EARLY TESTING - AN OVERVIEW WITH EMPHASIS ON LOBLOLLY PINE

Clements C. Lambeth

Abstract.--"Early testing" for growth rate has the potential to reduce the generation cycle in loblolly pine by 4-8 years as compared to conventional field testing, though it is not yet on operational procedure. Research in this area has been hampered by a scarcity of well-designed and economically mature genetic tests by which the "early test" is gauged and sampling problems associated with characterizing family rank correlations between experiments when heritabilities are low to moderate.

Nonetheless, there are sufficient positive results from recent studies to warrant the establishment of experimental populations where "early testing" and accelerated breeding are used to cycle populations through generations as rapidly as possible to determine the validity of the procedures. A six- or seven-year cycle is possible.

Techniques in "early testing" for fusiform rust resistance and drought resistance have been developed and are currently in practice. Other adaptability traits lend themselves well to "early testing".

INTRODUCTION

The reality of reducing the breeding-testing cycle by conducting selection at very young ages has, by and large, escaped the forest geneticist though the hope still remains. Recent and successful techniques to induce early flowering have greatly reduced the breeding phase of the generation cycle in loblolly pine but for over a decade there has been little change in the duration of the testing phase. Most operational programs are based on 5 to 10-year-old selections fro, genetic tests. 4

"Early testing" is usually pictured as a process whereby trees are selected after being grown at close spacing in a greenhouse, growth chamber, or nursery for one or two years. Such testing has the potential to increase genetic gain per year by significantly shortening the generation cycle if family ranks in the "early test" are reasonably consistent with those in longer-term field tests. Furthermore, an "early test" would considerably increase the payoff for tree improvement investments by greatly reducing testing costs and the time required to capture genetic gains in production orchards.

[1/] Tree Improvement Scientist, Weyerhaeuser Co., South. For. Res. Center, Hot Springs, Arkansas.

Because "early testing" has tremendous potential to impact tree improvement efforts, if successful, it is paramount that research in this area be reviewed periodically for potential applications and to generate new ideas for research emphases.

HOW LARGE A CORRELATION?

As is often the case in scientific inquiry, "early testing" is considered "guilty until proven innocent". That is, until it is shown to be workable, or at least better than conventional testing, it will receive little use. As will be shown, proving the "innocence" of "early testing" is not a simple task even if such is the case. The question is: How strong a genetic correlation between the "early test" and later performance is needed to make "early testing" a workable procedure? To compare the effectiveness of "early testing" with selection at mature ages requires a look at their genetic gain equations. The gain (G_M) from direct selection at maturity (economic rotation age) is expressed as:

$$G_M = i_M h_M^2 \sigma_M^2$$

while the correlated gain in the mature trait from selection on a juvenile trait (sometime before maturity) is (Falconer, 1960):

$$CG_M = i_J h_J h_M r_{J,M} \sigma_M,$$

Where: J, M = subscripts that denote the juvenile or mature trait
i = selection intensity
h^2 = heritability
r = genetic correlation
σ = phenotypic standard deviation.

To determine the gain per year for each of these testing schemes requires that each be divided by T, the number of years to complete a cycle. The efficiency (E) of "early testing" as compared to testing to maturity is therefore:

$$E = \frac{CG_M/T_J}{G_M/T_M} = \frac{i_J h_J r_{J,M} \sigma_M T_M}{i_M h_M^2 \sigma_M T_J} = \frac{i_J h_J r_{J,M} T_M}{i_M h_M \quad T_J}$$

If E = 1 then equal gain per year will be realized with either scheme. In fairness though, an economic analysis is required to determine their relative values. Indeed, this is how the efficiency of "early testing" should be assessed. Working against "early testing", in an economic sense, is the fact that breeding and testing must be repeated several times during one mature selection cycle. On the other hand, some increment of gain is realized after the first "early testing" cycle and in small increments for subsequent generations, whereas with mature selection no incremental gain is realized for many years.

For the sake of argument some simplifying assumptions will be made. Assume

$$i_J = i_M,$$

$$h^2_J = h^2_M,$$

$$T_J = \text{selection age (2 years)} + 5 \text{ years to breed} = 7 \text{ years},$$

$$\text{and } T_M = \text{selection age (30 years)} + 5 \text{ years to breed} = 35 \text{ years}.$$

In reality, the selection intensity for the "early test" (i_J) should be greater than i_M since more of the smaller plants could be tested in a given amount of space, therefore, this assumption works in favor of mature selection in calculations of E. The impact of the assumption regarding equal heritabilities is unknown but it does not seem unrealistic although h^2_J could conceivably be manipulated by the proper choice of "early test" environment which reduces environmental variance and thus increases h_J. The generation cycles, T_J and T_M, are based on a 2-year nursery test versus a 30-year test (economic rotation age) plus five years to complete the breeding in a greenhouse (Mike Greenwood, pers. comm.).

