OPTIMAL AGE FOR SELECTING LOBLOLLY PINE SEED SOURCES

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Abstract:--Five methods to estimate the optimal age for selection were compared using measurement of total tree height of 15 provenances at 5, 10, 15, 20, and 25 years of age obtained from a south-wide loblolly pine seed source study. The best time to separate seed sources, based on the comparison of F-values, is at age 15, when the heritability is also at its peak. However, because phenotypic variance increases with age, maximum genetic gain at a given selection intensity occurs five years later, at age 20. Based on the annual genetic gain, selection should be at age 10. Correlation between initial growth and periodic growth becomes negative after age 15. Thus, the optimal age for selecting trees for height growth among loblolly pine of different provenances should be between age 10 and 20 years.

Keywords: Pinus taeda L., provenance test, genetic gain.

INTRODUCTION

Loblolly pine is a commercially important species of the eastern United States. Long-term seed source trials have been established in its native range (Wells 1983), at the fringe of its range (Rink and Thor, 1971, Talbert and Strub, 1987), and outside of its native range (Rink and Wells, 1988). In recent years, sudden mortality of individual dominant and codominant trees were observed at about age 23 in southern Arkansas (Wells and Lambeth, 1983), and about age 35 in southern Illinois (Wells and Rink, 1984). The problem of late mortality may have been the manifestation of maladaptation on off-sites. The result of stress necessitates long-term observation of provenance test through a complete rotation.

However, when loblolly pine was planted within its native range, self-thinning occurred between ages 25 and 30 (Schmidtling 1988). Thus, if we did not consider selection for mortality rate, which may be either due to maladaptation or due to self-thinning, but to concentrate only on the single trait of height growth, then, when would be the optimal age for making a seed source recommendation?

The best time to determine selection age is at an age when the differences among seed source are most prominent. Variation among seed sources should be significantly greater than differences among trees within seed sources. In statistical terms, the age with the largest F-value should be the selection age.

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The second method is based on the argument that genetic control should be fully demonstrated at the selection age. Thus, the age with the highest heritability should be chosen. It will be illustrated later in this paper that this method gives the same result as the first method.

For a trait whose variance is not static and changes with time, one may argue that emphasis should be placed on the maximization of selection differential. For a given culling intensity, selection differential should be at its maximum when one make a seed source recommendation. This approach may be impractical for total growth whose variance always increases with time so that one must keep on waiting forever. Furthermore, Because heritability may vary within the life time of the seed source study, one should consider both selection differential and heritability at the same time. Thus, the selection age should be located at the peak of genetic gain, which is the product of selection differential and heritability. This is the third method.

The fourth method follows the above argument but goes a step farther. If one considers the time element, (after all, time is money) then one should place the selection age at the peak of average annual genetic gain. The average annual genetic gain is the genetic gain divided by the age of selection.

The fifth method involves comparing correlation coefficients between periodic increment and the total growth at the beginning of the period and at some putative selection age. If there is a positive correlation between the two growth traits, or the fast growing seed sources are still growing faster than the poor seed sources, it may be worthwhile to wait for the farther separation of seed source performance. On the other hand, if the correlation should become zero, then, waiting would not improve separation of seedlots. Finally, if the correlation should turn from positive to negative, then waiting is wasting of time. Because the longer you wait, the less is the differentiation among seed sources, even to the degree that it may work against the result of early selection.

In this paper, total height of trees in the south-wide loblolly pine seed source study is used to illustrate the five different methods in choosing the optimal selection age.

MATERIALS AND METHODS

The south-wide loblolly pine seed source study represented 15 seed sources in 15 plantations (Wells and Wakeley, 1966). Data used for this paper were extracted from a computer tape which was kindly provided by Dr. O. 0. Wells and the Southern Forest Experiment station. I used all available trees measured at age 5, 10, 15, 20, and 25 to calculate the average height for each seedlot in each plantation. These provenance-plantation means then were used as observations in a two-way analysis of variance. The F-value for provenance effects was extracted and from it the heritability for provenance differences was calculated. The standard deviation of phenotypic provenance means were extracted from previous publication (Kung, 1987). The 5-year periodic growth was computed by the height difference observed in a 5 year interval. Data were analyzed using Statistical Analysis System package programs (SAS, 1985).

RESULTS AND DISCUSSION

Maximum F-value

Using the general linear model for a two-way analysis of variance, the random seed sources effects are significant for all 5 ages. The maximum F-value was found at age 15 (Table 1).

