EFFECTS OF GENETICALLY IMPROVED STANDS ON GROWTH AND YIELD PRINCIPLES

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Abstract.--Economic and biological evaluation of tree improvement programs is dependent on quantifying the long term inputs of improved selections on growth and yield response surfaces. Components and principles of growth and yield systems that may be affected by genetically improved stands are given. Specific examples of genotypic population effects on the height-age relationship and on the early dominant height-rotation yield relationship are presented. Suggestions are given for future research needs and direction.

Additional keywords: height-age, evaluation, loblolly pine, *Pinus taeda.*

The impact of tree improvement programs on forest management practices is considerable and seems to be increasing. Demand for genetically improved material has been based on the premise that the subsequent stands of selected trees will have better survival, growth rates, or quality characteristics, resulting in better yields and economic returns than stands of unimproved trees. However, present management decisions and future plans concerning the role of superior trees in an operational setting have been based largely on individual tree characteristics observed over the early years of selected research studies. Long-term studies covering a range of sites and silvicultural treatments, and containing large scale plantings of genotypic populations are not numerous, but they are critical for determining the dynamic growth and yield response surfaces and economic returns of genetically improved stands. These responses must be understood, quantified and integrated so that decision making systems can assess the true economic consequences of genetic improvement. An understanding of the effects of genetically improved stands on growth and yield is a necessary and logical starting point. My objective today is to discuss how genetically improved stands may affect growth and yield principles with specific reference to the height-age relationship.

GROWTH AND YIELD SYSTEMS

There are various components and principles of growth and yield models that can be affected by genetically improved material. The components of a growth and yield system will vary depending on the type of system. There are three basic systems: individual tree, diameter distribution and whole stand. An individual tree system has a tree as the basic modeling unit, while a diameter distribution system has a number of trees by diameter class as the modeling unit, and a whole tree system has a stand as the modeling unit.

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The sophistication of a system, that is, the type of biological components and their interrelationships, and the level of output resolution, decreases from the individual tree model to the diameter distribution model to the whole stand model. For example, the individual tree model PTAEDA (Daniels and Burkhart 1975) for loblolly pine (*Pinus taeda* L.) contains the following functions describing biological components for the unmanaged portion of the program:

Pre-competition Phase	Post-competition Phase
Spatial distribution	
Point-of-competition	Competition index, crown ratio
Mortality	Probability of mortality
Height-age (site index)	Height-age (site index)
Diameter distribution	Diameter increment
Height, crown length	Height increment
	Volume, unit conversions

These components are not independent of each other. Although the parameters for each are estimated as if they are independent, they are actually interrelated in that an estimate from one function is often used in another function. Yield estimates are determined from the integration of these 4 interrelationships. The output information in this system could include stand and stock tables for any specified age, and stand level statistics for individual tree characteristics of average diameter, height, crown length and competition index, and stand level characteristics of average basal area, yield and biomass. In addition, subprograms exist that can incorporate the effects of site preparation, fertilization and thinning.

In contrast, a whole stand model has only one biological component that incorporates all of the above individual tree components into one. For example, Burkhart et al. (1972) developed loblolly pine stand yield as a linear function of age, height of the dominants, and number of trees surviving. This function requires essentially the same input as the individual tree system, but the whole stand model supplies only one piece of information - an aggregate yield for a specified input.

The effects of genetic improvement may be found in any or all of the components of any of the yield systems. Since geneticists select genotypes on the basis of survival (e.g., drought hardy), growth rates (dominant height), productivity (specific gravity) and quality (disease resistance) characteristics, it would seem that the growth and yield components characterized by these selection criteria would be naturally affected. However, the growth and yield components, as in the case of an individual tree model, are interrelated meaning that if one component is affected by genetic selections, then most of the remaining components will be affected by that single change as well as any final yield estimates. For example, in the case of PTAEDA, if the site index or height-age function is adjusted for differences in genotypic populations, there will be associated changes in survival, tree size attributes, distributions, growth responses, and taper. In the end, the proposed genetic adjustment in height-age may not result in the desired adjustment in total yield because of the resulting interactions (Sprinz 1986).

