

EARLY TESTING AND JUVENILE SELECTION
IN LOBLOLLY PINE

by

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Abstract.--Two independent studies have shown that it is possible to predict heights of loblolly pine half-sib families after eight years in field tests from a single year's leader growth. Shoot elongation patterns on sixth-year leaders suggested that families have different characteristic growth strategies that may be used in early genetic evaluation. In the second study, leader growth after the free growth phase (cyclic growth) of seedlings at 31, 41 and 58 growing weeks after germination was moderately correlated (approx. +0.60) with eight-year heights of siblings in older field trials.

Additional keywords: Early genetic evaluation, shoot morphogenesis, cyclic growth, Pinus taeda L..

Successful operational procedures for early genetic evaluation must be reliable. They must also be economical, which implies that the increase in present value arising from time saved must more than offset any loss of absolute genetic gain (revenue) or increased costs. Thus, the best early genetic evaluation procedure would, for example, maximize net present value. To date, the most profitable age is earlier than the most efficient biological age.

The biological evidence suggests that the most efficient selection age for loblolly pine, (Pinus taeda L.) is between five and ten years (Lambeth 1980, Lambeth et al. 1983). This is corroborated by a recent analysis of first-generation loblolly pine genetic tests (Anonymous). Genetic gain per year for growth was optimum if selection was done after eight years in field tests. However, present value analysis (which did not consider costs) of these data suggested that selection should be made after only four years (the youngest age for which data were available). Further reduction of the test age is not likely to be profitable even if costs do not increase dramatically, since juvenile-mature correlations for juvenile ages younger than four are not reliable (e.g. Lambeth 1980). Thus, research to reduce the selection age to less than four years has moved away from age-age comparisons in conventional genetic tests. There are several factors that may contribute to the unreliability of these juvenile-mature correlations based on age four. Genetic tests are typically established at commercial spacings which increase the likelihood of high microsite heterogeneity early in the life of the stand. Competing vegetation and planting shock may also reduce the efficiency of the test design in the early years after planting (e.g. Rehfeldt, 1983; Namkoong et al. 1972). Furthermore, age-age correlations tend to be upwardly biased by re-measurement of the same individuals at different ages (Franklin, 1977). Finally, the results from older field trials may be equivocal as it was

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frequently necessary to use unsophisticated averaging procedures to estimate the performance of half-sib families from unbalanced mating and field designs (Hatcher, et al. 1981).

In current early evaluation research, the "juvenile" and "mature" tests are generally separate. This has reduced the bias due to design and serial correlation problems and increased the rapidity with which genetic testing approaches can be assessed. Remnant seeds from families already established in genetic tests ("mature" tests) are compared with the same families in short-term (juvenile) tests. These retrospective tests (after Lambeth et al. 1982) measure the association between a family's field ranking and its performance in the greenhouse or nursery.

There have been notable successes with retrospective tests (Lambeth, 1983), particularly with a Texas loblolly pine source (van Buijtenen, In press). However, there have been two obstacles: 1) the understanding of shoot growth differences between fast- and slow-growing families is lacking and 2) repeatability has often been low. We shall discuss the results of early evaluation studies on loblolly pines that addressed these obstacles in Section I and II, respectively.

I. SHOOT GROWTH COMPONENTS AND JUVENILE EVALUATION

The analysis of shoot growth components was proposed as a method to better understand the influence of genetic differences and cultural responses (Cannell 1979). The current understanding of juvenile-mature correlations could be improved if one could test the hypothesis that all fast-growing families have similar shoot growth patterns. For example, Northern pines which elongate one flush per year from a bud formed the previous year show that differences in stem unit numbers may account for differences in shoot length (tanner 1976, Cannell et al. 1976). Thus, the rate and/or duration of stem unit production and/or elongation among genotypes could be used to forecast family growth potential.

