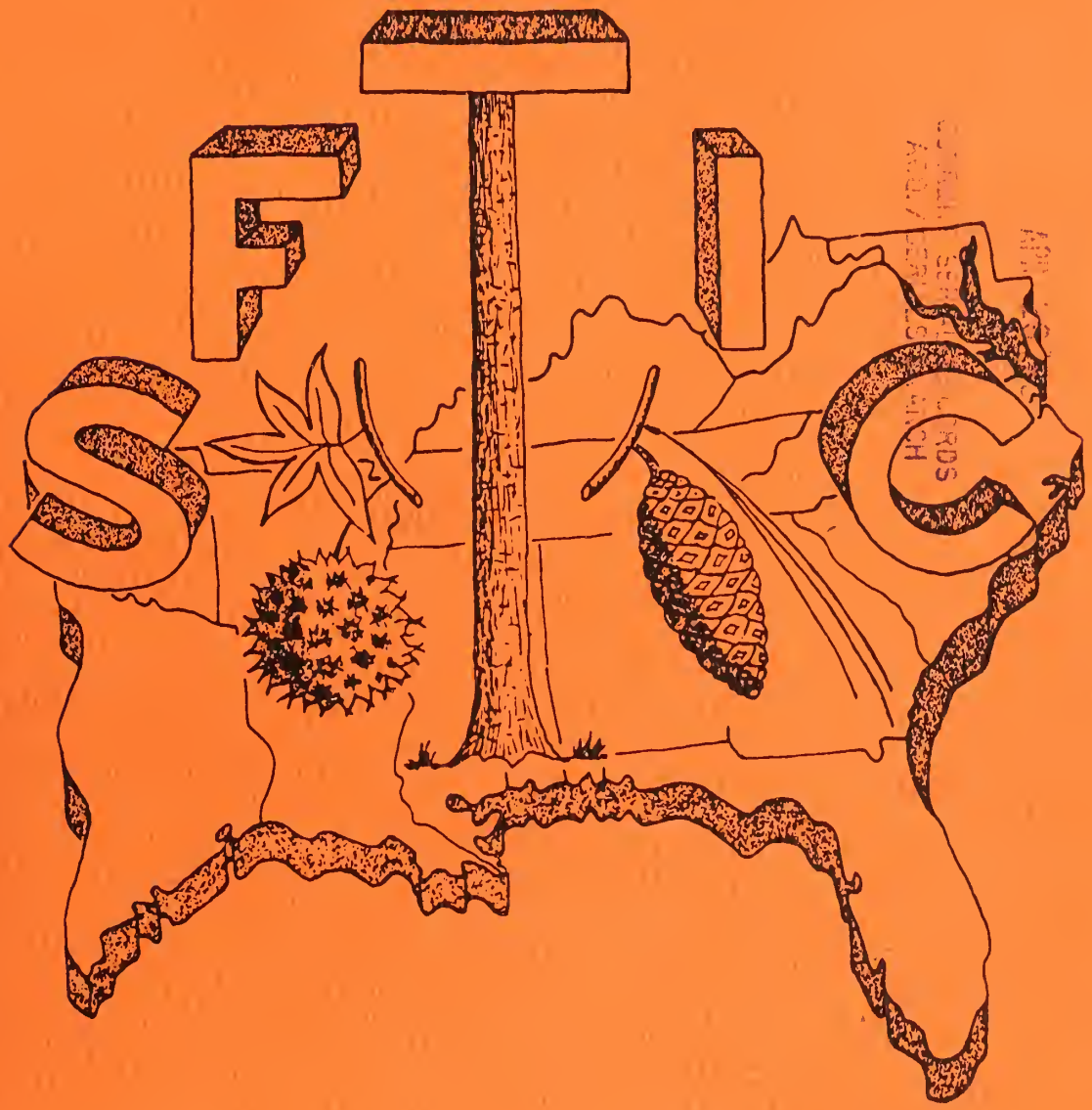
16th Southern Forest Tree Improvement Conference



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THE SOUTHERN FOREST TREE IMPROVEMENT COMMITTEE

May 27-28, 1981

VIRGINIA POLYTECHNIC INSTITUTE and STATE UNIVERSITY

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FORWARD

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Hybridization - Then and Now?

J. W. Duffield[1/]

Technologies have a way of changing, if they remain important for human welfare and economic development. As new techniques and approaches are tried and adopted, old ones become outmoded. The outmoded approaches retain interest for the historically-minded, but occasionally they may be dusted off and put to use again - witness the dusted-off technology of wood-burning stoves.

I believe it is fair to state that species hybridization has ceased, at least for the present, to be an important approach in tree improvement. Many of today's workers probably ask themselves: "What was all the fuss about species hybridization thirty and forty years ago?" As one of those tree-climbers of forty years ago, I recall the circumstances, compulsions, and rationales that shaped our programs. Some of these considerations are no longer relevant: others, I believe may warrant a renewal of interest in species hybridization on the part of tree imporvement workers.

But first, why did tree improvers devote so much effort to hybridization in the past? It would be accurate to say that ignorance and naivete played a large part, but these are curable human failings, and the curing process is often quite interesting.

Let's start with Germany's, or more precisely Prussia's energy crisis of a century and a half ago. Biomass, as it was not then called, was one way out, and a professor of botany named Klotsch conceived the notion that if trees could be made to channel the products of photosynthesis largely or exclusively to wood production rather than diverting them to reproductive tissues, they would be much more useful. The conventional wisdom in Klotsch's day was that hybrids were generally sterile, so he proposed to produce sterile hybrids by interspecies crossing, and one of his trials was an attempt to cross Pinus sylvestris with P. nigra. He reported that he made the cross, one fine spring in the 1840's, and in the autumn of the same year collected the resulting seed, which duly germinated and produced plants which exhibited hybrid vigor. His work has been cited more frequently than it has been read with care, and as one of those who cited it has written: " - - no further experiments were made and his pioneer work fell into oblivion".

But species hybridization in forest trees did occur, if not by design, then by accident. The accidents occurred in botanical gardens and on large estates where allopatric species were brought together. Some ex-

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amples are the London plane (involving Platanus orientalis and occidentalis), the Dunkeld larch (Larix decidua and kaempferi) and the red horsechestnut (Aesculus pavia and hippocastanum). The latter eventually proved to be of exceptional interest since it was shown to be an amphidiploid and as such is more or less true-breeding. It is worth noting that two of these hybrids are horticultural successes; the London plane is widely used as a city and garden tree, but its parents must be sought in their native haunts. Red horsechestnut has not displaced Aesculus hippocastanum as a street and garden tree, but is nevertheless widely grown. The hybrid larch has been produced in large numbers by mass pollination, largely at the instigation of Syrach Larsen, and has been found valuable as a forest tree in Denmark.

These three examples, although of little direct relevance to forest tree improvement practice in this country, were among the stimuli to forest tree breeders here fifty years ago. Other stimuli were the Salix hybrids made by Heribert-Nilsson and the Populus crosses of Augustine Henry. These roused the interest of A. B. Stout of the New York Botanical Garden, who, with the assistance of E. J. Schreiner and the support of the Oxford Paper Company in Maine, started, in 1924, the first systematic tree improvement program in this country, concentrated on the genus Populus. This program, as a consequence of progress in pulping technology and economic stress in the 1930's, eventually gave rise to the forest genetics project of the Northeastern Forest Experiment Station under Schreiner's direction.

At the Northeastern Station, work with Populus continued at a reduced intensity, while the scope of the project was expanded to cover most of the genera, broadleaved and coniferous, native to the region. The project could not be accurately termed a tree improvement effort; it was rather, and quite properly, involved in exploring the reproductive biology of forest trees, the technology of control of parentage, and propagation. Species hybrids in Acer, Betula, and Quercus were produced before 1942, and after 1946 in Picea and Pinus.

In 1925, the Eddy Tree Breeding Station, later to become the Institute of Forest Genetics, was established in Placerville, California. Its program was early concentrated on the genus Pinus and the first major activity was the assembling of a world-encompassing arboretum of pine species. Before this arboretum reached an age to permit a comprehensive program of species crossing, two hybrids were made on indigenous trees in 1927. The first was the attenuata x radiata cross, reproducing a natural hybrid found in at least one location in coastal California. The other was the ponderosa x engelmannii cross. Meanwhile, the emphasis shifted to assembling a comprehensive provenance collection of P. ponderosa and two open-pollinated progeny tests of ponderosa from a wide range of elevations in a restricted region of the central Sierra Nevada. By 1942, the program emphasis had reverted to species hybridization. Among the trees assembled in the arboretum at Placerville are several southern pine hybrids made by Phil Wakeley in the early 1930's.

From our present perspective, it is not too clear why forest geneticists of 50 years ago put in so much effort on species crossing and so little on

selection in native populations. To understand their reasoning, we have to remind ourselves of the "state of the art" (to use a current cliche) at the time. Much work in cytogenetics and plant breeding dealt with polyploidy and its artificial induction. It was thought that hybrids which combined the desirable properties of the parent lines or species could be made into true-breeding amphiploids by colchicine or other polyploidy-inducing treatments. It turned out that in the pines, at least, colchicine-induced polyploids were dwarfs of greatly reduced viability. At the same time, selection theory was barely off the pages of the works of Fisher, Wright, and Haldane and far from the practical application given impetus by Lush and others. It is true that improvement by selection is an ancient art, but the attention of forest geneticists of the 1930's was attracted by current and exciting work in cytogenetics rather than by applied plant breeding. Moreover, the few localitieswhere forest geneticists were at work provided little in the way of extensive even-aged stands of simple species composition. To be sure, one of the motivations of the tree hybridizers was that the variation to be found in F_2 and subsequent generations would be utilized in selection programs. Schreiner, for example, frequently wrote and spoke of "hybridization and selective breeding" as linked activities.

Then there was the expectation of realizing hybrid vigor. Indeed, embryological studies by Buchholz at the Institute of Forest Genetics demonstrated in the early forties that at least one pine cross (contorta x banksiana) resulted in embryos which developed faster than those resulting from open pollination of lodgepole pine. Eventually it became clear that hybrid vigor in forest trees, expecially in those cases where the parent species are allopatric, is difficult to define. Nevertheless, several species crossings in the white pines supported the notion that crosses between closely related but widely allopatric species are likely to result in vigorous offspring.

So far, I have attempted to give what might be termed the reasonable or respectable rationale for early programs of species crossing. There were other motivations as well. Simple minded as it may sound, success in producing recognizably hybrid progenies was an important validation of the techniques being worked out. Moreover, the plain delight at producing something new was a reward for the sometimes strenuous work involved. Both Schreiner and Righter enjoyed climbing trees - in Righter's case, the bigger the better, and in the Sierra Nevada, there are some big pines. Finally, the ability to exhibit hybrids readily recognized as such was used as a demonstration that forest trees, like agricultural plants, were subject to genetic manipulation by plant breeders. Because this notion was not at first widely accepted, these demonstrations were important in securing continuing support for programs. These "tree shows" as they were termed by Syrach Larsen, a master at the promotion of forest tree breeding, were short on experimental design, but long on audience appeal.

Species crossing in the pines has had one spin-off not directly relevant to tree improvement. As the number of recorded species hybrids in the pines increases, it appears that species crossability is one indicator of relationship, and this is of interest to pine taxonomists. Much remains to be done in quantifying degrees of pine species crossabilities along the

lines laid down by Jens Clausen and his colleagues working with wild herbaceous plants in California, and summarized in his 1951 work on the Evolution of Plant Species.

So much for species hybridization as a curtain-raiser for present-day tree improvement activities. What part does it play today, and what role can it have in the future?

A most striking utilization of the strategy of combining useful properties of two species is the work of Hyun in South Korea, where thousands of hand pollinations in existing scrubby plantations of Pinus rigida produced operational quantities of rigida x taeda hybrids. These were of practical value in an environment where the seed parent contributed hardiness and the pollen parent good stem form. Recent reports from South Korea suggest that wind pollinated F_2 and back-cross progenies of the original F_1 are quite satisfactory in form and hardiness.

Nikles, in Queensland, is reporting that on swampy sites, of which there are large areas, the cross between P. elliottii and caribaea hondurensis is outgrowing both parents. He is also finding that the nominal F_2 populations from seed orchards constituted of F_1 hybrids are quite usable even though somewhat inferior, in terms of variability, to the hand-pollinated F_1 populations.

What is common to these two instances is the fact that both parent species are exotic to the sites where the hybrids out-perform them. In a sense, as Nikles puts it, these hybrids are finding hybrid habitats hospitable.

At first sight, it appears that what we call the "southern pine region" is not likely to provide "hybrid habitats" for pines, since our commercial species are not exotic, and, in general terms this appears to be the case. But, on the ground, the "southern pine region" is not the homogeneous environment portrayed by the large green area shown on the maps. Moreover, foresters have found that some of the hardwood and mixed forest sites of the south can produce useful pine stands. It seems likely that as finer tuning is applied to the technology of suiting planting stock to site, reliance on the "big three" pines - loblolly, shortleaf, and slash - will become less pervasive, and that hybridization may be involved to some extent in the pedigrees of the planting stock.

There is a nagging practical question about the direct use of hybrids, namely cost of production. Hyun solved this problem by giving hordes of school children some healthy outdoor exercise, but one may speculate that this may have proven a short-term solution and certainly one hard to duplicate here. I suspect that despite the general effectiveness of southern pine seed orchards in producing seed, most seed orchard operators are less than completely satisfied with the practice of leaving the matchmaking to the vagaries of flowering times of individual clones and the weather. Moreover, it takes strong faith to believe that what goes on in a multiclonal seed orchard - or even a multi-family seed orchard - remotely approaches panmictic crossing. What I am suggesting is that, leaving aside

for the moment the question of mass production of hybrids, single-species seed orchard technology will be greatly strengthened when the technology of mass low-cost artificial pollination is more widely used. Bruce Devitt in British Columbia has developed mass pollen handling techniques for supplementing the natural pollination in a Douglas fir seed orchard. When this technology, which should be much easier in the pines, comes into wide use, it will become a bit more practical to talk about the operational use of F_1 species hybrids.

There has been reluctance to use the nominal F_2 and backcross populations resulting from open pollination within F_1 populations. To some extent this reluctance derives from the observed variability in these F_2 populations, but I suspect that it is also caused by consideration of the textbook examples of F_2 segregation following the original hybridization between established varieties or pure lines. The situation may prove to be less unfavorable in the case of wild species hybridization. To work both sides of the street, one may argue that considerations of cost of open-pollinated F_2 relative to controlled-pollinated F_1 seed, added to the silviculturally questionable value of a high degree of uniformity in forest stands, make F_2 and backcross populations worth considering in operational plantations.

In the west, at least, we hear a bit about the "clonal option", to use Bill Libby's phrase. To date, vegetative propagation techniques for our commercial conifers have not reached an operationally feasible stage, but the technology of producing container-grown seedlings in quantities and at costs competitive with bare-root nursery stock may soon be mated to rooting techniques to multiply hybrid - or other - clones for operational plantations. The clonal option is not new, even in forestry, as it has been the mode of operation in poplar plantation technology for at least a century in southern Europe. The disasters that plague poplar clonal monoculture are an object lesson one hopes will be heeded when the use of conifer clones becomes generally feasible.

The direct operational use of hybrids may be much less important in tree improvement, in the long run, than the use of hybrid derivatives to provide the materials for selection. So far, there seems to be no evidence that tree improvement programs in this country have started to run out of usable heritable variation within species, but it would seem prudent to get at the job of stockpiling species and provenance hybrids in various environments. After all, it is probably not accidental that most of our oldest and most indispensable agricultural crop plants have considerable hybridization in their pedigrees.

GROWTH AND YIELD MODELING -- A PLACE FOR GENETIC IMPROVEMENT EFFECTS

Harold E. Burkhart and Thomas G. Matney [1/]

Abstract.--A wide array of growth and yield models, ranging from whole stand models to individual tree models, has been developed for southern species. These models for "woods run" stock can potentially be modified to provide preliminary estimates of growth and yield in stands established from genetically improved stock. The approach necessary and the likelihood of success in incorporating genetic improvement effects in growth and yield models depends on the components of the model, the predictor variables used, the interdependence of the components, and, of course, the extent and nature of the data base on genetic effects.

Additional keywords: Yield tables, stand models, simulation

INTRODUCTION

For over two decades considerable effort has been devoted to the selection and propagation of forest trees for seed orchard establishment in the South. Seed collected from these orchards is now providing genetically improved stock for stand establishment. During the 1979-80 planting season, the forest products industry in the Southern U. S. planted 787,743,422 pine and hardwood seedlings. Of the more than three-quarters of a billion seedlings planted, a record 327,341,410 were from seed orchard-produced stock (information provided by Southern Forest Institute). At present, information concerning the effect of genetic variation on yield is limited. Yield tables that are currently available apply only to natural stands or plantations established from "woods run" stock. It is essential that yield estimates be developed for the increasing acreage of genetically improved stands if prudent forest management decisions and realistic wood supply projections are to be made.

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The purpose of our paper is two fold: (1) to present an overview of growth and yield modeling approaches that have been commonly employed in the past, and (2) to suggest how the effects of genetic gain might be incorporated into the various types of models.

OVERVIEW OF GROWTH AND YIELD MODELING APPROACHES

Modern quantitative analysis of forest growth and yield dates to MacKinney and Chaiken's (1939) application of multiple regression techniques to the problem of variable-density yield estimation in natural stands of loblolly pine. Since that time, a wide variety of approaches has been taken to growth and yield estimation. Throughout this discussion emphasis will be placed on techniques and approaches taken to growth and yield modeling for even-aged stands of southern species. The current modeling approaches may be considered to lie on a continuum with respect to structural complexity and output detail. This continuum may be broken into three broad categories: (1) whole stand models, (2) size class distribution models, and (3) individual tree models.

Whole Stand Models

Many investigators have used multiple regression techniques to predict growth and/or yield for the total stand or for some merchantable portion of the stand (such as Beck and Della-Bianca 1972, Bennett 1970, Bennett et al. 1959, Brender and Clutter 1970, Burkhart et al. 1972a, b, Clutter 1963, Coile and Schumacher 1964, Dale 1972, Farrar 1979, Goebel and Warner 1969, Murphy and Sternitzke 1979, Schumacher and Coile 1960, Smith et al. 1975, Sullivan and Clutter 1972, Sullivan and Williston 1977). Stand level variables such as age, site index, basal area or number of trees per unit area are utilized in the whole stand approach to predict some specified aggregate stand volume. Volume distribution by size class is not provided. A commonly used multiple linear regression model for natural stands is:

$$\log(Y) = b_0 + b_1 (1/A) + b_2 (SI) + b_3 \log(BA)$$

where

Y = net yield per unit area
A = stand age
SI = site index
BA = basal area per unit area
b_i's = parameters to be estimated from the data

Whole stand models for plantations generally involve number of trees rather than basal area per unit area as the expression for stand density.

Net growth is estimated by differencing predicted yield at two points in time. When obtaining growth estimates by differencing a yield equation, it is necessary to have a function that describes the change in stand density over time. For natural stands this has generally involved an equation to project basal area as a function of site index, initial basal area and age, and the length of the projection period. Numbers of trees per unit area must be projected for typical models of planted stands. These "survival curves" commonly express the number of live trees at any given time as a function of the number planted, site index and age.

Many of the published multiple regression models are highly empirical "best fits to the data," although some work has been reported on biologically-based model forms (for example, Pienaar and Turnbull 1973). A major improvement in model specification methodology was suggested by Clutter (1963) when he derived compatible growth and yield models for loblolly pine. Clutter's (1963) definition of compatibility was that the yield model should be obtainable through mathematical integration of the growth model.

Size Class Distribution Models

A number of models have been developed which consider the stand in terms of the distribution of the number of trees per unit area by size-class. In most cases dbh classes have been used. The most common stand models for southern species in this general category are based on a diameter distribution analysis procedure (for example, Beck and Della-Bianca 1970, Bennett and Clutter 1968, Burkhart and Strub 1974, Clutter and Belcher 1978, Dell et al. 1979, Feduccia et al. 1979, Lenhart 1972, Lenhart and Clutter 1971, Schreuder et al. 1979, Smalley and Bailey 1974a, b). In this approach, the number of trees per unit area in each diameter class is estimated through the use of a probability density function (pdf) which provides the relative frequency of trees by diameters. Mean total tree heights are predicted for trees of given diameters growing under given stand conditions. Volume per diameter class is calculated by substituting the predicted mean tree heights and the diameter class midpoints into tree volume equations. Yield estimates are obtained by summing the diameter classes of interest. Although only overall stand values (such as age, site index, and number of trees per acre) are needed as input, detailed stand distributional information is obtainable as output.

The various diameter distribution models differ chiefly in the function used to describe the diameter distribution. Initial applications of this technique (Beck and Della-Bianca 1970, Bennett and Clutter 1968, Burkhart and Strub 1974, Lenhart 1972, and Lenhart and Clutter 1971) used the beta probability density function, whereas more recent applications have utilized the Weibull function (Clutter and Belcher 1978, Dell et al. 1979, Feduccia et al. 1979, Schreuder et al. 1979, and Smalley and Bailey 1974a, b).

Regardless of the probability density function used, the procedure involves estimating the pdf parameters for each plot in the data set (usually by the method of moments or maximum likelihood) and then developing regression equations to relate these parameter estimates to stand characteristics such as age, site index and number of trees per unit area. Unfortunately, functions for relating the pdf parameters to stand characteristics have not been fully satisfactory. Currently, there is much interest in an alternative to the conventional methods for estimating diameter distribution. This alternative, sometimes called a "parameter recovery method," consists of forecasting overall stand attributes (such as total cubic volume, total basal area) and solving for the parameters of a theoretical diameter distribution model (such as the beta or Weibull) that will give rise to the overall stand attributes. Although there is little published on this technique, it does have potential for producing more consistent diameter distributions and it provides a direct mathematical link between the overall stand volume and the distribution of that volume. Additional information on parameter recovery methods can be found in the recent papers by Hyink (in press) and Matney and Sullivan (in press).

Individual Tree Models

Approaches to predicting stand yields which use individual trees as the basic unit will be referred to as "individual tree models". The components of tree growth in these models are commonly linked together through a computer program which simulates the growth of each tree and then aggregates these to provide estimates of stand growth and yield. This approach, while receiving extensive attention and application in the Western and Lake States regions of the U. S. as well as in Canada, has not been applied widely in the South.

Individual tree models are generally divided into two classes, distance dependent and distance independent depending on whether or not individual tree locations are required tree attributes. Distance independent models project tree growth either individually or by size classes, usually as a function of present size and stand level variables such as site index and basal area per unit area. These models vary widely in structure; examples of distance independent models are Dale (1975) and Stage (1973).

Distance dependent models that have been developed vary in detail but are quite similar in overall concept and structure. Initial data of a stand are input or generated and each tree is assigned a coordinate location. The growth of each tree is simulated as a function of its attributes, the site quality, and a measure of competition from neighbors. The competition index varies from model to model but in general is a function of the size of the subject tree and the size of and distance to competitors. Tree growth is commonly adjusted by a random component representing genetic and/or microsite variability, and survival is controlled either stochastically or deterministically as a function of competition and/or individual tree attributes. Yield estimates are obtained by summing the individual tree volumes (computed from tree volume equations) and multiplying by appropriate expansion factors. Models of this type have been developed by Arney (1974), Daniels and Burkhart (1975), Ek and Monserud (1974), Hegyi (1974), Newnham and Smith (1964), and others. The loblolly pine stand simulator published by Daniels and Burkhart (1975) is presently the only fully operational distance-dependent stand model for a southern species.

INCORPORATING GENETIC IMPROVEMENT EFFECTS IN GROWTH AND YIELD MODELS

Preliminary estimates of growth and yield are needed for stands established from genetically improved stock prior to large acreages reaching merchantable size. Modification of existing growth and yield models for "woods run" stock will likely be the most feasible means of developing these preliminary estimates.

Past Studies

Relatively little work has been done on modeling genetic improvement effects on growth and yield. Tisdale (1973) evaluated a whole stand model and a diameter distribution model for loblolly pine plantations to determine which could best predict dry weight yield after constant growth increases in diameter and height and increases in specific gravity were incorporated. He found the diameter distribution model was more readily modified to include assumed changes in growth characteristics and that the predicted yields from the modified diameter distribution model conformed more closely to expected values than did those from the whole stand model.

Mitchell (1975) modified the mean and variance in height growth in his Douglas-fir stand simulator to depict the effects of hypothetical selection programs on yields. His results indicated that a

simultaneous increase in the mean and decrease in the variance of height growth may result in little or no increase in total volume and will probably decrease the volume in the larger "crop trees".

Nance and Bey (1979) modified four relationships in Daniels and Burkhart's (1975) individual tree model to reflect genetic differences. Predicted yields from the modified version were then compared to yields with the original model. These comparisons indicated that early height growth gains must be maintained throughout the rotation to materially affect final yield, that mixing of seed could be more desirable than separate plantings of woods run and improved seed, and that reducing phenotypic variance may reduce total volume production.

Genetic improvement effects on "optimal" rotation age of loblolly pine plantations were studied by Thurmes (1980). Using Daniels and Burkhart's (1975) stand model, he found that arbitrarily increasing height growth decreased optimal rotation age in the same manner as experienced by increasing site index. Thurmes also decreased the stochastic variability in the model in an attempt to simulate genetic selection. This decreased variability (without any shift in the mean) resulted in fewer peeler-sized trees and decreased the stand value.

Some Possible Approaches for Future Studies

In the ensuing discussion of possible approaches for future studies aimed at incorporating the effects of genetic improvement in growth and yield models, we assume that an existing model for "woods run" stock is to be modified. When modifying an extant model, it will be necessary to develop biological paradigms of how genetically improved stock might grow, specify mathematical models of these paradigms, and evaluate the resultant predictions against conventional wisdom and experimental data. As additional data from genetically improved stands become available, this information can be used to evaluate the appropriateness of the original models and to estimate coefficients in growth and yield models.

The approach to incorporating genetic improvement effects in growth and yield models will be determined by the type of model(s) and the extent and nature of data on realized genetic gain that are available. Genetic improvement may affect many different aspects of tree growth and stand development. First we will examine some of the individual components and suggest how modifications may be made to reflect the effects of genetic selection.

Specific gravity modification can be modeled by simply changing the constant for converting cubic volume to dry weight.

Form changes can be incorporated by modifying the tree volume or taper equations that are used to convert dbh and height values to tree volumes.

Disease resistance, for example resistance to fusiform rust, can be partially incorporated by modifying the survival curve. If selection for disease resistance affects the distribution as well as the total amount of mortality, this shift must also be incorporated to provide realistic estimates of surviving volume by size class.

Diameter growth changes can be incorporated into the diameter growth function, or, depending on the type of models, perhaps into the basal area projection equation.

Height growth modification may be reflected through a height growth function or through a shift in the site index value.

Selection for any one factor is not necessarily independent of the other factors, of course. Thus, it would not be realistic to assume a simple change in diameter or height growth with no corresponding change in factors such as tree form and mortality rates. In many instances, models are structured such that a change in one factor will affect many other factors. For example, if height growth is increased without any increase in diameter growth and both dbh and height are used to estimate tree volume, an improvement in form is implied even if the coefficients in the tree volume or taper equation are not modified.

As a further example, consider how mortality might be affected by genetic selection. In growth and yield models where mortality is expressed as a function of initial number of trees planted and stand age, increased (or decreased) diameter or height growth would not influence survival. If, however, surviving number of trees is modeled as a function of stand age, basal area, average height of the dominant stand, and initial number of trees planted, then an increase in diameter or height growth (or both) would affect survival. In cases where the components are interrelated, a change in only one component may affect all other components. When the components are not interrelated it may be necessary to modify several functions to appropriately

reflect a change in a single factor. The approach necessary and the likelihood of success in incorporating genetic improvement effects in growth and yield models depends on the components of the model, the predictor variables used, and the interdependence of the components.

Decreased variability is often a result of selective breeding. In deterministic models, decreased variability can be modeled by adjusting growth equations so that trees are more uniform in size. This decreased variability is commonly expressed in stochastic models by the adjustment of the variance of selected random components in the model. An appropriate variance reduction for random components is difficult to determine, however, because these components reflect both microsite and genetic variability. In general, stochastic models provide some advantages over deterministic models when attempting to model many genetic gain effects because either growth functions or random components (or both) can be modified.

SUMMARY AND CONCLUSION

In summary, a wide array of growth and yield models -- ranging from whole stand models to size class distribution models, to individual tree models -- have been developed for southern species. With the increasing acreage of stands established from genetically improved stock, it is essential that growth and yield estimates be developed for these conditions as quickly as feasible. Preliminary estimates can be derived through the modification of existing growth and yield models for "woods run" stock. The approach to this modification will depend on the type of model(s) available and the extent and nature of data on genetic gain. Incorporation of genetic improvement effects into growth and yield models must proceed in light of components of the model, the predictor variables used, and the interdependence of the components. Until adequate validation data are available, these tentative estimates of the effects of genetic selection should be used cautiously.

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STAND PRODUCTIVITY: Some Considerations in Evaluating Genetic Improvement

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Abstract. The productivity of forest stands depends on the potential of their constituent abiotic and biotic elements. The patterns of stand and tree growth differ, and performance estimates based on free growing trees, which are mainly based on time, are not directly transferable to stands, where performance includes the additional dimension of space. The development of stands, whether from selected or unselected growing stock, will follow the classic growth curve and will be under the control of its determinants. Improving the rates of growth of the main biotic elements of stands will chiefly decrease the time required to reach the relatively fixed carrying capacity of the site. This improved rate will enable or require shorter rotations and more frequent thinnings to realize the genetic gains. The realities of these changes are briefly considered.

Additional Keywords: Carrying capacity; growth curves; stand dynamics.

INTRODUCTION

Stand productivity* is the focus of a diversity of disciplines associated with the forest resource. In forestry, it has traditionally been addressed by forest mensuration and has centered on the growth and yield of the utilized portion of the crop - wood. Such information has satisfied the practical needs of forest management, but it has not measurably contributed to an understanding of the productive processes of forest stands. The relationships between the biota and the environment that determine the productivity of stands has always been a challenge to practical ecologists such as silviculturist and agronomist (Baker 1950, Jenny 1980, Evans 1980). Fortunately, the early efforts of Moller (1945) and others in silviculture who attempted to quantify and understand these processes continues today. An understanding of the productive processes of forest stands is important now and in the future, as the forest is made more productive for mankind.

The success achieved by efforts in tree improvement during the last three decades requires an evaluation by those concerned with the

*The productivity of ecological systems can be expressed in various ways. Productivity is expressed here as either stem volume or basal area growth, the traditional terms used with forest stands.

productivity of forest stands. What will be the productivity and culture of stands composed of trees possessing improved growth rates, increased resin production, greater disease resistance, etc.? The following thoughts are restricted to the effects of improved rates of growth and do not consider any qualitative characteristics, although their importance and the contribution that genetic improvement has on their character is recognized. The relative compatibility of maximizing the potential of the individual tree and that of the stand is the principal thrust of these thoughts.

GENERAL CONSIDERATIONS

Forest Stands and Productivity

Forest stands are ecological systems, and their productivity is dependent on the potential of their biotic and abiotic elements and the interactions of these elements. The variation found in the productivity of forest stands is a reflection of the variation in these elements and their interactions. Foresters and others have tacitly recognized this variation and interaction by noting that the productivity of an area must be expressed in terms that are specific to a particular species.

The biotic and abiotic elements of forest stands are not equally amenable to management. The biotic elements are much more flexible and their modification and control constitutes the bulk of silvicultural practice, e.g. the control of composition, density, structure, etc. In comparison, the abiotic elements are relatively fixed and one has to mainly work within the confines of climate, soil, or whatever else is at hand. However, modification of the abiotic elements, either improving or degrading, is usually much more lasting.

Stand versus Tree Productivity

The productivity of forest stands is expressed in the behavior of the populations and communities that constitute the biotic elements assembled on an area. At the stand level productivity is expressed in terms of quantity per unit of time and space. In contrast, assessments of the productivity of individual trees usually ignore space. Thus, the growth patterns of trees and stands differ; the growth of the tree is continuous while the stand approaches a maximum quantity which is thereafter roughly maintained (Figure 1).

The growth rates of both trees and stands is also affected by the allotment of growing space. Increased growing space permits a greater expression of the potential of the individual tree. For example, beyond ten years wider spaced trees in loblolly pine plantations have twice as much basal area as closer spaced trees (Figure 1A). The effects of increased growing space on stand basal area is the reverse of that of the mean tree, since the stand includes considerations of population size and space. Increased growing space for the trees within the stand reduces the rate of approach of the stand to the maximum and constant levels which the site can apparently support. Thus, the stand with closer spacing reaches a rather constant level of basal area sooner than a stand with a wider spacing (14 years versus 22 years, Figure 1B).