Under these assumptions a $r_{J,M}$ of only .20 is required to make E = I. At first glance this low value look'encouraging in that repeated experimentation should almost certainly result in discovery of some early trait measured in the right environment which would result in a correlation at least as large as .20. However, there are practical problems that will deter the establishment of the true genetic correlation between the "early" and "mature" test situations not the least of which is the fact that well-designed genetic tests of an economical] mature age are almost impossible to find. Very often, rank performance of families in a greenhouse or nursery are compared, instead, with the ranks oft same families tested under field circumstances but measured at ages much younger than economic maturity. Such comparisons are still useful if field tested families are at an age suitable for selection, as determined by other evidence. As mentioned earlier, selection is often conducted in 5 to 10-year-old genetic tests. Now, how efficient is an "early test" as compared with, say, an 8-year-old test which is assumed to be optimum for field selection? Under the above assumptions and regarding 8 years as the "mature" selection age, a much larger $r_{j,m}$ = .54 is needed for E 1.

RESEARCH PROBLEMS

Sampling

Correlation analysis is the most commonly employed research into the effectiveness of "early testing", i.e., family performance in the "early test" is correlated with older field performance. While older field tests provide an excellent opportunity to determine the value of "early tests", the correlation approach is faught with difficulties. A study designed to determine the true genetic correlation between family performances in two circumstances is much more difficult than designing a study simply to determine whether or not there are among family differences for a certain trait because of the inherent problems associated with sampling in a bivariate population.

The correlations plotted in Figure 1 were generated by independent samples from a population with a between groups variance (σ_F^2) of .07 and a within group variance (σ_W^2) of .93. If the groups are families then the ratio

$$\frac{\sigma_F^2}{\sigma_F^2 \sigma_W^2} = .07.$$

would represent a heritability of .14 for full-sib families or .28 for half-sib families or somewhere in between for open-pollinated families (assuming no dominace variance or epistasis), all realistic heritability values for a genetic test. A correlation was generated with the computer as follows:

1. A set of random values estimating a variance of .07 and mean of zero were generated. These represent a population of "family" means from which two independent samples of "individuals" within "families" were generated.

2. "Individuals" within each "family" were generated by drawing random numbers from a population with a variance of .93 and a mean determined by the "family" value obtained in (1). Two sets of "individuals" within "families" were drawn.

3. A rank correlation between "family" means as estimated from the two independent sets of "individuals" within families was calculated. Each solid point (▲ or ●) represents the average of ten such correlations. The open points (△ or ○) are the highest and lowest of the ten correlations.

Even though the underlying correlation is r = 1.0, none of the sample correlations reached that level and most were well below. The correlations increase, and the range decreases dramatically as the number of "individuals" within "families" increases. The correlations based on 10 rather than 25 "families" were generally lower and their range wider. With 150 "families" and 200 "individuals" per "family" the mean correlation is r = .92 with a range of .90 to .94.

If these correlations are realistic in terms of what could be expected from "early testing" studies, then the sample sizes (numbers of families and individuals within families) are extremely critical in detecting the true relationship between "early testing" and field testing. A study based on too few families and individuals could yield almost any correlation.