Loblolly pine shoot growth is complex in that several cycles of growth may be produced annually. The first cycle, the spring shoot, is overwintered in the terminal bud while subsequent summer shoots are initiated and elongated sequentially (Greenwood 1980). Thus, the formation and elongation of each cycle is influenced by changing environmental conditions throughout the growing season (Allen and McGregor 1962, Zahner 1962, Stransky and Wilson 1964, Allen and Scarbrough 1970, Boyer 1970, and Griffing and Elam 1971).

An exploratory study on sixth-year leader increments on loblolly pine families was undertaken in 1982 to determine whether stem units were distributed differently on leaders and to deduce the possible implications of different leader elongation patterns on family performance over a broad range of sites. Studying shoot morphogenesis on trees near the age at which selection in field tests is commonly done avoids the problem of having to use equivocal mature-tree data. It was hoped that understanding leader elongation patterns on older trees would suggest a new approach to future seedling studies.

Shoot growth components were studied on leaders of six half-sib families at two sites in eastern North Carolina (Bridgwater et al. 1985). It was found that (1) variation among families in annual leader lengths arose primarily

from differences in numbers of stem units rather than differences in the average length of leader per stem unit and (2) some families produced longer leaders by elongating more stem units for the first through third cycles, while other families had more trees which produced more stem units in fourth, fifth or sixth cycles. Furthermore, these patterns were consistent over two sites of different quality. It was hypothesized that loblolly pine families exhibited one of two leader elongation strategies. Type I growth was characterized by more stem units in cycles elongated earlier in the growing season, while Type II growth had more cycles of growth, perhaps by growing later into the season.

The implication of these hypothetical growth types is illustrated in Figure 1, A-C. If environmental conditions were the same throughout the growing season, neither growth type would be favored (Figure 1A). If favorable growing conditions existed during the first part of the growing season and were unfavorable thereafter, Type I growth would be the best strategy (Figure 1B). Type II growth would be best if unfavorable growing conditions early in the season improved later (Figure 1C).

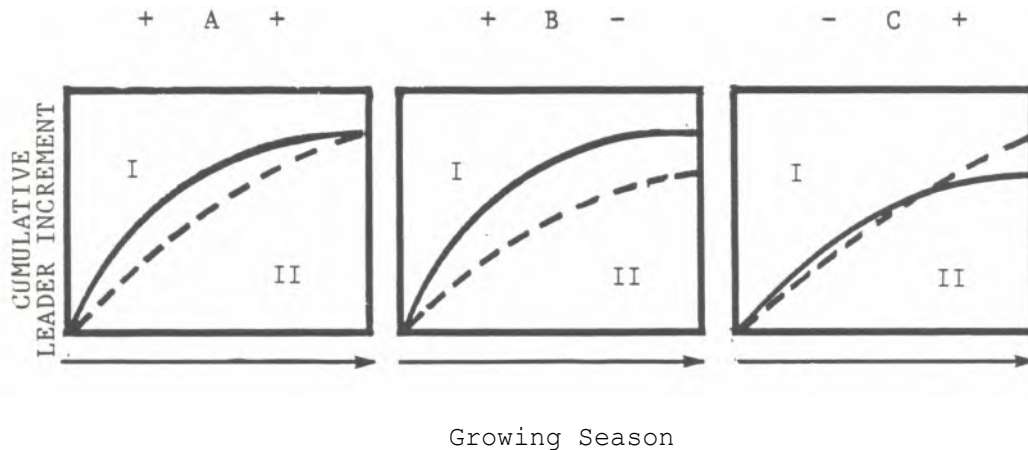


Figure 1.--Illustration of the interaction between changing environmental conditions during a growing season (+ = favorable, - = unfavorable) and two hypothetical growth types (I, II).