There are some important growth and yield principles that may be also affected by genetically improved stands. Langsaeter's growth-growing stock (1944, taken from Smith 1986), maximum stocking line (Reineke 1933, Drew and Flewelling 1977) and carrying capacity are other biological relationships that have been hypothesized for testing to determine if significant effects from tree improvement exist (Nance et al. 1986). Information from analyzing genetic effects on these principles will have important ramifications on how growth and yield systems perform as an aggregate. In the example above, a proposed change in site index due to genetic differences would affect these principles as well as the components of growth and yield systems.

GENETIC EFFECTS ON HEIGHT-AGE

With this idea of growth and yield as a system of interrelated components, I would like to present some results from analyzing the effects of different genotypic populations on one component - the height-age relationship. Height has been an important trait that geneticists have used in selecting superior genotypes and in determining potential gains at later dates. It has also been one of the methods discussed as a way to incorporate the effects of tree improvement into growth and yield modeling.

Most of the reported height-age work has centered on quantifying effects of genetic populations on the shape and level of this relationship, and on determining subsequent effects of changes in this relationship on aggregate yields. Nance and Wells (1981b) and Buford and Burkhart (1985) have analyzed loblolly pine genotypic population effects on the shape and level attributes of a logarithm of height and inverse of age model. They found significant differences in the level of the height-age relationship by population. This result would indicate that adjustments in site index values may be a valid method in adjusting growth and yield models for differences in genetic populations. In other research, Schmidtling (1984) found shape and level differences between loblolly families selected for high and low specific gravity using the same height-age model.

Few studies exist that have repeated measurements of height over time corresponding to actual yields for the entire length of a rotation. Through a growth and yield simulation of loblolly pine, Nance and Bey (1979) determined that in general, height gains that diminished over the length of the rotation (i.e., shape differences) had minimal effect on final yields; however, a consistent height gain over the length of a rotation (level differences) had a considerable impact on final yields. Diminishing height gains can be thought of as temporary lift in site index, while consistent height gains can be thought of as a permanent lift in site index (Fig. 1). Nance and Wells (1981a) incorporated dominant height differences in a growth and yield model and found greater source differences in yield than were actually observed. Taking an early percent height gain as a percent site index gain, Talbert (1982) simulated final yields and determined that yields were tending to converge by age 35. Wells (1983) used dominant height differences at age 25 to determine potential yield differences. He found that estimated yields at age 25 of seed sources grown in Arkansas were generally not different.

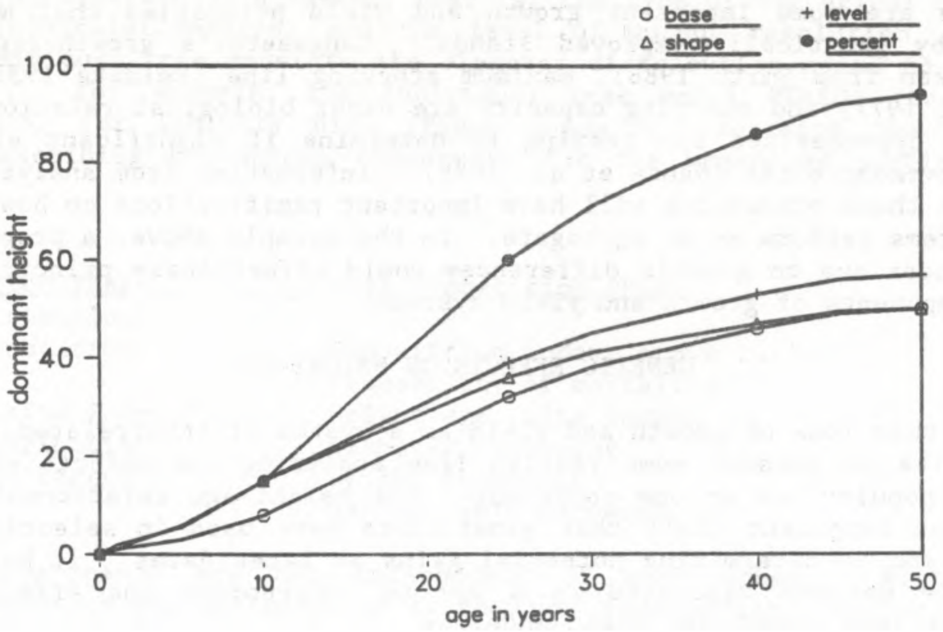

Figure 1. Dominant height-age trends showing level, shape and percent differences of an assumed height increment at age 10.