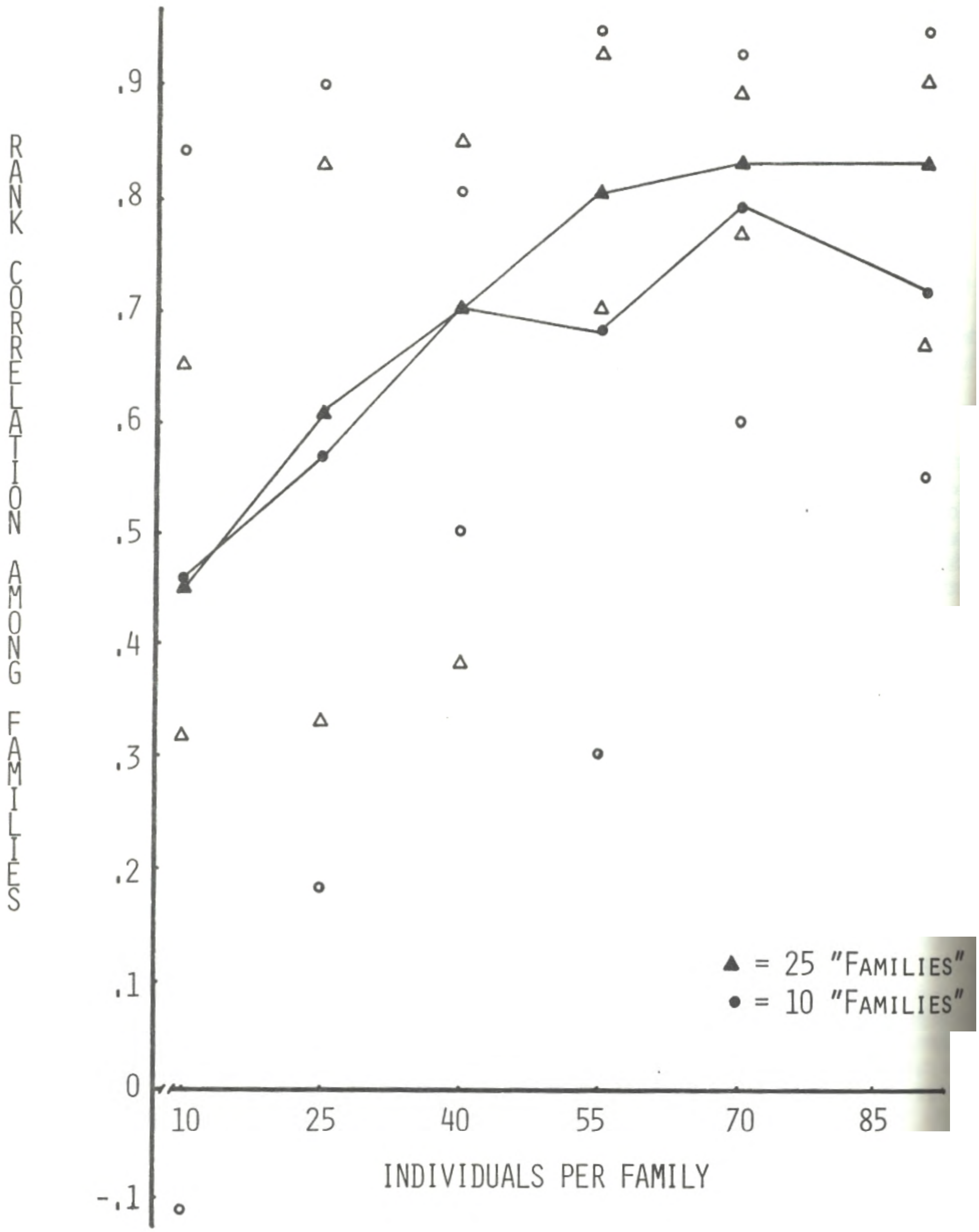

Figure 1. Computer-simulated rank correlation among "family" means when two independent sets of individuals are used to calculate the "family" mean. The estimated variances were .07 and .93 for among and within "family" variances, respectively. Solid points represent a mean of ten runs while the open points represent the high and low values of ten runs.

If one samples from a population whose underlying correlation is less than r = 1.0 then the problems associated with sampling error are even worse. In fact, it may be virtually impossible to detect and characterize some low to moderate genetic correlations between the "early test" and the field test due to biological limitations, even though the correlation may be of sufficient magnitude to be useful in an operational tree improvement program. Perhaps this is one reason that, after decades of research in this area, there is no general consensus on whether or not "early testing" can work.

The sampling problems associated with correlation analysis in "early testing" must be understood by the researcher. The important lesson here is that compromises in experiment size may lead to inconclusive or misleading conclusions. There is an especially strong temptation to make compromises in sample size when measuring certain physiological or otherwise complicated processes in the "early test" because of the time and cost associated with measurement.

Miller (1982) and Waxier and van Buijtenen (1981) avoided some of the sampling problems associated with estimating a correlation between the "early test" and field test by testing extremes. They used the same set of five fast- and five slow-growing families in 10- to 20-year-old field tests and simply tried to classify the families properly based on greenhouse testing. In both studies, mean total dry weight of families in several environments correctly classified four of five families, i.e. four of the top 5 greenhouse families were also classified as fast-growing in field tests.