Table 1. F-value, heritability (h^2), standard deviation of provenance means (Sp), genetic gain, annual gain, and correlation (r) between periodic increment and total growth in loblolly pine from age 5 to 25 years.

	Age				
	5	10	15	20	25
F-value	2.33	5.45	6.85*	6.40	4.49
h^2	0.570	0.817	0.854*	0.844	0.777
Sp	0.823	1.592	1.974	2.205	2.227
Genetic gain	0.469	1.300	1.686	1.861*	1.730
Annual gain	0.094	0.130*	0.112	0.093	0.069
r	0.729	0.808	-0.068	-0.129	

* Maximum of 5 values across a row to indicate the optimal selection age.

Using age as independent variable and the F-value as dependent variable in a second order regression, we have,

$$F\text{-value} = -2.432 + 1.126 * Age - 0.034 * Age * Age \qquad R^2 = .9992$$

and the peak F-value of 6.89 is expected at age 16.5 years (Figure 1).

Maximum Heritability

The heritability of provenance means is calculated from the F-value as follows (Kung, 1979):

$$h^2 = 1 - (1 / F)$$

The maximum heritability was found at age 15 (Table 1). The results are the same as method one because heritability is a direct linear transformation of the F-value. However, the second order regression is slightly different from the previous one:

$$h^2 = 0.303 + .0667 * Age - .00193 * Age * Age \qquad R^2 = .949$$

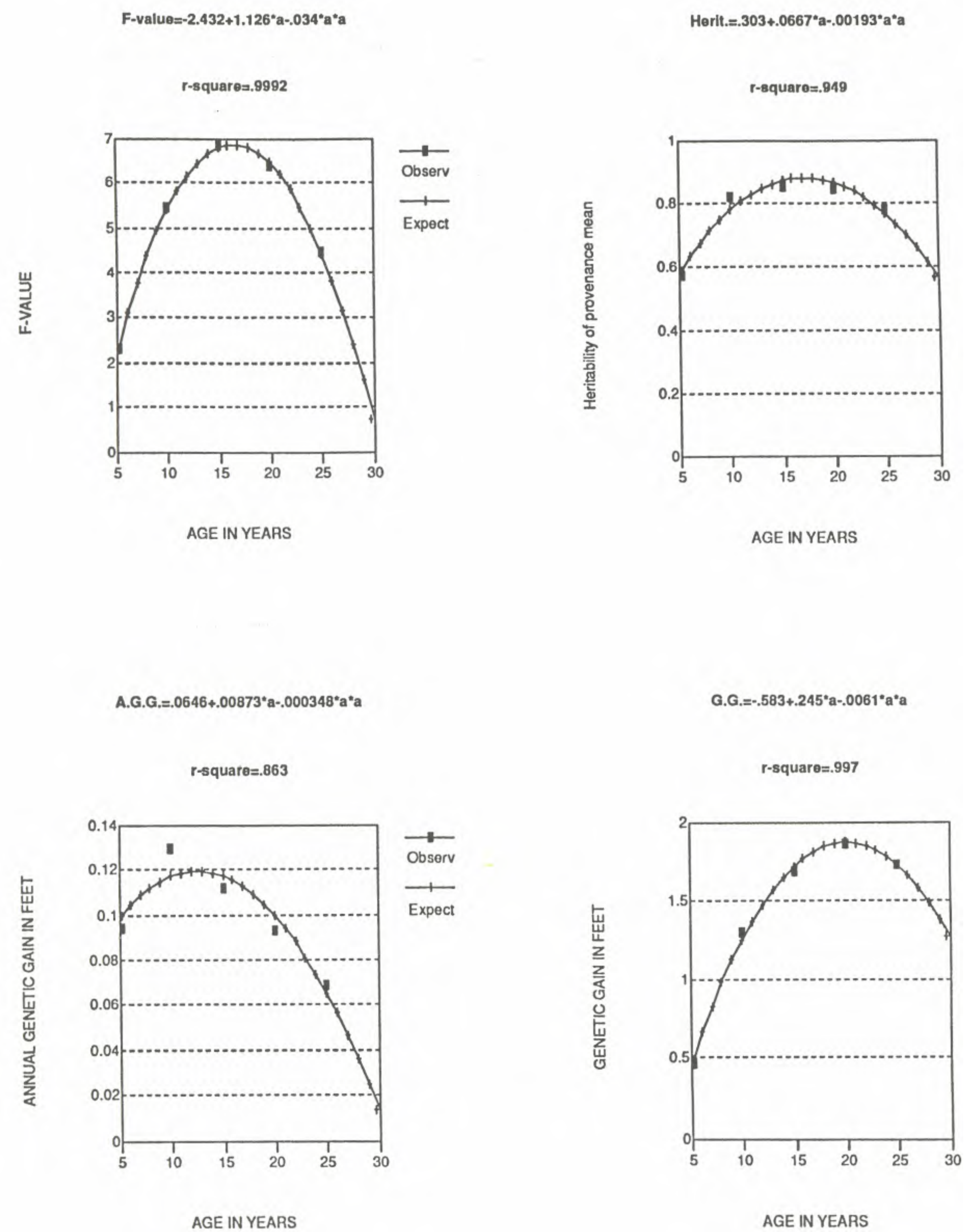

Figure 1. Relationship between age and F-value (upper left), heritability (upper right), genetic gain (lower right), and annual genetic gain (lower left).

The maximum heritability calculated from this function is 0.879 at the age of 17.3 years (Figure 1).

Maximum Genetic Gain

Assuming that the selection intensity (i) is the same for all ages, genetic gain is simply a function of Sp * h^2, in feet. The values of genetic gain in Table 1 represent one unit of selection intensity (i=1.0), or 38% of selection proportion. Changing the common selection proportion or selection intensity will change the absolute value for genetic gain but will not change the location for the peak performance. Genetic gain was maximized at age 20 in Table 1. This is the same age calculated from a regression developed from the five pairs of observations:

$$\text{Genetic Gain} = -.5832 + .2447 * \text{Age} - .0061 * \text{Age} * \text{Age} \qquad R^2 = .997$$

Maximum Annual Genetic Gain

Comparison of the five values for annual genetic gain indicates that the optimal selection age is at 10 years. It becomes age 12.5 (Figure 1) if the following regression is considered:

$$\text{Annual Genetic Gain} = .06458 + .00873*\text{Age} - .000348*\text{Age}*\text{Age} \qquad R^2 = .863$$

Correlation Between Periodic and Total Growth