Standardized measures of field performance of eight-year-old siblings in other field studies could be predicted for these six families quite accurately using both the numbers of stem units produced early (on second cycles) and later (average numbers of cycles) on sixth-year leaders. Thus, eight-year family performance could be predicted from examining leader growth during a single season. However, the regression equation derived from the sixth-year leader data weighted the two variables differently for each of the two study sites. In other words, the total number of cycles produced during the season received more weight in the regression equation at one of the two sites in order to accurately predict eight-year performance. This implies that the conditions under which growth of a single annual leader are produced may change the ranking of families for field performance over a broad range of sites. But, these six loblolly pine families each exhibited similar growth patterns over the two sites, even though family ranks changed. Juvenile evaluation might be improved if these patterns were exhibited in future studies on seedlings and were consistent over a range of environmental conditions.

II. SEEDLING ONTOGENY AND ITS RELATIONSHIP TO JUVENILE-MATURE CORRELATIONS

Unrepeatable results have been another problem in early evaluation of growth traits. In one North Carolina loblolly pine population, retrospective tests have yielded positive (Lambeth, 1983) to zero or negative correlations (Williams, 1986; Dalmacio, 1982) between the same seedling growth traits and field rankings based on height or volume. Differences were not due to sampling errors and ontogenetic development differed among the studies. A genetic phase change was proposed to occur in the first year of seedling development which in turn altered juvenile-mature correlations. Measurement after the change was expected to yield higher correlations than measurement before the change.

The typical first-year shoot of loblolly pine seedlings from seed (Figure 2) produces primary needles at the apex, then secondary needles acropetally until the first bud forms at the apex. Unlike temperate zone pines, the bud will either overwinter a single flush, or break within the first season. The phase before first budset (Figure 2D) is "free growth" (after Sweet and Bollman, 1976) which is atypical of the remainder of the life cycle. Growth after first budset, cyclic growth, can be "fixed" (overwintered) (overwintered) growth or summer growth where the bud is initiated and elongated in the same season.