<u>Seed Effects</u>

Traits such as seed weight and germination rate may influence very early performance of families. If these effects are short-lived the result may be to confound "early test" family ranks and thus reduce the correlation with older field performance which may not be related to seed effects. Lambeth et al. (1982) showed that seed weight, speed of germination and average number of cotyledons were related to greenhouse and growth chamber performance of Douglas-fir full-sib families but not with 6th-year height in three field tests. Waxier and van Buijtenen (1981) report similar findings for loblolly pine. In the Douglas-fir study, family AA X BB had the heaviest seed, quickest germination rate and the largest number of cotyledons per tree. It also ranked highest in mean total dry weight in 12 phytotron environments. Since this family did not perform well (rank 11th of 16 families) after six years in the field, it appears to be an outlier when "early test" family ranks are plotted against field ranks (Figure 2). When this family is dropped, the correlation between the early test and field results increases from r = .56* to r = .67**. An inspection of annual field measurements revealed that this family was also top-ranked in the first few years immediately following planting but its performance rank fell in subsequent years.

The influences of seed on "early test" performance need to be better understood. Perhaps one way to get beyond seed influences would be to grow larger plants in a two-year, nursery or greenhouse test.

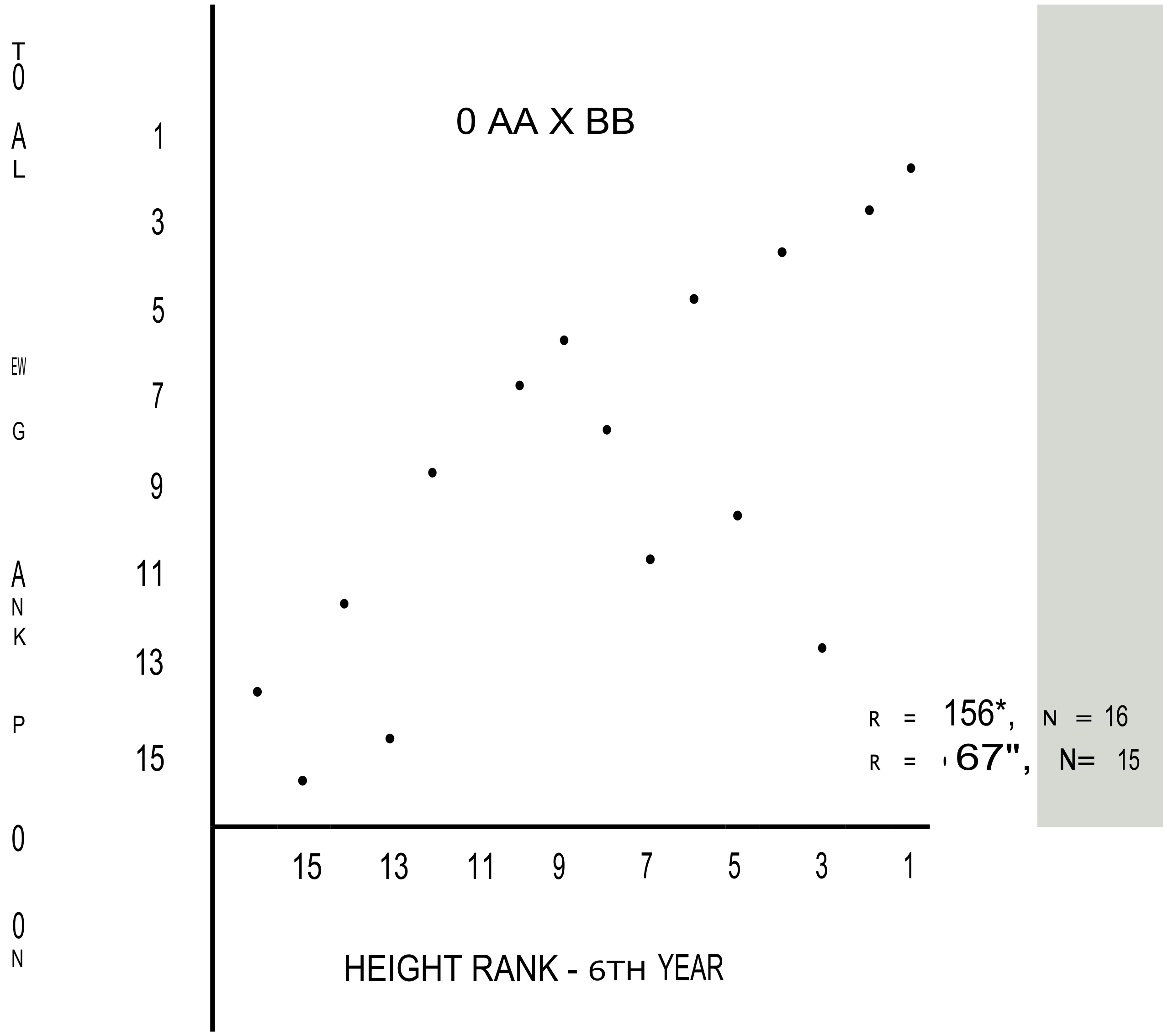

Figure 2. Phytotron versus sixth-year field height rank of Douglas-fir full-sib families (1 = Best, 16 = Worst). Total dry weight is the mean of the family in all 12 phytotron environments. The circled point represents the best family in the phytotron (presumably due to seed effects) which ranked only 11th of 16 in the field. Correlations shown are for all points (n = 16) and after deletion of family AA X BB (n = 15).