STUDY AREAS

Texas A&M University and Weyerhaeuser Company have worked closely over the last two years collecting information from several loblolly pine genetic trials. One study was the Southern Pine Seed Source Study (SPSSS) located in southwestern Arkansas, while the others were Texas Forest Service half-sib block plantings located in western Louisiana.

The particular portion of the SPSSS that we sampled consists of four spatially separated completely randomized blocks of 36 geographic seed sources representing the native range of loblolly pine. Historical data on diameter at breast height, total height and survival were available (Grigsby 1973, Grigsby 1977, Wells and Lambeth 1983) through age 26 from seed. Wells and Lambeth (1983) from their analyses subdivided the sources into 7 geographic regions (Fig. 2). At age 29 from seed, the study was measured for diameters and heights, with a destructive subsample taken for stem analysis. This procedure entails cutting a tree into 5-ft sections and then splitting the sections to determine the exact height at each age through flush or whorl counts. The height and age pairs were recorded on 279 trees.

The Texas Forest Service studies consist of completely randomized blocks of selected genotypes. One study contains 7 superior half-sib families planted adjacent to corresponding check families. The block plantings were either 31 or 34 years from seed when 56 trees were stem analyzed for height-age pairs. Another study contained 20 block plantings of families selected for high or low specific gravity. In this case there were 48 trees sampled at age 31 years from seed.

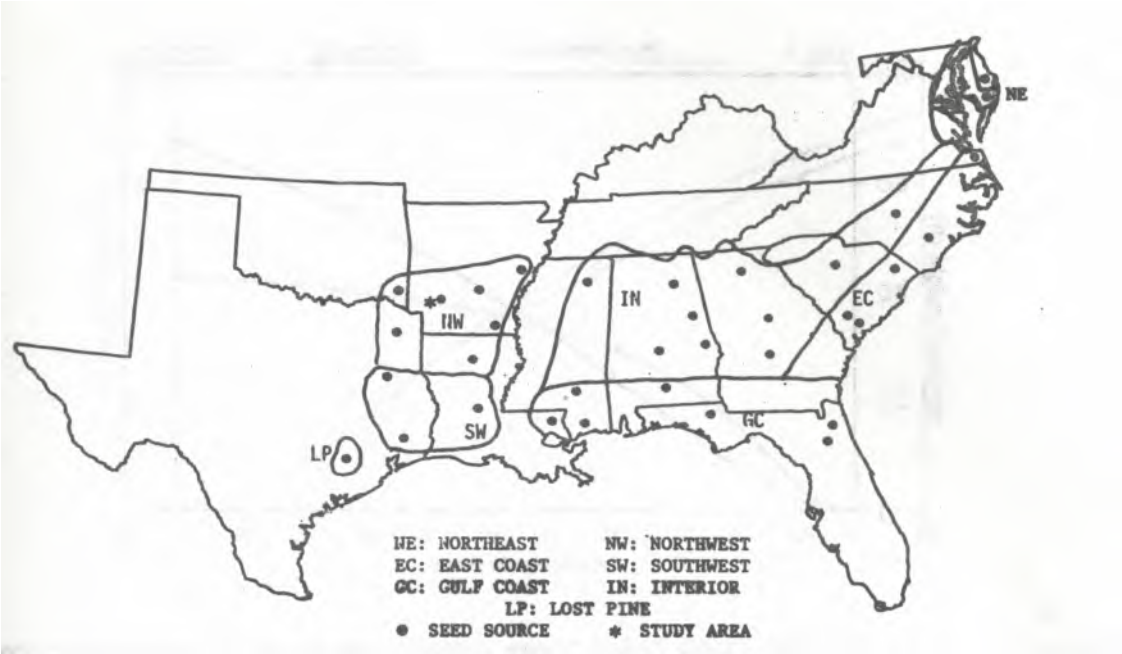

Figure 2. Map indicating regional groupings, seed source groupings and study area.