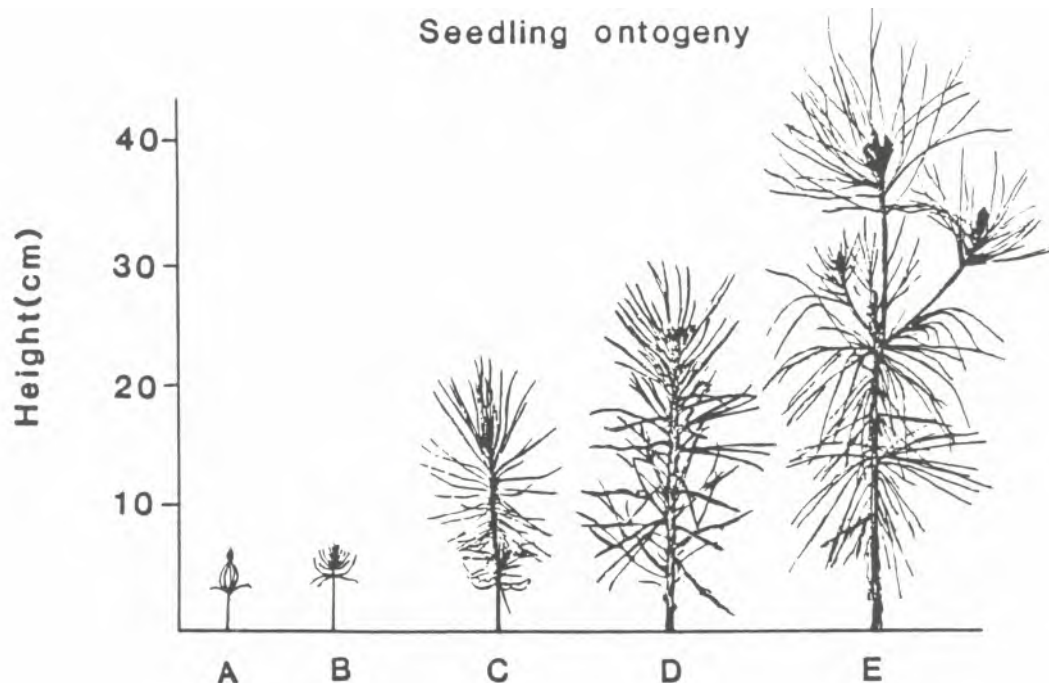


Figure 2.--Typical shoot ontogeny of first-year loblolly pine seedlings. A - cotyledon emergence with seed coat attached. B - Emerging primary needles form rosette above cotyledons. C - primary needles predominant; plant approaches minimum height for basal emergency of secondary needles. D - secondary needles emerge and split into 3's; budset begins after secondary needles emerge. This is the "threshold" stage; this part of the seedling will be carried as the juvenile stem axis. E - After first budset, cyclic growth begins. Lateral branch buds form and break and an area of sterile cataphylls separate each cycle. Morphological description based on greenhouse observations (from Williams 1986).

The family means from samples taken at 6, 8, 14 and 18 months from germination (20, 31, 41 and 58 growing season weeks) were correlated with field trial assessments. The correlation between family means based on eight-year field height and height at the four measurement periods increased as the proportion of cyclic growth increased (Figure 3). Cyclic growth length itself had a consistently high (approx. + .60) family mean correlation, and it correctly ranked two checklots of known, extreme performance. The data suggested that the free growth phase was poorly related to field growth, but that the correlation improved with increasing cyclic growth contribution. If additional experimental evidence bears this out, one should avoid the measurement of growth accumulated in the free growth phase.

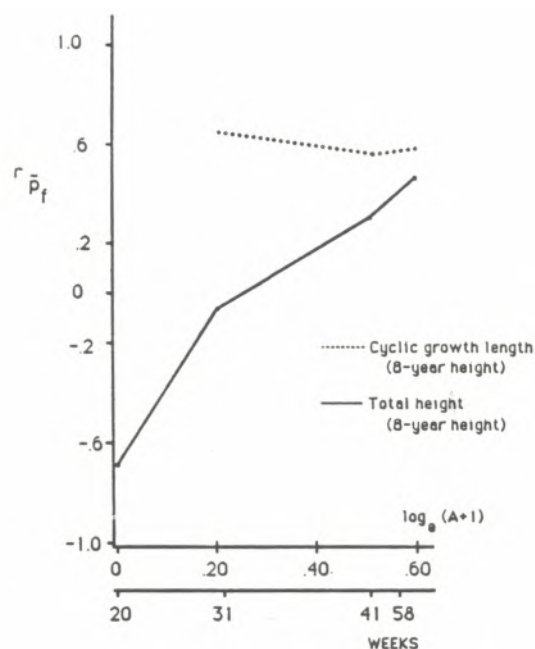


Figure 3. The family mean correlations (r_{p_f}) for height and cyclic growth length over time and ontogenetic progression. $\log_e(A+1)$ denotes the logarithm of the proportion of cyclic growth over total height. (After Williams, 1986).

In this study, late season height increment in the second year had little effect on expression of growth potential in older field tests. This study (Williams 1986) did not corroborate the model hypothesized by Bridgwater et al. (1985). If this is borne out by additional experimental evidence, then it implies that loblolly pine families that perform best over a broad range of field sites may simply produce and elongate the most stem units per unit of time.

At present, work is underway to try to quantify the effects of soil moisture stress and ambient air temperatures on leader elongation patterns. This work is expected to result in further refinements in the early evaluation process. More experimental evidence continues to corroborate the efficacy of family evaluation by age two in closely spaced genetic tests. Utility of this testing methodology (see Greenwood 1986, these proceedings) would be timely.