CHOICE OF TRAIT IMPORTANT

Recent studies (Miller 1982, Lambeth et al. 1982, Duke and Lambeth 1982, Wazler and van Buijtenen 1981) have suggested that family shoot or total dry weight may be better predictors of field performance than total height or, especially, height growth increment when dealing with small trees of the size usually encountered in greenhouse "early tests". The tendency of conifers to periodically halt height growth and set a resting bud, even when the environment is held constant, contributes to the inaccuracy of height increment as a predictor; i.e., some families are resting while others are growing. Nonetheless, when a plant has a resting bud it may still grow considerably in biomass if the environment is favorable. Over a period of a few months in the greenhouse, total height can be an adequate predictor of family field performance though it is usually still not as reliable as total dry weight.

There has been some hope that measurement of certain physiological processes that contribute to early size may be better indicators of later growth potential than early size itself. To my knowledge this is yet an unproven hypothesis.

GENOTYPE - ENVIRONMENT INTERACTION

Whether or not genotype-environment interactions are important to success in "early testing" is still unresovled. If they exist then the degree of correlation with field results will depend strongly on the choice of "early test" environment. The four studies mentioned in the preceding section were all multiple-environment experiments and all resulted in the conclusion that there were no serious genotype-environment interactions. Family ranks were reasonably consistent from one greenhouse environment to another. Family rank changes did occur but they were not beyond the realm of what might be attributed to sampling error.

Lambeth et al. (1982) found that the traits which showed the best correlation between family ranks in the phytotron and 6th-year field height also showed the least evidence of genotype-environment interaction. In an analysis of 12 phytotron environments (varying fertility, moisture, lighting, temperature and relative humidity), total dry weight showed almost no variation attributable to full-sib family-by-environment interaction. There were 16 families and 25 trees per family in each environment. The family rank correlations with 6th year field height on three sites varied considerably (Table 1) by environment from r = .07 to r = .75**; a result consistent with the variance of sampled correlations in Figure 1. Overall, the correlations were certainly encouraging. By contrast, height increment showed considerable variance due to genotype-environment interaction and poor correlation with field results (Table 1).

Table 1.--Correlations between family ranks for total dry weight and height increment in 12 phytotron environments and 6th-year height in field tests (Lambeth et al., 1982).

	Environment											
	1	2	3	4	5	6	7	8	9	10	11	12
Total Dry Wt.	.53*	.55*	.49*	.59*	.59*	.41	.75*	.61*	.07	.14	.41	.50*
Height Increment	.12	.64*	.00	.37	-.54*	-.13	.02	-.18	-.14	.04	-.14	-.14

Until genotype-environment interactions are better understood it is probably best to conduct multiple - rather than single-environment "early tests". A single-environment test may yield poor correlation with field results if it so happens that the choice of environment results in unusual ranking of families.

One approach currently being studied is to conduct a multiple-environment "early test" and screen families not only for overall performance rank but for stability of rank as well. The circled points in Figure 3 represent open-pollinated families with poor rank stability in a greenhouse test of loblolly pine in three environments (Duke and Lambeth, 1982). These tend to lie to the outside of a significant regression with a correlation of r = .51* with 8th-year field volume. When these points are deleted, the correlation improves to r = .74**. Thus the probability of making the correct choice of families in the "early test" improves if families with unstable ranks are first screened from consideration. This hypothesis holds up for three other data sets and is currently under further investigation. Whether or not the rank instability of these families is due to experimental error or genetic response to changing environments is unknown but, whatever the cause, if the geneticist does not have confidence in the overall rank of a family in the "early test", then that family would also be a poor choice for varying field environments that would certainly be encountered.

ADAPTATION

Development of "early testing" methods requires concentration on other traits as well as growth rate, especially in areas where the environment requires populations with good resistance to drought, frost, snow bend or disease. Selection for growth rate alone in an artificial environment could lead to the development of populations poorly adapted to the rigors of field environments.