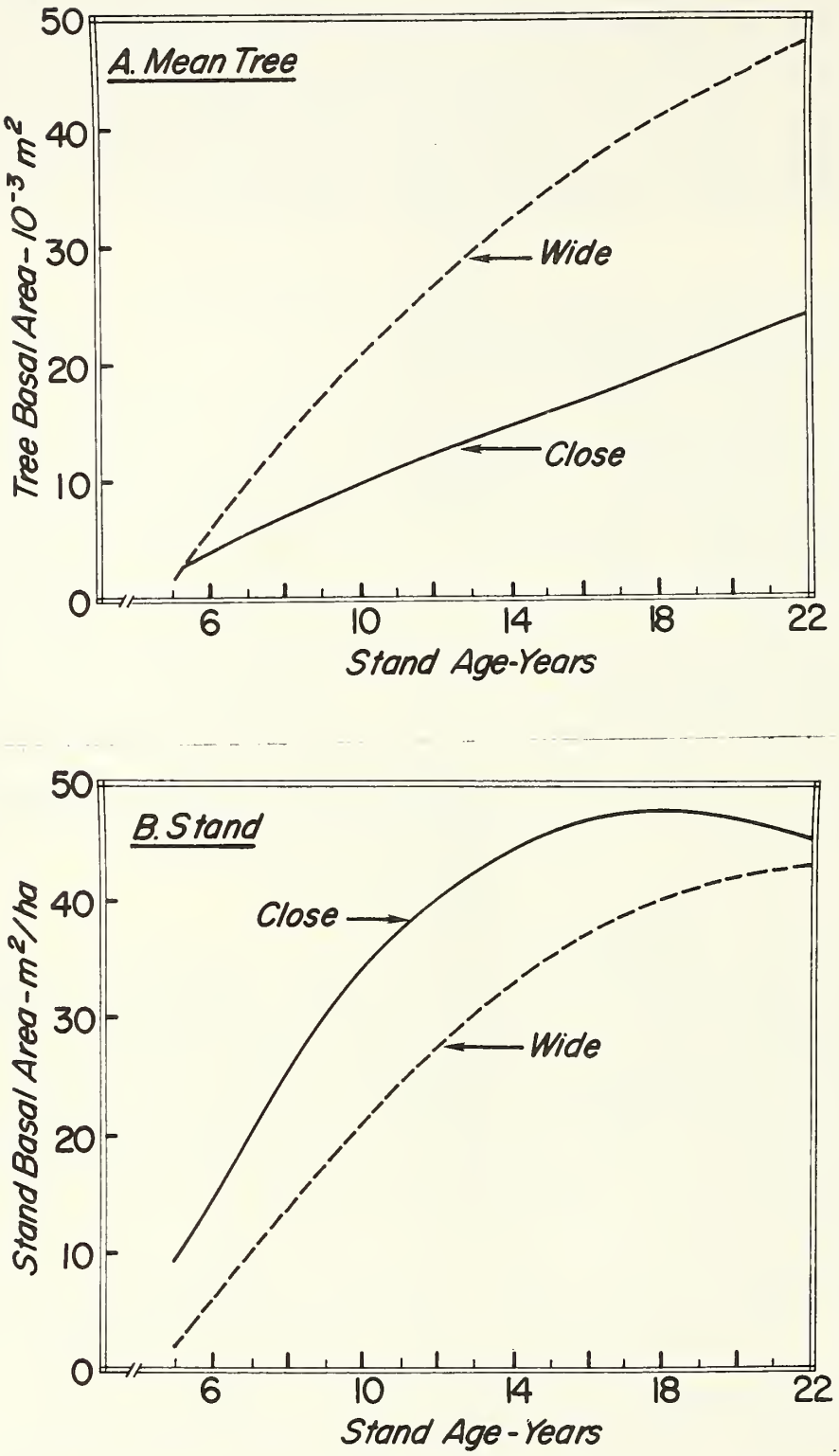

Figure 1. A comparison of the basal area development of the mean tree and the stand in loblolly pine plantations at wide (1200 trees/ha) and close (4300 trees/ha) initial spacings. The site index of the area is 29 m at 50 years.

The objectives of maximizing the potential of the individual tree and the stand are not compatible in forest management. Maximizing the potential of the individual involves performance in an unrestricted or "open grown" environment. In contrast, the objective in stand management is to maximize the productivity per unit of land area by optimizing the balance between the potential of the individual, the population, and the site. Therefore, assays of productivity based on free growing individual trees — such as those arrived at in convential progeny trials — are not directly transferable to stands or populations which face the confines of space.

GROWTH CURVES AND SELECTION

Characteristics and Determinants

The previously described pattern of stand basal area growth is characteristic of the classic growth curve that applies to biologic populations in limited space and resources (Hutchinson 1978). The periods of population growth follow the common sequence of acceleration, linearity, deceleration, and constancy (Figure 2). This common pattern of behavior results from the integrated expression of the determinants of the growth curve identified as biotic potential, environmental resistance, and carrying capacity (K). Biotic potential is the inherent capacity for growth in an environment of unlimited resources and is a property of both individuals, populations, and communities. Carrying capacity is principally an expression of the limits of the relatively fixed abiotic elements of the environment to support life and is expressed in quantity per unit area. Environmental resistance is an

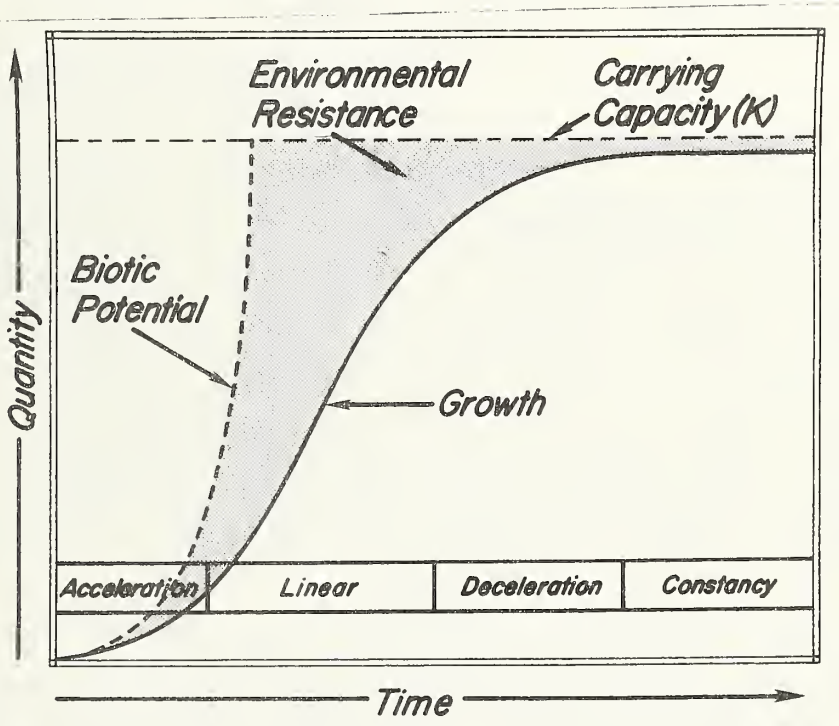

Figure 2. The periods of development and determinants of the classic growth curve.

expression of the opportunities for growth and is lowest during the early life of a stand when opportunities for growth are greater. It increases as time elapses and carrying capacity is approached.

During stand development conditions change from low levels of density and competition to high densities with more intense levels of competition. These changes bring about two types of selection in the life of the stand: r and K selection (MacArthur, 1972). r selection is independent of density and occurs early in the life of the stand when increased growth rates are favored by the low densities and temporal habitats offered before carrying capacity is reached. In contrast, K selection is density dependent and is expressed as the stand approaches and is at carrying capacity. K selection favors persistence at reduced growth rates and greater efficiency in the use of resources. These two types of selection have relevance in tree improvement since considerable selection effort is centered on improved rates of growth in low density environments (r selection). Little regard has been placed on increased efficiencies at the high densities associated with K selection. In addition, most of the species presently of interest in tree improvement are those which naturally preempt the low density and temporal habitats of the early stages of succession. Such species exemplify r selection.

Applications

The equations that mathematicians use to characterize population growth also recognize these determinants of behavior. The one used in the subsequent examples is that of Chapman and Richards (Pienaar and Turnbull 1973) where:

$$\text{Quantity} = KR$$

$$\text{and } R = (1 - e^{a\ \text{Time}})^{b}.$$

In this equation K is the carrying capacity of an area and is visualized as being constant. R is the degree of approach to K and is a function of biotic potential and time. It ranges from zero to one and is zero at time zero and approaches one as time increases and K is reached. When applied to forest stands K can be expressed by the various measures used to quantify stand properties such as basal area, volume, leaf area, and dry weight. However, for each of these expressions of K the level and rate of approach differs; e.g., the carrying capacity for foliage is achieved relatively early in the life of a stand while that of volume is much later. Two examples based on data from the literature are used to illustrate the expression of the growth curve determinants in forest stands. In the first example, carrying capacity varies and biotic potential is the same; in the second, biotic potential varies and carrying capacity is approximately the same.

The first example uses the performance of loblolly pine at the two limits of its observed productivity, i.e., site indices of 18 and 36 meters at 50 years (Figure 3A). The volume carrying capacities at these limits are 300 and 800 m^3/ha, respectively. These carrying capacities differ by almost three-fold and represent the potential limits expressed

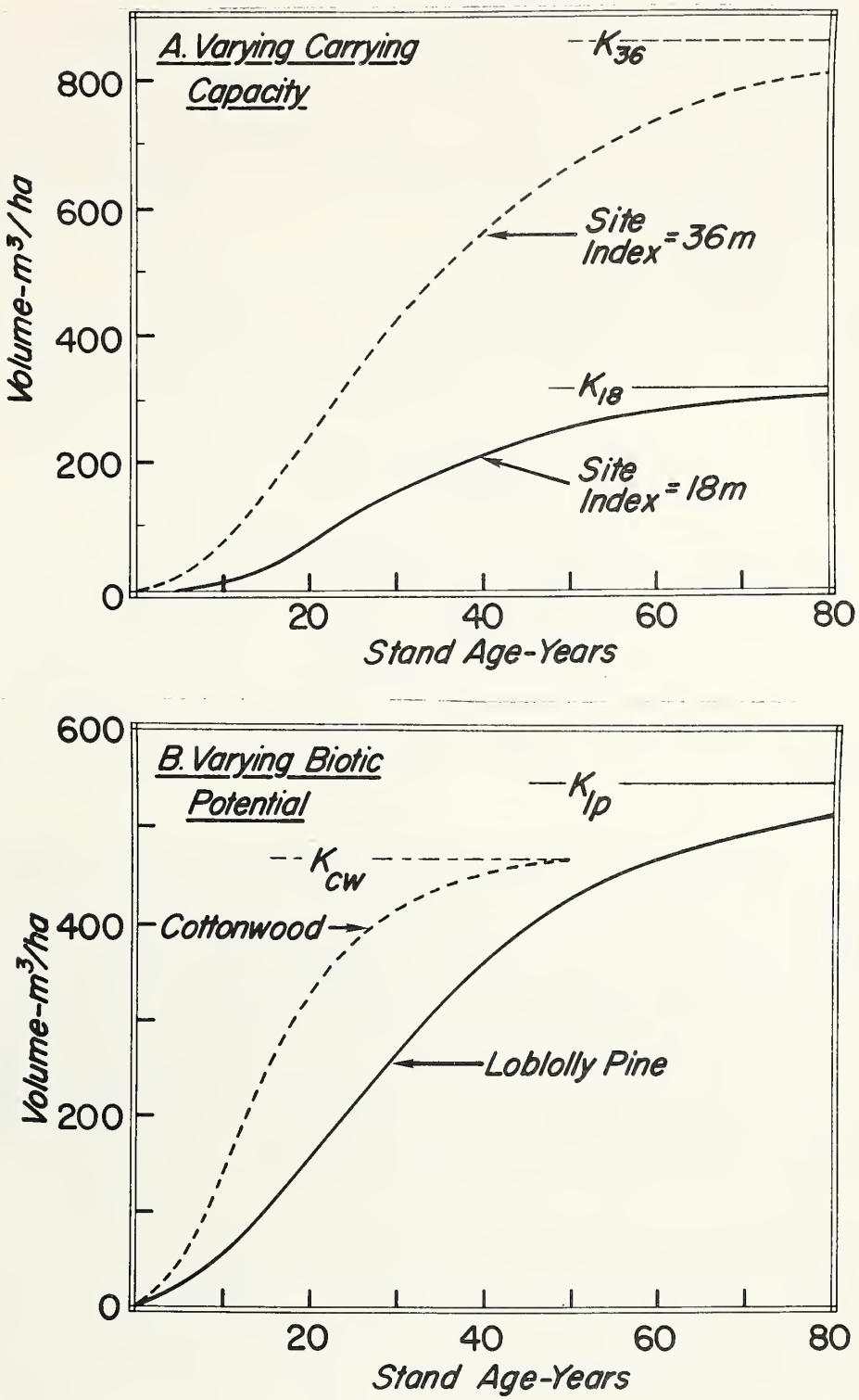

Figure 3. A comparison of the volume growth curves for: (A) varying carrying capacities and similar biotic potentials, and (B) varying biotic potentials and similar carrying capacities. The growth curves were fit with nonlinear regression using the Chapman-Richards equation. All data are based on site indices at 50 years and are from USDA (1929) for loblolly pine and Williamson (1913) for cottonwood.

by the species. In contrast, the values for R, considered to be an expression of the biotic potential of this species, are essentially the same for both carrying capacities. For example, at 40 years of age, 65 percent of K has been attained on both sites. This similarity of R on both sites indicates that the biotic potential of the species is the same. Thus, the difference between the two sites is principally the extent to which the carrying capacities have permitted the expression of biotic potential.

Cottonwood and loblolly pine are compared in the second example which considers comparable levels of K (around 500 m^3/ha)* and different levels of biotic potential (Figure 3B). This choice of species is perhaps a bit extreme but it usefully illustrates the point. The rate of approach to the "comparable" carrying capacities differs for the two species. For example, at 20 years the volume for the natural cottonwood stands is about 350 m^3/ha which is about 70 percent of K. At the same age the volume for the loblolly pine stands is only 150 m^3/ha or only 30 percent of K. Thus, there is more than a 2-fold difference in R at this age. Although two species were used here to demonstrate differences in R, genetic selection within a species can also result in increased biotic potential, though perhaps less than the 2-fold increases in this example. However, any gains in biotic potential will result in a shortening of the time required to reach K.

STAND DYNAMICS

Differentiation

The characteristics and determinants of the growth curve can be applied at both the individual tree and stand level. The growth curve of the stand is essentially a composite of the gains made by the growth of individual trees and the losses through tree mortality. However, the growth curves of the individual trees making up the stand are not the same, since the trees grow at different rates. Analysis of the growth of individual trees is very complicated since there can be as many patterns of growth as there are trees. However, the development of individual trees within a stand can be expressed by differentiating the stand population into size classes. The process of differentiation described here uses the distribution of height classes in loblolly pine plantations during the early years of development.

Differentiation commences early in the life of the stand and continues through the stand's development, although the rates diminish with age. For example, at planting there is a marked central tendency in height class distribution, and the range in heights is only 0.3 m (Figure 4). However with increasing age, differences in the rates of height growth within the population result in a widening of the distribution of heights, and by 4 years the range in heights has increased to

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* Although these volume carrying capacities are about equal, the site indices are 41 m and 27 m for cottonwood and loblolly pine at 50 years, respectively.

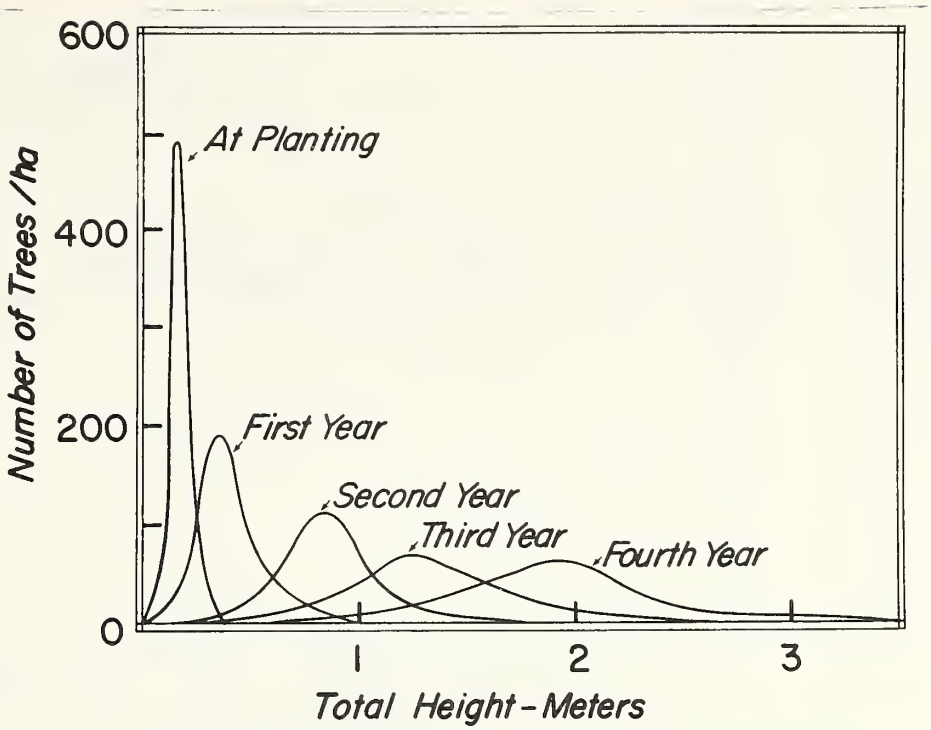

Figure 4. The distribution of height classes (3 cm) during the first 4 years of development of loblolly pine plantations planted with 1920 trees/ha and with a site index of 29 m at 50 years.

3 m. During these early years of development the leading edge of the distribution is growing at a rate about three times faster than that of the trailing edge. These early differences in growth rates occur before canopy closure and when the trees are relatively free growing. They are mainly atributable to the genetic makeup of individuals, micro-variation in the environment, and their interactions. Random variation also exerts an influence on differences in growth rates, since factors such as insect damage, top breakage, etc. are essentially random events. However, these early differences in growth rates are an expression of r selection and are a major criterion in advanced generation selection.

Subsequent Development

What are the implications of these early differences in rates of height growth on the subsequent development of the stand and its productivity? To resolve this, the performance of segments of the height distribution existing at 5 years in a loblolly pine plantation were followed through 20 years. The distribution at 5 years was grouped into ten segments of equal numbers (deciles). The first decile is the shortest 10% of the population and the tenth decile is the tallest. Repeated measurement of the trees permits tracking the development of each decile through time.

The current annual volume growth of trees through 20 years is strongly related to their decile at 5 years (Figure 5). The differences among deciles occur early in plantation development and increase through

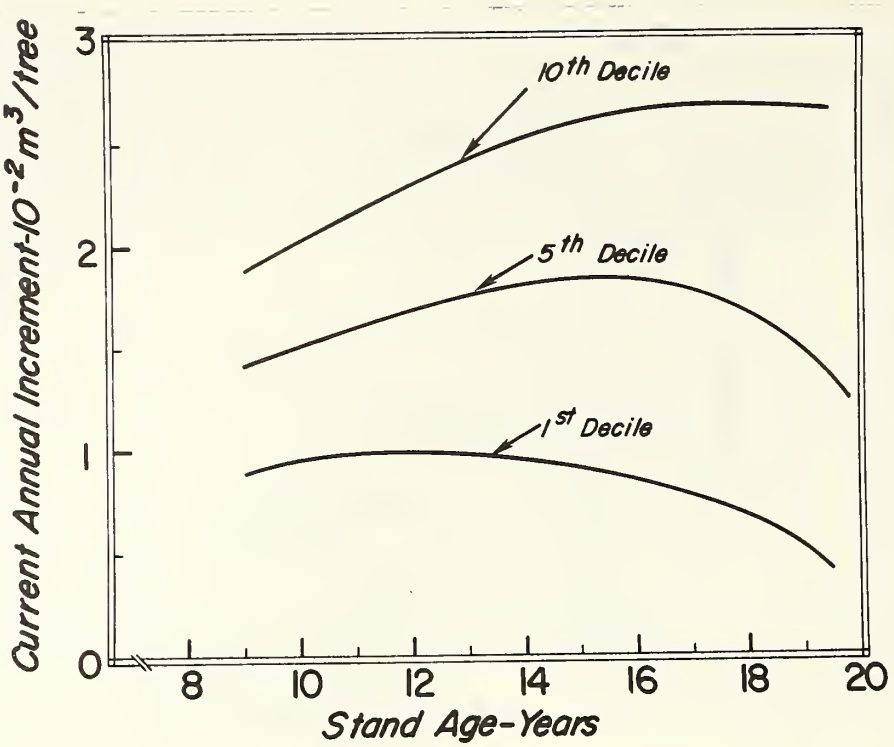

Figure 5. The patterns of current annual increment for the identified deciles in a loblolly pine plantation. The plantation was planted with 1920 trees/ha and has a site index of 29 m at 50 years. The deciles were identified from the height distribution at 5 years.

time. For example, at 8 years the tenth decile is growing twice as fast as the first decile. Further, this difference between these two deciles increases to five times by 20 years. Thus, the volume growth of the shortest trees at 5 years generally declines through time, while that of the tallest trees increases through 15 years and is maintained thereafter. The differences in the growth rates of the deciles are undoubtedly related to changes in the relative canopy positions of the trees. The trees in the lower deciles are constantly being shifted to subordinant positions within the canopy where their growth rates decline. In contrast, the superior canopy positions of the tallest trees enables them to maintain their high rates of growth.

The relative size of trees when the canopy closes is strongly related to their subsequent development. At 20 years the tenth decile trees are 60% greater in diameter than the first decile trees and have almost three times more volume (Table 1). The high rates of growth and low mortality of the tallest trees at 5 years enables them to make large contributions to the second decade volume growth (Table 1). Thus, the contribution to the total volume growth during the second decade is not equally distributed among the deciles. The tenth or tallest decile produces almost 25 times the volume growth of the first decile. In addition, the taller 50% of the trees at 5 years produces 70% of the second decade volume increment.

Table 1. The average properties at 20 years of the population deciles identified at 5 years and their percentage contribution to second decade volume increment.

Decile at 5 years	Twentieth year			Second Decade Volume Increment
	Mean DBH	Volume	Survival	
	-cm-	$-10^{-2}\ m^3-$	-%-	-%-
1	14	13	21	< 1
2	16	16	65	4
3	17	18	70	6
4	18	21	86	9
5	19	24	92	11
6	20	25	95	12
7	20	26	94	12
8	21	28	95	14
9	22	30	97	14
10	23	34	97	17

The trees in the lower deciles also have lower survival because of their subordinant canopy position. For example, only 20% of the trees in the first decile at 5 years are still living at 20 years, while the upper five deciles average 95% (Table 1). In addition, nearly 90% of the mortality from 5 to 20 years occurs in the shorter 50% of the trees at 5 years.

Components of Productivity

General Patterns. The volume and basal area increment of forest stands can be partitioned between gross, net, and mortality. Gross increment is the total productivity for a time period, net is the change in the standing crop during the period, and mortality is the loss for the period. Thus, net = gross - mortality. Mortality is a reality in natural populations whether they are from selected materials or not, although this phenomenon has been poorly quantified in past studies of stand performance. The pattern of mortality during stand development is important in shaping the growth curve of stands and is related to the four periods that characterize this curve (Figure 6).

During the acceleration period mortality is negligible and thus net increment is equal to the gross increment. The attainment of K during this period is low (< 20%) and the opportunities for growth are great. The trees have not fully occupied the site and thus the high rates of growth are a fair reflection of the biotic potential. The stand is also rapidly increasing in foliar mass, and at the end of the period maximum levels of foliage are achieved. During this period small increases in the approach to K result in large increases in the current annual increment. For example, with an increase from 5 to 10% of K, net increment increases by almost one-half. In contrast, an increase from 10 to 15% of K results in only a 10% increase in increment.

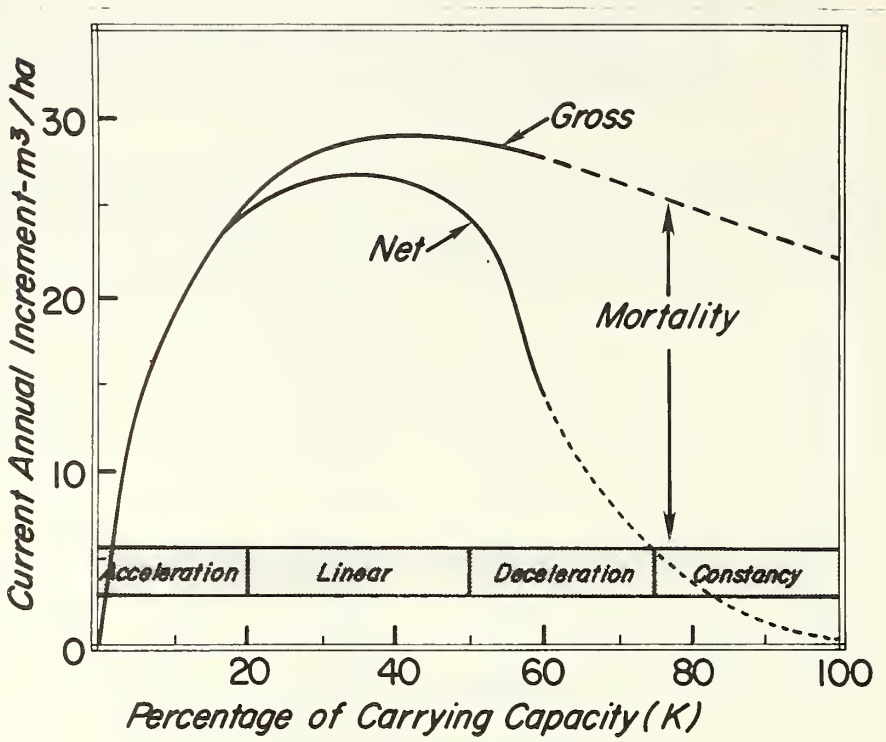

Figure 6. The relationship of the components of current annual volume increment and the volume of the standing crop expressed as a percentage of the sites carrying capacity (600 m^3/ha). Data through 60% of K are from a loblolly pine spacing study, with a site index of 29 m at 50 years. The dashed portion of the curves are speculative.

The maximum rates of gross and net increment approach 25 m^3/ha during the linear period, which extends from 20 to 50% of K. The foliar mass of the stand is maintained at constant levels during this period, and thus, increases in the crown size of individual trees are at the expense of its neighbors. As a consequence, mortality commences and the net increment falls below the gross increment.

The continued impress of mortality is reflected in the decline of net increment during the deceleration period, which extends from 50 to 80% of K. The increased rates of mortality result from the declining growth rates of the trees in the lower canopy, while those in the upper canopy continue to grow at high rates. The trees in the lower canopy are shifted to even lower positions, where they are unable to sustain life.

Since the carrying capacity is reached during the constancy period, net increment approaches zero, and thereafter, the standing crop is maintained at a constant level. Thus, a steady state exists where the gains from gross increment are offset by losses to mortality. In reality there are temporal flucuations about the carrying capacity (Bormann and Likens 1979), and this value represents a longterm mean.

Implications. The improvement of growth rates realized from genetic selection will undoubtedly modify the behavior of population development. However, the growth of the population will still be restricted by the determinants of the growth curve. Within the current limits of forest management, the values of K are primarily fixed by the abiotic elements of the environment (Jenny 1980), while R is more flexible and can be modified by management techniques, such as using improved growing stock or varying the initial spacing.

A comparison of the effects of improved growth rates on the basal area development of loblolly pine plantations is illustrated in Figure 7. In this comparison, the improved growth rates achieved through the use of closer initial spacings are considered to be comparable to those attained by genetic selection. The stand with a closer spacing reaches full occupancy of the site earlier than that with a wider spacing. For example, the carrying capacity of the site (40-45 m^2/ha) is reached at 13 years with the closer spacing while the wider spacing takes 19 years. This pattern of stand behavior is similar to that observed with improved growth rates in agronomic crops (Evans 1980) and is also anticipated in stands comprised of trees with improved growth rates.

As a result of the more rapid attainment of carrying capacity the gross increment of the closer spacing at 20 years is 25% greater than that of the wider spacing. However, the increased growth rate represented by the closer spacing intensifies the competition of trees for limited resources, and through 20 years, mortality is five times greater in the closer spacing than in the wider. Thus, at 20 years, mortality has offset the gains from increased growth and the net production of basal area at that age is the same for both spacings. Therefore, capitalization on improved rates of stand growth, whether from closer

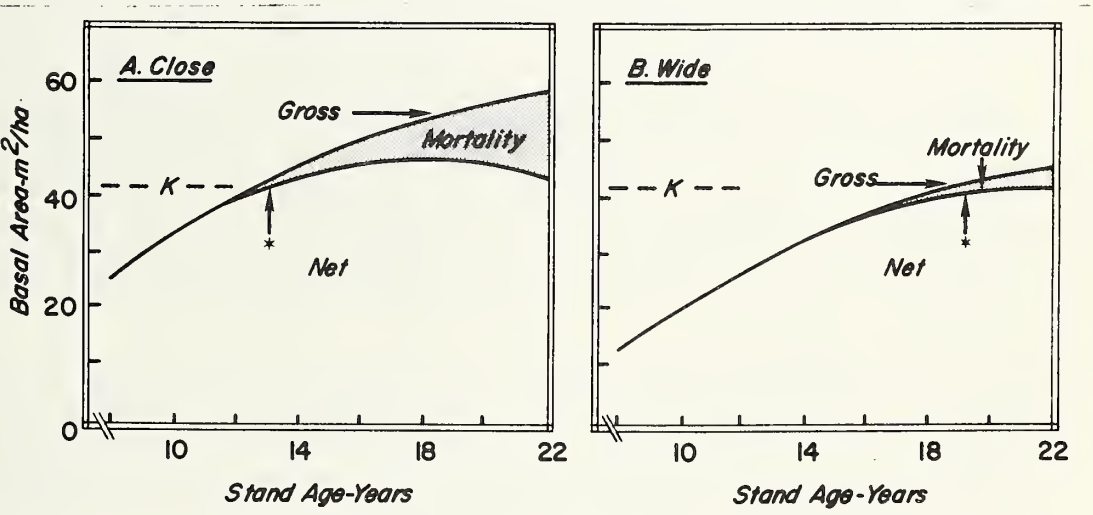

Figure 7. The components of basal area development in loblolly pine plantations at different initial spacings. (A) Close spacings (4300 trees/ha) represent improved rates of growth. (B) Wide spacings (1200 trees/ha) represent unimproved rates of growth. The starred arrows indicate when 90% of the sites carrying capacity is reached.

spacings or genetically improved growing stock, will require or enable the use of shorter rotations and frequent thinnings. These thinnings will lower the level of the standing crop below K and maintain the stand in the linear period of growth. Improved growth rates coupled with improved quality may also permit wider initial spacings in plantations, earlier achievement of desirable merchantable size, and a rapid realization of K.

CONCLUSIONS

The determinants of stand productivity are the relatively fixed abiotic elements and the comparatively flexible biotic elements. The flexibility of the biotic elements permits modification of their character through the silvicultural manipulation of stand structure, composition, density, etc. All of these stand properties are related to genetic character. The modification of the biotic elements requires effort and the application of skills. However, such efforts are not equal to those required to modify the relatively fixed abiotic elements, although such modifications, beneficial or detrimental, may be more lasting. The increased yields of present day agriculture have been achieved by simultaneously modifying both the biotic and abiotic elements (Pimentel et al. 1973) and are therefore not likely to be broadly applicable in forestry. The scale of time and area in forestry and the comparative value of forest crops sharply limits the wholesale transfer of such technology. Also, real crop yields in agriculture are often only about one-half to one-third of those attained under experimental conditions (Milthorpe and Moorby 1974). If the geometry and logistics of agriculture (Frink and Horsfall 1980) has this magnitude of influence on realized yields, what are the realities for forest management?

The determinants of the classic growth curve have implications in evaluating genetic improvement. Firstly, they indicate that evaluations of growth rates based on individual tree behavior are not applicable to stand conditions since they do not consider the limitations of space and/or resources (Ford 1976). Secondly, the determinants indicate that improved growth rates will enable or require the use of more intensive stand culture to realize the gains, i. e. shorter rotations, more frequent thinnings, etc. This requirement needs to be recognized and its desirability evaluated. Thirdly, if the experience with agronomic crops is valid for the forest (Evans 1980), the relatively fixed carrying capacity is not likely to be changed by selection based on improved rates of growth.

The results of our efforts to improve the performance of forest trees through applied genetics are generally real and in some cases noteworthy. However, the realities of using this improvement in the varied area of applied forest management has not been sufficiently evaluated. Until then, the traits that improve the quality of forest stands will undoubtedly be the most genuine improvements.

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PREDICTING GROWTH AND YIELD OF FORAGE CROPS

Glenn W. Burton[1/]

Abstract -- The first year's growth and yield of space planted seedlings of bermudagrass, Cynodon spp., and bahiagrass, Paspalum notatum, was positively correlated (r = +.34 to +.43) with later average yields when seedlings establishment and management was kept as uniform as possible. Being able to propagate superior genotypes of bermudagrass vegetatively has greatly facilitated the improvement of this species. Recurrent restricted phenotypic selection has been 4 times as efficient as mass selection in improving forage yields of Pensacola bahiagrass.

Additional keywords: Bermudagrass, Cynodon spp., bahiagrass, Paspalum notatum, correlation coefficients.

Increasing growth and yield is one of the major objectives of the forage crop breeder. Although the ultimate objective is increased yield of meat or milk from the animals consuming the forage, it is usually realized by increasing the growth rate and yield of the forage consumed. Thus the forage breeder is always concerned with increasing yield. To do this, he must be able to predict and measure yield controlled by growth rate.

Since April 30, 1936, we have been trying to increase the yield of perennial cross pollinated grasses. The two grasses with which we have worked more than others are bermudagrass, Cynodon spp. and bahiagrass, Paspalum notatum. Commercial vegetative propagation of superior bermudagrass hybrids such as Coastal has greatly facilitated the genetic improvement of this grass. Although bahiagrass can be propagated vegetatively, its much slower establishment rate from sprigs has made seed propagation its only commercial method of increase to date. Our experience improving yields of these two grasses may be helpful to the breeders of trees and it is to this end that this paper is written.

BREEDING BETTER BERMUDAGRASSES (1)

Many years ago, H. K. Hays, with years of plant breeding experience said, "Use the best parents you can find. They usually have the best offspring". Our experience confirms this statement. But how do you find them?

Coastal bermudagrass is the best of 5000 F_1 hybrids between two excellent parents (2). J. L. Stephens saw a superior bermudagrass plant in a cotton patch on the Coastal Plain Experiment Station, increased it, compared it with a common bermuda check and named it Tift bermudagrass. An unknown person in South Africa used his eyes to select the other parent for Coastal. Both parents were grown in single plots along with other bermudagrasses in a uniform environment in our introduction garden. By observing them throughout the season and comparing their entire season's growth in the fall, we were able to detect growth rate differences that would have been difficult to detect on a short-time basis. We could also note resistance to diseases, absence of seed heads and other characteristics desired in the new variety.