METHODS OF ANALYSIS

There were two main methods used to evaluate genetic effects on the height-age trends. One method involved testing significant differences among average values and specific contrasts with an analysis of variance procedure.

The second method entailed testing significant differences among parameters of a height-age model with a full and reduced model procedure. Two models were tested. A logarithm height and inverse of age model was initially tested, but proved to be inappropriate in describing the sigmoidal curve exiting between height and age (Fig. 3) (Sprinz 1986). The other model, popularized by Pienaar and Turnbull (1973), proved to be very flexible and suitable for this analysis (Fig. 3). This model is characterized as

$$H = a(1 - \exp(-b*A))^c \qquad (1)$$

where,

H – total height (ft) based on stem analysis
A – age from seed (years)
exp – exponential
a,b,c – regression coefficients.

The parameters of this model have important interpretations that may be useful in describing the effects of genetics on the height-age relationship. The asymptote of the curve is describe by the 'a' parameter, the rate of development is indicated by the 'b' parameter, while the pattern of development is measured by the 'c' parameter. Namkoong et al. (1972) found that the parameters of model (1) were not significantly affected by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) populations even though other analyses indicated significant population differences in height.

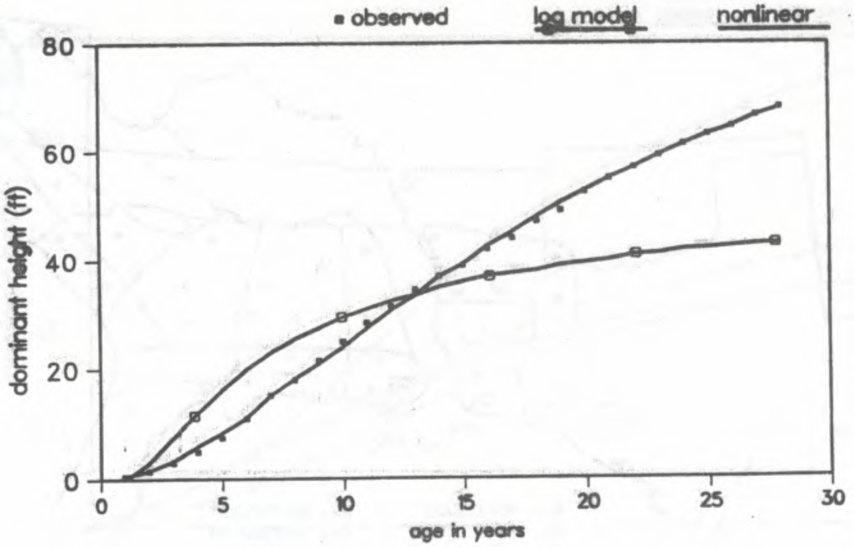

Figure 3. Observed dominant height-age trend compared to predicted values from a logarithm of height and inverse of age model, and a nonlinear model (1), proposed by Pienaar and Turnbull (1973).

Significant differences between these parameters will give an indication of where genetically improved stands are affecting the height-age relationship and how these effects can be incorporated into growth and yield models. One method to determine significant differences is to compare the residual mean square associated with models fit to each region separately (i.e., full model) to the residual mean square associated with models combining regions (reduced model) (Neter et al. 1983). For example, a model containing one asymptote parameter and region specific rate and pattern parameters may have a similar residual mean square as a model containing region specific asymptote, rate and pattern parameters. In this example, the inference would be that genetic gains were found in the shape of the height-age trend, but not the level.

