle model. and in the basic model, earliest x which generates y = 1 could be considered as optimum selection age.

The multiple cyle model presented here does not generate any information that is significantly different from the basic model, except that the x is translated into n. However, the model is important because it defines a reference point which can connect the single cycle models and multiple cycle models.

Literature Cited

Dickerson, G. E. and L. N. Hazel: Effectiveness of selection on progeny performance as a supplement to earlier culling in livestock. J. Agr. Res. 69: 459—476 (1944). — Franklin, E. C.: Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica 28: 207—212 (1979). — Kang, H.: Components of a tree breeding plan. Proc. IUFRO Joint Meeting of Working Parties on Genetics about Breeding Strategies Including Multiclonal Varieties. Sensenstein, W. Germany. Sept. 6—10. Pp 119—135 (1982). — Lambeth, C. C.: Juvenile-mature correlations in *Pinaceae* and implications for early selection. Forest Science 26: 571—580 (1980). — Lundgren, A. L.: Cost-price: A useful way to evaluate timber growing alternatives. USDA, Forest Service, Research Paper NC-95, 16 pp. (1973). — Namkoong, G., and M. T. Conkle: Time trends in genetic control of height growth in ponderosa pine. Forest Science 22: 2—12. (1976). — Namkoong, G., R. H. Usanis, and R. R. Silen: Age-related variation in genetic control of height growth in Douglas-fir. Theore. and Appl. Genet. 42: 151—159 (1972). — Rudolph, T. D.: Female stroboli on 12-month-old jack pine. Tree Planters' Notes 30: 24—26 (1979). — Squillace, A. E., and C. R. Gansel: Juvenile-mature correlations in slash pine. Forest Science 20: 225—229 (1974).

Provenance Study of Douglas-Fir in the Pacific Northwest Region IV. Field Performance at Age 25 Years*)

By T. L. White and K. K. Ching**)

Summary

Twenty-five-year results are reported for 14 Pacific Northwest provenances of Douglas-fir growing in 5 thinned, fast-growing plantations. In all plantations, the southern Oregon provenance was the poorest performer for all response variables (height, diameter at breast height, height: diameter ratio, volume per hectare, and site index). It produced 30 percent less volume than the average of the other provenances. Differences among the other 13 provenances were smaller and often not statistically significant. Provenance $\times$ plantation interactions were generally not significant when the southern Oregon source was omitted from the analyses. These results seemingly contradict experiments with seedlings and young plantations which indicate an extremely tight adaptation of Douglas-fir populations to the local environment in which they evolved. Of the several possible explanations for the apparent discrepancies, the most likely is a lack of experimental precision in the present study.

Key words: Douglas-fir, provenance, yield, genotype $\times$ environment interaction.