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The plant breeder hybridizes to combine desired characters and to obtain hybrid vigor. We knew nothing about the parents for Coastal bermudagrass except that they possessed the characteristics desired and appeared to yield as well or better than any other bermudagrass in our nursery. Variation we had observed in common bermudagrass suggested that these parents were heterozygous. We could have spent several years testing all of our potential parents. We believed, however, that we would be able to propagate bermudagrass vegetatively and that we needed only to create and isolate a superior plant. It seemed more efficient; therefore, to start our breeding program by studying a large population of hybrids from these parents. If the parents were heterozygous, as assumed, each hybrid would carry a different set of gametes and one or more might possess the hybrid vigor necessary to increase yield. Because the parents came from different parts of the world and were probably unrelated, we expected them to have a good chance of producing the high yielding F_1 hybrid desired.

The hybrid seeds produced in the summer of 1937 were planted at uniform rates in flats of soil in the greenhouse in December and were transplanted to 2-inch clay pots in February. In April, 1938, they were set in the field on 5-foot centers in a sandy soil without fertilizer and were kept free of weeds throughout the season. A visual yield rating was made June 13, 1938, and height and diameter measurements, heading dates, and disease resistance ratings were made throughout the summer. In the fall, using the plant appearance at that time as much as our copious notes, we selected 128 plants (the range of types and the larger plants) and started three 4-inch pots of each in the greenhouse. Total dry matter produced by these potted plants cut at 3-week intervals during the winter failed to correlate with the total seasonal production of these selections in replicated field plots in 1940. These potted plants (one in the center of each 4 x 24 foot plot), were used to establish this clipping test with 3 replications in 1939. Weeds were controlled and most plots were completely sodded over by the fall of 1939.

A visual yield rating made June 13, 1938 less than 3 months after the 2" potted seedlings were set in the field correlated with the total 1940 yield ($r = +.34$, $P = .05$), suggesting that superior yield could be recognized early in some plants. However, several years of measuring yield in two replicated tests and other criteria were required to prove that Coastal was superior to many other bermudagrass hybrids produced in 1937.

As we have continued our bermudagrass breeding work releasing Suwannee, Midland, Coastcross-1, and Tifton 44, we have concluded that:

1. Coastal bermudagrass is an excellent parent transmitting many of its superior traits to its offspring.
2. Superior bermudagrass parent plants are usually heterozygous, giving highly variable offspring when crossed with Coastal or any other parent. Usually, several hundred F_1 hybrids of any cross must be screened to give one plant significantly more productive than Coastal.
3. By keeping everything as uniform as possible from the time the seeds are planted in the greenhouse until they are spaced on 9 x 9 foot centers in a uniform deep sand soil, we believe it is possible to select the highest yielding 5% of the plants visually at the end of the first season.

4. Yield data collected from a replicated clipping test conducted for 3 years will usually separate the best from the better clones and will indicate how it compares with its parents and other check varieties. Occasionally outstanding hybrids can be detected at the end of the first year in a replicated clipping test.

BREEDING PENSACOLA BAHIAGRASS

Pensacola bahiagrass is a stoloniferous perennial that can spread 12 to 18 inches per year. It is a sexual diploid that is presently propagated by seed. Most plants are highly self-incompatable and may, therefore, be considered F_1 hybrids. The variability between individual plants is substantial. We are presently using two plant breeding procedures to increase the forage yield of this grass. They are recurrent restricted phenotypic selection, (a more efficient form of mass selection) and the production of commercial F_1 hybrids. Seed for such hybrids will be produced by harvesting all seed from isolated fields vegetatively planted to alternate strips of two self-sterile cross-fertile clones that give high yielding hybrids. A brief description of each follows.

Recurrent restricted phenotypic selection (RRPS) is based on early research that proved that yields of spaced plants cut at the end of one season were positively correlated with 5-year yields of the same plants when compared in a vegetatively planted replicated clipping test conducted for 5 years ($r = +.43$ and $+.39$) (3). RRPS begun in 1960 initially involved spaced plant populations of at least 1000 plants evaluated with green plant yields taken in two consecutive seasons. Using the total forage yield for two years, we selected the five top yielding plants in each 25 spaced plant (5 x 5) block. Two culms with roots attached ready to flower the next day were taken from each selection, were placed in buckets of water and were grouped together in a space less than 1 meter in diameter in the laboratory by a north window. Each morning thereafter as they flowered, they were agitated to insure complete intermating between the 200 selections. When mature, seeds from these culms were harvested and used to start plants in the greenhouse for the next spaced-plant nursery. The 25-plant grid selection technique helped to reduce soil heterogeneity effects and the polycross procedure allowed selection on both the male and the female side and thus doubled the progress expected from mass selection that takes open pollinated seed from the field for the next cycle.

As we advanced through successive cycles of RRPS, we observed that most of the plants collected after yields or yield ratings were taken in the second year were the same that would have been selected at the end of the first year. We observed further, that, if great care was exercised to keep everything uniform, we could have selected visually in July, most of the plants that yielded more when cut in October. It appeared possible, therefore, to double our efficiency again by getting one cycle per year instead of one cycle every two or more years.

For the last two years, we have successfully completed one cycle per year as follows:

1. The soil in the field for space planting is fumigated in late March with methyl bromide to control weeds. Bahiagrass seedlings grow better after this treatment than following the use of other herbicides.

2. Following a spring growth rating that reflects winter injury, we study all date including actual yields taken on the previous year's spaced plant nursery and discard the seedling progenies from the poorest one-sixth of the maternal plants.

3. The remaining 166 progeny are given accession numbers ranging from 1 to 166. Each of six plants from each selection is placed in a separate one-half pound kraft bag numbered with its accession number. These are then placed in six different garbage cans so that one plant of each accession occurs in each can.

4. In mid April as these potted plants are set in the field (4) (each garbage can making a separate replication), their accession number is recorded in a graph-paper planting plan. Such a planting and such records allow an analysis of the performance of the 6-plant progeny of each selection and permits one to trace the pedigree of any seedling.

5. By mid-July when all the better plants are producing flowering culms, the five better plants in each 5 x 5 grid are checked on a graph-paper field plan.

6. The following morning, we collect two culms ready to flower from each selection, tag them with a row and plant number and group them together in the laboratory polycross previously described.

7. Each morning a tent made from paper suspended over the polycross is agitated to create a thorough mixing of the pollen produced. As soon as anthesis is complete, the tent is removed to give the culms access to the indirect light from large north windows.

8. When mature, the seeds from each selection are harvested, threshed, and blown to separate empty florets and chaff from florets containing caryopses.

9. In early-December, we plant in the greenhouse, 125 caryopses from each selection in 18-inch rows spaced 2 inches apart in flats of steam sterilized soil.

10. In mid-January, we transplant the seven most vigorous plants from each row into 2" clay pots of steam sterilized soil. These are set in sand on a greenhouse bench where they grow into large vigorous plants by mid-April.

11. All records including winter injury and spring growth are then studied and the poorest one-sixth of the progenies are discarded.

12. By mid-April the roots of each plant have formed a mat inside the 2-inch pot that holds the soil intact as the plants are pulled from the pots and put into the one-half pound kraft bags for field planting.

The original seed lots and seed from the space planting of each cycle of improvement have been kept in cold storage to permit a measure of progress achieved. Studies of replicated space plant plots from each cycle indicate that RRPS has produced higher yielding single plants as well as populations with higher mean yields. Through cycle 6 there has been a straight line increase in population yield of 2.5%/year in seeded plots and 8.7%/year in spaced plantings.

Our Pensacola bahiagrass breeding program directed toward the development of commercial F_1 hybrids assumes the following:

1. Self-sterile cross-fertile clones can be found that will give high yielding F_1 hybrids. We have clones that qualify and produce F_1 hybrids that have yielded 30% more than the check (commercial Pensacola bahia) in replicated clipped plots over a 3-year test period.
2. It will be possible to establish commercial seed production fields with alternate strips of such a pair of clones planted vegetatively. We have established small pilot fields, setting clonal material with vegetable planters. We believe we can greatly reduce the hand labor required for such plantings by using the Bermuda King bermudagrass sprig digger to harvest sprigs and the Bermuda King fairway planter to plant them. More research to confirm preliminary tests is required.
3. Herbicides can be used to keep seeds falling to the ground from developing plants until the sprigs are sodded over. Seeds that fall to the ground in well established bahiagrass sod rarely produce plants.
4. Once established such seed fields should produce hybrid seed of the perennial Pensacola bahiagrass for many years by merely combining all seed produced in the field. Seed harvested from small pilot fields confirm this conclusion.

Breeding in this commercial hybrid program consists of finding excellent clones that seed well and give the highest yielding F_1 hybrids when crossed. Because all clones are single crosses, 2-clone single crosses are in effect double crosses. Single crosses can be easily produced by placing together in 3 x 14 inch glassing bags culms from two parents that will flower at the same time, putting them in water in the laboratory and shaking them daily until anthesis is complete. Following this procedure we produced seed for a partial diallel involving eight superior clones selected from RRPS cycle 4.

In December, these seeds were planted in flats of soil and 60 seedlings from each cross were transplanted to 2-inch clay pots as in the RRPS breeding procedure. In mid-April 4 x 14 foot plots replicated five times were established by planting in methyl bromide treated soil, 12 of these potted seedlings one foot apart in the center of each plot. By the end of the first year, these plants had spread to make a solid sod strip at least 18 inches wide. By July of the second year, the width of the sod exceeded the two foot wide strip cut for forage yield determinations. Forage yields were usually taken 3 times in the first year and 4 times in succeeding years. Average annual yields of the 29 single crosses in this test ranged from 9,547 to 15, 930 pounds/acre of dry matter. The top yielding hybrid produced 31% more dry matter than the check.

Four of the clones included in a replicated plot test and cut four times per year gave average annual yields ranging from 14,882 to 17,987 lbs/A. The mean yields of the single crosses involving these four clones correlated well with the clone yields ($r = +.89$).

To date we have obtained three-year dry matter yields from replicated plots of 41 selected Pensacola bahiagrass clones. These have given average annual yields ranging from 11,888 to 17,987 lb/A of dry matter. Seed yields for these clones has ranged from 391 to 1188 lb/A, indicating that the choice of clones for commercial hybrid seed production can greatly influence the cost of the hybrid seed produced.

These 41 clones have been test crossed with two of our best clones and the crosses have been compared in replicated yield trials (5 replications) for 2 years. Correlation coefficients between these 2-year yields and the 3-year yields of the 41 clones were $r = +.365$ and $+.374$ $P = .01$, respectively. We had hoped that they would be higher.

In this hybrid program, the clones must be evaluated for seed yield and other traits. The positive correlations though small, indicate that the higher yielding clones will tend to give higher yielding two-clone hybrids. However, the small size of the correlation coefficients indicate that two-clone hybrids must be yield tested to find the best one.

In conclusion, we would like to suggest that breeding cross-pollinated trees may not differ greatly from breeding cross-pollinated grasses. More time per generation (from seed to seed) will be required for most, if not all tree species and probably more years for evaluation will be needed. I believe the genetic principles will be essentially the same.

Just as there has been a great advantage in being able to propagate a superior genotype of bermudagrass vegetatively, there should be a similar, perhaps even greater, advantage for the vegetative propagation of forest trees. Breeders of fruit and ornamental trees have demonstrated the need for and the value of vegetative propagation with their crops. Most of the offspring from crosses between two superior heterozygous clones of bermudagrass or bahiagrass have yielded less than their parents. I would expect most of the offspring of two superior heterozygous clones of a forest tree species to have a slower growth rate than their parents. After 20 to 30 years, the difference in the yield of wood between the superior vegetatively propagated genotype and the seedlings from two superior clones could make vegetative propagation profitable. Certainly the breeder of superior forest tree varieties will be able to make greater progress in less time at lower cost if practical methods of vegetative propagation can be found. We have found significant differences in the ease with which bahiagrass genotypes can be propagated vegetatively. I would expect a similar relationship in forest tree genotypes.

Regardless of the manner in which the end product of forest tree breeding is used, the breeder and the industry will profit from research designed to reduce the time required to grow one generation. When we started breeding pearl millet, we grew one generation a year. When we added greenhouses we could grow two. Using short days, high temperatures, and seed treatments to break dormancy, we can now grow four generations per year. For some breeding objectives, particularly introducing resistance genes to protect a variety from a disease, learning to grow four generations a year was a very significant plant breeding advance.

Our experience with grasses suggests that the relative growth rate of a tree can be estimated early in its life cycle. The problem will be the development of a uniform screening system that will subject every genotype in a population to the same, or very similar, environmental pressure. The need to maximize uniformity throughout the screening procedure is apparent. The gain in efficiency that could most certainly result from such early screening for growth rate will certainly warrant a substantial investment in research designed to develop such a screen.

Finally I would like to suggest that every fascet of your current forest tree breeding program can be made more efficient. For many year, we, me and my entire staff, have been reminding ourselves that "We haven't found the best way to do anything yet". This repeated reminder has significantly improved the efficiency of our plant breeding research and I believe it can improve yours.

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ESTIMATING VOLUME POTENTIAL IN GENETIC TESTS USING GROWTH AND YIELD MODELS

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Abstract.--Genetic field tests are subjected to many disturbances such as damage from diseases, insects, fire, wind, and ice. The differences in standing volume among plots in many older genetic field tests largely reflect differences in density due to uncontrolled disturbances rather than inherent differences in growth rate. Hence, standing volume is often subject to large experimental errors which makes it unsatisfactory for measuring genetic differences in growth rate.

Height of dominant-codominant trees is much less dependent on density and therefore is a better measure of inherent growth rate differences. Growth and yield models can be used to translate differences in dominant-codominant height into volume differences expected in the absence of uncontrolled disturbances. This approach is illustrated with loblolly pine data from the Southwide Pine Seed Source Study.

Additional keywords: Plot size, provenance testing, loblolly, *Pinus taeda*.

Genetic field tests of forest trees, like operational plantations, are subject to fire, insects, disease, high winds, and other disturbances. These disturbances kill trees and hence lower the density (number of surviving trees per acre) of affected plots, thus altering plot volume, diameter growth, basal area, and most other common measures of productivity. Thinning has similar effects. Plot-to-plot variations in density often induce large experimental errors and destroy the utility of volume and other density-dependent traits as measures of genetic potential.

Fortunately, not all growth traits are density-dependent. In fact, the height growth of dominant-codominant trees in even-aged stands is relatively free of density effects over a wide range of densities (Smith 1962). This is one reason foresters have long used site index, which is the mean height of dominant-codominant trees at a specified index age, as a universal measure of the potential productivity of forest land.

In large-plot field tests of genetic material (in contrast to individual tree or row plots), the mean height of the dominant-codominant trees within a plot should be relatively free of density effects. If one genetic group produces taller dominant-codominant trees than another group of the same age on

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the same site, then the taller group is expected to have higher volume production. Whether the taller group consistently produces more volume than the shorter one will depend largely on the density variation among plots in the field test, a nongenetic effect.

The Southwide Pine Seed Source Study is an example of a large-plot genetic field test in which large differences in dominant-codominant heights between seed sources are easily detected; yet volume differences are generally neither large nor strongly related to dominant-codominant height growth after nearly 30 years in the field. Typically, the field plots have been affected by fusiform rust, bark beetles, high winds, thinnings, and other disturbances. Therefore actual volume production of a seed source probably does not reflect its potential volume for the cases where density is controlled.

In this paper, we develop a method for obtaining expected plot volumes for large-plot genetic field tests. The method is based on the application of a growth and yield model (Feduccia et al. 1979) which uses the site index and initial density of a plot as variables to produce the expected volume of that plot--assuming it develops in the absence of disturbances. We applied the method to the loblolly pine phase of the Southwide Pine Seed Source Study. Extensions of the method to other problems in assessing genetic potential in field tests are discussed.

MATERIALS AND METHODS

Complete details of the loblolly phase of the Southwide Pine Seed Source Study are given by Wells and Wakeley (1966) and Wells (1969). Fifteen seed sources are represented, and 16 plantings survive after 25 years in the field. The seed sources and plantings are divided into two series. Series 1 sources represent the major part of the range. Series 2, with the exception of the southeastern Louisiana seed source, is restricted to an east-west transect from North Carolina to Arkansas. Seed was collected in 1951 from at least 20 trees in each area, and seed from all trees within a source was composited. A randomized complete-block design with four replications was used for each planting. Plots consist of 121 trees at 6- by 6-foot spacing; the inner 49 trees were periodically measured, and the outer two rows served as buffers against competition from other trees.

Measurements were made at 1, 3, 5, 10, 15, 20, and 25 years after planting in most plantations, but occasionally they were made at 16, 22, or 27 years in some plantations. Total height of all trees was recorded at each measurement age along with survival and damage from insects or disease. Diameter at breast height (d.b.h.) was recorded for each tree starting with the 10th-year measurement.

Light thinnings were done in most plantings to equalize the number of trees in each plot, but despite efforts to avoid it, wide variations in density from plot to plot still occurred because of mortality due to disease, insects, and other uncontrollable factors.

The total outside bark volume for all living trees at the last measurement age was computed by the standard conic formula:

$$V = 0.02909 \cdot DBH^2 \cdot H$$

where

V = outside bark volume in cubic feet
DBH = diameter at breast height in inches
H = total height in feet

The sum of these volumes for all trees on each plot was then computed and will be referred to herein as the "actual volume."

The growth and yield model (Feduccia et al. 1979) was developed for unthinned plantations of loblolly pine growing on cutover sites in the west gulf region of the United States. It is available in a computer program (named USLYCOWG) written in FORTRAN. Before describing the model further, it is necessary to introduce several terms and notations.

Notation	Meaning
Ap	Plantation age, the number of growing seasons since the seedlings were planted.
S_I	Site index, the average height of dominant and codominant trees at a given index age (usually 25 years).
Tp	Number of trees planted per acre.
Ts	Number of trees per acre surviving at a given age Ap.

Basically, the model accepts three input values and from these predicts plot volume. The three input values are Ap, S_I, and either Ts, or Tp. Hence, there are two combinations, or survival options, allowed as input as defined below:

Survival Option	Input Values	Output
1	Ap, S_I, Ts	Predicted plot volume at age Ap for plot growing on land with site index S_I with Ts surviving trees per acre at age Ap. It is assumed that the plot developed to age Ap in the absence of artificial thinning, disease, or insect damage.
2	Ap, S_I, Tp	Predicted plot volume at age Ap for plot growing on land with site index S_I with Tp trees per acre initially planted. The model predicts survival at age Ap assuming the plot would experience about 30 percent mortality by age 3 and subsequently develop in the absence of artificial thinning, disease, or insect damage to age Ap.

Since the number of surviving trees at age Ap (Ts) is given, option 1 does not require a survival model. Option 2 requires that a survival function predict Ts at age Ap, assuming the planting mortality to be around 30 percent (varying slightly with S_I). Hence, the program essentially reduces option 2 to option 1 by first predicting Ts and then generating volumes using that Ts, Ap, and S_I.

Option 1 volume predictions apply to the case where one knows the number of trees surviving on a plot, the plot's age, and enough of the plot's history to determine that the plot has not been disturbed by artificial thinning, disease, or insect damage. Of course, the plots in this data set do not satisfy the last assumption, but it is interesting to compare the actual plot volume with that predicted by option 1. We used option 1 as a rough check on the model's ability to duplicate actual volume on our plots. On plots that were disturbed only slightly, option 1 volumes should be close to actual volumes.

Option 2 volume predictions apply to the case where one knows the number of trees planted (Tp) and the site index of the planting site (S_I) and wants to predict volume at age Ap, assuming that the plantation will not be disturbed by thinnings, disease, or insects. The model uses a survival function to first predict the number of surviving trees at age Ap and then predicts the volume of that stand using that Ts and the site index of the planting. In the present application, option 2 estimates seed source potential under conditions of average planting survival and stand development without disturbance by damaging agents or thinning.

We used both options of the model on data for each plot within each planting to predict total outside bark volume. For each plot, we input Ap equal to the last measurement age (either 25 or 27 years) and S_I equal to the mean dominant-codominant height at that age. The mean dominant-codominant height was computed as the average of the tallest two-thirds of the trees in the plot.

We analysed actual plot volumes and predicted plot volumes from option 2 for each planting using an analysis of variance of the following form:

Source of variation	Degrees of freedom	Mean square	F-ratio
Blocks	$(b - 1)$	MSB	$F_B = MSB/MSE$
Seed Sources	$(s - 1)$	MSS	$F_S = MSS/MSE$
Error	$(b - 1)\cdot(s - 1)$	MSE	

Occasionally, a plot was missing in which case we used a missing plot substitution method. We also computed the coefficient of variation for each planting using the following formula:

$$CV = (\sqrt{MSE} \; / \; \bar{X}) \cdot 100$$

where

CV = coefficient of variation in percent
MSE = mean square error from analysis of variance
$\bar{X}$ = overall planting mean

RESULTS AND DISCUSSION

The correlations between actual and predicted seed source volumes using option 1 of the growth and yield model were quite high. In 14 of the 16 plantings the correlations were .80 or above and in 7 were .90 or above. It appears that the main effect of the disturbances was to simply reduce the number of surviving trees below that expected if suppression mortality had acted alone. The result is reassuring, since it tends to confirm that the model can provide realistic estimates of standing volume, given the number of surviving trees, the site index, and the age of the plot.

Since option 1 volumes are not used again, we refer to option 2-derived volumes as "model-derived volumes," and concentrate on comparing these with actual volumes.

The coefficients of variation for model-derived volumes were smaller than those for actual volumes in all plantings (table 1). Each of the plantings has been damaged by destructive agents to some degree, and experimental error for actual volume is sensitive to this damage as shown by the high coefficients of variation. Only 1 planting had a coefficient of variation for actual volume under 10 percent, compared with 11 for model-derived volumes.

Significant F-ratios (at the 5 percent level) for seed source differences in actual volumes occurred in only five plantings, compared with nine for model-derived volumes. In 12 of 16 plantings F-ratios for model-derived volumes were greater than those for actual volumes. In four plantings however, the trend was reversed and inspection showed seed source variation in traits in addition to dominant-codominant height.

Fusiform rust resistance of certain sources strongly influenced volumes in one of the four plantings, for example, as did seed source-related variation in planting survival in another. When nonheight-related variation among seed sources was primarily responsible for survival at the last measurement age, the model-derived volume is not appropriate. These extreme cases are relatively uncommon but are not less important. Fortunately, an extension of the present method (Nance et al. 1981) has been developed for situations where disturbances such as fusiform rust or planting mortality must be considered in combination with growth traits in assessing genetic potential.

Table 1.--Comparison in 16 seed source plantings, of ANV of volume calcuated by 2 methods (sum of d^2h) and model-derived

Planting			Site index of local source	Computing method	Seed source F-ratio	Coefficient of variation
Location	Series	Age	*Feet*			*Percent*
03 1M	1	20	56	Actual	4.6*	15.9
				Model	11.0*	7.1
07 1O	1	25	69	Actual	1.4	31.6
				Model	1.5	11.5
07 1P	1	25	66	Actual	0.6	40.2
				Model	2.6*	8.5
15 1M	1	25	55	Actual	4.4*	9.3
				Model	7.1*	5.7
26 1M	1	25	69	Actual	0.6	24.8
				Model	1.9	8.1
28 1M	1	27	57	Actual	1.1	37.3
				Model	1.7	18.3
32 1M	1	27	74	Actual	0.7	27.8
				Model	3.6*	7.7
36 1M	1	20	58	Actual	2.5	29.6
				Model	0.9	15.2
40 1M	1	25	59	Actual	0.6	19.5
				Model	3.6	6.7
07 2M	2	25	72	Actual	1.0	36.1
				Model	4.0*	8.6
13 2M	2	25	57	Actual	4.0*	21.0
				Model	2.4	14.0
25 2M	2	25	60	Actual	2.4	30.9
				Model	1.7	12.8
28 2M	2	27	56	Actual	4.7*	17.9
				Model	9.8*	5.1
29 2M	2	25	68	Actual	4.1*	30.4
				Model	3.0*	4.7
32 2M	2	27	76	Actual	2.7	23.8
				Model	4.9*	6.9
40 2M	2	25	62	Actual	0.6	27.0
				Model	4.1*	6.3

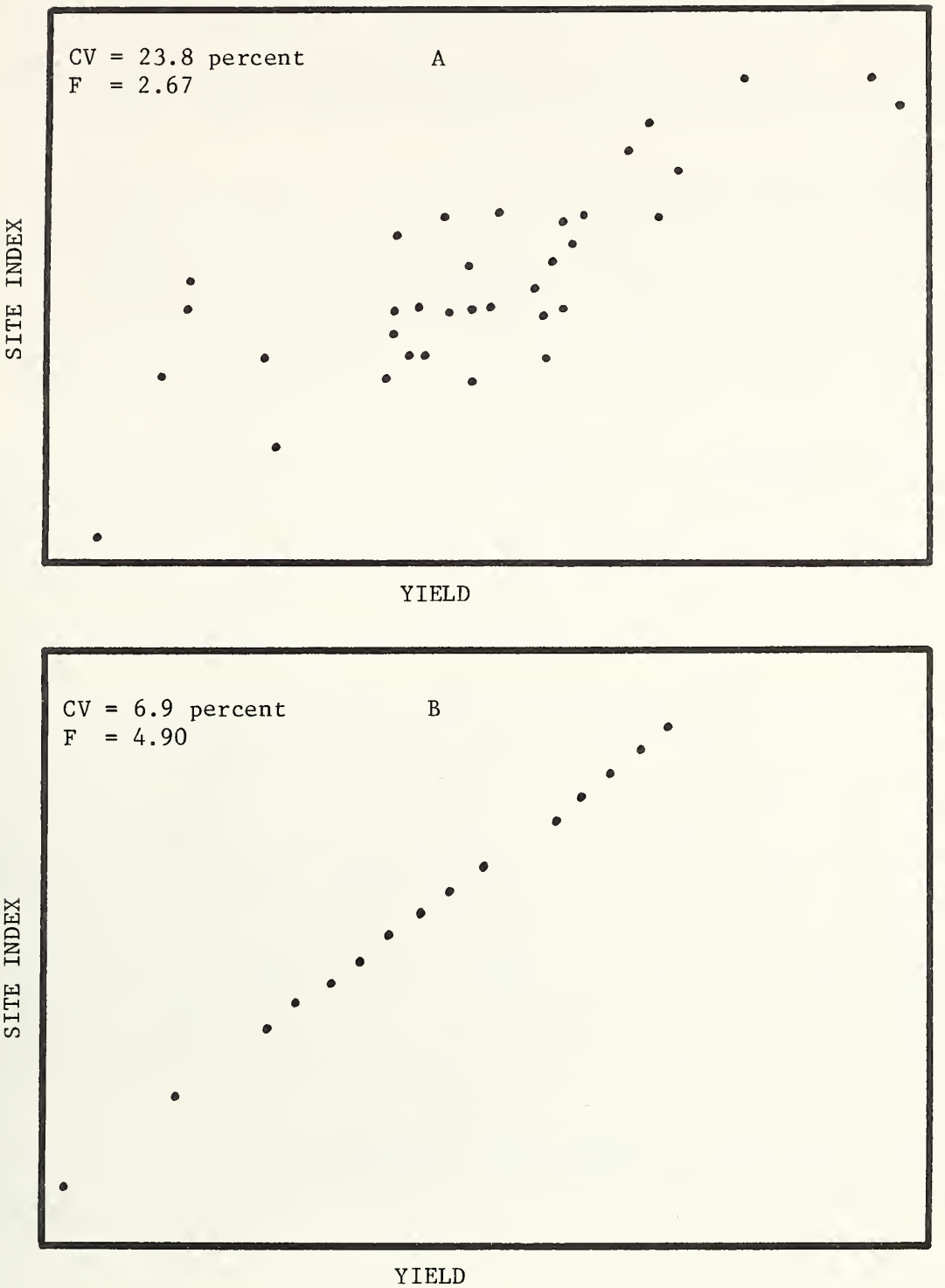

Figure 1.--Relationship of site index and yield for one plantation with actual volume (A) and model-derived volume (B).

A planting in southeastern Louisiana in Series 2 is representative of the way actual and model-derived volumes compare. The planting was on a fertile site (S_I = 65); had a typical planting survival by age 3 of 70 percent; about 10 percent of the planted trees died with fusiform rust cankers by age 10; there was a light thinning at age 10; and many plots were recurrently damaged by bark beetles between years 15 and 27.

The sum of these events resulted in actual volumes at age 27 that were so variable that differences among seed sources were not significant at that time, although the sources varied significantly in dominant-codominant height. The relationship between site index and actual volume at age 27 on a plot-by-plot basis was not strong as one would expect under ideal conditions (fig. 1A). Model-derived volumes for each plot, on the other hand, were directly proportional to the site index of the plot and the F-value for seed source differences at age 27 rose to a significant 4.90 (fig. 1B).

The present use of a growth and yield model provides a way of assessing the volume production of each seed source while, in effect, holding uncontrolled disturbances constant. It resembles covariance adjustment but it is much more effective in that it "corrects" for many disturbances simultaneously. This approach is appropriate for most situations in which growth is the dominant trait influencing volume.

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MODELING DIAMETERS AND HEIGHTS OF IMPROVED SLASH PINE (PINUS ELLIOTTII ENGELM. VAR. ELLIOTTII) USING WEIBULL DISTRIBUTIONS

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Abstract.--To model the heights and DBH distributions of 15-year-old slash pine progenies in southeast Georgia, the two and three parameter Weibull functions were used. Both fit the data equally well, but the three parameter form, due to its more meaningful interpretation, was used to examine changes in the distributions over time, site, and among progenies. Age and site significantly influenced both the location and scale parameters of the height and DBH distributions. Across ages and sites, progeny differences were detected only in the shape parameter of the DBH distribution. However, a balanced subset of progenies and checklots suggested that the DBH distributions of progenies and checks differ in location and shape parameters. The findings reported here will be used in the development of yield functions for genetically improved slash pine.

Additional keywords: Growth and yield studies, diameter distributions, height distributions, tree improvement.

Growth and yield functions currently used in pine plantations of the Southeast are based on data gathered from genetically unimproved stands. Of the 73 slash pine growth and yield studies listed by Williston (1975) none were concerned with genetically improved stock.

Modeling diameter (DBH) and height distributions is the first step toward the development of yield formulae. Bailey and Dell (1973) list several examples of previous diameter distribution models. Predictions of these distributions can help the forester forecast the future value of a stand, estimate the number of trees which meet merchantability requirements, plan thinning operations and determine harvesting costs.

This paper discusses modeling the DBH and height distributions of half-sib progenies of 15-year-old slash pine in southeast Georgia. The estimated parameters of the distribution models are then evaluated for the effects of test (site), age, and progeny.

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MATERIALS AND METHODS

Progeny Tests

Five half-sib slash pine progeny tests maintained by Brunswick Pulp Land Company in Appling, Brantly, and Wayne Counties, Georgia, were included in this study (Table 1). The tests were planted at a 7' x 12' spacing following a site preparation with KGing, raking, harrowing, and bedding. All tests were planted in a randomized complete block design with two or three checklots replicated within each block. The tests vary in size, number of families, number of replications, type of family plot, and site index at base age 25.

Table 1.--Description of half-sib progeny tests included in this study.

Test	Location	Established	Site Index	No. of Progenies	No. of Reps	Type of Plot	Measurement Ages
1-3	Wayne Co.	1963	60	9 (2)[1/]	10	10-tree row	5,7,10,15
1-4	Wayne Co.	1963	65	7 (2)	10	10-tree row	5,7,10,15
1-5	Wayne Co.	1963	70	14 (2)	40	Single tree	3,5,10,15
1-6	Appling Co.	1964	65	38 (3)	5	2-tree row	7,10,15
1-7	Brantly Co.	1964	60	38 (3)	5	7-tree row	7,10,15

[1/] Number of checklots.

Statistical Analysis

The two and three parameter Weibull distribution functions were selected because of their flexibility to model tree diameters and heights (Bailey and Dell, 1973). The two parameter Weibull probability density function is of the form:

$$f(x) = \left(\frac{c}{b}\right)\left(\frac{x}{b}\right)^{c-1} e^{-\left(\frac{x}{b}\right)^{c}} \quad \text{where } x \geq o,\ b > o,\ c > o.$$

The more general three parameter Weibull probability density function is as follows:

$$f(x) = \left(\frac{c}{b}\right)\left(\frac{x-a}{b}\right)^{c-1} e^{-\left(\frac{x-a}{b}\right)^{c}};\ x \geq a \geq o,\ b > o,\ c > o.$$

In the expressions above, x represents DBH or height with the parameters a, b, and c estimated from the data. For this study the statistics for the two parameter Weibull were estimated by the maximum likelihood method (Thoman, Bain, and Antle, 1969). For the three parameter Weibull, estimates were obtained by the simple percentile procedure (Zanakis, 1979). Parameter estimates for both Weibull models were calculated using diameter or height measurements from each surviving tree of a given progeny within a given test at each measurement age. The modified Komogarov-Smirnov statistic was used to determine which model best fit a given distribution.

The three estimated Weibull parameters of each distribution were used as response variables for analysis of variance with test, age, and progeny as factors. Eleven progenies and two checklots were included in the analysis. Individual progenies were represented in at least three tests and all measurement ages with DBH distributions analysed at age 7 and above. Additional analyses were calculated for the 10- and 15-year DBH distributions using parameter estimates of the four progenies and two checklots common to all five tests.

RESULTS

Though both Weibull models fit the data equally well the three parameter Weibull was chosen for further analysis because its parameters have a more meaningful interpretation. This choice was made in spite of the fact that the maximum likelihood estimates of the two parameter Weibull are generally regarded as better estimates.

In the three parameter Weibull, "a", the location parameter, shifts the distribution along the x axis. In progeny test 1-3 the height distribution value for "a", averaged over the progenies at age 15 was 19.71 feet (Table 2). This parameter represents the smallest possible element in the distribution. The scale parameter, "b", controls the spread of the distribution with a+b defining the point at which 63% of the trees are smaller. This parameter was the greatest in the height distributions of test 1-6. The symmetry of the distribution is explained by "c". At c = 3.6 the curve is symmetrical and approximates normal. When "c" decreases, the curve becomes positively skewed with a tail increasing to the right. As "c" increases beyond 3.6 the distribution becomes negatively skewed. All the progenies in test 1-5 at age 15 had DBH distributions that were positively skewed.