Fortunately, many adaptation problems show up early in stand development. Mortality due to moisture stress occurs primarily in the two years after planting in most areas where loblolly pine is planted. "Early tests" in stress beds are successful at identifying drought resistance seed sources and families (van Buijten 1966, Lambeth and Burris 1982). Testing of seed sources for use

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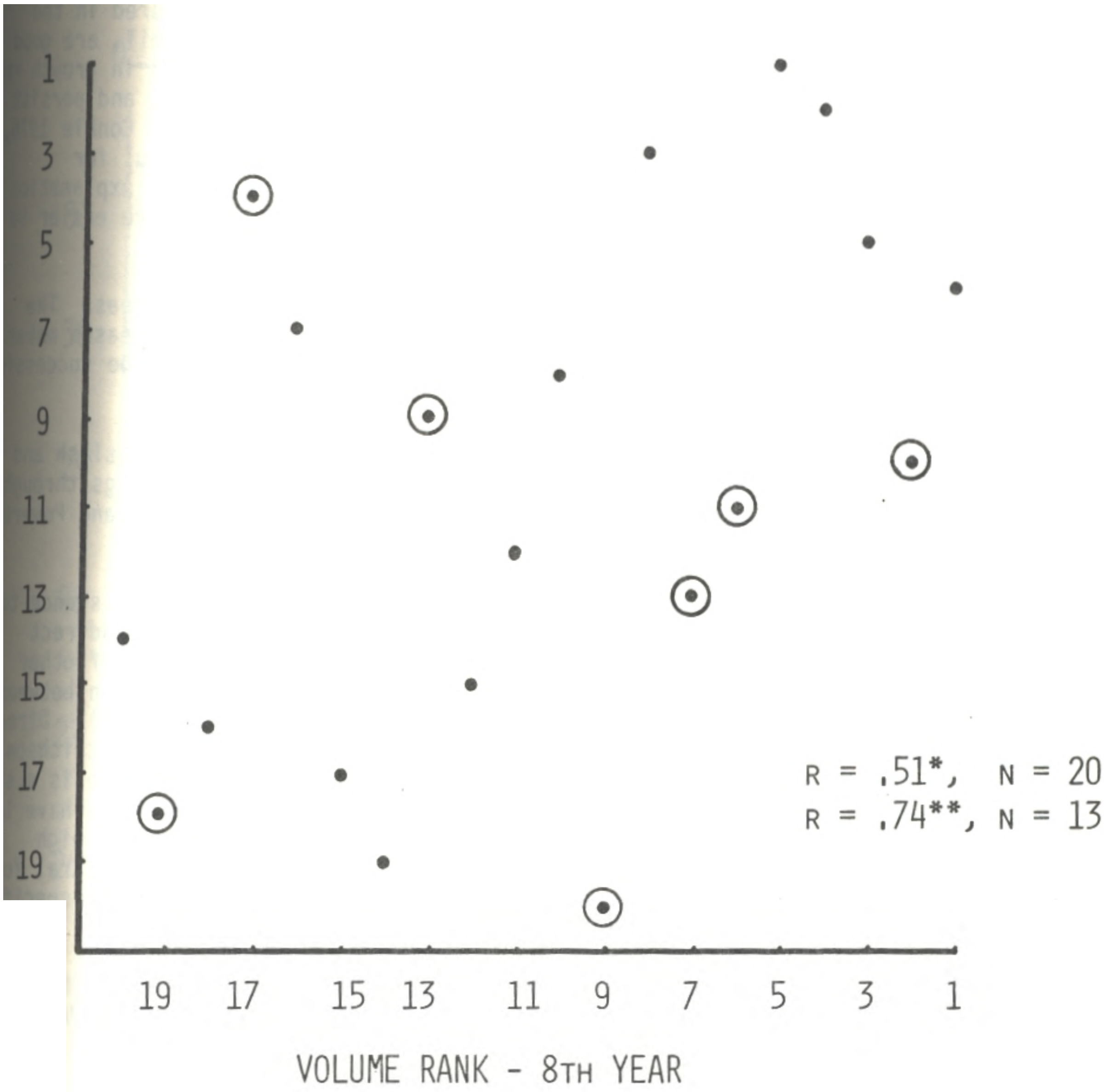

Figure 3. Greenhouse versus eighth-year field volume rank of open-pollinated families of loblolly pine (1 = Best, 20 = Worst). Circled points are families with poor rank stability across the three greenhouse environments. Correlations shown are for all points (n = 20) and after deletion of circled points (n = 13).

at the northwestern fringe of the natural loblolly pine range in Arkansas and Oklahoma have shown good agreement between growth rate, as measured in the greenhouse, and survivability, as measured in a sandy nursery soil, are good measures of field performance (Figure 4). The large differences in growth rate among seed sources, are very often exhibited at very young ages, and persist through to economic maturity (Namkoong et al. 1972, Namkoong and Conkle 1976, Nanson 1974). "Early testing" for growth has been more successful for provenances than for families within provenances. A most likely explanation is that differences among provenances are usually large and therefore easier to detect experimentally.