The correlations between the 5-year periodic growth and the cumulative growth at the beginning of a growth period were positive for age 5 and 10, but were negative for age 15 and 20. Thus, the fast growing seed sources are growing faster before age 15, but are slower after age 15. Therefore, optimal selection age should be set at 15, unless growth rates change again after the end point of the present study.

Comparison of Results

The earliest selection age is given by the annual genetic gain criterion (Method 4). Because the annual genetic gain is computed as genetic gain divided by age, choosing this criterion will favor younger ages. In black walnut progeny tests, clonal selection could be made as early as age 4-5 years when the selection efficiency was judged by a ratio of genetic gain per year between early and later years (McKeand, Beineke, and Todhunter, 1979).

The latest selection age is given by the genetic gain criterion (Method 3). Genetic gain is the product of three components: selection intensity, standard deviation of the selection units, and heritability. If we compare this method with methods 1 and 2, given that all three methods have comparable selection intensity and heritability, but with the additional factor in method 3 (phenotypic variance of total growth) which tends to increase with age, then we can see that this genetic gain criterion will favor selection age in later years.

Using the criteria of F-value, heritability, or correlation between periodic and total growth, will favor the selection ages within the mature genotypic phase of stand development. The duration of this phase ranges from 5 to 20 years in loblolly pine and slash pine, 15 to 40 years for Douglas-fir and ponderosa pine (Franklin, 1979).

The transition into negative correlation between periodic and total growth may be explained as follows. As the trees mature sexually, height growth may be subject to restrictions imposed by the need to maintain a competitive position in the canopy and the need to allocate energy to reproductive needs. Hence, height growth may be subject to a population form of developmental canalization (Namkoong, Usnais, and Silen, 1972).

CONCLUSIONS

As illustrated in this paper, the optimal selection age changed slightly with the use of different criteria. For the height growth in loblolly pine, it may be somewhere between 10 to 20 years.

The choice of criterion may be more or less subjective, but judging by costs and benefits, the annual genetic gain criterion seems to be economically sound. If the phenotypic variance were stable over the years (for example, observations were transformed to stabilize the variance), then the three criteria (F-test, heritability, and genetic gain) would have the same results, and the F-value is the simplest to use. The F-value is already available from the analysis of variance table for the provenance test.

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