Univariate analyses of variance of the three Weibull parameters for total tree heights indicate that the location parameter, "a", is significantly affected by age and test (Table 3). The scale parameter, "b" also has significant test and age components of variation with age having the greatest effect. There were no significant main effects in the shape parameter, "c". The test by age and the test by progeny interactions were significant in all the parameters of the height distributions. Figure 1a shows the changes in the height distribution of one progeny in the single-tree plot test through time. The effects of tests are shown in Figure 1b for one progeny's height distribution on a poor site (Test 1-3) and a good site (Test 1-5).

Table 2.--Average and range of progeny values for estimated Weibull parameters for the height and DBH distributions at age 15.

Test	Height Distribution			DBH Distribution		
	Parameter a	Parameter b	Parameter c	Parameter a	Parameter b	Parameter c
1-3	19.71[1/]	20.93	4.04	2.75	3.09	3.32
	10.94-25.19[2/]	14.50-31.56	2.24-6.81	1.47-3.47	2.20-4.56	4.56-5.49
1-4	23.19	21.38	4.88	2.89	3.54	3.63
	5.29-34.00	10.30-39.71	2.54-8.04	2.01-4.30	2.20-4.39	2.03-5.05
1-5	43.52	11.70	2.63	5.28	2.70	2.42
	39.75-49.92	7.08-15.64	1.17-4.51	3.52-6.10	2.00-4.58	1.51-3.33
1-6	15.09	29.88	4.30	2.02	4.32	3.31
	0.00-28.47	15.53-46.99	1.84-7.77	0.00-3.67	2.43-6.65	1.51-5.91
1-7	25.29	27.68	4.85	2.97	4.20	3.26
	0.00-41.91	9.09-51.99	1.03-10.69	0.00-4.24	3.01-7.50	1.95-7.86

[1/] Mean.

[2/] Range.

Table 3.--Analysis of variance of the 3 Weibull parameters of the height and DBH distributions.

Source	Height Distribution				DBH Distribution			
	df	a	b	c	df	a	b	c
Tests (T)	4	21.45**	6.75**	1.60	4	17.04**	2.89*	0.65
Ages (A)	4	19.33**	13.85**	2.61	2	9.54*	19.34**	2.64
Progenies (P)	4	0.85	0.88	1.56	12	0.82	1.12	2.09*
T x A	9	4.99**	3.05**	2.39*	7	2.40*	3.34**	1.93*
T x P	36	1.95**	1.84*	1.77*	36	2.00**	2.01**	1.84*
A x P	48	0.85	0.89	1.28	24	1.37	1.52*	1.28

* and ** Significant at 5 and 1% levels, respectively.

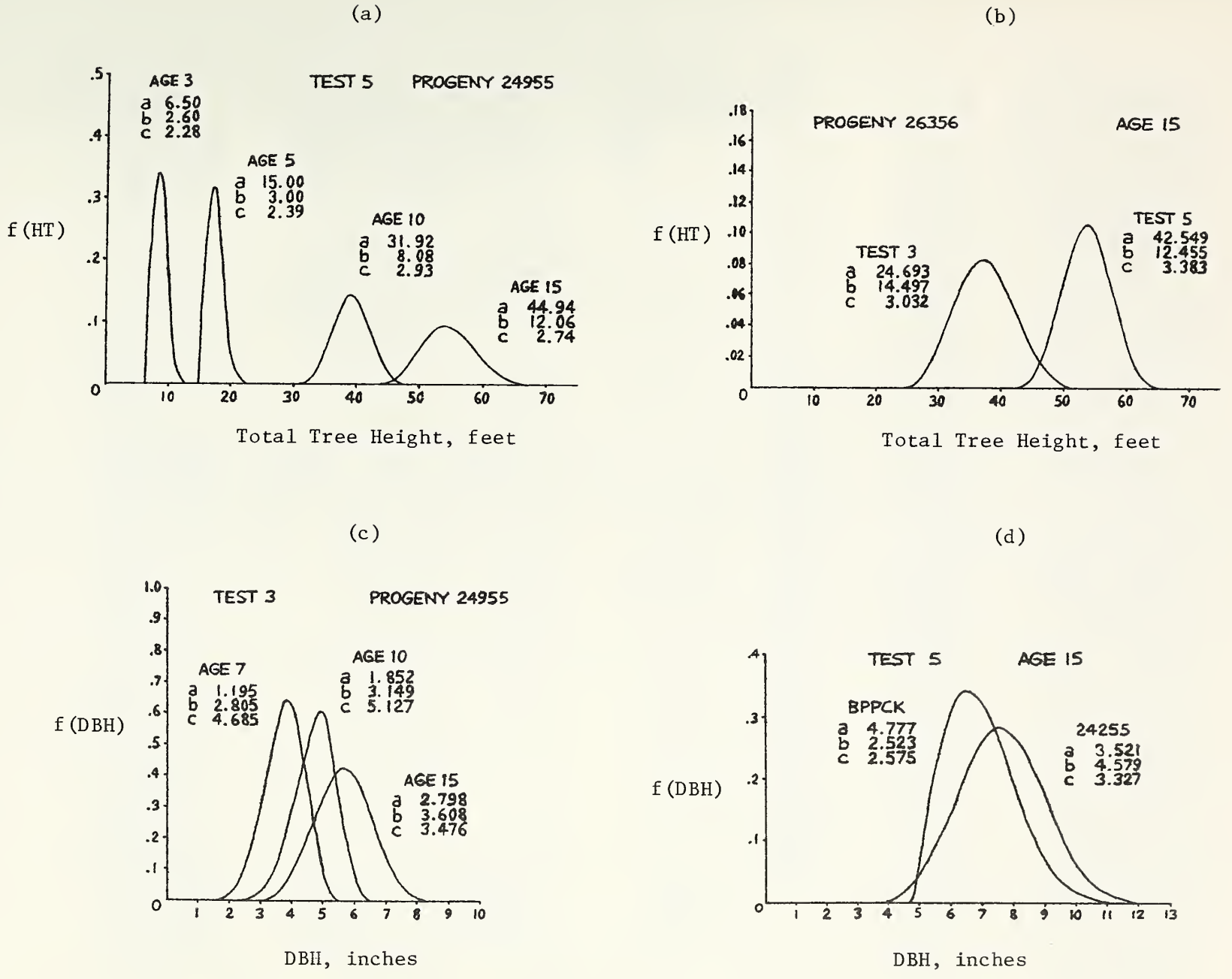

Figure 1. Influence of various factors on height and DBH distribution: a) age on height, b) site on height, c) age on DBH, d) progeny on DBH.

Univariate analyses of variance for the three parameters of the DBH distribution show that the location parameter, "a", is significantly influenced by age, test and the interactions between test and progeny, and test and age (Table 3). This parameter is greatly controlled by test (site) and age. The scale parameter, "b", showed significant effects due to test, the three interactions and particularly age. The shape parameter has significant progeny, test by age and test by progeny effects. Figure 1c gives an example of the DBH distribution's changes through time. Also shown (Figure 1d) is a comparison of a check and an improved progeny in test 1-4 at age 15.

The analysis of variance for the DBH distributions of the progeny common to all the tests showed no significant parameter differences between the two checklots, but showed significant differences in the "b" and "c" parameters between the improved progeny (Table 4). Significant check-vs.-improved progeny contrasts were detected in both the "a" and "c" parameters.

Table 4.--Analysis of variance of the 3 Weibull parameters of the DBH distributions over ages 10 and 15, and of the 6 progenies common to all five tests.

Source	df	a	b	c
Test (T)	4	10.14**	1.57	2.34*
Age (A)	1	26.09**	23.15**	3.09
Progenies (P)				
Checks	1	0.22	0.03	0.00
Improved	3	1.33	3.56*	5.50*
Checks-vs.-Improved	1	4.39*	1.57	11.35**
T x A	4	1.18	1.26	0.68
T x P				
Checks	4	3.74	3.21	6.14
Improved	12	5.64**	4.50**	1.25
Checks-vs.-Improved	4	3.99	4.07	8.53**
A x P				
Checks	1	3.17	2.81	10.28*
Improved	3	1.19	1.38	0.20
Checks-vs.-Improved	1	0.00	0.01	0.03

* and ** Significant at 5 and 1% levels, respectively.

DISCUSSION

As expected, the age of the plantations greatly affected the DBH and height distributions. When trees are planted, they have approximately uniform size. The DBH and height distributions of a very young stand have very little spread and appear as a spike over some low value. As age increases, diameter and height distributions shift to the right, as indicated by the larger location parameter, "a". With time, the spread of the distribution increases, changing the scale parameter, "b".

The effects of the test, which should reflect site effects, are greatest in the location parameter. Site affects tree height and DBH, with some effect on the spread of the distribution, and no significant effect on the shape. The significant test-age interaction is probably due to faster growth on better sites.

The progeny effect was only significant in the shape parameter of the DBH distribution. The analysis of the six progenies common to all five tests over ages 10 and 15 showed that the improved progenies' DBH distributions had significant differences in shape, but most of the shape parameter's significance was due to the check-vs.-progeny contrast. This second analysis also showed significance in the checks-vs.-progeny contrast of the location parameter "a". These two significant contrasts suggest that the improved progenies have a greater proportion of larger diameter trees than the checklots. Also the test by progeny interaction indicates that progenies perform differently in different tests.

The estimation procedure used here to calculate the three Weibull statistics was very sensitive to outlying trees, especially very small trees. This may be the reason for the shape parameter of the DBH distribution being the only significant progeny effect. Other estimation techniques may produce different results.

Knowing the effects of age, test, and genetics on the DBH and height distributions will be extremely helpful in the further development of growth and yield formulae. The next step toward these yield functions will be the formulation of multiple regression equations to predict values of the distribution parameters as functions of age, site index, planting density and some measure of the genetic component.

CONCLUSIONS

For our data, progeny test and stand age have significant effects on the estimated "a" and "b" Weibull parameters in both the height and DBH distributions. Progeny was only significant for the shape of "c" parameter of the DBH distribution. The parameter estimation procedure used was very sensitive to outlying trees. A method of screening the data to remove these outliers should reduce the error terms and result in more significant progeny effects.

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Evaluation of Full-Sib Families of Douglas-fir in a Nelder Design.

Roy Stonecypher and Rex McCullough

ABSTRACT

Thirty Douglas-fir full-sib families and an unselected check were evaluated in a Nelder's design covering a range of densities from 735 to 26,300 trees/ha. Regression analysis resulted in good overall fits of volume and caliper to density with the power function ($y = ax^b$), and indicated differential response of families to density.

Key words: Pseudotsuga menziesii, spacing, spacing x genetic interaction, heritability, juvenile-mature correlations.

Evaluation of Full-Sib Families of Douglas-fir in a Nelder Design.

Roy Stonecypher and Rex McCullough[1]

INTRODUCTION

The use of systematic designs for spacing experiments was first proposed by Nelder (1962) and later recommended by Namkoong (1966) as potentially valuable for examining genetic variation in density response in forest tree improvement research.

The sampling of an adequate range of densities in genetic studies utilizing rectangular plots, requires large areas, many trees for each genetic entry, and results in differential precision of estimates and inefficient use of genetic material and experimental area (Namkoong 1966). The systematic designs proposed by Nelder (1962) offer an alternative which effectively addresses the problems associated with multiple-tree plot spacing experiments. In using such systematic designs, however, it should be recognized that certain assumptions normally associated with traditional randomized designs are not valid and analyses must be appropriately modified.

The objectives of the Nelder planting of selected families of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) reported here were:

1. To examine genetic response to density.

2. To examine the impacts of density on genetic variances and juvenile-mature correlations over time.

3. To examine the effects of density on mensurational traits.

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4. To compare performance of genetic material grown under varying densities with performance in field tests.

This paper will report results related to the first three objectives stated above.

METHODS

Four circles of a Nelder's design were established in 1973 at the Weyerhaeuser seed orchard near Jefferson, Oregon at latitude 44°45' N and longitude 123°2' W. The site is in the central Willamette Valley of Oregon and has an elevation of approximately 61 m. The area used was formerly under agriculture and has minimum soil and topographic variation. The soils consist of sandy river alluvium and are well drained.

Four circles of the design were established utilizing full-sib families and two unselected check sources. The genetic entries were derived from 60 selected parents of Weyerhaeuser Company's low-elevation Coos Bay, Oregon breeding program. The parents are located near the central coast of Oregon and range in latitude from 43°21' N to 43°27' N and in elevation from 122 to 366 meters. The unselected control entries were derived from two seed lots which were obtained from stands of the type normally used in operational collection of seed for planting at Coos Bay.

The actual genetic material was obtained from excess seedlings of a two-parent mating design which is part of an operational genetic test for Weyerhaeuser's Coos Bay tree breeding program. There were thus 30 full-sib families and 2 unselected checks established in the four circles.

The spacings and densities used in the design are presented in Table 1. The genetic entries were randomly assigned on rays in two of the circles, and on the arcs in the other two. Thus, in circles 1 and 2 individuals are competing with their full-sibs within the ray, while in circles 3 and 4 competition is random in relation to families. Unfortunately, the need to utilize circle 1 material to replace mortality in the other circles precluded the general use of circle 1 in the analyses.

Decisions as to the range of spacings used and the physical layout were largely driven by the amount of material and experimental area available.

Table 1. Spacing and number of trees for 11 arcs used in the Nelder Design.

Arc	Spacing		Trees	
	m^2	(ft^2)	/ha	/acre
2	0.38	(4.1)	26,300	(10,625)
3	0.54	(5.8)	18,500	(7,510)
4	0.76	(8.3)	13,160	(5,248)
5	1.13	(12.0)	8,850	(3,630)
6	1.59	(17.1)	6,290	(2,547)
7	2.26	(24.4)	4,425	(1,785)
8	3.25	(35.0)	3,077	(1,245)
9	4.62	(50.0)	2,164	(871)
10	6.64	(71.5)	1,506	(609)
11	9.52	(102.5)	1,050	(425)
12	13.60	(146.4)	735	(298)

The circles thus established had 33 rays and 13 arcs (Figure 1). The first and last arcs were guard trees and one of the rays was a filler. The shape of the growing space was held constant in the design used and thus conform to type Ia of Nelder (1962).

Measurements of total height were made annually with the exception of the sixth year. Caliper at 50 cm above ground line was measured starting in the third year and continued as the height measurements. Volume was calculated using equations developed by Kovats (1977).

As indicated earlier, systematic designs are generally not suited to traditional analysis of variance techniques. Although we did use analysis of variance for satisfying one of the objectives of this study, the majority of the analyses used regression.

Increasing mortality, presumably related to competitive stress, was observed as early as the fourth year in arcs 2-4 and extended to arcs 5, 6, and 7 by the fifth year and beyond. Since analyses would be expected to be influenced by mortality, adjustments of spacing were made to account for space created by loss of competing trees.

RESULTS

Density-Growth Relationships

Plots of volume versus density by years indicate that patterns of response to density were developed as early as the fourth year and became definite and clear by the seventh year (Figures 2, 3, and 4). Caliper response was very similar to volume as would be expected, but height indicated a negative response at both the high and low densities (Figures 5 and 6). It is emphasized, however, that the range of densities examined in this study were extreme at the higher end. In using the extremely high densities of these plantings, competition becomes manifest at an early age and its influence on growth is greatly enhanced. It is tempting to speculate, however, that the responses observed at the higher densities at young ages in this study, may be representative of those at older ages with material grown under more realistic densities.

Examination of plots for volume, caliper and height of eighth year data versus density indicated that curves of the form indicated in Figures 4 through 6 would adequately describe the growth-density responses. The growth data summarized by density are presented along with the $\log_e$ transformed regression equations in Table 2.

Table 2. Means and regressions for eight-year data averaged over all families.

Trees/ha	Volume (dm^3)	Height (m)	Caliper (cm)
26300	9.2	6.7	6.3
18500	9.5	6.7	6.4
13160	12.6	6.9	7.4
8850	15.2	7.1	7.9
6290	17.8	7.1	8.7
4425	23.6	7.3	10.3
3077	27.1	7.0	11.3
2164	34.9	7.1	13.2
1506	41.7	6.9	14.5
1050	49.3	6.8	15.9
735	53.2	6.5	17.4

1. $\ln(\text{volume}) = 7.68 - 0.55 \ln(\text{trees/ha})$; $r^2 = 99\%$

2. $\ln(\text{height}) = 6.16 + 0.053 \ln(\text{trees/ha}) - 8.59 \times 10^{-6}(\text{trees/ha})$; $r^2 = 70\%$

3. $\ln(\text{caliper}) = 4.95 - 0.31 \ln(\text{trees/ha})$; $r^2 = 99\%$

Genetic Variation in Density Response

The major objective of this study was to determine if spacing x genotype interactions were evident. Regressions of the form

$$\ln(\text{volume}) = a + b \ln(\text{trees/ha})$$

were calculated for each of the 30 families and unselected check (Table 4). The analysis of variance of the regression coefficients over groups indicates that there are significant differences among entries in slope and/or intercept (Table 3).

Table 3. Analysis of variance of regression coefficients over groups.

Source	DF	Mean square	F
Groups	61	1.366	4.24**
Within groups	901	0.322	

** Significant at 0.01 level

An examination of Table 4 indicates large differences among families in volume and in slope or response to density. Plots of selected entries are presented in Figure 7. Family 1 is an extremely fast growing family with a response slope equal to the population average while family 30 is a relatively high performing family with a slope well below the average. It appears that family 30 is performing relatively poorly at the lower densities. Note also that the unselected check has a steeper slope than average and is performing very poorly at the higher densities.

Particularly strong evidence for spacing x density interaction is presented in Figure 8. Although families 102 and 57 had rather similar performance in average volume at 8 years, family 57 is performing much better at higher densities.

Density-Genetics Variance Relationships

Recently, information has been published that indicates that onset of inter-tree competition in genetic tests results in changes in genetic variances of growth traits and in juvenile-mature correlations (Franklin 1979). Insofar as the extremely high densities of this study may represent onset of competition in older, more conventionally spaced tests, it was felt that an examination of heritabilities at contrasting densities over time would be useful. Separate analyses of variance and cross products were, therefore, carried out for the three growth traits for each of two classes of density, three circles, thirty full-sib families, and the five measurement years. Density classes were divided into high and low using the curves of Figures 2 and 3 as guides. Arc 6 (see Table 1) was used as the division point. The high

density class was thus represented by densities of 6,290 to 26,300 trees/ha and the low density class by 735 to 4425 trees/ha. Estimates of the full-sib family components and heritability by spacing class for the three growth traits were then developed (Table 5). Comparisons of heritability for the high and low density classes indicate a decrease with increasing age for the lower density class. There is thus an indication that as the material in the lower density comes under competition heritability decreases. However, Table 6 indicates little evidence for change in genetic correlations related to density classes.

CONCLUSIONS

Relationships between density and average tree volume and caliper were well defined by the seventh year of the test (Table 2 and Figure 3). The estimated response slopes for volume and caliper were -0.55 and -0.31 respectively.

Regression analyses of the response of individual families to density indicated the presence of family x density interactions (Table 4 and Figures 7 and 8). There did not appear to be a correlation between family mean growth performance and response to density (Table 4). Whether such interaction would occur at older ages under more realistic densities is conjectural. If such is the case, however, the implications for breeding programs designed to increase yield per unit area in Douglas-fir would be significant. We plan to continue to examine this planting, and to initiate new Nelder plantings using a more realistic range of densities with genetic material of specific interest to our breeding program.

An examination of the effect of onset of inter-tree competition on heritability estimates indicated slight impact in this study. While there was a tendency for estimates of heritability to decrease with age, there was no evidence that increasing competition changed juvenile-mature correlations (Table 5 and Figures 9 and 10).

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Table 4. Regressions for eight-year volume by family.

Family	$\hat{a}$	$\hat{b}$	$S(\hat{b})$	Mean dm^3	S.E.	Rank
Check	8.44	-0.71	0.07	19.3	1.19	29
1	7.71	-0.50	0.07	44.7	3.03	1
3	7.39	-0.50	0.07	31.9	2.44	9
5	6.64	-0.46	0.12	22.9	1.14	24
7	7.76	-0.58	0.07	23.0	1.63	23
9	8.14	-0.65	0.08	22.6	1.47	26
14	8.35	-0.62	0.08	32.4	2.18	8
16	7.63	-0.54	0.11	33.1	2.27	5
20	6.86	-0.45	0.08	28.4	1.94	14
22	8.07	-0.62	0.08	24.7	1.76	20
23	8.07	-0.68	0.09	16.7	1.31	31
28	7.61	-0.55	0.12	28.8	1.93	15
30	5.98	-0.32	0.09	32.7	1.97	6
44	8.70	-0.70	0.10	27.8	2.53	18
46	6.64	-0.42	0.10	28.8	2.25	16
47	6.18	-0.39	0.14	24.7	1.77	21
48	7.35	-0.51	0.14	30.5	2.25	12
53	7.84	-0.56	0.08	32.5	2.39	7
57	5.72	-0.34	0.10	22.4	1.31	27
58	8.09	-0.60	0.09	30.9	2.33	11
59	8.12	-0.63	0.10	26.1	2.13	19
60	8.32	-0.62	0.09	31.3	2.40	10
61	8.54	-0.62	0.08	37.6	2.62	3
62	8.72	-0.67	0.08	33.3	2.42	4
68	7.96	-0.64	0.07	18.4	1.18	30
70	7.58	-0.61	0.14	20.0	1.74	28
72	6.93	-0.48	0.12	28.2	2.33	17
75	8.56	-0.66	0.08	30.5	1.96	13
83	8.60	-0.62	0.08	40.3	3.00	2
101	7.97	-0.61	0.06	22.8	1.44	25
102	9.03	-0.75	0.10	24.4	1.95	22

Table 5. Heritability estimates for two spacing classes by years.

Year	High Density $\hat{\sigma}^2 f$	High Density $S(\hat{\sigma}^2 f)$	High Density h^2	Low Density $\hat{\sigma}^2 f$	Low Density $S(\hat{\sigma}^2 f)$	Low Density h^2
			VOLUME			
3	0.034	0.012	0.36	0.070	0.020	0.60
4	0.204	0.071	0.43	0.336	0.108	0.47
5	1.125	0.461	0.34	2.106	0.844	0.30
7	4.124	1.770	0.28	17.002	6.009	0.28
8	8.971	4.237	0.25	60.945	20.818	0.25

Year	High Density $\hat{\sigma}^2 f$	High Density $S(\hat{\sigma}^2 f)$	High Density h^2	Low Density $\hat{\sigma}^2 f$	Low Density $S(\hat{\sigma}^2 f)$	Low Density h^2
			HEIGHT			
3	282.62	119.49	0.24	450.95	145.70	0.40
4	305.36	177.91	0.13	608.24	193.48	0.36
5	568.80	227.57	0.30	488.08	194.70	0.26
7	731.40	354.32	0.21	337.60	239.67	0.08
8	1364.93	584.07	0.29	827.97	368.08	0.18

Year	High Density $\hat{\sigma}^2 f$	High Density $S(\hat{\sigma}^2 f)$	High Density h^2	Low Density $\hat{\sigma}^2 f$	Low Density $S(\hat{\sigma}^2 f)$	Low Density h^2
			CALIPER			
3	0.040	0.016	0.27	0.076	0.023	0.47
4	0.156	0.059	0.35	0.242	0.077	0.45
5	0.347	0.154	0.28	0.489	0.194	0.24
7	0.623	0.273	0.26	1.401	0.456	0.27
8	0.685	0.354	0.23	3.473	1.030	0.33

Table 6. Juvenile-mature correlations for two spacing classes.

	High Density					Low Density			
Year	4	5	7	8	Year	4	5	7	8
				VOLUME					
3	1.00	1.00	0.90	0.96	3	0.98	0.88	0.84	0.86
4		0.96	0.80	0.88	4		0.99	0.93	0.88
5			0.95	1.00	5			0.98	1.00
7				0.97	7				0.99

	High Density					Low Density			
Year	4	5	7	8	Year	4	5	7	8
				HEIGHT					
3	0.93	0.79	0.85	0.78	3	0.98	0.88	1.00	0.73
4		0.75	0.60	0.70	4		0.98	1.00	0.82
5			0.81	0.98	5			1.00	1.00
7				0.86	7				0.96

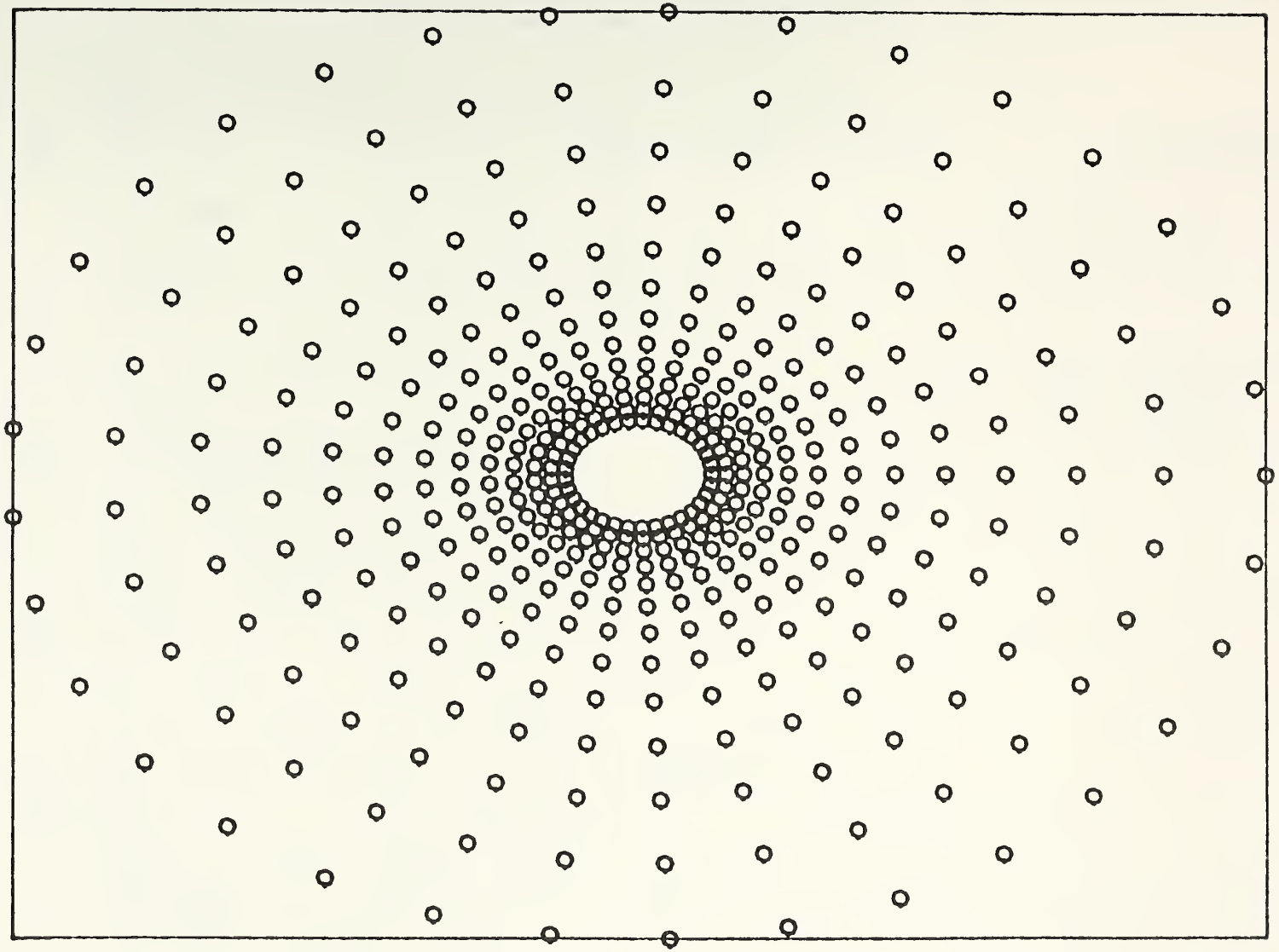

Figure 1: Diagrammatic representation of the Nelder's design used. There are 33 rays and 13 arcs in the circle

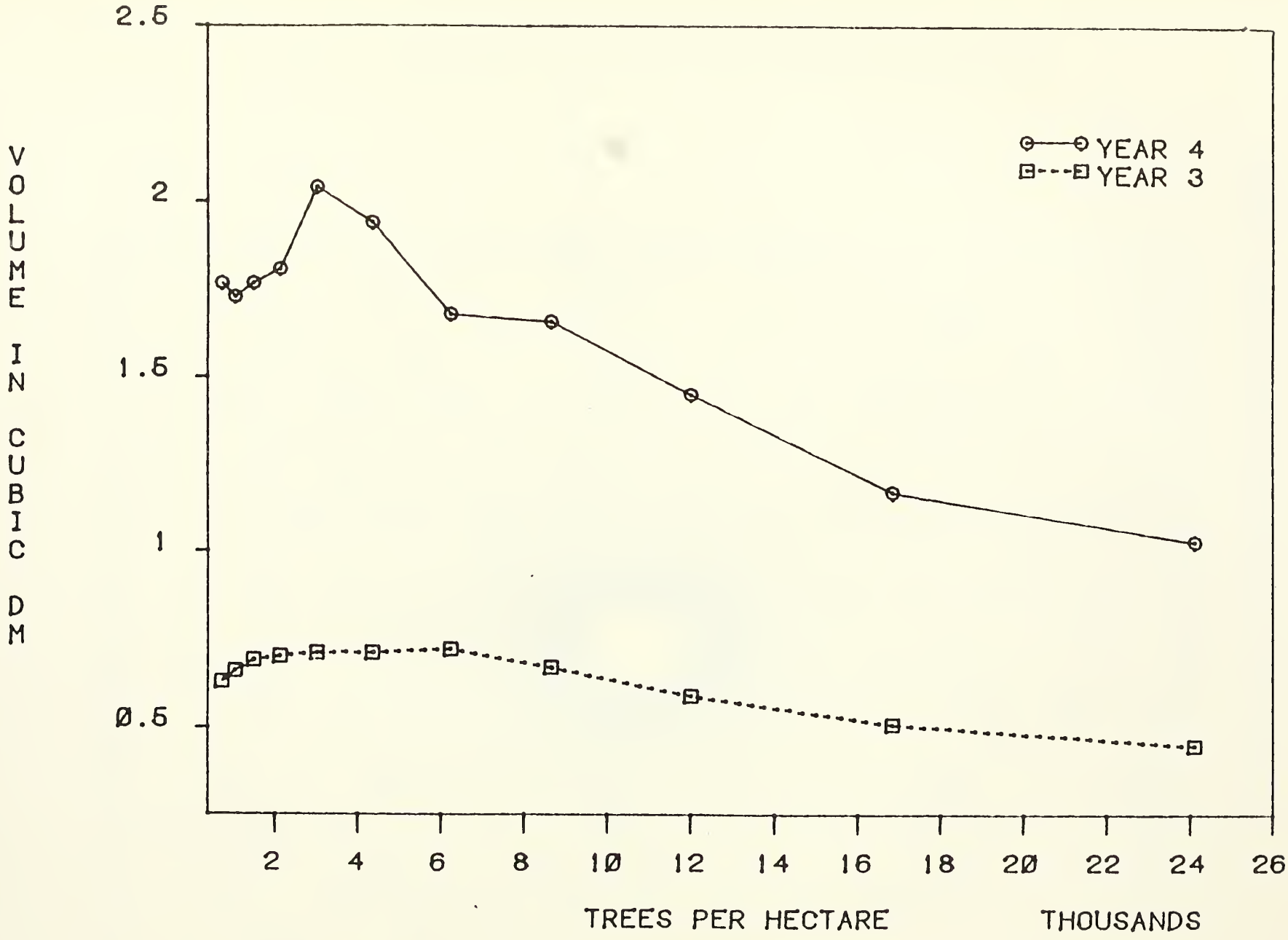

Figure 2: Average volume for all spacings and families for years 3 and 4.

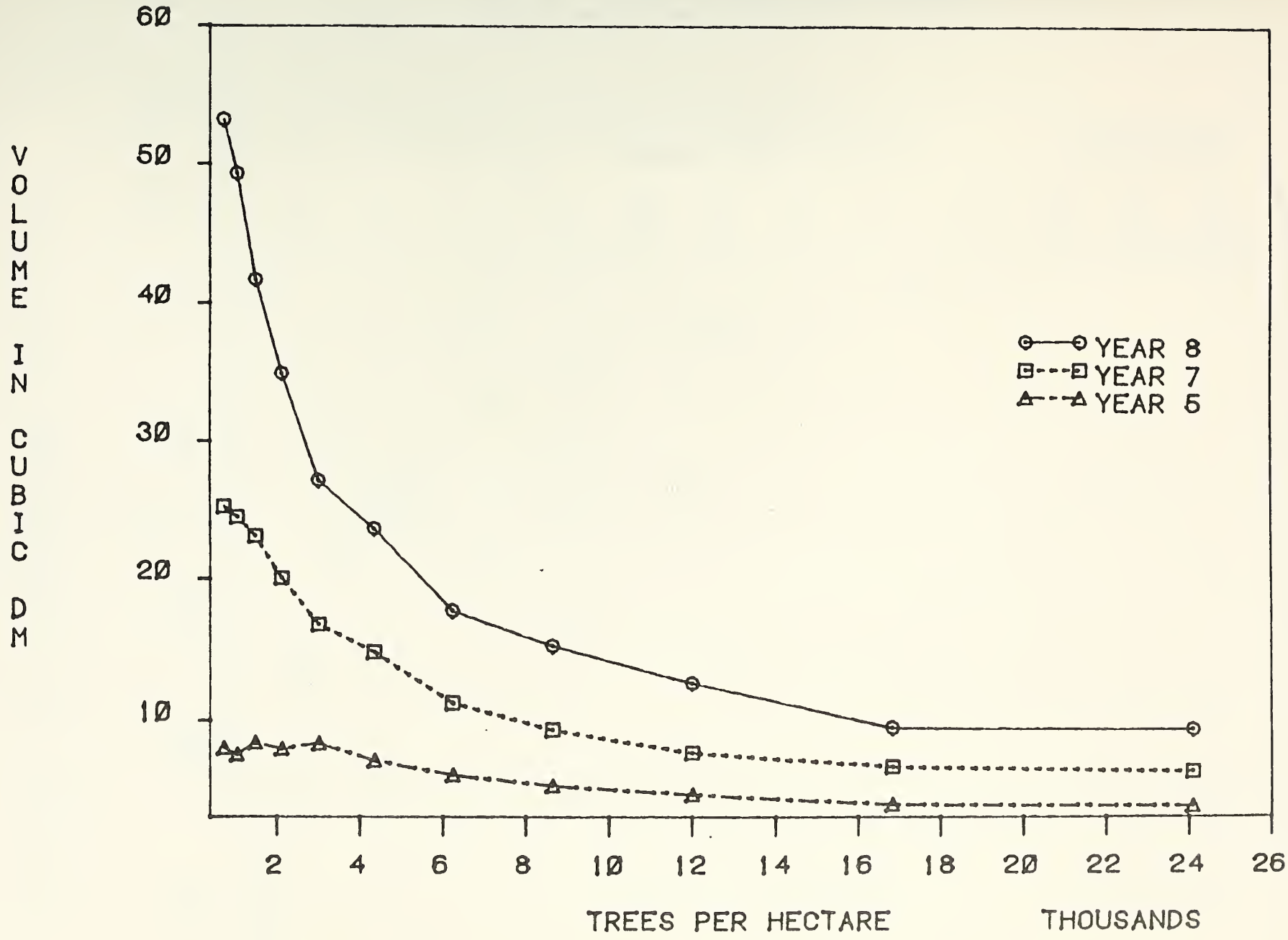

Figure 3: Average volume for all spacings and families for years 5, 7 and 8.