RESULTS AND DISCUSSION

Average total height and dominant height in the seed source trials were consistently and significantly taller for eastern versus western sources, and for East Coast versus Northwest sources over the 29-year period.[a] Dominant heights for the eastern sources were 1.3 ft (4.7%) taller than the western sources at age 11, and 4.5 ft (6.7%) taller at age 29 (Fig. 4). The East Coast sources were 2.5 ft (9.3%) taller than the Northwest sources at age 11 and were 5.2 ft (7.7%) taller by age 29 (Fig. 5). These differences translated in a 4.0 ft increase in site index at base age 25 for the eastern sources compared to the western sources, and 5.1 ft increase for the East Coast versus Northwest sources.

Results from Model (1) suggested that the general shape of the height-age trend was affected by the geographic populations. It was found that a common asymptote parameter with source related rate and pattern parameters could be used across the regions. This would suggest that the maximum dominant and codominant heights among seed sources are similar; however, the height-age

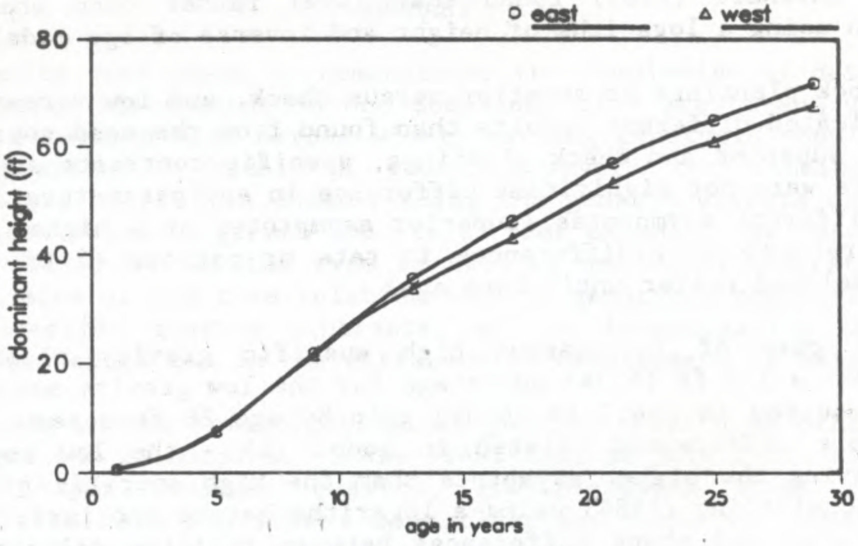

Figure 4. Observed dominant height-age trends from western and eastern loblolly pine seed sources grown in Arkansas.

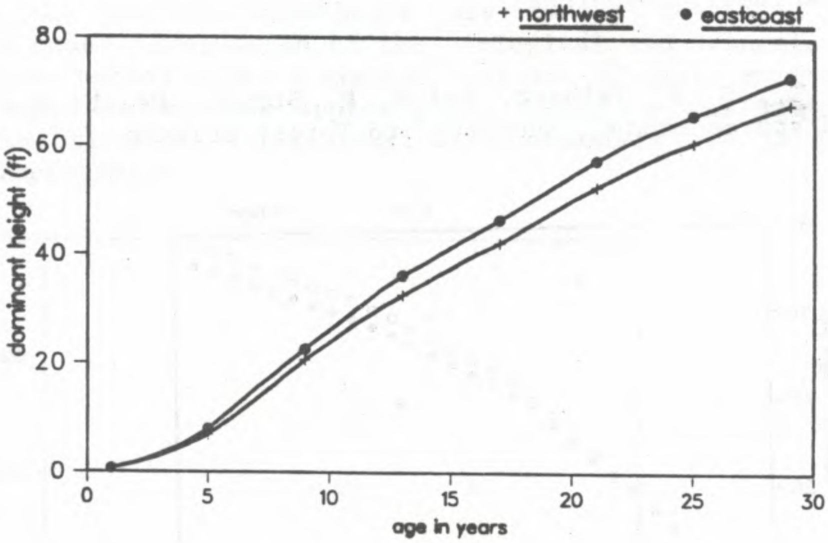

Figure 5. Observed dominant height-age trends from the Northwest and East Coast loblolly pine seed sources grown in Arkansas.

relationship prior to the maximum is different. Nance and Wells (1981b) and Buford and Burkhart (1985) found that level rather than shape differences existed when using a logarithm of height and inverse of age model.