Frost damage also plagues seedlings more often than large trees. The tendency of seedlings to break bud early and grow late into the season makes them more susceptible. "Early tests" of frost resistance should be successful under the right testing circumstances.

As more data comes in, confidence in the ability to identify slash and loblolly pine families with good rust resistance for field plantings through artificial inoculation procedures in the greenhouse grows (Miller and Powers, 1983).

Direct assessment of some traits such as straightness and resistance to bending by snow and ice will be difficult in an "early test" but indirect selection for these qualities may be possible through measurement of other traits such as specific gravity which tends to have high correlation between juvenile and mature wood (McKinley et al. 1982, Talbert et al. 1983). Direct evidence that high specific gravity is related to straightness (Dietrichson 1964, McKinley et al. 1982) is also supported by the fact that there is a strong correlation which shows that trees with a high Modulus of Elasticity have low specific gravity (Pearson and Gilmore 1980). It seems logical that high elasticity would result in the tendency to crooked growth due to natural forces that bend the tree but more direct study of the relationship between specific gravity and straightness is needed.

In summary, adaptation traits seem to lend themselves better to "early testing" than does growth rate, but the methodologies have not been determined for all traits of concern.

WHERE ARE WE AND WHERE DO WE GO FROM HERE?

Research

Obviously, more work is needed to determine the value of "early testing" for growth rate. Studies examining the relationship between greenhouse or nursery performance versus longer term field performance are quick and valuable However, more efforts of the type where "early" family selections are made and then carried through to field tests will provide the most conclusive evidence o the "utility or futility" of "early testing". A study of this type by Robinson et al. (1983) showed that "early" screening of families for growth rate result in a 28% 5th-year volume gain in follow-up field tests. Twenty-seven of 28 select families outperformed their check lot.