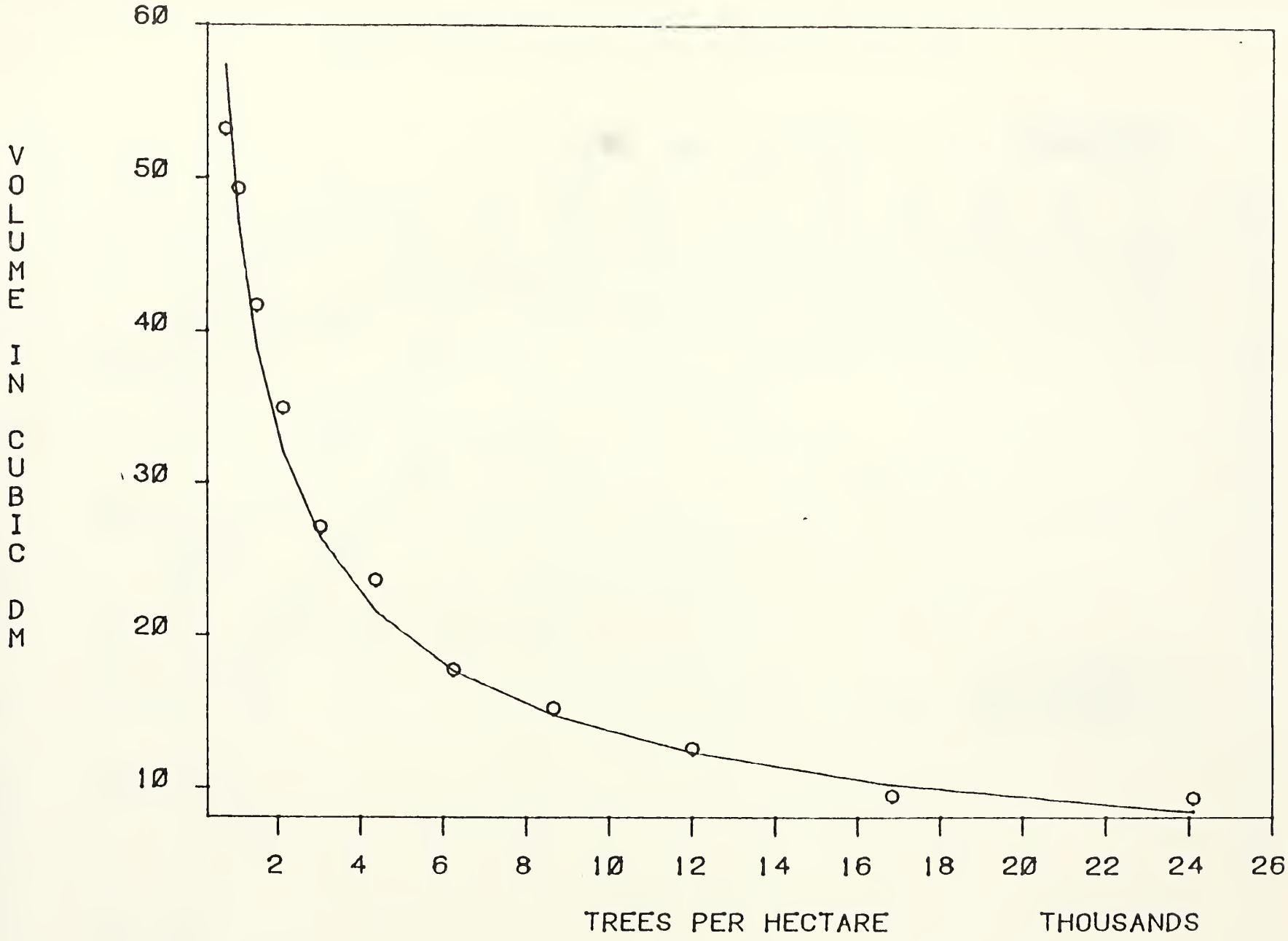

Figure 4: Fit of 8-year average volume for spacings and families. (Volume = 2165 (trees/ha)-0.55

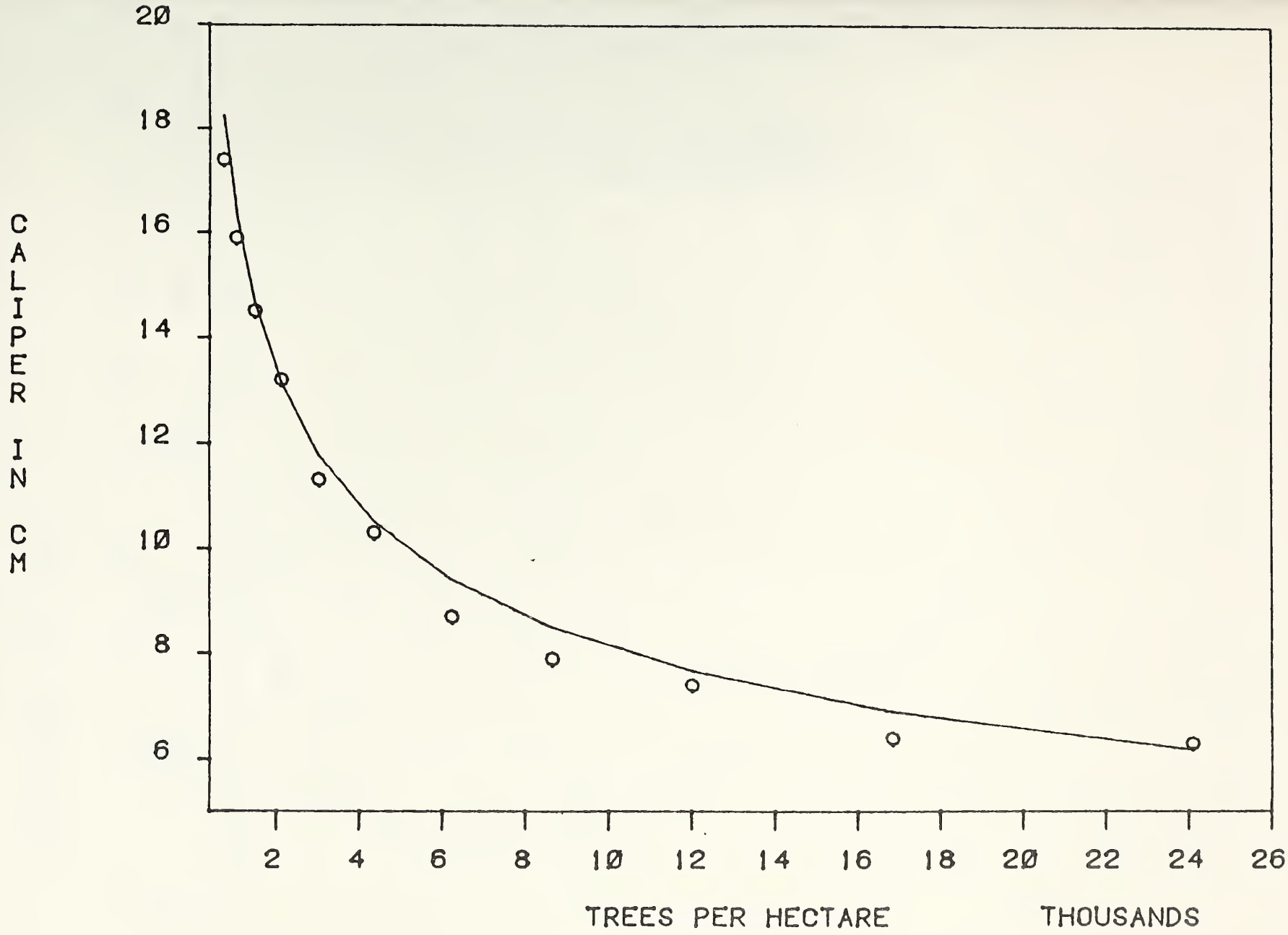

Figure 5: Fit of 8-year average caliper for spacings and families. Caliper = 141 (trees/ha)$^{-0.31}$

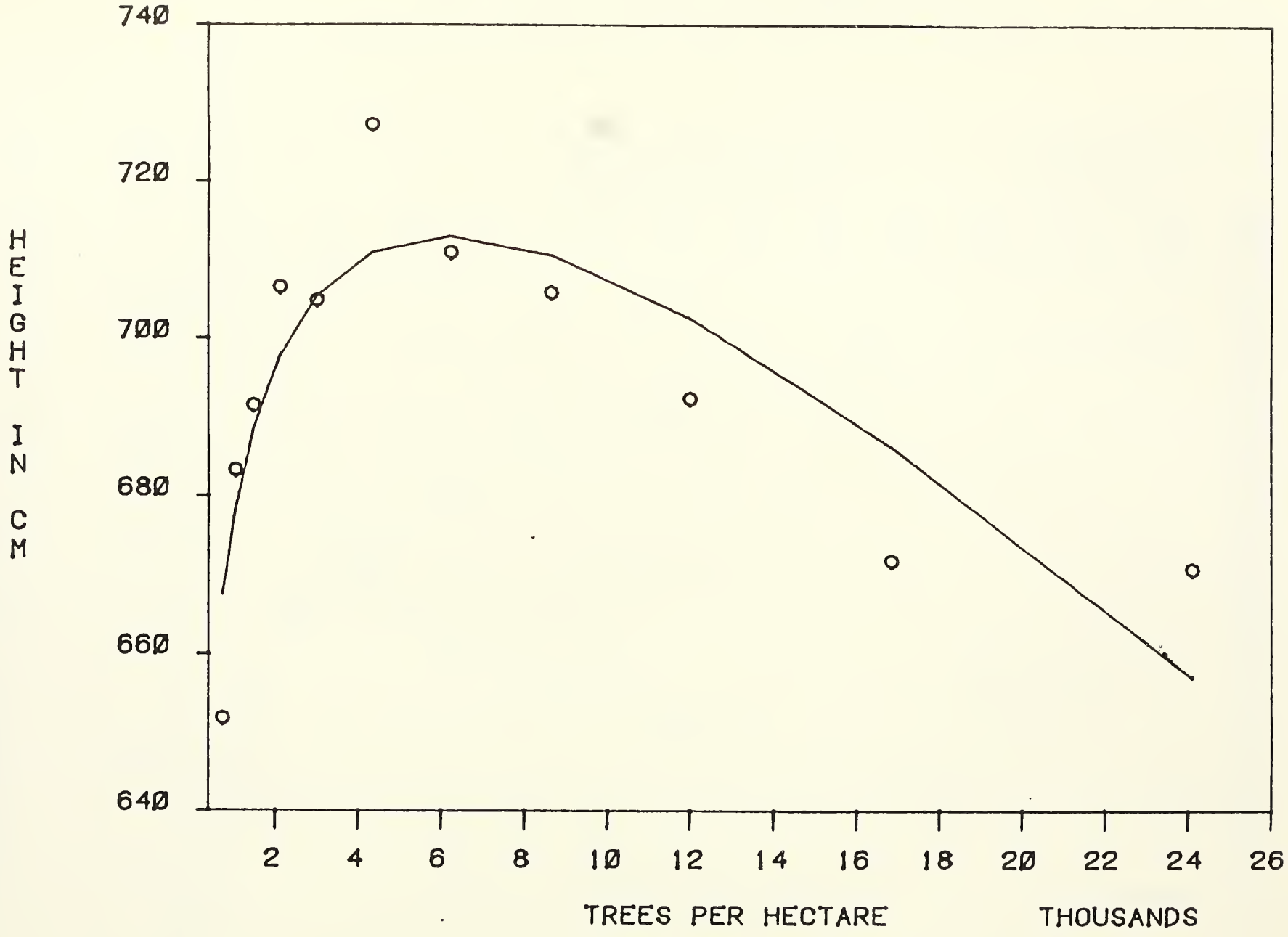

Figure 6: Fit of 8-year average height for all spacings and families. Height = 473 (trees/ha)/e (8.59x10-6trees/ha)

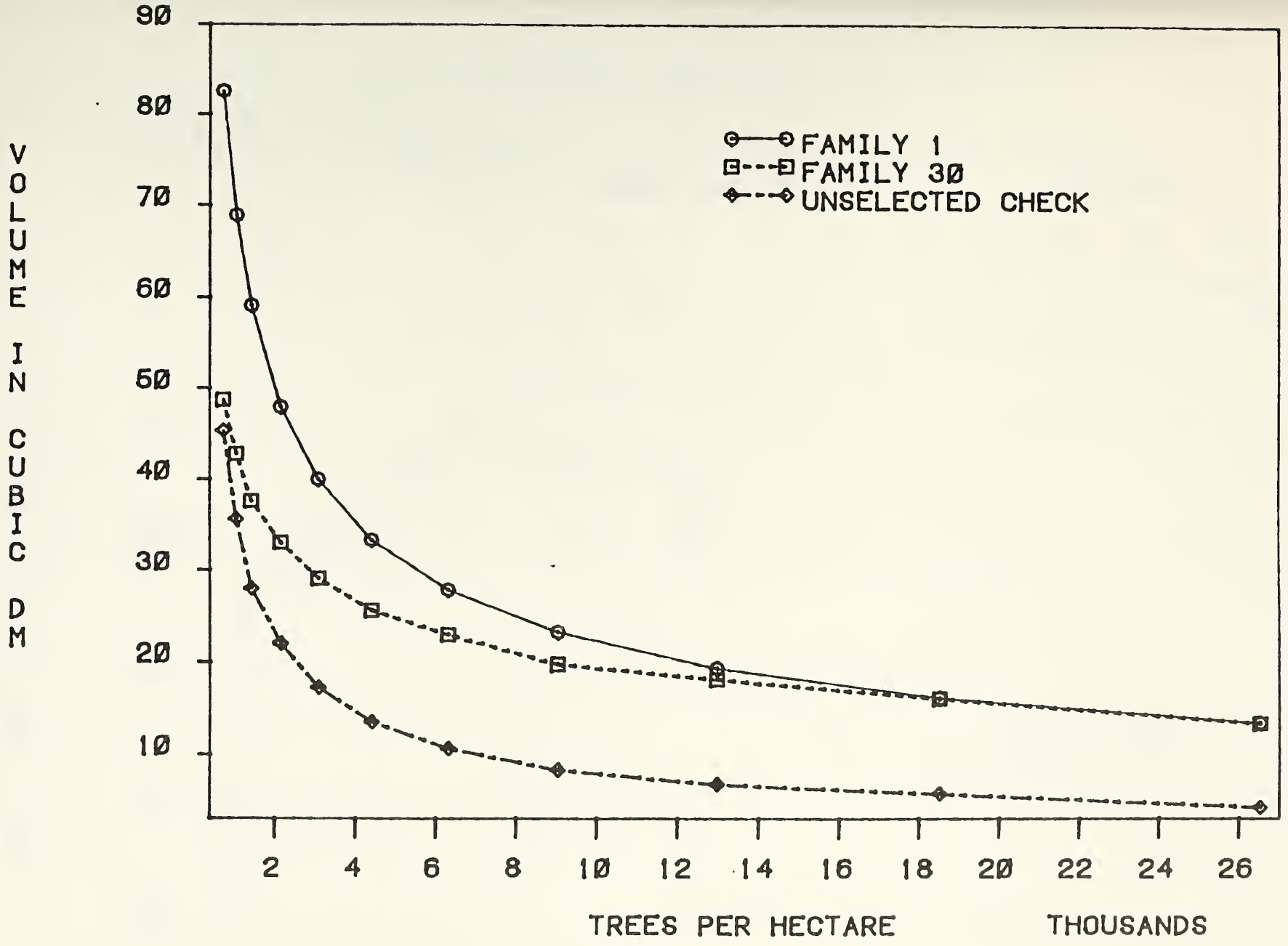

Figure 7: Fit of 8-year average volume for two families and unselected check.

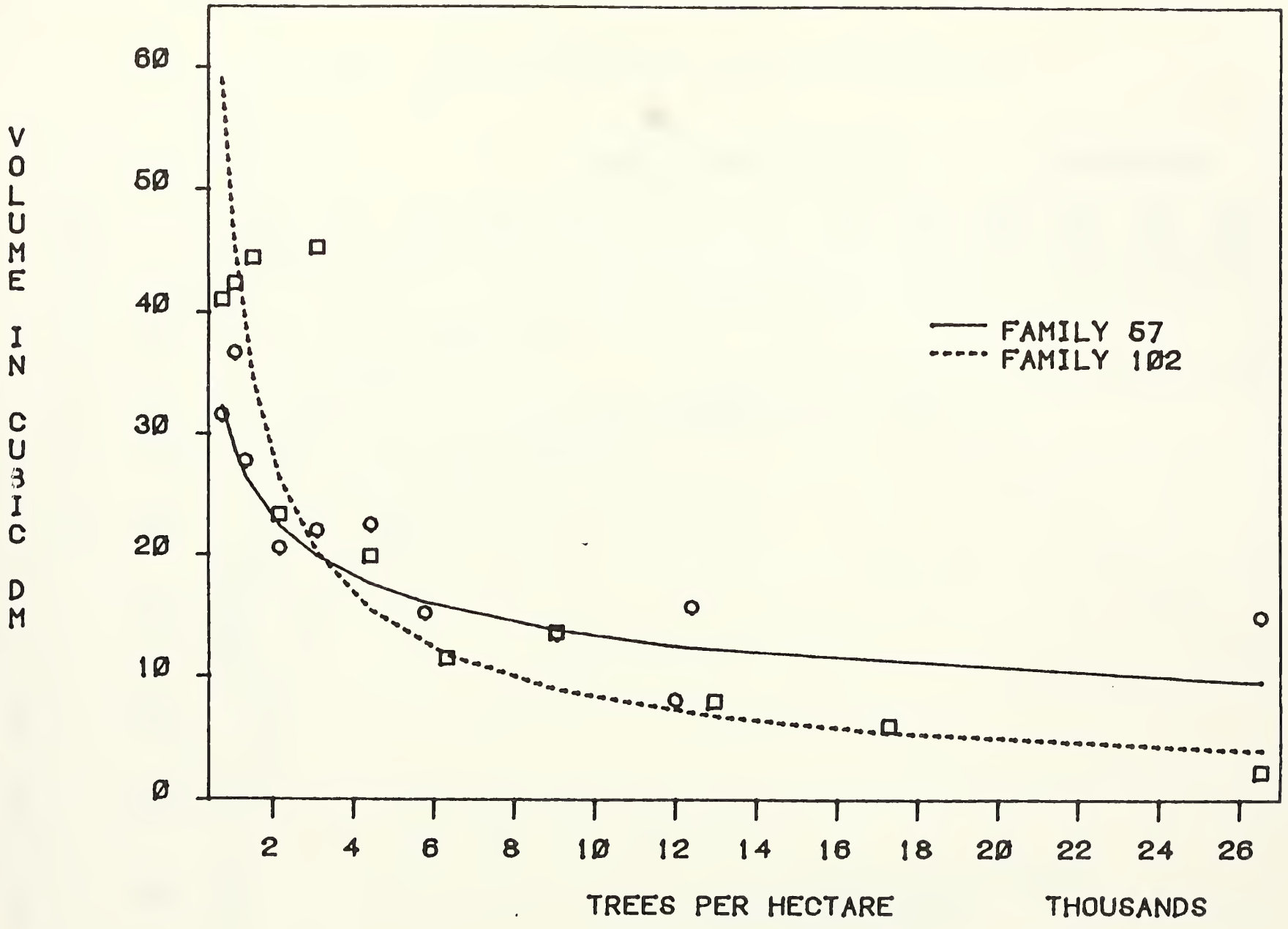

Figure 8: Fit of 8-year average volume for two families with equal volume but contrasting slopes.

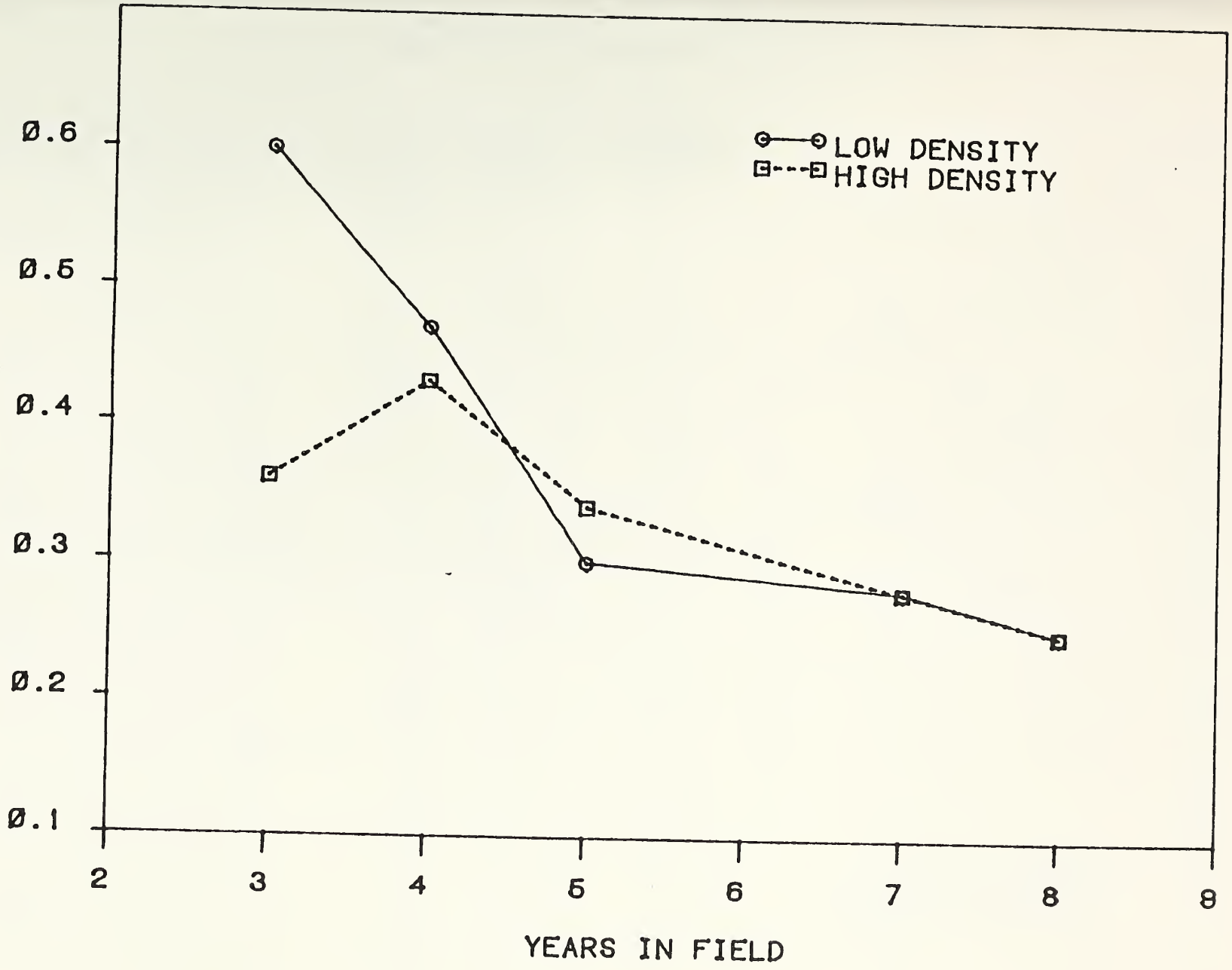

Figure 9: Comparisons of heritability estimates for volume by density class.

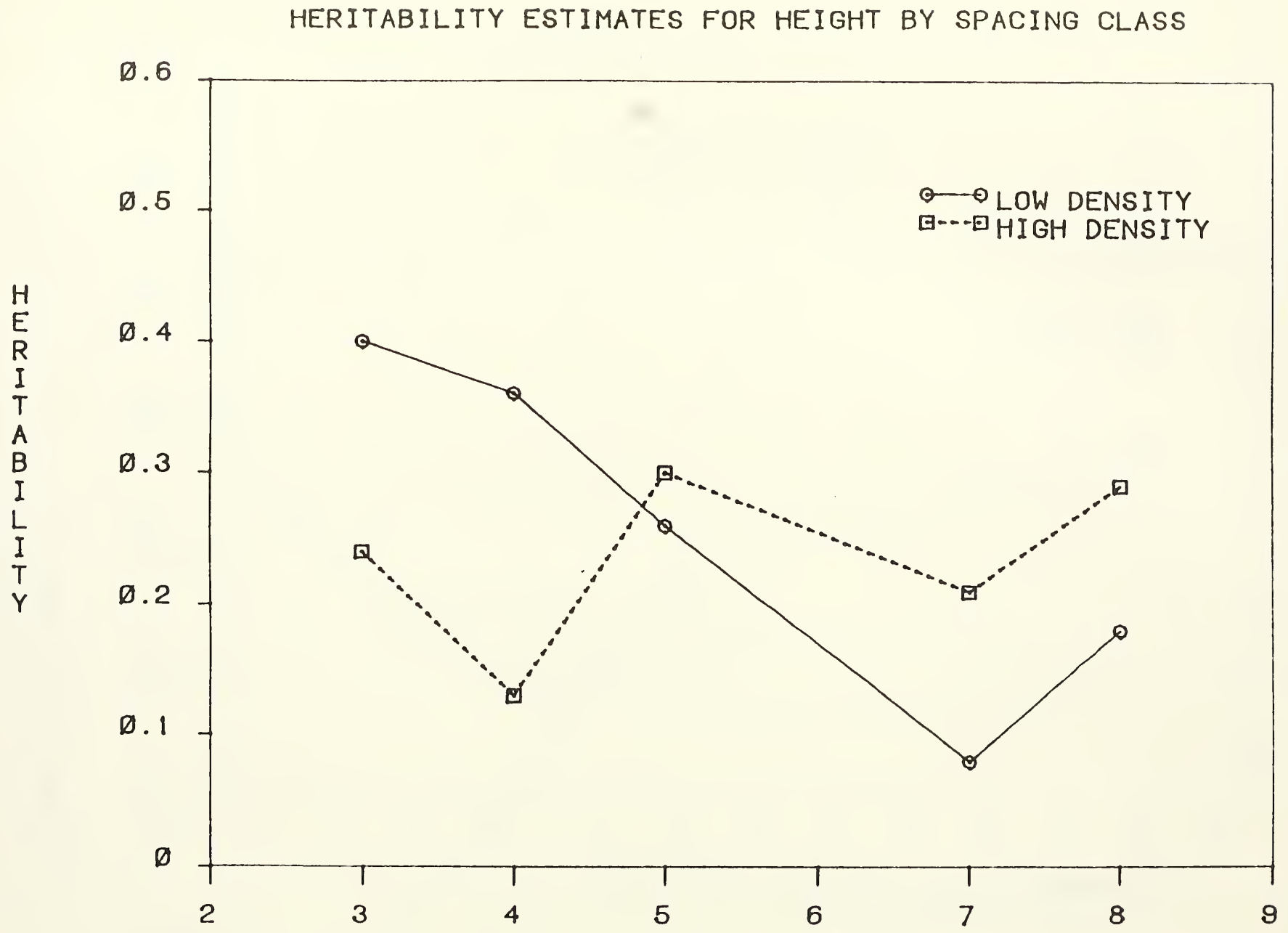

Figure 10: Comparisons of heritability estimates for height by density class.

GENETIC, SPACING, AND GENOTYPE X SPACING INFLUENCES ON GROWTH OF EUCALYPTUS GRANDIS IN SOUTH FLORIDA

Donald L. Rockwood[1/] and George Meskimen[2/]

Abstract.--Thirty-three E. grandis progenies in three studies and a related spacing study were used to document genetic, spacing, and genotype x spacing factors for growth up to 2.5 years. Variation among progenies was substantial for total height, diameter, tree volume, and volume/ha. Although progeny comparisons across studies were inconsistent, similarities within studies between traits over ages suggest that early progeny assessment may be possible. Spacing can be modified to alter juvenile yields dramatically, while use of the better progenies, due to the lack of spacing x progeny interaction, will permit yield increases for different cultural systems.

Additional keywords: Biomass, competition, genotype x environment interaction, early progeny assessment, selection.

Eucalyptus grandis Hill ex Maid., widely utilized worldwide (Eldridge, 1978), can be grown in south Florida for pulpwood (Franklin, 1978) or energy (Purdy et al., 1979). Three generations of selection by the USDA Forest Service (FS) have resulted in gains similar to those achieved by other E. grandis breeding programs (van Wyk, 1977; Campinhos and Ikemori, 1977).

Presently, FS E. grandis genetic base populations are planted at 1916 trees/ha and selected and rogued based on 2.5-year measurements. The current seedling orchard provides improved seed for pulpwood plantations established at 1389 trees/ha with an 8-year rotation. Shorter selection cycles and much closer spacings seem possible and appropriate for biomass base populations.

Reported below are results on 1) trait interrelationships among E. grandis progenies at juvenile ages, 2) spacing influences, 3) variation among progenies, and 4) genetic x spacing factors.

METHODS

In July 1979, open-pollinated progenies provided by FS were established near Labelle, Florida, in three biomass studies by the University of Florida (UF). Details of these studies plus the FS base population established in July 1977 near Labelle are presented in Table 1. UF studies were measured variously at .4, .7, 1.4, and 1.7 years for survival, height, and diameter. FS Base was measured for survival and height at .6 years and for survival, height, and dbh at 1.5 and 2.5

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years. Whole stem volume was estimated by the formula

$$dm^3 = .00008333(D^2H)^{.9525} - .000000055(D^2H)^{1.2535}$$

first derived by J. Saucier and metricated by T. Lloyd (both USDA Forest Service, personal communication) where D is dbh in mm and H is total height in dm. Data sets were analyzed separately by appropriate analyses of variance and Duncan's Multiple Range Tests. Within data sets, correlation coefficients among traits were obtained using progeny means. Comparison of progenies across tests were based on correlation coefficients also derived from progeny means.

Table 1.--Description of E. grandis studies.

Study	No. of Progenies	Planting Densities (trees/ha)	Experimental Design	Plot Type	No. of Reps
UF Nelder	33	40,000 25,000 14,706 8,403 4,444	RCB, Nelder's circles (Design 1a)	single-tree	8
UF Selection	20	10,000	RCB	25-tree square	3
UF Spacing	49 bulk	20,000 10,000 6,667	CRD	100-tree square	3
FS Base	33 [1/] (of 529)	1,916	CRD	single-tree	approx. 60

[1/] These progenies common to all studies.

RESULTS AND DISCUSSION

Variation among progenies was appreciable in most studies (Table 2). Survival in FS Base was relatively uniform, while progeny differences for height and stem volume were evident at all measurement ages. Progenies in UF Nelder, when compiled over all five spacings, also differed, and early differences among progenies were evident in UF Selection. Edge effect bias in UF Selection at 1.4 years resulted in elimination of 24 of 57 plots and reduction of precision. Consequently, substantial differences among progeny means, while similar to those in FS Base and UF Nelder, were not statistically significant.

Table 2.--Average, range, coefficient of variation, and significance of progeny means in E. grandis studies.

Study - Trait - Age	n	$\bar{x}$	Range	CV	Significance of Progenies[1/]
FS Base					
Survival - .6 years (%)	33	98.3	94 - 100	1.7	--
Height - .6 years	33	19.1	16.6 - 20.4	4.2	**
(dm) - 1.5 years	33	47.5	41.5 - 52.9	6.7	*
- 2.5 years	33	74.9	63.8 - 84.4	7.6	**
Stem - 1.5 years	33	5.6	4.0 - 8.1	19.6	*
Volume - 2.5 years (dm^3)	33	21.5	12.9 - 31.6	21.9	**
Volume - 1.5 years	33	10.4	7.7 - 14.5	18.4	No
/ha - 2.5 years (m^3)	33	40.9	24.7 - 57.6	21.4	**
UF Nelder					
Height - .4 years	33	14.8	10.5 - 17.4	8.8	**
(dm) - .7 years	33	18.1	12.5 - 21.3	8.8	**
- 1.4 years	33	42.4	25.0 - 45.9	9.7	**
Stem - .7 years	33	.670	.269 - 1.034	21.3	**
Volume - 1.4 years (dm^3)	33	1.88	.41 - 2.73	26.1	**
UF Selection					
Survival - .4 years (%)	20	91.3	73 - 99	7.0	**
Height - .4 years	20	16.3	14.6 - 19.1	8.0	**
(dm) - 1.4 years	19	47.0	40.5 - 54.1	8.1	No
Stem - 1.4 years Volume (dm^3)	19	2.37	1.72 - 3.15	15.6	No
Volume - 1.4 years /ha (m^3)	19	21.4	15.3 - 30.6	19.6	No

[1/] -- = not calculated, No = non-significant, * and ** = significant at the 5% and 1% levels, respectively.