The block plantings of superior versus check, and low versus high specific gravity indicated different results than found from the seed source trials. In the case of superior and check plantings, specific contrasts suggested that in 2 cases there were not significant difference in any parameters, in 2 cases were only different asymptotes (superior asymptotes at a higher level), and in 3 cases there were only differences in rate or pattern (2 of the 3 superior families developed taller until base age).

In the case of low versus high specific gravity plantings, it was indicated that a 1.7 ft (4.9%) advantage for the low gravity material at age 11 from seed resulted in a 4.3 ft (6.4%) gain by age 26 from seed. In addition, only asymptote differences existed in model (1) - the low specific gravity plantings having the higher asymptote than the high specific gravity material (Fig. 6). Schmidtling (1984) using a logarithm height and inverse of age model found both level and shape differences between families selected for low and high specific gravity: low specific gravity families were taller than high specific gravity families to age 21 at which point the high gravity families became taller than the low gravity families.

Problems also exist if early attribute data from plantings are used to make long term projections of final aggregate yields. If early dominant height differences from these studies are related to actual yields at rotation age, trends were not obvious. Within each study, the height gains indicated at age 11 from seed were regressed with the final standing yields. An absolute or percentage gain in height was not related to final yield in any of the studies as shown in Figure 7 with the seed source trials and Figure 8 with the superior-check family plantings.

Sprinz, P. T., C. B. Talbert, and M. R. Strub. Height-age trends from an Arkansas seed source study. Submitted to Forest Science.

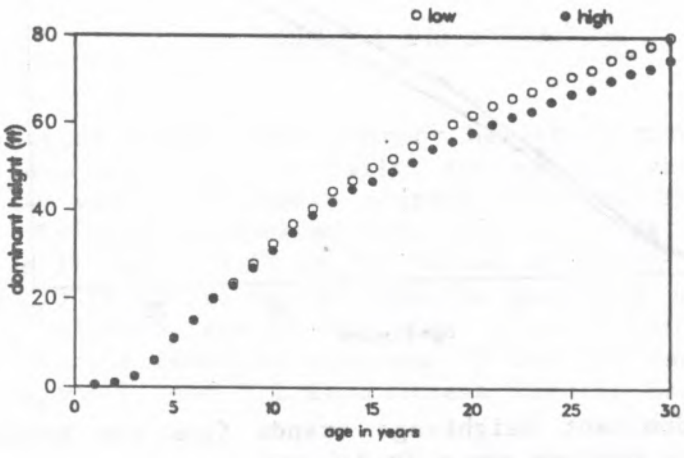

Figure 6. Observed dominant height-age trend from half-sib block plantings of families selected for low and high specific gravity.

SUMMARY

These results were given to demonstrate the complexity of determining the effects of genetic improvement on one component of a growth and yield system. As a mixture of results from across widely varying genotypic populations these may be disconcerting. Within a study, however, the findings are very meaningful and are helpful in understanding the genetic effects on the dynamic response surfaces found in growth and yield. For example, the results from the seed source trials provided the type of data we needed to understand the long term stand dynamics of and tree relationships in genotypic populations. In the case of the specific gravity contrasts, we are investigating the different growth strategies exhibited in the differential development of height.

At Texas A&M we are investigating the genetic effects on other growth and yield components and principles. These areas include height-diameter, diameter distributions, taper, volume, quality, growth-growing stock and carrying capacity. Results have not always been clear and cohesive, especially as we look across a wide spread of genotypic populations; however, it is a start to understanding, quantifying and incorporating genetic improvement into growth and yield.