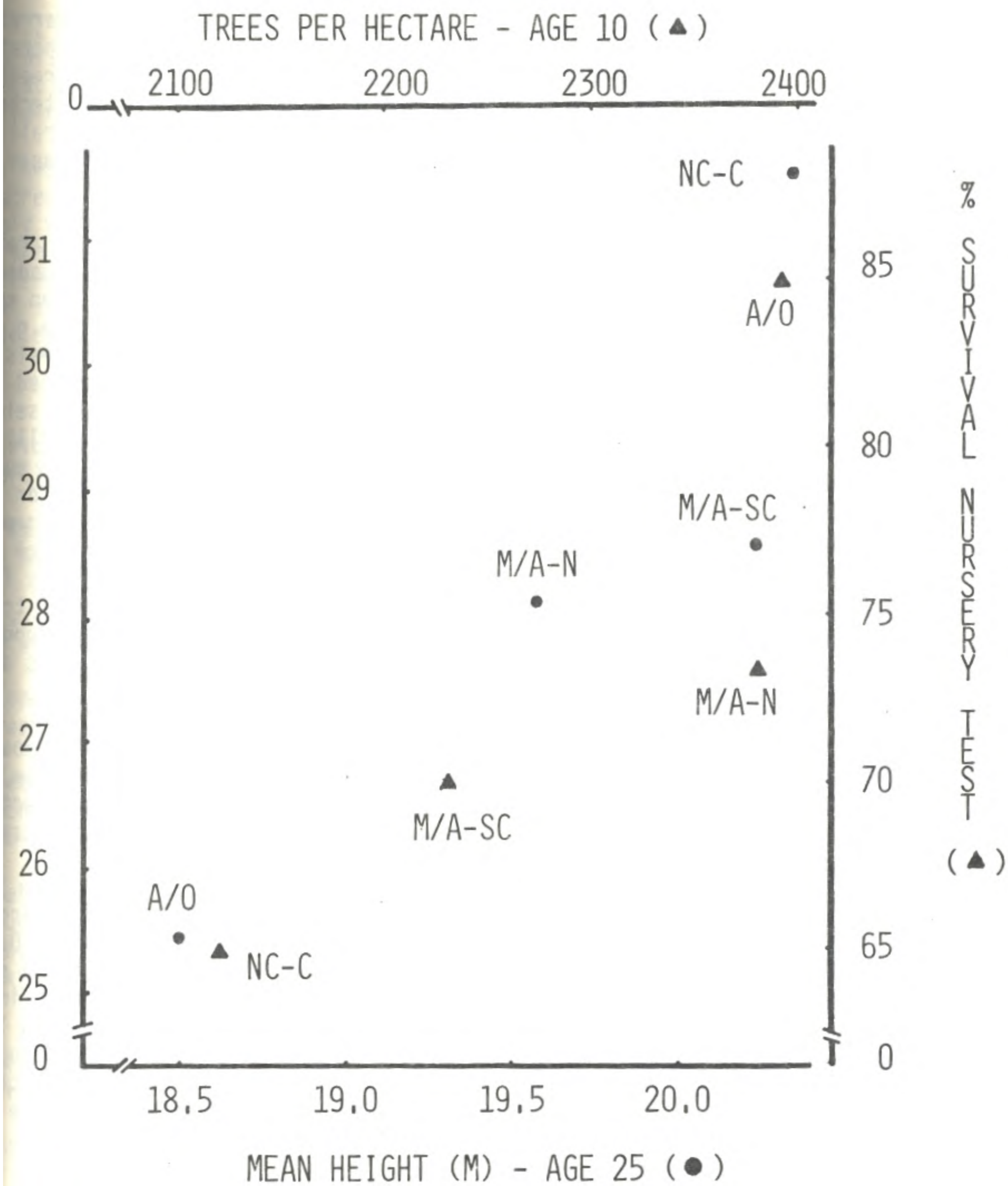

Figure 4. Height and survival assessments of loblolly pine seed sources in greenhouse and nursery tests versus a long-term field test (Wells and Lambeth, 1983).

NCC = North Carolina Coast
A/O = Arkansas and Oklahoma
M/A-N = Northern Mississippi and Alabama
M/A-SC = South Central Mississippi and Alabama

Enough positive evidence from "early testing" research to date warrants the establishment of experimental populations which are cycled through generations as rapidly as possible by employing "early testing" and accelerated breeding. A six- to seven-year generation cycle should be possible with existing technology. These could be specialized populations where selection for a single trait might yield varieties with high specific gravity, good fusiform rust resistance, drought resistance or high volume yield.

In other populations, selection could be carried out for several traits in each generation. One approach would be to test for different traits under different types of "early tests". "Early tests" seem to work best when specifically designed to accentuate the expression of the trait of concern, e.g., fusiform rust resistance through greenhouse inoculation and drought resistance by inducing mortality in stress beds. A proposed scheme for accelerated generation cycling with primary emphasis on growth rate may involve intense selection on size at the family and individual levels combined with low level culling of families for adaptability traits. To ensure that the population does not move away from adaptation to field environments, families could be culled for poor survivability and the nursery test for growth rate occurs in the same geographic area where the material would be commercially planted to ensure exposure to local winter conditions. Poor rust resistance and low specific gravity families could also be screened out through culling levels independent of other traits. Culling on secondary characteristics is conducted to ensure that the population does not lose ground in these traits for whatever reason; e.g., genetic drift or negative genetic correlations between growth and other traits.

The fact that these accelerated breeding and testing populations start out as experimental populations would not preclude their operational use if the techniques are successful. These populations should be periodically tested against material from conventional tree improvement programs in long-term field trials.

Forestry needs an effort akin to the oil and protein improvement program in maize at the Illinois Agricultural Experiment Station (Dudley, 1974). Over eighty generations of selection that started with only one variety have produced results far beyond the expectations of those who worked in the program in its infancy and continued gains are being realized. The program started in 1896, before the rediscovery of Mendel's papers, and has had only rare interruptions. Invaluable data regarding responses to various types of artificial selection have been the reward. Undoubtedly, such commitment in forestry would be similarly rewarded.

Applications

Some "early testing" is already in practice. Techniques in "early testing" for drought resistance in loblolly pine that are being used to develop drought hardy strains for use in east Texas (van Buijtenen 1966). Fusiform rust resistance screening in slash pine is also an operational reality. To my knowledge, fusiform rust resistance screening is not presently being used operationally in loblolly pine though such should be the case in the very near future.

It is conceivable that enough data to warrant "early testing" for growth rate will be in within 5 to 10 years. The first attempts may involve alternating generations of "early testing" and longer term field tests until complete confidence in the latter is sufficient.

Research has yielded sufficient evidence to indicate that "early testing" to screen out the very slow growing families from field testing is possible. Rarely would the very worst families in a short-term greenhouse or nursery test perform well in older field tests. This form of "early testing" does not shorten the generation cycle since the long-term field test is still used for final selection. It is purely intended to make the overall testing process more efficient or less expensive.

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