Progeny differences in each study were consistent with age (Table 3). By age 1.5 years in FS Base, differences appeared to be established. At the closer spacings and higher competition in the UF studies, progeny differences evident as early as .4 years existed at 1.4 years. Correlations among height and volume traits at the same age were strong.

Table 3.--Correlation coefficients among progeny means within each E. grandis study.

		Height		Stem Volume	
		1.5 years	2.5 years	1.5 years	2.5 years
FS Base:					
Height -	.6 years	.29	.22	.20	.10
-	1.5 years		.90**	.91**	.82**
-	2.5 years			.88**	.93**
Stem Vol. -	1.5 years				.84**

		1.4 years	.7 years	1.4 years
UF Nelder:				
Height -	.7 years	.79**	.92**	.80**
-	1.4 years		.72**	.87**
Stem Vol. -	.7 years			.84**

		.4 years	1.4 years	1.4 years
UF Selection:				
Survival -	.4 years	.05	.14	.30
Height -	.4 years		.77**	.71**
-	1.4 years			.58**

*, ** - Significant at the 5 and 1% levels, respectively.

Table 4.--Correlations coefficients among means of 33 progenies common to FS Base and UF Nelder.

		UF Nelder			
		Height		Stem Volume	
FS Base:		.7 years	1.4 years	.7 years	1.4 years
	.6 years	.29	.33	.07	.14
Height -	1.5 years	.26	.38*	.13	.26
	2.5 years	.20	.41*	.09	.25
Stem -	1.5 years	.09	.28	.01	.18
Volume -	2.5 years	.05	.33	-.02	.19

*Significant at the 5% level.

Progeny performance across the various studies was not consistent. While correlations between height growth of the 33 progenies in FS Base and UF Nelder at 1.4 years were evident, the correlations between height and stem volume and between stem volumes in the two studies were not significant (Table 4). On the basis of the 19 progenies occurring in all three studies, heights at age 1.4 years in the UF studies were correlated with FS Base heights in four of the six possible cases and in one instance 1.4 year height in UF Nelder was correlated with 1.5 year stem volume in FS Base (Table 5). The 19 progenies common to the two UF studies had similar performance at 1.4 year heights only; stem volume correlations were not evident.

Table 5.--Correlation coefficients among means of 19 progenies common to UF Base, UF Nelder, and UF Selection.

		UF Nelder				
		Height			Stem Volume	
FS Base:	Years:	.4	.7	1.4	.7	1.4
	- .6 years	.32	.39	.52*	.19	.32
Height	- 1.5 years	.32	.35	.56*	.22	.50*
	- 2.5 years	.22	.23	.54*	.18	.45
Stem	- 1.5 years	.13	.14	.46*	.08	.39
Volume	- 2.5 years	.03	.02	.43	.01	.34

		UF Selection			
		Height		Stem Vol.	Vol./ha
FS Base:	Years:	.4	1.4	1.4	1.4
	- .6 years	.53*	.50*	.31	.26
Height	- 1.5 years	-.17	-.03	-.47	-.30
	- 2.5 years	-.01	.12	-.26	-.09
Stem	- 1.5 years	-.27	-.03	-.47	-.26
Volume	- 2.5 years	-.16	.06	-.28	-.10

		UF Selection			
		Height		Stem Vol.	Vol./ha
UF Nelder:	Years:	.4	1.4	1.4	1.4
	- .4 years	.27	.26	-.02	-.05
Height	- .7 years	.29	.25	-.01	-.06
	- 1.4 years	.35	.52*	.05	.06
Stem	- .7 years	.21	.22	.00	-.04
Volume	- 1.4 years	.19	.41	-.01	-.03

*Significant at the 5% level.

The lack of consistency of progeny performance may be due to many factors. In view of the degree of similarity in height growth, stem volume inconsistencies may be attributed to the different spacing or competitive regimes in the studies. The relatively wide spacing in FS Base may not create the level of competition through 2.5 years that was present at 1.4 years in UF Selection or at even younger ages in the closer spacings in UF Nelder. Although the two sites are within 8 km of each other, site factors, as have been detected in very limited areas, may cause some genotype x environment interaction. Another possible explanation for progeny instability between FS Base and UF studies may be different seed crop years, but this factor appears minimal because of the lack of correlation just within the UF studies.

The potential for short-term, close-spacing progeny testing for pulpwood rotation systems consequently is not established. Consistency of performance over age within the UF biomass studies gives encouragement for the approach, but longer-term growth data are needed.

Differences among the 33 progenies when grouped by generation identify the progress that has been made by selection and also the same inconsistency in progeny performance discussed earlier. In FS Base, 1.5-year stem volumes of progenies of second and third generation selects compared to progenies of first generation selects averaged 12% and 25% greater, respectively. (These differences may be affected by the inter-genotypic competition introduced by the single-tree plot layout.) However, the same comparisons in UF Nelder for 1.4 year stem volume resulted in differences of only 3% and 7%, suggesting that the selection criteria for pulpwood and biomass cultures are only weakly related.

Spacing had considerable influence on growth in UF Nelder (Tables 6 and 7). Total tree height at .4 and .7 years was greater at the two closest spacings,

Table 6.--Height, stem volume, and volume/ha means for UF Nelder and UF Spacing.

Study-Spacing (trees/ha)	Years:	Height .4 (dm)	Height .7 (dm)	Height 1.4 (dm)	Stem Volume .7 (dm^3)	Stem Volume 1.4 (dm^3)	Volume/ha .7 (m^3)	Volume/ha 1.4 (m^3)
UF Nelder -								
40,000		16.5^{a} [1/]	20.6^{a}	41.5^{a}	.54^{a}	1.08^{ab}	21.6^{a}	43.3^{a}
25,000		15.4^{b}	19.2^{b}	42.5^{a}	.61^{ab}	1.43^{b}	15.3^{b}	35.8^{b}
14,706		14.2^{c}	17.1^{c}	41.8^{a}	.63^{bc}	1.61^{c}	8.9^{c}	22.9^{c}
8,404		13.8^{c}	16.5^{c}	41.8^{a}	.72^{bc}	2.11^{d}	6.1^{d}	17.7^{d}
4,444		13.9^{c}	16.6^{c}	44.0^{a}	.84^{c}	3.15^{d}	3.7^{e}	14.0^{d}
UF Spacing -								
20,000		12.6^{a}	--	43.3^{a}	--	1.89^{a}	--	33.7^{a}
10,000		13.0^{a}	--	43.5^{a}	--	2.42^{b}	--	22.9^{b}
6.667		12.6^{a}	--	42.0^{a}	--	2.72^{c}	--	16.2^{c}

[1/] Means within a trait and study not sharing the same superscript are significantly different at the 5% level.

Table 7.--Summary of F-values resulting from analyses of variance for UF Nelder.

Source	Approx. df.	Height at Age .4 Years	at Age .7 Years				at Age 1.4 Years			
			Height	DBH	Stem Volume	Vol./ ha	Height	DBH	Stem Volume	Vol./ ha
Reps (R)	7	17.41**	13.91**	9.49**	12.25**	6.02**	4.57**	1.49	2.52**	.88
Spacings (S)	4	9.61**	16.23**	18.26**	4.23**	89.72**	1.61	45.14**	37.93**	56.86**
Progenies (P)	32	3.46**	2.99**	2.37**	2.24**	2.72**	4.98**	3.64**	2.75**	3.42**
R x S	28	4.30**	2.72**	2.87**	4.50**	2.53**	1.99**	1.87**	2.00**	1.38
R x P	224	2.28**	3.85**	1.46**	1.81**	1.53**	1.53**	1.34**	1.45**	1.21*
S x P	128	1.17	1.06	.96	1.10	1.07	1.03	1.09	1.19	1.17
Error	896									
	1319									

* and ** Significant at the 5% and 1% levels, respectively.

but by 1.4 years heights were comparable to all spacings. Diameter was strongly affected by spacing and produced three-fold tree volume differences at 1.4 years. Environmental variation was evident as differences among the eight reps located on the .3 ha area were significant for each trait and age except DBH at 1.4 years. Rep x Spacing and Rep x Progeny interactions were also present.

The absence of progeny by spacing interaction for all traits in UF Nelder (Table 7) is especially notable. For the alternative spacings being considered for biomass plantations, the better performing progenies will apparently do well at any of the spacings. However, because no pulpwood spacings are involved in the examination of interaction, any extrapolation to progeny performance at planting densities less than 4,444 trees/ha is risky.

Volume yields from the four studies mesh in consistent inverse relation to planting density while mean heights are surprisingly uniform (Table 8). These consistent results from different studies, separate sites, different seed crop years, and different planting years suggest that the yields obtained characterize productivity achievable over the vast area of similar sites available in south Florida.

Our results indicate that a thorough genotype x spacing study needs to be initiated in order to characterize definitively the performance of E. grandis progenies across the range of spacings to be considered for pulpwood and biomass systems. Such a study, with adequate plot size, buffer, and replication, would involve major commitments of plant material, land, and personnel.

Table 8.--Summary of mean heights and volumes for all E. grandis studies ordered by planting density.

Study	Trees/ha	Age	Height	Volume	
				Total	Per Year
		(yr)	(dm)	------m^3/ha---------	
UF Nelder	40,000	1.4	41.5	43.3	30.9
UF Nelder	25,000	1.4	42.5	35.8	24.6
UF Spacing	20,000	1.4	43.3	33.7	24.1
UF Nelder	14,706	1.4	41.8	22.9	16.4
UF Spacing	10,000	1.4	43.5	22.9	16.4
UF Selection	10,000	1.4	47.0	21.4	15.3
UF Nelder	8,403	1.4	41.8	17.7	12.6
UF Spacing	6,677	1.4	42.0	16.2	11.6
UF Nelder	4,444	1.4	44.0	14.0	10.0
FS Base	1,916	1.5	47.5	10.5	7.0

CONCLUSIONS

Considerable variation for juvenile height and volume growth exists among E. grandis progenies. Progeny differences were consistent over age within each study but were inconsistent over studies possibly due to varying levels of competition and limited time of observation. Short-term, close-spacing systems for progeny evaluation may be possible if longer-term evaluation conforms to present patterns. Close spacings radically affected short-term productivity levels, with the closest spacing resulting in total stem biomass/ha four times larger than that achieved with 1,916 trees/ha. Spacing x progeny interaction appears minor.

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SITE INDEX MODELS FOR HEIGHT GROWTH OF PLANTED LOBLOLLY PINE (*Pinus taeda* L.) SEED SOURCES

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Abstract.--The loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley 1966) was analysed to assess the effect of seed source on site index variation. Height growth differences among seed sources were evaluated using site index models, and the results presented as coefficients that can be used in existing growth and yield models for loblolly pine. A practical interpretation of the results was based on the time required to achieve a given size.

In most of the plantations, there was a significant effect of seed source on site index at index ages 25 or 27. Differences in site index between seed sources were consistently greater than 5 feet, and occasionally greater than 10 feet in the 15 plantations studied. Except for one plantation in south Mississippi, seed source effects on the form of the site index curves was not large.

Additional keywords: Geographic variation, growth and yield modeling.

In American forestry, site index, or the mean height achieved by dominant and codominant trees by a given index age, is almost universally accepted as the fundamental indicator of site quality. This is clearly an oversimplification in that the site index of a given forest site depends on the potential growth rate of the trees occupying the site. So it is common to name the species for which the site index applies. A fundamental question arises as to whether this refinement should be extended to the point of specifying the site index that applies to each seed source, half-sib family, full-sib family, or any other definable genetic group that could be planted on the site.

The answer is of fundamental importance to both forest geneticists and forest managers. If geneticists have improved the growth potential of improved stock compared with woodsrun stock--and there are many indications that they have--then these gains should be quantifiable in terms familiar to managers. By expressing genetic improvement in terms of site index, geneticists can accomplish this step and perhaps in the process gain a better understanding of the biology of the system they are attempting to change.

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Forest managers need answers to such questions to effectively handle improved planting stock. Just as managers handle better sites differently than they do poor sites, improved stock may require different strategies than woodsrun stock. For example, better sites are managed on shorter rotations, thinned more often, and can be planted with fewer trees. If they are not managed differently, much of the advantage may be lost. In the same way, improved stock may require similar refinement to maximize economic gain.

Unfortunately, much of the existing data on genetic effects on growth rate are based on unsuitable small row plots. However, in certain genetic field tests, large plots of relatively homogeneous material are replicated on different sites. It should be possible in these tests to estimate site index for each plot and, within the limits of the experimental design, assess the effect of genetics on site index.

In this paper we analyse the loblolly phase of the Southwide Pine Seed Source Study (Wells and Wakeley 1966) to assess the effect of seed source on site index variation. Height growth differences among seed sources are evaluated using site index models. The results are presented as coefficients that can be used in existing growth and yield models for loblolly pine. A practical interpretation of the results is based on the time required to achieve a given size.

MATERIAL AND METHODS

The Southwide Pine Seed Source Study is sponsored by the Southern Forest Tree Improvement Committee. It was established in 1952-53 by numerous industrial cooperators under the direction of Philip C. Wakeley, Southern Forest Experiment Station, now retired. The study sought to determine to what degree inherent geographic variation (i.e., genetic variation) in four southern pines is associated with geographic variation in climate and physiography.

Details of the loblolly phase of this study appear in Wells and Wakeley (1966). Fifteen seed collection areas, or seed sources, were selected and bulk seed from at least 20 trees in each area was collected in 1951. The seed sources were grouped into two sets, or series, with nine sources in each series--six unique to a series and three common to both series. Seedlings were placed in 19 test plantations during the winter of 1952-53.

The experimental design of each plantation is a randomized complete block with four blocks--usually of nine seed sources from one series and eight from the other. Each seed source plot contains 121 trees (11 x 11 trees) with 72 outer trees used as borders and the inner 49 as test trees. Spacing was 6 x 6 feet.

Each of the 49 interior test trees in each plot was measured at 1, 3, 5, 10, 15, 20, and 25 years after planting, except for occasional measurements made at 16, 22, or 27 years instead of 15, 20, or 25. Total height, survival, and damage from insects, disease, and other agents were recorded at each measurement age. Diameter at breast height (d.b.h.) was recorded at measurement ages past 5 years.

Most of the plantations were thinned by cooperators some time after the 10th year. The thinning rules were designed to eliminate diseased or suppressed trees and improve the internal spacing of plots. Thinning to a prescribed density (25 test trees per plot, or 617 trees per acre) was the goal rather than a prescribed residual basal area. Throughout the 25-year period, and despite efforts to avoid it, wide variations in density from plot to plot still occurred because of disease, insects, and other uncontrollable factors.

Fortunately, the failure to control density does not preclude a realistic assessment of the effect of seed source on growth potential. The primary measure of growth potential, height growth of dominant-codominant trees, is essentially independent of density except for extremely high or low densities (Smith 1962). Other measures of growth rate, such as diameter, volume growth, basal area, and biomass are sensitive to density and not as useful in comparing growth potential. The almost universal acceptance of site index (the mean height of dominant-codominant trees at a given index age) as a measure of the productivity, or potential productivity, of forest land attests to the utility of this method.

We designated the tallest two-thirds of the surviving trees at age 25 (or 27) as dominant-codominants at all measurement ages. In plots with fewer than nine surviving trees at the last measurement age, we designated the tallest five as dominant-codominants.

A two-way plot of mean dominant-codominant height over age provides a site index guide curve. Mathematical models of such curves play a central role in growth and yield prediction systems. Also, site index models provide a convenient method of summarizing large amounts of height growth data using only a few statistics. This allows statistical comparisons of site index curves from different data sets. For these reasons, we chose the site index curve as the basic unit of observation for growth analysis.

Basically, variation between site index curves reflects fundamental differences in growth rate due to biotic and abiotic factors. Variation associated with seed source reflects genetic differences in growth rate, whereas variation related to blocks or plantations reflects environmental effects and possibly genetic by environmental interaction effects on growth rate. Our approach to the statistical analysis of variation between site index curves consists of (1) characterizing the site index curves with an appropriate mathematical model, (2) partitioning the variation in model coefficients according to the controlled factors in the experimental design (seed source and blocks), and (3) performing statistical tests to judge whether the variation attributable to controlled factors can be considered significant in light of the experimental error variation between model coefficients.

We chose a mathematical model for site index curves proposed by Smalley and Bower (1971) for loblolly pine:

$$H_D = (S_I) \cdot 10^{B_1 \cdot (1/\sqrt{A} - 1/\sqrt{I})} \qquad (1)$$

where

H_D = mean height of dominant-codominant trees
A = age in years since planting
I = index age in years
S_I = site index, or the value of H at age I
B_1 = model coefficient

The model is linear when expressed in logarithmic form:

$$LOG_{10}(H_D) = B_0 + B_1 \cdot (1/\sqrt{A}) \qquad (2)$$

where

LOG_{10} = logarithm to the base 10

$$B_0 = [LOG_{10}(S_I) - B_1 \cdot (1/\sqrt{I})]$$

When expressed in this form, it is clear that a graph with $LOG_{10}(H_D)$ as ordinate and $1/\sqrt{A}$ as abscicca should linearize the site index curve if the model is a good representation of the data. We did this for the data from each plot in the data base and found that the transformation linearized all height data beyond 5 years, but in general did not linearize height data at ages 1, 3, and 5. For this reason, we eliminated the first three height measurements from further analyses and used only the height data beyond age 5 to represent the site index curve. This seems justifiable in light of the fact that nursery effects, planting shock, and other short-term effects influence early height growth, even though they are not related to long-term site productivity.

The logarithmic form, equation (2), expresses the general relationship between height and age for a set of data that are uniform in the sense that each site index curve has the same slope (B_1) but not necessarily the same intercept (B_0). In growth and yield terminology, such data "follow the same guide curve." Hence, defining B_1 is equivalent to defining a guide curve that may be used to generate a site index curve for any site index at any index age simply by setting B_0 to the desired value. For example, the site index curve for site index 60 feet at age 25 can be generated by:

$$LOG_{10}(H_D) = [LOG_{10}(60) - B_1(1/\sqrt{25}] + B_1(1/\sqrt{A})$$

or

$$H_D = (60)10^{B_1(1/\sqrt{A} - 1/\sqrt{25})}$$

We fit each plot to equation (2) separately, using simple unweighted linear regression methods. The lack of fit for each plot was measured by first generating a predicted site index curve for the plot using the plot's site index and B_1 coefficient. Deviations from prediction, in feet, were then taken and their average squared deviation computed. Finally, the square root of this value was used as a measure of lack of fit.

Once estimates of B_1 were obtained for each plot within a plantation, we used analysis of variance procedures to partition the plot-to-plot variation between coefficients within a plantation as follows:

Source of variation	Degrees of freedom	Mean square	F-ratio
Blocks	b-1	MSB	F_B = MSB/MSE
Seed Source	s-1	MSS	F_S = MSS/MSE
Error	(b-1)(s-1)	MSE	

The same analysis of variance procedures were also applied to the site index of each plot, i.e., the observed value of H_D at the last measurement. For these analyses most plantations were balanced. But whenever there were missing plots, substitution methods as described by Snedecor (1948) were employed. Four of the original 19 plantations suffered excessive damage from fire or other agents and were eliminated.

Overall estimates of B_1 were obtained by simply pooling (H_D,A) pairs for all plots within a plantation and fitting one B_1 coefficient. Estimates of B_1 for each seed source in each plantation were obtained by first computing the plantation mean value of H_D for each seed source at each measurement age and then fitting the B_1 coefficient to the mean values.

Site index performance can be expressed in terms of time. For example, the following question may be posed: How long would it take a plot to reach a given mean dominant-codominant height assuming the plot grew in accordance with the mathematical model used to represent its site index curve? We answered with the following formula:

$$T_H = [\ B_1/(LOG_{10}(H_D)-LOG_{10}(S_I)+B_1/\sqrt{I})]^2$$

where

T_H = time in years to reach a given height H_D

and B_1 and S_I are specific to the plot in question.

RESULTS AND DISCUSSION

The overall regression coefficients (B_1's) for each planting varied widely (table 1). Differences in climate, soil moisture regime, and site preparation (Wells and Wakeley 1966) probably contributed. The southwestern Georgia plantation exhibited the smallest "error", with only a 0.20 foot average deviation from predicted height. The two southern Mississippi plantations fit worst, with an average deviation of nearly 1 foot.

Table 1.--Analysis of variance of model coefficient (B_1) and observed site index (S_I) variation between plots within plantations

Plantation		Overall Fit		ANOVA of S_I			ANOVA of B_1		
Location	Series	B_1	Error [1/]	F_B	F_S	MSE [2/]	F_B	F_S	MSE
				[3/]					
E NC	1	-2.51371	0.84	29.80*	1.41	21.82	14.33*	0.68	0.1088
SW GA	1	-3.04114	0.20	1.41	7.04*	3.61	5.47*	6.16*	0.0177
E NC	1	-2.58167	0.52	5.07*	2.61*	12.28	1.90	0.40	0.0647
W SC	2	-2.36299	0.43	1.81	2.32	20.98	2.71	3.02*	0.0496
N MS	2	-3.78783	0.45	1.95	3.14*	9.63	0.96	1.15	0.0410
N AL	1	-2.87898	0.34	0.00	1.42	17.88	4.63	1.60	0.0126
E NC	2	-2.66222	0.54	6.32*	3.87*	13.59	26.27*	1.69	0.0314
C AL	2	-3.03082	0.81	14.00*	1.65	21.11	11.84*	1.09	0.1399
SW AR	1	-2.68197	0.60	9.18*	4.60*	13.80	0.11	2.70	0.0220
SW AR	1	-2.98396	0.56	14.83*	4.13*	7.88	7.76*	3.00*	0.0391
E MD	1	-3.09563	0.55	3.72*	10.67*	3.68	0.97	0.65	0.1326
SE LA	2	-2.52170	0.62	1.73	4.75*	9.87	3.24	0.63	0.0301
S MS	1	-3.05636	0.98	6.15	1.70	31.86	0.01	8.37*	0.0334
SE LA	1	-2.43230	0.78	1.55	3.65*	13.25	0.84	3.65*	0.0470
S MS	2	-3.17342	0.96	8.00*	9.77*	2.25	2.60	2.67	0.0476

1/ Error = average deviation from predicted plot height, in feet.
2/ MSE = mean square error from the analysis of variance.
3/ An asterisk denotes significance at the 0.05 probability level.

The analyses of variance for plot-to-plot variation in both site index and model coefficients also appear in table 1. Of the 15 plantations, 7 showed significant (at the .05 level) effects of seed source on site index without showing significant seed source effects on B_1 coefficients. Three plantations showed significant seed source effects in both site index and B_1 coefficients, while two showed significant seed source effects only in B_1 coefficients. The remaining three plantations did not show significant seed source effects in either site index or B_1 coefficients.

The B_1 coefficients and site index values for each seed source in each plantation are given in tables 2 and 3. Except for the series 1 plantation in south Mississippi, the variation in B_1 coefficients was not large. Conversely, differences in site index values were consistently greater than 5 feet and occasionally greater than 10 feet.

Table 2.--Site index (S_I) and model coefficients (B_1) for series one seed sources in each planting

Plantation		Seed Source								
		E MD	SE NC	E NC	SW GA	N AL	N AL	SE LA	E TX	SW AR
E NC	B_1	-2.27	-2.78	-2.55	-2.72	-----	-2.42	-2.38	-2.50	-2.65
	S_I	64.50	69.50	68.00	65.00	-----	60.00	66.00	62.00	58.00
SW GA	B_1	-3.24	-2.98	-3.11	-3.03	-3.18	-3.19	-2.74	-2.86	-3.02
	S_I	55.95	56.50	56.50	55.25	51.00	52.00	56.50	53.25	50.25
E NC	B_1	-2.60	-2.69	-2.54	-2.54	---	-2.58	-2.66	-2.45	-2.57
	S_I	63.25	71.50	66.25	65.75	---	63.75	66.00	63.25	63.00
N AL	B_1	-2.87	-2.79	-2.86	-2.88	-2.93	-3.03	-2.76	-2.77	-3.02
	S_I	68.50	73.00	75.50	72.00	67.50	69.00	72.50	66.50	64.50
SW AR	B_1	-2.90	-2.78	-2.66	-2.71	-2.83	-2.82	-2.60	-2.37	-2.39
	S_I	68.25	68.75	70.23	67.75	67.00	66.50	65.50	60.50	57.75
S MS	B_1	-3.32	-3.00	-3.17	-3.57	-----	-3.14	-2.41	-2.63	-2.95
	S_I	56.50	49.50	53.50	54.50	-----	52.00	57.00	45.50	42.50
E MD	B_1	-2.82	-3.07	-3.00	-3.21	-3.03	-3.02	-3.42	-3.31	-2.99
	S_I	56.00	52.75	52.50	48.00	49.50	48.00	46.00	49.25	48.00
SE LA	B_1	-2.41	-2.12	-2.69	-2.29	-----	-2.70	-2.27	-2.56	-2.42
	S_I	65.75	67.25	76.00	70.25	-----	71.75	73.50	71.75	67.50

Table 3.--Site index (S_I) and model coefficients (B_1) for series two seed sources in each planting

Plantation number		Seed Source								
		SE NC	W SC	NE GA	NE AL	NE MS	SE LA	SW AR	W TN	NW GA
W SC	B_1	-2.13	-2.46	-2.44	-2.39	-2.47	-2.02	-2.26	-2.50	-2.61
	S_I	52.75	57.25	59.50	52.00	56.25	50.25	51.75	56.00	59.75
N MS	B_1	-3.69	-3.70	-3.79	-3.94	-3.85	-3.73	-3.78	-3.93	-3.64
	S_I	70.75	63.25	66.25	64.50	64.76	70.50	67.75	64.75	66.25
E NC	B_1	-2.66	-2.77	-2.52	-2.77	-2.62	-2.68	-2.81	-2.52	-2.60
	S_I	71.75	70.00	64.25	68.25	67.50	68.50	62.75	60.50	65.00
C AL	B_1	-2.76	-3.04	-3.25	-3.03	-3.05	-2.78	-2.62	-3.18	-3.07
	S_I	57.00	56.75	60.00	59.75	59.25	64.25	53.50	57.75	59.75
S MS	B_1	-3.11	-3.18	-3.09	-3.39	-3.38	-2.69	-3.28	-3.48	-2.90
	S_I	53.50	52.00	52.00	52.00	49.50	56.50	50.00	46.50	46.00
SW AR	B_1	-2.81	-2.95	-3.10	-3.16	-2.94	-2.70	-2.86	-3.18	-3.08
	S_I	70.75	70.00	70.50	69.75	69.50	68.00	61.75	67.00	70.75
SE LA	B_1	-2.47	-2.46	-2.52	-2.42	-2.63	-2.56	-2.52	-2.60	-2.54
	S_I	73.75	68.50	69.00	66.25	67.25	75.75	67.50	65.50	70.00

Table 4.--Gain or loss in time required for nonlocal seed sources to grow to same height as local seed source in series two plantations

Plantation number	Measurement age (Years)	Mean height of local source (Feet)	Gain (+) or loss (-) in years to indicated height for seed source								
			SE NC	W SC	NW GA	NE AL	NE MS	SE LA	SW AR	W TN	NW GA
				1/							
W SC	15	41.92	-1.4	*0.0*	+0.4	-2.5	-0.9	-2.4	-2.2	-1.0	+0.1
	20	49.03	-1.6	*0.0*	+1.7	-2.5	-0.1	-3.5	-2.4	-0.1	+1.6
	25	57.38	-4.9	*0.0*	+1.4	-5.1	-1.1	-8.7	-5.5	-1.2	+1.7
N MS	15	41.01	+0.6	-0.9	-0.4	-1.0	*0.0*	+0.6	-0.1	-0.9	-0.0
	20	55.64	+0.8	-1.6	-0.6	-1.4	*0.0*	+0.7	-0.2	-1.2	-0.3
	25	68.10	+1.0	-2.3	-0.8	-1.6	*0.0*	+1.0	-0.2	-1.3	-0.6
E NC	15	48.36	*0.0*	-0.0	-1.2	-0.5	-0.2	+0.3	-2.2	-2.6	-1.1
	20	60.44	*0.0*	-0.1	-2.6	-0.9	-0.8	+0.2	-3.5	-5.0	-2.2
	25	71.76	*0.0*	-1.0	-5.6	-2.2	-2.5	-0.8	-5.9	-9.4	-4.6
C AL	15	41.30	-0.9	-1.6	-1.0	*0.0*	-0.8	+1.2	-2.0	-1.6	-0.8
	20	52.82	-2.2	-2.6	-1.2	*0.0*	-1.4	+1.2	-4.5	-2.3	-1.2
	25	59.67	-1.9	-1.9	+0.2	*0.0*	-0.3	+2.7	-5.3	-1.3	-0.1
SW AR	15	45.10	+2.4	+1.9	+1.6	+1.4	+1.8	+2.1	*0.0*	+0.8	+1.7
	20	56.84	+3.7	+3.3	+3.0	+2.8	+3.1	+3.1	*0.0*	+2.0	+3.2
	25	68.74	+4.4	+4.0	+3.9	+3.7	+3.7	+3.3	*0.0*	+2.6	+4.1
SE LA	16	56.11	-1.3	-3.3	-3.2	-4.4	-4.3	*0.0*	-3.9	-5.1	-2.9
	20	65.84	-2.2	-5.1	-4.8	-6.9	-6.1	*0.0*	-5.9	-7.3	-4.3
	27	75.76	-0.0	-4.1	-3.4	-6.6	-4.9	*0.0*	-5.0	-6.7	-2.7
S MS	15	42.65	-4.9	-5.9	-5.8	-5.9	-7.2	*0.0*	-6.9	-9.2	-8.9
	22	51.93	-3.8	-5.2	-5.2	-4.7	-6.7	*0.0*	-6.5	-9.4	-10.7
	27	56.65	-2.3	-3.9	-4.0	-3.1	-5.4	*0.0*	-5.3	-8.5	-11.1

1/ Italicized values designate local seed source.

Table 5.--Gain or loss in time required for nonlocal seed sources to grow to same height as local seed source in series one plantations

Plantation number	Measurement age (Years)	Mean height of local source (Feet)	Gain (+) or loss (-) in years to indicated height for seed source								
			E MD	SE NC	E NC	SW GA	N AL	N AL	NE AL	E TX	SW AR
					1/						
E NC	15	48.06	-0.3	+0.0	*0.0*	-1.2	----	-2.5	-0.1	-1.9	-3.5
	20	59.00	-1.3	+0.4	*0.0*	-1.4	----	-4.4	-0.6	-3.2	-5.3
	25	68.39	-3.2	+0.7	*0.0*	-2.0	----	-7.4	-1.8	-5.2	-7.8
SW GA	15	37.05	-0.4	+0.4	+0.1	*0.0*	-1.9	-1.5	+1.0	-0.3	-1.8
	20	47.07	-0.1	+0.5	+0.4	*0.0*	-2.5	-1.9	+1.0	-0.8	-2.7
	25	55.48	+0.3	+0.7	+0.7	*0.0*	-3.2	-2.3	+0.8	-1.5	-3.9
E NC	15	45.99	-0.7	+1.4	*0.0*	+0.3	----	-0.4	-0.5	-0.6	-0.6
	20	56.30	-0.9	+2.5	*0.0*	+0.5	----	-0.5	-0.5	-1.2	-0.9
	25	66.47	-2.4	+2.7	*0.0*	-0.5	----	-1.8	-1.6	-3.3	-2.5
N AL	15	46.98	-0.1	+1.2	+1.5	+0.8	-0.5	*0.0*	+1.1	-0.4	-1.5
	20	58.29	+0.1	+2.0	+2.5	+1.5	-0.2	*0.0*	+1.7	-0.6	-1.6
	25	69.23	-0.4	+2.1	+2.9	+1.5	-0.8	*0.0*	+1.7	-1.7	-2.6
SW AR	15	44.22	+1.5	+2.1	+1.8	+1.8	+1.2	+1.3	+1.1	+0.6	*0.0*
	20	53.88	+3.0	+3.7	+3.1	+3.1	+2.5	+2.7	+2.0	+0.7	*0.0*
	25	58.88	+5.9	+6.7	+5.9	+5.9	+5.3	+5.5	+4.5	+2.6	*0.0*
E MD	15	41.89	*0.0*	-0.3	+0.2	-0.8	-0.6	-1.1	-2.0	-1.0	-1.4
	20	56.15	*0.0*	-1.8	-1.2	-2.2	-2.5	-3.3	-3.8	-2.3	-4.0
	25	65.99	*0.0*	-0.4	+0.4	-0.6	-1.4	-2.5	-2.4	-0.6	-3.6
SE LA	16	54.02	-2.8	-1.8	-0.3	-1.0	----	-1.6	*0.0*	-1.3	-2.5
	20	64.00	-4.9	-4.4	-0.6	-2.6	----	-2.4	*0.0*	-2.4	-4.6
	27	73.55	-5.6	-6.1	+1.4	-2.6	----	-1.0	*0.0*	-1.3	-5.0
S MS	15	46.44	-6.1	-4.6	-7.4	-7.1	-7.9	-3.9	*0.0*	-6.1	-16.2
	22	50.78	-1.6	-0.1	-3.3	-2.5	-3.9	+0.2	*0.0*	-2.3	-14.4
	27	57.25	-0.7	+0.9	-3.0	-1.5	-3.9	+0.0	*0.0*	-2.8	-18.6

1/ Italicized values designate local source.

Summarizing the differences between seed sources in terms of time required to reach a given height is a convenient and practical way to express differences in site index curves. If the nearest seed source to each planting site is designated as "local," one might pose the following question: How much more (or less) time would be required for each "nonlocal" seed source to grow to the same height as the local source? The answer for selected ages beyond 10 appears in tables 4 and 5. For example, in the two southwestern Arkansas plantations, the nonlocal seed sources grew at a much faster rate than the local source, and this advantage translated into a gain of more than 5 years on a 25-year rotation. Wherever southwestern Arkansas or eastern Texas seed were planted, the slower growth amounted to a time lag of up to 5 or more years on a 25-year rotation.