LITERATURE CITED

- Allen, R. M., and McGregor, W.H.D. 1962. Seedling growth of three southern pine species under long and short days. *Silvae Genet.* 11:43-45.
- Allen, R. M., and Scarbrough, N. M. 1970. Morphology and length correlated in terminal flushes of longleaf pine saplings. USDA Forest Serv. Res. Pap. S0-53, 15 p.
- Anonymous, 1986. North Carolina State Univ.-Industry Cooperative Tree Improvement Program 30th Annual Report, N. C. State Univ., Raleigh, N. C., pp. 11-24.
- Boyer, W. D. 1970. Shoot growth patterns of young loblolly pine. *Forest Sci.* 16:472-482.
- Bridgwater, F. E., Williams, C. G., and Campbell, R. G. 1985. Patterns of leader elongation in loblolly pine families. *For. Sci.* 31(4):933-944.
- Cannell, M.G.R., Thompson, S., and Lines, R. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. In: *Tree physiology and yield improvement* (M. G. Cannell and F. T. Last, eds.), p. 173-205. Academic Press, New York. 567 p.
- Cannell, M.G.R. 1979. Components of conifer shoot growth. In: *Proc. of the 5th N. Amer. For. Biol. Workshop, U. of Fla., Gainesville, Fla., March 13-15, 1978*, pp. 313-318.
- Dalmacio, R. V. 1982. The effect of nursery management on progeny test results in loblolly pine (*Pinus taeda* L.). Ph.D. dissertation, Dept. of Forestry, North Carolina State Univ., Raleigh. University Microfilms, Int., Ann Arbor, Michigan.
- Franklin, E. C. 1977. Juvenile-mature correlations. IUFRO Workshop, Brisbane, Australia, April 1977.
- Greenwood, M. S. 1980. Reproductive development in loblolly pine. I. The early development of male and female strobili in relation to the long shoot growth behavior. *A.J.B.* 67(10):1414-1422.
- Griffing, C. G., and Elam, W. W. 1971. Height growth patterns of loblolly pine saplings. *Forest Sci.* 17:52-54.
- Hatcher, A. F., Bridgwater, F. E., and Weir, R. J. 1981. Performance level-standardized score for progeny test performance. *Silvae Genet.* 30(6):184-187.
- Lambeth, C. C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *For. Sci.* 26(4):571-580.
- Lambeth, C. C. 1983. Early testing - overview with emphasis on loblolly pine. *Proc. 17th So. For. Tree Impr. Conf., Athens, GA.* pp. 297-311.

- Lambeth, C. C., Stonecypher, R. W., and Zobel, B. J. 1982. Early testing of Douglas fir in phytotron environments--the effects of selection traits and genotype-environment interactions. In: Proc. 6th N. Amer. For. Biol. Conf., Lexington, KY. pp. 137-148.
- Lambeth, C. C., van Buijtenen, J. P., Duke, S. D., and McCullough, R. B. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. *Silv. Gen.* 32(5-6):210-215.
- Lanner, R. M. 1976. Patterns of shoot development in Pinus and their relationship to growth potential. In: Tree physiology and yield improvement (M.G.R. Cannell and F. T. Last, eds.), p. 223-243. Academic Press, New York. 567 p.
- Namkoong, G., Usanis, R. A., and Silen, R. R. 1972. Age-related variation in genetic control of height growth in Douglas fir. *TAG* 42:151-159.
- Rehfeldt, G. D. 1983. Veracity of short-term testing. In: Progeny Testing. Proc. Servicewide Genetics Workshop. Charleston, SC. pp. 118-148.
- Stransky, J. J. and Wilson, D. R. 1964. Terminal elongation of loblolly and shortleaf pine seedlings under soil moisture stress. *Soil Sci. Soc. Proc.*, pp. 439-440.
- Sweet, G. B., and Bollmann, M. P. 1976. Terminology of pine shoot growth. *N. Z. J. For. Sci.* 6(3):393-396.
- van Buijtenen, J. P. An integrated accelerate breeding system. In: Proc. of a Workshop on Advanced Generation Breeding, June 6-7, 1984, Baton Rouge, LA. 10 pp. (In Press).
- Williams, C. G. 1986. Early genetic testing for loblolly pine growth traits. Ph.D. Dissertation, N. C. State Univ., Raleigh, N. C. 78 pp.
- Zahner, R. 1962. Terminal growth and wood formation by juvenile loblolly pine under two soil moisture regimes. *Forest Sci.* 8:345-352.