The greatest handicap that the tree improvement program has is the time factor. A 30-year period is not an acceptable period for evaluating a cross; however, evaluating row plots at age 10 without an understanding of intraspecific competition effects on stand attributes is also not acceptable. Studies exist now and <u>designed</u> studies can be established that will enable scientists to quantify population dynamics of genetically improved stands, which in turn will provide a sounder basis for evaluating early selections and for projecting rotation gains. This research will have to transcend disciplines if the correct hypotheses are to be developed and correct inferences to be made. Evaluation of the biological and economical aspects of genetic improvement necessitates a systems approach if there will be success in this endeavor. Only a systems approach can integrate the knowledge of the geneticists, biometricians, silviculturists, economists and land managers in assessing tree improvement.

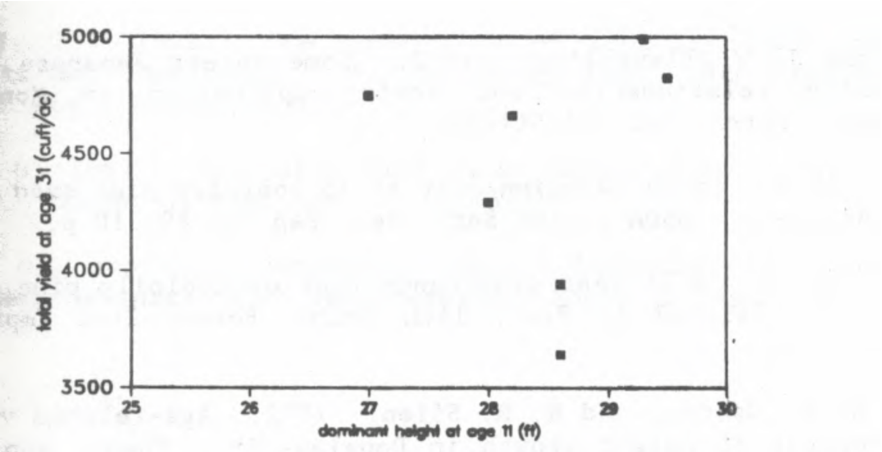

Figure 7. Comparisons of standing yield at age 31 and dominant height at age 11 of loblolly pine seed sources grown in Arkansas.

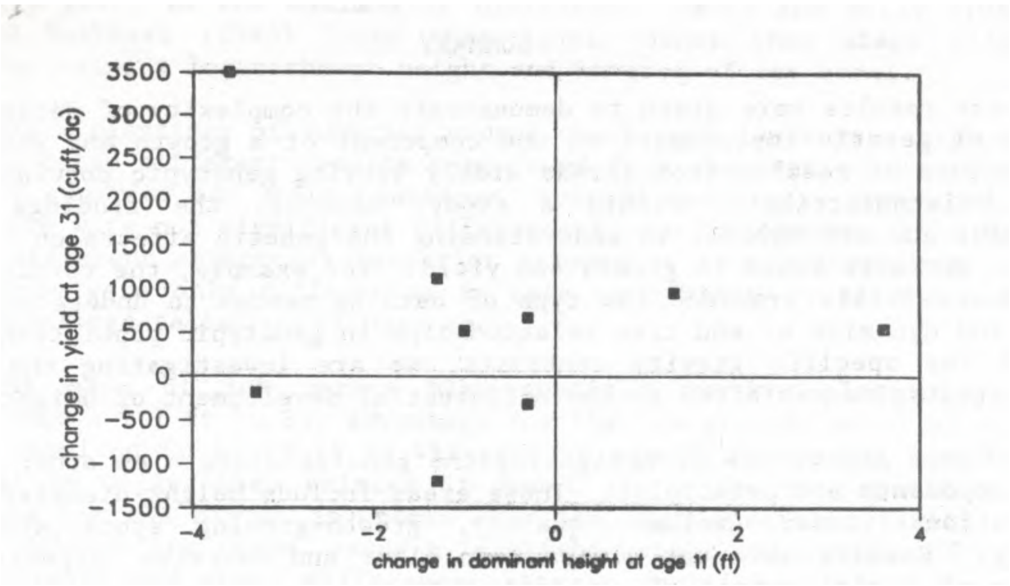

Figure 8. Incremental gain of superior over check half-sib families in terms of standing yields at age 31 and dominant height at age 11.

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