The results presented here support the general conclusion that, at least for forest management applications, seed source differences in height growth could be incorporated into existing growth and yield models simply by adjusting site index potential without modifying the form of the guide curve. However, for applications of growth and yield models that require more precision, individual guide curves for different seed sources and different sites may be required. We emphasize that these results apply only to seed source differences in site index in plantations relatively undisturbed by destructive agents. The other components of growth and yield models (such as survival functions) might also be affected by seed source.

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A HALF-DIALLEL CROSS AMONG LOBLOLLY PINES SELECTED FOR RESISTANCE TO FUSIFORM RUST

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Abstract.--Fifth-year infection data from progeny tests of seed orchard clones of loblolly pine were used to select 10 clones for further breeding for rust resistance. At age 5, the 45 progenies from a half-diallel cross showed no significant differences in survival but differed significantly in height and highly significantly in percentage of rust-free trees and number of cankers per tree. General combining abilities of the clones were nonsignificant for survival, significant for height, and highly significant for rust traits. Specific combining abilities were nonsignificant for all traits. Heritability was low for survival, moderate for height, and high for rust-resistance traits.

Additional keywords: Pinus taeda, Cronartium quercuum fusiforme, heritability, progeny testing, variation.

Southern fusiform rust (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) has become a major problem in plantations of loblolly pine (*Pinus taeda* L.) in the Southeastern United States (Czabator 1971; Powers and others 1975). No effective cultural practices to control infection and damage by the fungus have been found. The use of planting stock that is genetically resistant to fusiform rust appears to be the only way to handle the problem.

Practical breeding programs were begun a number of years ago concurrently with research on variation in and inheritance of resistance to fusiform rust in loblolly pine. Stonecypher (1966) described a large study conducted in Georgia. Results from that study showed that loblolly pine varies in resistance to fusiform rust (Kinloch and Stonecypher 1969), heritability of resistance is under moderately strong additive control (Blair 1970), and family plus within-family selection should result in considerable improvement in resistance (Blair and Zobel 1971). Progenies from three single crosses among five loblolly pines of known resistance to fusiform rust had greater resistance to infection than did wind-pollinated progenies from the same five trees (Powers and Duncan 1976). Furthermore, there was high correlation between single cross progeny and mid-parent in degree of resistance ($r = 0.98$).

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The clones in the Georgia Forestry Commission's loblolly pine seed orchard were progeny tested for rust resistance and other traits. The clones with above-average rust resistance were determined from the test data and 10 of them were crossed in a half-diallel (no reciprocals or selfs), producing 45 progenies. Based on the amount of information per experimental unit, the partial diallel is the best of four commonly used experimental designs for estimating heritability (Pederson 1972). This is a report of the 5th-year results from the outplanting of that diallel cross.

MATERIALS AND METHODS

The 10 clones used in the study were evaluated on the basis of 5th-year rust data from their progenies in several progeny test plantations located in Bleckley and Houston Counties, Georgia. Progenies of the clones ranged from 39 to 81 percent above their respective plantation means in rust resistance traits (table 1).

The clones were arranged in the half-diallel cross according to flowering phenology (Sluder 1977). Pollinations were made in 1972. Seedlings for the study were grown in peat pots in the greenhouse and field planted in Houston County, Georgia, in June 1974. The field design was randomized blocks, four replications, and 16-tree square plots with a tree spacing of 2.5 by 2.5 meters (8.2 by 8.2 feet). The study included the 45 crosses and three checklots. The checklots were two standard lots and a bulk seed orchard lot.

Progenies were assessed at age 5 for survival, height, number of rust cankers per tree, and the percentage of rust-free trees. Standard randomized block analysis of variance was made for all traits. In addition, diallel analysis was made for all traits according to methods of Griffing (1956) and Becker (1975), with clonal effects assumed to be random (table 2). Heritabilities (h^2) were estimated on family means for survival and percentage of rust-free trees. For height and numbers of rust cankers per tree, heritabilities were estimated on a family mean and on an individual tree basis.[1/]

1/ $h^2_{fam.} = \sigma^2_{GCA} \div (\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_e)$

$h^2_{ind.} = 4\sigma^2_{GCA} \div (\sigma^2_{GCA} + \sigma^2_w + \sigma^2_p)$

σ^2_{GCA} = general combining ability variance

σ^2_{SCA} = specific combining ability variance

σ^2_e = error variance

σ^2_w = within-plot variance

σ^2_p = variance among plots

Table 1.--*Loblolly pine clones used in the study and the superiority of their progenies in rust resistance at age 5 in the original progeny test plantations*[a/]

Clone		Superiority of progeny over plantation mean	
G.F.C. serial number	Tree identification	Percent	SD
518	Coweta 1	39.2	1.13
520	Coweta 3	50.2	3.45
541	Greene 5	71.9	1.51
542	Greene 6	50.9	1.46
566	Heard 15	47.9	1.93
578	Morgan 3	80.5	1.69
582	Morgan 7	80.9	2.34
600	Morgan 57	67.2	1.22
603	Putnam 4	74.1	0.96
617	Sumter 1	75.8	2.79
Mean		63.9	1.85

[a/] Resistance was based on percentage of rust-free trees or on the number of cankers per tree.

Table 2.--*Expected mean squares for the diallel analysis of variance*

Source	df	Expected mean squares[a/]
GCA	9	$0.0211\sigma^2_w + \sigma^2_{sca} + 8\sigma^2_{gca}$
SCA	35	$0.0211\sigma^2_w + \sigma^2_{sca}$
Error	33	$0.0211\sigma^2_w$

[a/] σ^2_w = variance among full sibs within plots; σ^2_{gca} = general combining ability variance; σ^2_{sca} = specific combining ability variance. The coefficient 0.0211 is the reciprocal of the harmonic mean number of full-sibs per cross, 47.45.

Variance components, general and specific combining abilities, and breeding values also were estimated. Confidence limits for combining abilities were calculated by multiplying their standard deviations which were calculated according to Griffing (1956) by the appropriate value from a standard t-distribution table. Genetic correlations between percentage of rust-free trees and number of cankers per tree and between percentage rust-free and height were calculated. Genetic gains in rust resistance with different intensities of selection were estimated.

RESULTS

Randomized Block Analysis

Differences among the 45 diallel progenies were nonsignificant for survival, significant for height, and highly significant for percentage rust-free and number of cankers per tree (table 3).

Table 3.--*Mean squares of randomized block analysis of variance and of diallel analysis of 5th-year data*

Source	df	MS			
		Survival	Height	Rust-free	Cankers/tree
			ANALYSIS OF VARIANCE		
Block	3	996.44**	3.47**	653.00**	72.86**
Progeny	44	253.31	0.20*	659.00**	19.14**
Error	132	220.92	0.12	152.18	3.83
			DIALLEL ANALYSIS		
GCA	9	72.95	0.098*	628.59**	17.35**
SCA	35	60.86	0.037	45.46	1.55
Error	33	55.23	0.031	38.04	0.96

GCA = general combining ability; SCA = specific combining ability.
* Significant at the 0.05 level.
** Significant at the 0.01 level.

Diallel Analysis

Neither general nor specific combining ability variation was significant for survival (table 3). For height, general combining ability (GCA) was significant but specific combining ability (SCA) was nonsignificant. GCA was highly significant both for percentage rust-free and number of cankers per tree, but neither trait exhibited significant variation in SCA.

Estimates of variance components for GCA and SCA and their standard deviations are shown in table 4. For SCA, the standard deviation is greater than the variance component for all traits except number of cankers per tree. For GCA, the standard deviation is greater than the variance component for survival only. Variance components expressed as percentage of total including error indicate that relative GCA variance is low for survival, moderate for height, and high for rust resistance (table 5). Relative SCA variance is low for all traits.

Table 4.--*Variance components for GCA and SCA and their standard deviations*

Variance source	Component	Standard deviation
	SURVIVAL	
GCA	1.5111	4.2714
SCA	5.6259	19.3522
	HEIGHT	
GCA	0.0077	0.0054
SCA	0.0063	0.0113
	PERCENTAGE RUST-FREE	
GCA	72.8911	33.5298
SCA	7.4133	13.9431
	CANKERS PER TREE	
GCA	1.9753	0.9261
SCA	0.5955	0.4271

GCA = general combining ability; SCA = specific combining ability.

Table 5.--*Variance components by trait expressed as percentage of total*

Variance source	Variance component			
	Survival	Height	Rust-free	Cankers/tree
	Percent			
GCA	2.4	17.3	61.6	56.0
SCA	9.0	14.1	6.3	16.9
Error	88.6	68.6	32.1	27.1

GCA = general combining ability; SCA = specific combining ability.

Mean data for the 10 clones are shown in table 6 and their general combining abilities in table 7. Two clones had general combining abilities for survival which exceeded the 0.05 confidence limits even though analysis of variance indicated no significant variation in GCA for that trait. Two or more combining abilities exceeded confidence limits in all instances where analysis of variance indicated significance.

Table 6.--*Fifth-year data means by clone and trait*[a/]

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	*m*	*Percent*	*No.*
617	90.9	3.39	10.9	7.75
518	85.1	3.21	12.6	5.34
541	85.1	3.31	25.4	4.22
600	86.3	3.47	19.3	5.15
603	86.8	3.25	14.2	5.96
520	83.9	3.26	22.8	5.30
542	85.6	3.21	10.1	7.21
578	84.7	3.15	24.2	3.88
566	80.4	3.19	16.1	4.73
582	83.4	3.36	34.8	3.94
Mean	85.2	3.28	19.0	5.35

[a/] Means for the nine crosses involving the clone.

Table 7.--*General combining abilities by trait for the 10 clones*

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	*m*	*Percent*	*No.*
617	6.4*	0.12*	-9.6**	2.70**
518	-0.2	-0.07	-7.2**	-0.01
541	-0.1	0.03	7.2**	-1.27**
600	1.2	0.21**	0.3	-0.22
603	1.7	-0.04	-5.3*	0.68*
520	-1.5	-0.02	4.3*	-0.05
542	0.5	-0.08	-10.0**	2.09**
578	-0.6	-0.14*	5.9**	-1.65**
566	-5.4*	-0.10	-3.4	-0.69*
582	-2.1	0.08	17.8**	-1.58**

* Exceeds the 0.05 confidence limits.
** Exceeds the 0.01 confidence limits.

Combining abilities are expressed as values above or below the diallel mean. Breeding values of the clones, however, are absolute values and can be compared with check means as well as among themselves (table 8). None of the clones showed a serious deficit in survival ability and height growth, in comparison with checks, but clones 518, 542, 603, and 617 proved low in rust resistance at this planting site. Clones 520, 541, 578, 582, and 600 showed good to high rust resistance.

Table 8.--*Breeding values of the 10 clones by trait*

Clone	Trait			
	Survival	Height	Rust-free	Cankers/tree
	Percent	*m*	*Percent*	*No.*
617	98.0	3.52	-0.3	10.7
518	84.9	3.14	4.6	5.3
541	84.9	3.34	33.4	2.8
600	87.6	3.70	19.7	4.9
603	88.7	3.20	8.3	6.7
520	82.3	3.24	27.6	5.2
542	86.2	3.12	-1.1	9.5
578	84.1	3.00	30.7	2.0
566	74.3	3.08	12.4	4.0
582	81.1	3.44	54.6	2.2
Diallel mean	85.2	3.28	19.0	5.3
Check mean	87.5	3.09	6.3	8.7
Percentage gain over check	-3	6	202	64

The correlation between the percentage of superiority of the clone progenies over their respective plantation means (table 1) and the breeding values calculated with the data from this diallel (table 8) was 0.48, non-significant, for the rust-free trait. This is a rather weak agreement between results from the original progeny tests and this diallel cross. The mean breeding value for the 10 clones, however, was 202 percent above the check mean for percentage rust-free, a good indication that some gain in rust resistance has been made.

Heritability was very low for survival in this study, moderate for height, and strong for rust-resistance traits (table 9). For height and cankers per tree, heritability was lower on an individual tree basis than on a family basis.

Phenotypic standard deviation of the traits are also shown in table 9. These values were used to estimate expected genetic gain in rust resistance for various intensities of selection which might be done on these families and individuals (table 10).

The genetic correlation between percentage rust-free and average number of cankers per tree was 0.87. It was 0.30 between percentage rust-free and average height.

Table 9.--*Heritability and phenotypic standard deviation of the traits at age 5 based on family means and individual trees*

Trait	Heritability		Phenotypic SD	
	Family	Individual	Family	Individual
Survival (%)	0.02	--	7.90	--
Height (m)	0.17	0.09	0.21	0.58
Rust-free (%)	0.62	--	10.89	--
Cankers/tree (No.)	0.56	0.26	1.88	5.53

Table 10.--*Expected genetic gain in rust resistance for six intensities of selection*

Selection intensity	Upper percentage	Trait gain		Percent of mean	
		Family	Individual	Family	Indiyidual
		PERCENTAGE RUST-FREE			
1.16	30	7.83	--	41.2	--
1.40	20	9.45	--	49.7	--
1.76	10	11.88	--	62.5	--
2.06	5	13.91	--	73.2	--
2.42	2	16.33	--	85.9	--
2.64	1	17.82	--	93.8	--
		CANKERS PER TREE			
1.16	30	-1.22	-1.67	-22.8	-31.2
1.40	20	-1.47	-2.01	-27.5	-37.6
1.76	10	-1.85	-2.53	-34.6	-47.3
2.06	5	-2.17	-2.96	-40.6	-55.3
2.42	2	-2.55	-3.48	-47.8	-65.0
2.64	1	-2.78	-3.80	-52.0	-71.1

DISCUSSION

Statistical significance in GCA and nonsignificance in SCA in this study indicate that variation in rust resistance among these clones is largely additive and standard selection procedures should be effective in producing gains in rust resistance. The high genetic correlation between percentage rust-free and number of cankers per tree indicates that either measure of rust resistance can be successfully used for selection purposes. The low genetic correlation between percentage rust-free and height indicates that both traits can be improved with little if any correlated response of one to the other.

The average breeding value of 19 percent rust-free for the 10 parents in this diallel does not reflect a level of rust resistance high enough to meet the needs for central Georgia. One generation of selection was not enough, but these study results show that further gains in rust resistance can be made in subsequent generations of selection and progeny testing.

For example, selecting the best 30 percent of these families will result in a gain in percentage rust-free of 41 percent of the mean (Table 10). In terms of cankers per tree, the same selection intensity for families will produce a 23 percent gain, with another 65 percent gain possible by selecting the best 2 percent of individuals within the selected families. These gains are similar to predicted gains reported by Blair and Zobel (1971).

There are two possible sources of inaccuracy in predicting gains with data from this study. One is that the clones do not represent a completely random population. They are a sample of clones which on the average have a degree of rust resistance somewhat above the general population mean. I have assumed, however, that variances have not been significantly altered by the degree of selection already effected. Another possible source of inaccuracy is that only one test site was used. This can lead to a genotype x environment interaction component in the numerator of the heritability equation (Namkoong and others 1966). However, the block x family interaction was not significant on this site for number of cankers per tree even though there were highly significant differences among the block means for the trait. Infection levels differed among the blocks, indicating differences in inoculum level. Therefore, differences in inoculum level among test sites probably would cause little if any nonadditive genetic variance in the heritability numerator but differences among locations in genotype of the fungus might (Snow and Kais 1970; Powers and others 1977).

CONCLUSIONS

Ten loblolly pine clones with above-average resistance to fusiform rust were crossed in a half diallel. At age 5, the 45 progenies from the half-diallel cross showed no significant differences in survival but differed significantly in height and highly significantly in percentage of rust-free trees and number of cankers per tree. General combining abilities and heritability of the 10 clones were high or highly significant for rust-resistance traits. Selection among and within these or similar progenies coupled with further breeding should produce large gains in resistance to southern fusiform rust.

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STABILITY OF FIELD RESISTANT SLASH PINE TO SELECTED ISOLATES OF FUSIFORM RUST FUNGUS

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Abstract.--In a series of 6 experiments, 22 open-pollinated families of field resistant slash pine and 6 full-sib families were tested for their reaction to isolates of fusiform rust. There was a greater range and more differences for percent rust infection among pine families than among rust isolates. The coefficient of variation ranged from 13 to 69 percent for the 22 families. The degree of variation was not related to the relative susceptibility. The family x isolate interaction was significant in all six experiments. In tree improvement, rather than determining specific rust isolates-pine family reactions, rust resistance breeding should concentrate on crossing individuals selected for moderate to high resistance to many individual or composite isolates of the rust fungus.

Additional keywords: *Pinus elliottii*, G x E interaction.

From the standpoint of genetic improvement, there is a need to better understand fusiform rust (caused by *Cronartium quercuum* [Berk.] Miyabe ex Shirai f. sp. *fusiforme*) resistance that exists in slash pine (*Pinus elliottii* Engelm. var. *elliottii*). Although there is no evidence of provenance variation for rust resistance (Goddard and Wells 1977), individual resistant trees throughout the range have been identified. In selecting resistant trees, there have been problems in getting consistent responses in field and greenhouse tests. The pollen mix in the orchard (Powers and Zobel 1978), the geographic location of the test (Goddard and Schmidt 1979), and the fungal isolate used for greenhouse inoculations (Snow et al. 1976) have been identified as being responsible for inconsistent results. Family x location and family x fungal isolate interactions reported for slash and loblolly pine (*P. taeda* L.) suggest that in selection of rust resistant trees, many factors must be considered (Powers et al. 1978).

In this greenhouse study, our objective was to characterize the resistance of 22 open-pollinated slash pine families and several full-sib families for their reaction to naturally occurring rust isolates. On the basis of percent infection and stability of the pine families, breeding implications are discussed.

MATERIALS AND METHODS

Seed was collected from 22 open-pollinated slash pine trees already selected and recognized by industries and the U.S. Forest Service as being rust resistant when they were progeny tested under field conditions. Most

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seed came from operational seed orchards where there had been little, if any, roguing for rust resistance. Since all these trees were not included in the same progeny test, we calculated a field performance rating according to the method of Walkinshaw et al. (1980) to compare families. In this rating, higher values indicate greater resistance.

Nine fungal isolates from slash pine in Louisiana, Mississippi, and Florida were selected for this study. The selected isolates varied from weak to strong in their ability to infect slash pine (Walkinshaw and Bey in press).

Aeciospores were collected from individual stem galls, stored according to the methods of Roncadori and Matthews (1966), and later used to produce telia and basidiospores on susceptible water oak (Quercus nigra L.). Density of 11-16 basidiospores/mm^2 was maintained with a forced-air apparatus (Snow and Kais 1972) by varying exposure time from 2.5-8 seconds and holding air flow to 3-5 standard liters per minute.

In the six experiments, eight families were tested each year from 1978 through 1980, with family 18-15 common to all experiments. In a split plot design, isolates were whole plots and families were subplots. The nine rust isolates were divided into two groups. Five were used in each inoculation, with isolate MS-15 common to all. Three replications per experiment (except two in experiment 2) were completed in 8 days. Each day we inoculated all pine families with one isolate before proceeding to the next. One seedling from each family was inoculated, and the process was repeated until all 12 seedlings for each family were completed. The 12 trees per family per isolate were considered the experimental unit.

In an adjunct to the main study, the same inoculation procedure was used for seven open-pollinated and six full-sib families, with a weak (MS-15) and a strong (LA-7) isolate.

Gall incidence was recorded at 6 or 9 months and converted to arc sine $\sqrt{\text{percent}}$ for use in analysis of variance (ANOVA).

RESULTS

The percent of seedlings with galls for pine family-fungal isolate combinations ranged from 0 to 100 percent with an overall average of 59 percent. The averages for families over 9 isolates ranged from 27 to 84 percent while isolate means for the 22 families ranged from 47 to 68 percent (tables 1 and 2). The high infection rates in greenhouse tests do not detract from the high field performance for these field resistant families. During the inoculation and in the growth chamber and greenhouse, the environmental conditions were kept near optimum for the fungus, not like normal field conditions. When we used the rust evaluation index recently developed by Walkinshaw et al. (1980) all families were classified as being field resistant (table 2).

Table 1.--Percentage galled slash pine seedlings listed by isolate of rust used in the greenhouse inoculations

Expt. No.	Rust isolate					Expt. No.	Rust isolate				
	MS-15	MS-4	LA-8-7	LA-1	FL-4		MS-15	LA-6	MS-10	FL-3	LA-7
1	50a[1/]	51a	62a	64a	70a	2	52a	53a	59a	63ab	78b
3	49ab	44a	68ab	66ab	74b	4	45a	57a	49a	57a	46a
5	50ab	46a	65b	61ab	60ab	6	57a	59a	61a	76a	64a
Isolate mean	50	47	65	64	68		51	56	56	65	63
Rank corr.[2/]	.72	.58	.43	.78	.79		.61	.66	.77	.70	.79

1/ Means within the same experiment separated by the same letter are not significantly different at the .05 level.

2/ Spearman rank correlation. Values show how well the individual rust isolates ranked the pine families compared to the overall pine family rankings. All values significant at .05 level.

There were significant differences among families in five of the six experiments (table 3). Within experiments, the family means for percent galled ranged from 25 percent for LA-11 to 92 percent for A-31. For statistical significance, family means generally had to be separated by at least 20 percent to be different. For most experiments, this separated only families with the lowest and highest infection rates. The level of infection for families was dependent on the fungal isolate, but in general five isolates seemed to adequately rank families and provide a reliable average for percent of seedlings infected. Families that were best with the first set of isolates generally were best with the second set. The generally uniform results in all six experiments of common isolate MS-15 on common family 18-55 adds further reliability to tests with a small number of fungal isolates.

Compared with pine family differences, there were relatively few differences among isolates. There were statistically significant isolate differences in three (2, 3, and 5) of the six experiments. In general, isolate means had to be separated by 20 percent or more to be statistically different. Means for isolates on eight families (within experiments) ranged from 44 to 78 percent, considerably less than the wide range for means for the pine families. The five isolates maintained their relative ranking from experiment to experiment (1 versus 3 versus 5 and 2 versus 4 versus 6). Isolates MS-15, MS-4, and LA-6 tended to be low while LA-1, FL-4, FL-3, and LA-7 tended to be high. Isolate LA-8-7, known to be highly virulent on progeny of pine parent 8-7 (Snow et al. 1976), was intermediate in this test. Some of the other isolates were just as virulent as LA-8-7 on pine family 8-7.

Table 2.--Percent galled, predicted field performance and corresponding coefficient of variation for 22 pine families. Values are based on plot means over two experiments

Pine family	Expt. no.	Percent galled		Rank correlation [1]	Rust evaluation index [2]		Pine family	Expt. no.	Percent galled		Rank correlation [1]	Rust evaluation index [2]	
		Mean	CV		Mean	CV			Mean	CV		Mean	CV
LA-11	5,6	27	66	NS	16.7	19	J-17	3,4	63	31	.71	7.4	48
J-1-5	3,4	42	56	NS	11.9	31	FA-7	3,4	64	34	NS	6.8	48
18-55	3,4	43	31	NS	12.0	23	35-55	3,4	65	30	NS	7.9	31
M-707	1,2	43	31	-.71	15.4	15	316-56	5,6	68	28	.45	9.2	36
24-54	3,4	44	33	.47	12.2	21	36-55	3,4	69	27	NS	7.1	41
179-55	5,6	45	39	NS	13.6	23	J-10	5,6	70	29	NS	7.3	53
18-55	1,2	46	43	-.38	13.9	22	H-7	1,2	70	34	NS	8.7	36
71-58	1,2	47	47	NS	13.4	20	PR-1	5,6	71	36	NS	8.7	60
18-55	5,6	50	31	-.35	12.6	19	A-31	5,6	71	34	NS	7.1	52
H-28	3,4	54	63	.71	12.2	63	7-55	5,6	78	29	NS	6.4	72
8-7	1,2	55	69	.39	12.3	63	FA-2	1,2	80	20	NS	7.1	40
18-27	1,2	59	28	NS	11.7	28	A-20	1,2	84	13	NS	7.1	23

[1] Spearman rank correlation. Values show how well the individual pine families ranked the isolates compared to the overall rust isolate rankings. All values shown are significant at the .05 level.

[2] From Walkinshaw et al. 1980. High resistance is associated with seedlings showing initial purple spot symptoms but few developing galls that are fat or smooth. With the forced-air system used in this study there were more seedlings with initial symptoms and no swelling than in the controlled basidiospore suspension system used at the Resistance Screening Center where the rust evaluation index was developed.

Table 3.--Mean squares from analysis of variance for infection of slash pine by rust isolate [1/]

	Df	Experiment number					
		1	2	3	4	5	6
Replications (days)	2	64	281	12	204	78	611
Isolates	4	1184^{NS}	1061*	2224*	486^{NS}	821*	698^{NS}
Error a (RxI)	8	27	188	159	78	112	176
Families	7	2117*	1202*	1097^{NS}	865*	1795*	3817*
Family x isolate (FxI)	28	667*	295*	581*	333*	283*	614*
Error b	70	134	111	92	89	148	89

[1/] *Denotes significance at .05 level. The FxI mean square was used for testing family and isolate main effects. Degrees of freedom for experiment 2 with only two replications were 1, 4, 4, 7, 28, and 35 accordingly.

The family x isolate interaction was significant in all six experiments. In every experiment, certain family-isolate combinations stand out against the general trends. For example, in experiment 1 isolate LA-1 was generally virulent, but not on family M-707, while isolates MS-15 and MS-4 were disproportionately weak on family 8-7. In experiment 6, MS-15 was unusually high (100 percent) on family 7-55, while isolate LA-6 was unusually low (14 percent). Such interaction might be responsible for some of the family x location interaction reported in field tests (Goddard and Schmidt 1979). As in field tests, certain families in these experiments possessed high resistance levels to most isolates.

The coefficient of variation (CV) is a measure of family stability to the nine rust isolates. It measures differences due to scale effects but not isolate rank changes. For the 22 families, the CV's ranged from 13 to 69 percent. The most variable families had low to moderate average infection rates. The slash pines in these experiments exhibited a wide diversity in average level of infection and in variation to the nine isolates (table 2). There were degrees from low infection and low variability to high infection and high variability. The CV's were computed across the experiments using plot means, and therefore include isolate differences, between experiment differences, and plot-to-plot within experiment differences. Accordingly, the values were unusually high.

In addition to the pine family differences for percent infection and coefficients of variation, there were differences among pine families in the way they ranked the isolates (table 2). For a comparison of individual families, we used as a standard the isolate rankings over all families. Using Spearman rank correlations, 16 out of 22 families did not rank the isolates

according to their overall rank. Only five families had a significant positive rank correlation, and one had a significant negative correlation. There was no relationship between the families with significant correlations and percent galled or the CV.

In contrast to the general lack of individual families correctly ranking the isolates, the individual isolates all ranked the pine families about equally (table 1). The rank correlations for isolates varied from 0.43 to 0.79 and were all significant.

DISCUSSION

In terms of breeding strategy, this is a "good news" paper. The range of average infection of families was much greater than for the range of average infection of isolates. Some of the highly resistant families had high CV's, but when expressed for predicted field performance values, the CV's for the highly resistant families were substantially reduced and the CV's for the more susceptible families were increased (table 2). Statistically, this suggests that in the development of the predictive equation, there was less variation in ratings for the resistant families than for the more susceptible ones. Biologically, it appears that high resistance and low variability may occur more frequently in the field than in these greenhouse tests. Perhaps trees with galls in the more resistant families are more likely to recover than trees with galls in the more susceptible families.

Preliminary results from the adjunct inoculations to the main study and results from another study (Griggs and Walkinshaw 1981) suggest that it is unnecessary to know specific family x isolate responses to make additional gains through crossing. Griggs and Walkinshaw have shown that general combining ability for percent infection is high. In this study, infection rates for the control-cross progeny were always lower than the average infection rate of the two wind-pollinated parents (table 4). The same relationship was noted for other families by Griggs and Walkinshaw. It appears that there are many host genes that control resistance for each rust isolate, and that they may be different in different pine families.

Table 4.--Percent infection for open- and control-pollinated progeny for fungal isolates MS-15 and LA-7

Open-pollinated pine family	Fungal isolate MS-15	LA-7	Control-pollinated pine family	Fungal isolate MS-15	LA-7
8-7	8	71	8-7 x 7-55	21	71
18-27	44	87	8-7 x 35-55	15	41
18-62	96	88	18-27 x 18-62	63	79
9-2	46	--	18-27 x 9-2	33	69
7-55	86	92	18-27 x 7-55	58	79
9-55	75	--	18-27 x 9-55	46	63
35-55	75	36			

For pine breeding, it is important to develop resistance to a wide variety of rust isolates. But since the exact isolates that will be encountered in the field are unknown, screening to match the host to the pathogen will be impossible. More important than determining the specific rust isolate-individual family reactions is the need to select for moderate to high resistance over many individual or composite isolates. From the standpoint of improvement for resistance, the breeding scheme among the resistant clones or families is probably not critical. However, crossing of many such resistant parents and planting mixtures of progeny from these crosses should be done to provide an ample buffer against the array of fungal isolates in the field.

Although we did not test for buildup of virulent isolates nor for erosion of resistance, these will not likely be serious problems in tree improvement programs. Snow et al. (1976) list five factors that will moderate the rate of increase of virulent strains. Although this study shows that many naturally occurring isolates can infect all "resistant" pine families, the situation in the field is far more complex. Where mixtures of pine families are used, infection of "resistant" families in plantations will likely take place from many isolates in the fungal population on slash and loblolly pine in the area. This is supported from a slash pine test (Snow and Griggs 1980) which showed that inocula from infected individual resistant families were neither consistently virulent on these families nor on seedlings grown from commercial seed.

In summary, the balance seems to be tipped in favor of the tree breeder and the trees. The potential for selection of resistant pine families is large, a procedure for identifying resistant families is available, and a breeding system for making gains appears to be reasonably straightforward.

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SCREENING FOR FUSIFORM RUST RESISTANCE IN LOBLOLLY PINE: A COMPARISON OF ARTIFICIAL INOCULATION WITH FIVE YEARS FIELD PERFORMANCE

by

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Seedlings of seven half-sib families of loblolly pine were inoculated at 6 weeks with basidiospores of Cronartium quercuum f. sp. fusiforme from two geographic sources using the Concentrated Basidiospore System (CBS) and examined for gall development after 9 months. Uninoculated, fourteen-month-old seedlings of the same seven families were outplanted in a high-hazard rust area of central Georgia and examined for fusiform rust incidence after five years.

The family rankings based on the percentage of seedlings infected following the two methods of evaluation were essentially the same.

	Artificial Inoculation		Outplanted	
Family	% galls after 9 months	Ranking	% galls after 5 years	Ranking
10-5	45	1	46	1
10-25	64	2	55	2
7-56	75	3	55	2
10-8	77	4	80	5
5-33	78	5	66	4
12-12	79	6	84	6
12-9	84	7	85	7

In this test, the CBS system not only identified the most resistant and most susceptible families but also accurately ranked the intermediate families that have traditionally been more variable in previous tests.

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BREEDING STRATEGY FOR E. ROBUSTA IN SOUTHERN FLORIDA

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Abstract.--Eucalyptus robusta Sm. has undergone two cycles of improvement in southern Florida. In the first cycle, mass selection produced the following realized gains at 4.5 years: height 20%; diameter 6%; and volume 17%. In the second cycle, family plus within family selection produced the following realized gains at 2.6 years: height 40%; diameter 37%; and volume 91%. Combined gains for both cycles indicated the following improvements: cold hardiness 19%; height 27%; diameter 33%; volume 63%; branch size and angle 14%; and stem straightness 9%. Introductions from natural stands in Australia proved to be vastly superior, especially in cold hardiness, to material obtained from naturalized stands in Florida. Future gene pool enrichment efforts in the E. robusta program will place emphasis on Australian collections. Sib analysis estimates of heritability were higher than realized heritability values for the traits assessed in the second and third generation based populations. Generally poor agreement between sib analysis estimates and realized heritability values suggests caution must be exercised in using these estimates of heritability in genetic gain prediction formulas for E. robusta in southern Florida.

Additional Keywords: Mass selection, combined (family plus within family) selection, realized gain, sib analysis, coefficient of relationship.

INTRODUCTION

The Eucalyptus robusta Sm. breeding program has undergone two cycles of improvement in southern Florida. A seedling seed orchard-progeny trial approach was used to provide improved seed to commercial nurseries in the shortest time. Mass selection was used in the first cycle of improvement. As family information was available for the second cycle, the mass selection strategy changed to a combination of family plus within family selection. The objective of this study was to determine the efficacy of the two selection methods for eucalyptus breeding programs. Realized gains were calculated on a per cycle basis and for both cycles combined. Predicted and realized gains were compared to determine the reliability of forecasted gains.

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ESTABLISHMENT OF BASE POPULATIONS

The two cycles of improvement in southern Florida result from the establishment of three generations of genetic base populations summarized below.

First generation: Immokalee

In 1961, the Florida Forests Foundation established a species screening trial near Immokalee, Florida. The trial included 7 eucalyptus species represented by 40 seed sources, 9 of which were E. robusta. Measurement at age 4.5 years showed that E. robusta offered the best combination of local adaptability, commercial growth rate and acceptable stem form expressed in a sufficient number of seed sources to provide reasonable breadth in a genetic base population.

In 1966, 119 E. robusta trees were mass-selected (from 2,304 originally planted) based on phenotypic superiority to their neighbors in the seed source plots. Selection traits were stem volume, stem straightness and branch habit. All nine seed sources of E. robusta contributed at least one select, but the better seed sources contributed most of the selects. All nonselect trees were rogued to convert the Immokalee site to a pollen-isolated, first-generation genetic base population and seed production area for E. robusta.

Second generation: Burgess

Only 57 of the Immokalee selects bore sufficient seed to contribute progeny families to the second-generation base population and progeny test planted in 1967 at the Burgess site. The Burgess planting also included five of the originally imported seedlots planted at Immokalee, which came to be referred to as "ancestral" seed sources. Two newly imported seedlots were also included at Burgess, bringing the base population to 57 families and 7 seed sources represented by 6,275 seedlings.

Based on freeze damage scores at 3.5 years and measurements at 4.25 years, 94 trees were selected from 39 families with no more than 4 selections in any family. Selection criteria combined individual and family values for wood production, stem straightness, branch habit, and cold hardiness. All nonselect trees were rogued to convert Burgess to a seedling-seed orchard.

Third generation: R-POP

Eighty-four selected trees at Burgess bore sufficient amount of seeds to be represented in the 1975 base population known as R-POP. Thirty-seven second-generation families, principally from Immokalee select trees that had not produced seed in time for the Burgess planting, but also offspring of phenotypically superior trees in other research plots of known origin, were also included in the R-POP seedling-seed orchard progeny study.

To broaden the E. robusta genetic base which was being narrowed by selection, seeds from 98 parent trees in natural stands in Australia and 105 parent trees from naturalized stands in central and south Florida were also included in the

R-POP study. It was hoped that the new genetic combinations from outcrosses with this naturalized material would be well adapted to the mosaic of microsites present in southern Florida. The Florida naturalized stands arose from E. robusta sources of unknown origin established around old homestead sites as amenity plantings as early as the turn of the century (Franklin and Meskimen, 1973). In addition to the 203 Australian and Florida families, 23 entries, consisting of E. robusta families from Hawaii and bulk collections from various regions around the world, and the 5 ancestral seedlots were included in the R-POP seedling seed orchard-progeny trial (Table 1, Figure 1).

METHODS

Realized gains were calculated on a per cycle basis from Immokalee to Burgess (first to second generation) and Burgess to R-POP (second to third generation). Realized heritability was calculated for selections at Immokalee and at Burgess. Realized gain, expressed as a percentage of the mean of the previous generation was calculated by:

$$\frac{\text{Response to selection}}{\text{Mean of parental population}} \times 100 \qquad (1)$$

Realized heritability was calculated by:

$$\frac{\text{Response to selection}}{\text{Selection differential}} \qquad (2)$$

Response to selection and the selection differential were standardized to adjust for different population variances and for environmental differences at the two sites. These calculations are detailed elsewhere (Franklin and Meskimen, 1973).

Estimates of narrow sense heritability were calculated from sib analyses (see Falconer, 1960). Analyses of variance from single-tree plot experiments at both Burgess and R-POP were conducted using the NESTED procedure of the Statistical Analysis System (SAS)®. Estimates of heritability were calculated from:

$$h^2 = \frac{3\,\sigma^2 f}{\sigma^2 P} \qquad (3)$$

where h^2 = narrow sense heritability

$\sigma^2 f$ = family component of variance of open-pollinated families

$\sigma^2 P$ = phenotypic variance on an individual basis

The coefficient of relationship among open-pollinated families is .25 if every offspring of a half-sib family is the result of the mating between a common female and different, unrelated males. This value probably underestimates the true coefficient of relationship since some offspring are likely to have a

Table 1.--Summary of information from genetic base populations of E. robusta in southern Florida.

Trial Name	Established	Location	Design	Spacing	Type of Selection
Immokalee	1961	Collier Co.	randomized complete block; 4 blocks of 64-tree plots	2.4m x 1.8m	Mass
Burgess	1967	Charlotte Co.	completely random single-tree plots; average 98 trees per family	3.6m x 1.8m	Family & within family
R-POP	1975	Glades Co.	completely random single-tree plots; average 69 trees per family	3.0m x 1.8m	

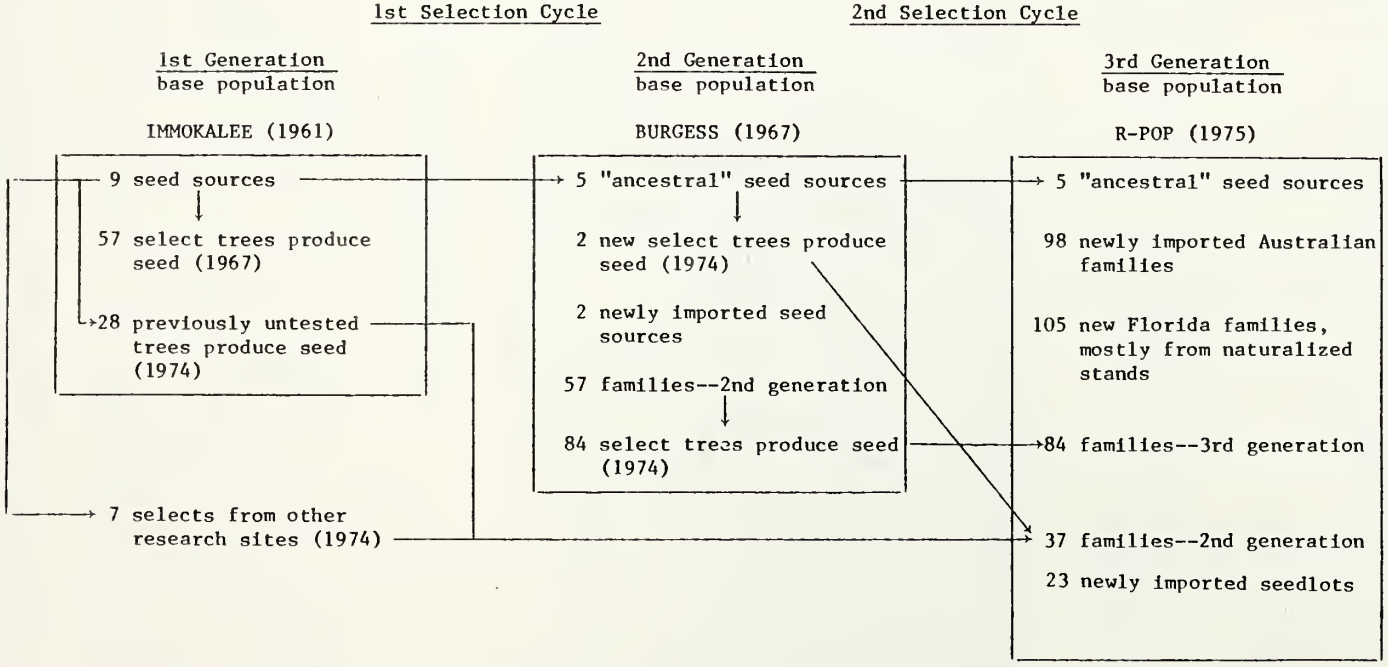

Figure 1.--Schematic diagram of two cycles of improvement for E. robusta in southern Florida.

common male parent and thus be related as full-sibs. The coefficient of relationship among full-sibs is .5. Based on these considerations, we chose to multiply the numerator by 3 (coefficient of relationship of .33) rather than 4 (coefficient of relationship of .25) because it assumes that some progenies are half-sibs and some are full-sibs (Squillace, 1974). The coefficient of relationship would also be inflated if male parents are related to the female parent.

Material at different levels of genetic advancement was included at R-POP. Realized gains were calculated for two cycles combined (Immokalee to Burgess to R-POP) from data collected at R-POP. The success of introducing material from Australia and Florida could also be quantified and compared. The common base to which all comparisons were made was the five ancestral seed sources. These ancestral seed sources consisted of three lots of bulk seed from Australia, one from Morocco and one from Zaire. Realized gains calculated from data collected only at R-POP were expressed as a percentage of the mean of the ancestral seed sources as follows:

$$\frac{\text{Mean of Population}}{\text{Mean of 5 ancestral seed sources}} \qquad (4)$$

RESULTS AND DISCUSSION

Realized gains for E. robusta for the first cycle of improvement (Immokalee to Burgess) were height 20%; diameter 6%; and volume 17% (Table 2). These values are similar in magnitude to the realized gains obtained in tests from rogued first generation seed orchards in the North Carolina State University-Industry loblolly pine tree improvement program (Weir, 1975). Realized gains for the second cycle (Burgess to R-POP) were height 40%; diameter 37% and volume 91% (Table 2). At least two factors contribute to more genetic gain in the second cycle than in the first. First, combined selection utilizes genetic information from sib analysis but mass selection relies only on phenotypic performance of candidates. Second, outcrossing of relatively inbred individuals between seed sources was enhanced by the completely randomized single-tree plot design at Burgess. This may have resulted in hybrid vigor in the offspring.

Table 2.--Realized percentage gains of E. robusta by cycles of improvement in southern Florida.

	Trait		
	Height	Diameter	Volume
1st cycle (Immokalee - Burgess)[a/]	20	6	17
2nd cycle (Burgess - R-POP)[b/]	40	37	91

[a/] expressed as the percentage of the mean of the Immokalee population and based on data from 40 open-pollinated families measured at 4.5 years.

[b/] expressed as the percentage of the mean of the Burgess population and based on data from 76 open-pollinated families measured at 2.5 years.

Reliable estimates of genetic gain depend on accurate estimates of heritability. Estimates of heritability using sib analysis were higher than realized heritability values for all traits assessed (Table 3).

Table 3.--Comparison of estimated heritability and realized heritability for 2 cycles of E. robusta improvement in southern Florida.

	Second Generation Base Population		Third Generation Base Population	
	Burgess[a/]		R-POP[b/]	
	Sib Analysis	Realized h^2	Sib Analysis	Realized h^2
Height	.46	.38	.38	.34
Diameter	.50	.09	.39	.24
Volume	.42	.08	.23	.11

a/ based on data from 40 open-pollinated families at 4.5 years of age.

b/ based on data from 76 open-pollinated families at 2.5 years of age.

Results indicate that caution must be exercised in using sib analysis estimates of heritability from E. robusta trials in southern Florida to predict genetic gains for future generations. This seems especially true for predictions of genetic gain for volume.

Realized gains calculated for material at different levels of genetic advancement at R-POP are presented in Table 4. Genetic material which had undergone two cycles of improvement in southern Florida showed sizable gains for height, 27%; diameter, 33%; and volume, 63%; at 2.6 years (Table 4). Realized gains estimated on a per cycle basis (Table 2) are different from those estimated for both cycles together (Table 4) because the reference base population used in making the calculations are different.

Table 4.--Performance of advanced generation and introduced material at R-POP 75. (Expressed as a percentage of increase or decrease of population means to mean of the ancestral seed source.)

Degree of genetic advancement	Cold Hardiness	Height	DBH	Volume	Branch Habit	Stem Straightness
Generation 3 (Immokalee - Burgess - R-POP	+19	+27	+33	+63	+14	+9
Introduced Material						
Australia (natural stands)	+24	+11	+20	+26	+8	0
Florida (natural stands)	-15	-4	-8	-13	-2	-3

Australian introductions were superior to Florida collections in all traits measured. The results suggest that future efforts to expand the genetic base of the E. robusta populations in southern Florida should concentrate on acquiring

new genetic material in Australia, not in Florida. Single-tree collections from good sources within the native range of a species may provide the best possible source of material for other hardwood breeding programs. Seed should be kept separate by individual trees in provenance trials so that provenance variation can be closely examined and selections of known pedigree can be made for advanced-generation programs.

Families obtained from Florida naturalized stands performed poorly. Florida naturalized areas are small in size and have originated from only one or a few parent trees of unknown origin. Selfing probably occurred which might have reduced the level of progeny performance.

SUMMARY

Relatively few results have been published on realized gains in hardwood programs in the United States. Results from the E. robusta program indicate that this exotic hardwood is extremely responsive to genetic manipulation. Mass selection resulted in moderate gains in volume for the first cycle of improvement in southern Florida. Combined (family plus within family) selection produced much greater percentage gains in volume in the second cycle. Progenies of trees from good sources of E. robusta in natural stands in Australia outperformed progenies of selections made in Florida naturalized stands. Estimates of heritability from sib analyses should be used with caution when predicting genetic gains for future generations of E. robusta in southern Florida.

The seedling seed orchard-progeny trial breeding strategy was effective in the E. robusta program. Tree improvement programs for other hardwood species should consider using the seedling seed orchard-progeny trial approach.

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GENETIC VARIATION, HERITABILITIES, AND SELECTION STRATEGIES FOR EARLY GROWTH OF SYCAMORE IN THE GULF SOUTH

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Abstract.--Open pollinated progenies from 160 trees representing 16 geographic seed sources in the Gulf South were planted in each of two years at each of four sites in Mississippi. Three years after outplanting, progenies from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana had the greatest stem volume. There were source-by-site interactions, but sources from south of the planting site and near the Mississippi River were usually better than sources from north of the site. Source-by-planting-year interactions were still present for root collar diameter and height after three years in the field, but had disappeared for stem volume by that time. Early screening trials of seed source variation should be repeated over both sites and planting years to avoid errors caused by these interactions. There was no variation among local stands within sources, but variation among families from trees within a stand was significant for all traits. Narrow-sense heritabilities on an individual-tree basis were low (.03 to .17). On a family-mean basis these heritabilities were ten times larger (.29 to .74). Heavy emphasis should be placed on progeny testing in a clonal seed orchard program. Gains from seedling orchards will not exceed those from clonal orchards, except when family selection intensity is low and mass selection intensity within families is high. Genetic correlations between traits measured at different ages were positive and increased as the difference between the ages decreased. However, the added number of trees that must be tested to get comparable gains from early selection as from direct selection may make the savings in time unjustifiable.

Additional keywords: Genetic correlations, genetic gains, Platanus occidentalis.

The rapid juvenile growth and relative ease of artificial regeneration of American sycamore (Platanus occidentalis L.) make it a prime candidate among southern hardwoods for short rotation energy and pulpwood plantations. Genetic improvement for early growth rate would increase productivity and returns from investments in these plantations. Information is presented here on genetic variation, heritabilities, genetic and phenotypic correlations, and selection strategies for stem size and volume at ages one, two, and four years from seed for trees from the Gulf South region of the United States.

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MATERIALS AND METHODS

Open-pollinated progenies of five trees within each of two stands at each of 16 geographic seed source locations in Mississippi, western Alabama, eastern Louisiana, and eastern Arkansas were planted in each of two years (1975 and 1976) at each of four sites in Mississippi (Figure 1). The seed sources were chosen to represent four latitudinal transects (30°45'N, 32°00'N, 33°15'N, and 34°30'N). There were four sources per transect, with one of the four coming from the banks of the Mississippi River and one from the Tombigbee River (along the Mississippi-Alabama border). Planting site #1 is located on an agricultural field site in the Upper Southern Coastal Plain (Soil Conservation Service et al. 1971) in Tishomingo County, Mississippi. The second site is found on an agricultural field site in the Interior Flatwoods section of the Southern Coastal Plain in Oktibbeha County. Site #3 in Jasper County is located in the Lower Southern Coastal Plain, and it was a forested upland pine site that was cleared and site prepared for planting. The fourth site is in the alluvial plain of the Mississippi River in Issaquena County, and it was a forested bottomland hardwood site that was cleared and site prepared.

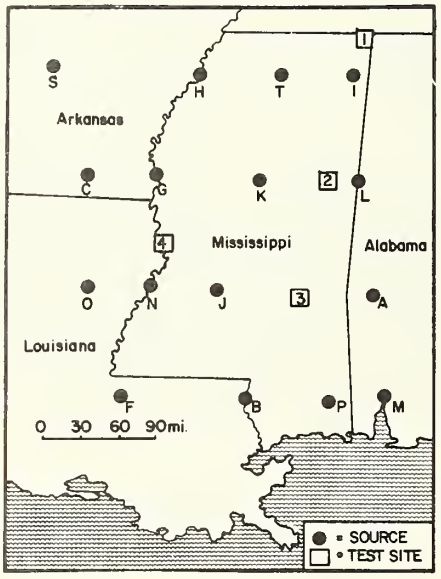

Figure 1.--Locations of seed sources and planting sites used for a provenance-progeny test of sycamore in the Gulf South

Seedlings of the 160 progeny families were grown for one year in a randomized complete block design with three replications at a state nursery in central Mississippi. Nursery bed density was controlled at approximately six seedlings per square foot by thinning. The same nursery procedures were used for each of the two years in which the study was repeated.

The 1-0 nursery seedlings were outplanted at the four sites in a series of split-plot experiments containing six replications and repeated in both space and time. Three-seedling family plots were used, and all families of a seed source were arranged together into compact family blocks within a replication. The three nursery replications were split, so that nursery

replication one provided seedlings for field replications one and two at each site, nursery replication two provided field replications three and four, etc.

Root collar diameters and tree heights were measured at the time of lifting the seedlings from the nursery (tree age one), one year after outplanting at the four sites (tree age two), and three years after outplanting (tree age four). Stem volume at age four was determined from root collar diameter, DBH, and height by treating the bottom 4.5 feet of the stem as the frustrum of a cone and the remaining top of the stem as a cone.

Analyses of variance and covariance had the form given in Table 1. Variance and covariance components were calculated by equating estimated with expected mean squares. The composition of the genetic and phenotypic variances (or covariances) from the variance and covariance components is shown at the bottom of the table. Estimates of narrow-sense heritabilities and genetic and phenotypic correlations were calculated from these genetic and phenotypic variances and covariances (Namkoong et al. 1966, Becker 1975). Standard deviations of estimates were derived by procedures outlined in Gordon et al. (1972) and Becker (1975).

RESULTS AND DISCUSSION

Survival after three growing seasons in the field was 98 percent over all sites and planting years. Trees at this age averaged 2.7 inches in root collar diameter, 15.2 feet in height, and 0.225 cubic feet in stem volume. At the time of lifting from the nursery these trees had a mean height of 3.1 feet and a mean root-collar code of 2.25 (code 1 = less than ¼ inch diameter, code 2 = ¼ to ½ inch, code 3 = ½ to 3/4 inch, and code 4 = greater than 3/4 inch diameter). The average root collar diameter and height at one year after outplanting was 0.8 inches and 4.0 feet, respectively.

Effects of Planting Years and Sites

Seedlings for the 1976 planting year were 20 percent larger than those for 1975. These size differences persisted through one growing season at the field sites, but disappeared after three growing seasons. Since the nursery site and nursery bed density were the same in both years, the year differences in seeding size were probably related to weather conditions during the nursery growing season.

At outplanting, seedlings from a family plot in the nursery were sorted to give the same initial average size for that family at all planting sites. Site differences in tree size increased with time following outplanting. After three field growing seasons, trees at site #4 near the Mississippi River were nearly four times larger in stem volume than the average for the other three sites. Obviously, the first step in an improvement program for short rotation sycamore plantations is site selection. Here, production was best on somewhat poorly drained to moderately well drained silt loam soils in an alluvial floodplain, which is characteristic of most major rivers in the Gulf South.

Effects of Seed Sources and Source x Environment Interactions

Trees from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana contained 24 percent more stem volume at age four

Table 1.--Composition of expected mean squares, genetic variance, and phenotypic variance for a sycamore provenance-progeny test repeated over planting sites and years

Source of Variation	EMS #	Expected Mean Square [a/] (EMS)
Sites		
Years		
Sites x Years		
Reps within Sites x Years		
Seed Sources	#15	$\#10 + 10\sigma^2_A + 60\sigma^2_{LYP} + 240\sigma^2_{YP} + 120\sigma^2_{LP} + 480\sigma^2_P$
Sites x Sources	#14	$\#8 + 10\sigma^2_A + 60\sigma^2_{LYP} + 120\sigma^2_{LP}$
Years x Sources	#13	$\#6 + 10\sigma^2_A + 60\sigma^2_{LYP} + 240\sigma^2_{YP}$
Sites x Years x Sources	#12	$\#4 + 10\sigma^2_A + 60\sigma^2_{LYP}$
Error (a)	#11	$\#2 + 10\sigma^2_A$
Stands within Sources	#10	$\#6 + 12\sigma^2_{LF(SP)} + 60\sigma^2_{LS(P)} + 48\sigma^2_{F(SP)} + 240\sigma^2_{S(P)}$
Families/Stands/Sources	#9	$\#5 + 12\sigma^2_{LF(SP)} + 48\sigma^2_{F(SP)}$
Sites x Stands/Sources	#8	$\#4 + 12\sigma^2_{LF(SP)} + 60\sigma^2_{LS(P)}$
Sites x Fam./Stands/So.	#7	$\#3 + 12\sigma^2_{LF(SP)}$
Years x Stands/Sources	#6	$\#4 + 24\sigma^2_{YF(SP)} + 120\sigma^2_{YS(P)}$
Years x Fam./Stands/So.	#5	$\#3 + 24\sigma^2_{YF(SP)}$
Sites x Years x St./So.	#4	$\#3 + 30\sigma^2_{LYS(P)}$
Sites x Years x F./St./So.	#3	$\#2 + 6\sigma^2_{LYF(SP)}$
Pooled Error (b)	#2	$(\sigma^2_W/h) + \sigma^2_B$
Within Plot	#1	σ^2_W

Additive Genetic Variance = GV = $4\{\sigma^2_{F(SP)}\}$

Phenotypic Variance:

Individual-tree basis = PVI = $\sigma^2_W + \sigma^2_B + \sigma^2_{LYF(SP)} + \sigma^2_{YF(SP)} + \sigma^2_{LF(SP)} + \sigma^2_{F(SP)}$

Family-mean basis = PVF = $[\sigma^2_W/48h] + [\sigma^2_B/48] + [\sigma^2_{LYF(SP)}/8] + [\sigma^2_{YF(SP)}/2] + [\sigma^2_{LF(SP)}/4] + \sigma^2_{F(SP)}$

a/ h = harmonic mean no. of trees per plot

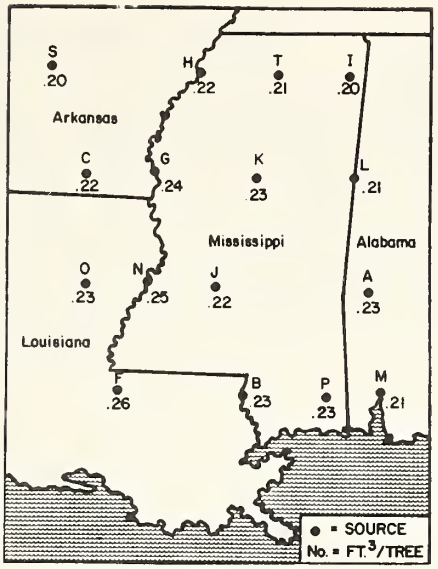

Figure 2.--Map with seed source means for stem volume of four-year-old trees in sycamore provenance-progeny tests in Mississippi

than trees from northeast Mississippi or central Arkansas (Figure 2). This was the only trait for which seed source variation was detected, and the significance test fell between the 0.1 and 0.05 probability levels (Table 2). Differences among sources increased as tree age increased, however, so that seed source variation may reach higher levels of significance at older ages.

Source-by-site interactions were not present after one growing season in the field, but had reached significance following three field growing seasons (Table 2). The interactions resulted from changes in ranks of sources within latitudinal transects, rather than from changes in ranks of latitude means for sources. Mean stem volume per tree was greater at all planting sites for latitudes south of the site than for latitudes north of the site. Even at site #1 in northeast Mississippi the trees from the southernmost latitudinal transect were equally as good as trees from the other transects. Although sources within transects changed in ranks from site to site, the source on the Mississippi River in each transect was always among the top two sources from that transect at every site. Therefore, even though source-by-site interactions occur, trees from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana should provide above average growth in stem volume at all sites in the Gulf South. There is no need to use specific sources for particular sites.

Interactions between seed source and year of planting were found for root collar diameter and tree height after one and three growing seasons in the field, but not for stem volume (Table 2). There was no pattern to the changes in source rankings from year to year. The interactions contribute to the inability to detect source variation in root collar diameter or height at these early ages. They provide a warning against the use of juvenile traits to interpret geographic patterns of seed source variation in sycamore, especially when results are based on only a single year's planting.

Table 2.--Significance and relative sizes of variance components for seed sources, stands, families, and their GxE interactions with sites and planting years

Variance Component	Root Collar Diameter			Tree Height			Stem Vol.
	1-Year (nursery)	2-Year (1 yr.field)	4-Year (3 yr.field)	1-Year (nursery)	2-Year (1 yr.field)	4-Year (3 yr.field)	4-Year (3 yr.field)
	- - - - - - - - - Variance Components Expressed as % of Total - - - - - - - - -						
Seed Sources (=SO)	5.0	0.0	1.7	3.6	4.3	10.1	12.4 a/
Sites x SO	0.9	4.4	14.8*	0.0	0.0	21.7*	33.3** b/
Years x SO	5.4	18.2*	13.3*	2.7	23.2*	15.7*	4.4
Sites x Years x SO	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stands in SO (=ST/SO)	0.0	0.0	1.2	0.0	4.9	4.1	0.6
Sites x ST/SO	0.0	3.2	4.8	0.0	2.3	0.0	0.0
Years x ST/SO	4.8	0.0	0.8	2.4	0.6	0.0	0.0
Sites x Years x ST/SO	0.6	10.1	0.2	0.4	2.0	4.0	2.8
Fams.in ST/SO (=F/ST/SO)	17.1*	34.2**	44.2**	21.7**	22.9**	29.0**	19.9**
Sites x F/ST/SO	0.0	2.8	0.0	0.0	1.3	0.0	22.2**
Years x F/ST/SO	66.2**	20.8**	0.7	69.2**	35.8**	1.9	0.9
Sites x Years x F/ST/SO	0.0	6.3	18.3	0.0	2.7	13.5	3.5
Total of Components	.01127	.00145	.01910	.07544	.04966	.37080	.000989

a/ Significance falls between the 0.1 and 0.05 probability levels.
b/ * = Significant at the 0.05 probability level; ** = significant at the 0.01 probability level.

Variation Among Local Stands Within Sources

There was no evidence of variation among stands within seed source locations for any of the traits studied (Table 2). Stands within a source were separated by one-half mile to 30 miles. This lack of variation among local stands provides indirect evidence for the absence of highly inbred, isolated stands in the natural population, since high inbreeding would be expected to result in large stand-to-stand genetic differences. No additional genetic gain in juvenile growth rate over that obtained from seed source selection can be expected from selection of phenotypically superior stands within sources to serve as seed production areas.

Variation Among Trees Within Stands, and GxE Interactions

Variation among families from trees within stands within sources was significant for all traits at all ages (Table 2). In every case this family component of variance was the largest of the three components: (i) sources, (ii) stands within sources, and (iii) families within stands within sources. The presence of such large variation indicates that the greatest genetic gains in juvenile growth rate will come from selection among individual trees within stands. This gain can be added to the gain from seed source selection by selecting the fastest growing families from the fastest growing seed sources.

Interactions between sites and families within stands were obtained only for stem volume after three growing seasons in the field (Table 2). However, the six highest families for volume were very stable in performance over all sites, as they never ranked lower than second out of the five families from their respective stands when planted at any site. Selection of specific genotypes for specific site types in the Gulf South should not be necessary.

Family-by-planting-year interactions were highly significant for root collar diameter and seedling height in the nursery and after one growing season in the field (Table 2). These interactions decreased with time, however, and were absent after three field growing seasons. Mohn and Randall (1973) reported no interactions between cottonwood clones and planting years for diameter or height of three-year-old trees, but they did not mention results for younger trees. The early interactions found here indicate that family selection for sycamore should not be conducted on very young material in either the nursery or field, unless the tests are repeated over more than one year.

Heritabilities and Expected Genetic Gains

Narrow-sense heritabilities on an individual-tree basis were very low for all traits, ranging from .03 to .17 (Table 3). When calculated on a family-mean basis, however, the heritabilities were as much as ten times larger (.29 to .74) than those for individual trees. Both types of heritability estimates increased with increasing age of the trees. Similar results were reported by Webb *et al.* (1973) for a sycamore progeny test on one site in Georgia, after adjustment of their estimates for genotype-by-site interactions. As pointed out by Webb *et al.*, the heritabilities presented here may be slightly overestimated, because some individuals within the open-pollinated families may be more closely related than half sibs (Namkoong 1966). In the following discussion of genetic gains the conclusions will not be affected by

Table 3.--Estimates of additive genetic variances, phenotypic variances, and heritabilities for stem dimensions of one-, two-, and four-year-old sycamore trees in progeny tests in Mississippi

Trait and Age of Tree from Seed	Additive Genetic Variance	Phenotypic Variance		Narrow-Sense Heritability a/	
		Individual Trees	Family Means	Individual Trees	Family Means
	GV (±std.dev.)	PVI (±std.dev.)	PVF (±std.dev.)	h_I^2 (±std.dev.)	h_F^2 (±std.dev.)
Root Collar Diameter					
1-year-old	.0070 (±.0040)	.2361 (±.0029)	.0066 (±.0015)	.03 (±.017)	.29 (±.095)
2-years-old	.0020 (±.0005)	.0343 (±.0004)	.0010 (±.0002)	.06 (±.015)	.52 (±.055)
4-years-old	.0338 (±.0060)	.3029 (±.0037)	.0115 (±.0018)	.11 (±.019)	.74 (±.035)
Tree Height					
1-year-old	.0653 (±.0255)	.3778 (±.0119)	.0435 (±.0086)	.17 (±.063)	.38 (±.080)
2-years-old	.0488 (±.0158)	.7833 (±.0104)	.0272 (±.0054)	.06 (±.020)	.42 (±.071)
4-years-old	.4302 (±.0815)	3.8604 (±.0499)	.1535 (±.0248)	.11 (±.020)	.70 (±.037)
Stem Volume					
4-years-old	.00079(±.00020)	.01217(±.00015)	.00036(±.00006)	.07 (±.016)	.54 (±.053)

a/ $h_I^2 = GV/PVI$; $h_F^2 = (\frac{1}{4}GV)/PVF$

See Table 1 for composition of GV, PVI, and PVF.

this bias, but the actual estimates of gains should be considered as maximum values.

Expected genetic gains from various combinations of mass selection and progeny test selection for clonal seed orchards can be calculated from equations given by Namkoong et al. (1966) [equations (1) and (2) in Table 4]. Gains will increase when greater selection emphasis is placed upon family performance of a tree's progenies, rather than upon the tree's own phenotype [compare cases (a), (b), (c), and (d) in Table 4]. However, progeny tests are more expensive than mass selection, and there is a limit to how many families can be effectively tested in a field progeny test. Even though case (d) would give the greatest gain of the four cases, one would need to progeny test 2000 families to get a 20-clone rogued orchard. Case (a) would be the least expensive, requiring only the phenotypic measurement of 2000 trees to get a 20-clone orchard, but the gain would be only one-half of that for case (b). A combination of mass selection and progeny testing will usually prove most desirable. A goal must be set determining what amount of genetic gain is needed to justify a tree improvement program. Then, by substituting that gain into equation (1) of Table 4, one can determine what practical combination of intensities for mass selection and family selection will accomplish the goal.

Clonal and seedling seed orchards can be compared for expected genetic gains by holding selection intensities the same in both for mass selection of parent trees and for family selection in progeny tests (Table 4). Gains from seedling orchards will not exceed those from clonal orchards, except when family selection intensity is low and mass selection intensity within progeny families is high. This is attributable to the high heritabilities on a family-mean basis and very low heritabilities for mass selection. Using parents of tested genetic worth for seed production makes a great difference in genetic gain under such conditions.

Genetic Correlations and Correlated Gains

Genetic and phenotypic correlations between measurements on the four-year-old trees and earlier measurements were positive and increased as the time between the two measurements decreased (Table 5). Tree height at an earlier age was not as good an indicator of four-year stem volume as was root collar diameter. Correlations between root collar diameter and height at age four were positive and high.

These estimates of "juvenile-mature" correlations can be used to compare expected gains in a four-year-old trait from (i) selecting for a trait at an earlier age versus (ii) selecting directly for the four-year-old trait. Consider gains from a clonal orchard, where both mass selection and progeny test selection are utilized. When the younger trait is "X" and the four-year trait is "Y", the equation for the correlated gain in "Y" from selection for "X" is (Falconer 1960):

$$(3)\quad CR_y = i_1\sqrt{h^2_{Ix}}\sqrt{h^2_{Iy}}\,Rg_{xy}\sqrt{PVI_y} + 2i_2\sqrt{h^2_{Fx}}\sqrt{h^2_{Fy}}\,Rg_{xy}\sqrt{PVF_y}.$$

As an illustration, one can ask what effort would be needed to get as much genetic gain in four-year stem volume from selecting for two-year root collar diameter as from directly selecting for four-year volume. Placing the appropriate values from Tables 3 and 5 into equation (3), one gets:

Table 4.--Expected genetic gains in stem volume of sycamore trees at age four from using various selection strategies for clonal seed orchards and seedling seed orchards

GAIN EQUATIONS (Namkoong et al. 1966):

(1) Clonal Orchard: Gain = (Mass Sel. Gain) + (Family Sel. Gain from Progeny Test)

$$= i_1 h_I^2 \sqrt{PVI} + 2 i_2 h_F^2 \sqrt{PVF}$$

$$= .00717\ i_1 + .02053\ i_2$$

(2) Seedling Orchard: Gain = (Mass Sel. Gain) + (Family Sel. Gain) + (Mass Sel. Gain w/i Families)

$$= i_1 h_I^2 \sqrt{PVI} + i_2 h_F^2 \sqrt{PVF} + i_3 h_W^2 \sqrt{PVW}$$

$$= .00717\ i_1 + .01032\ i_2 + .00721\ i_3$$

where: $PVW = PVI - (\frac{1}{4}GV)$ and $h_W^2 = (3/4)GV/PVW$

EXPECTED GAINS FOR VARIOUS SELECTION STRATEGIES: (proportion sel. held constant at 1/100 for mass+fam.sel.)

(Case)	Mass Selection		Family Selection		w/i Fam.Selection		% Gain from S.O.	
	Proportion	i_1	Proportion	i_2	Proportion	i_3	Clonal	Seedling
(a)	1/100	2.66	1/1	0.00	1/1	0.00	8.5	8.5
(b)	1/50	2.42	1/2	0.80	1/1	0.00	15.0	11.4
					1/2	0.80	15.0	13.9
					1/4	1.27	15.0	15.4
					1/10	1.75	15.0	17.0
(c)	1/25	2.15	1/4	1.27	1/1	0.00	18.5	12.7
					1/4	1.27	18.5	16.7
					1/10	1.75	18.5	18.3
(d)	1/1	0.00	1/100	2.66	1/1	0.00	24.4	12.2
					1/10	1.75	24.4	17.8
					1/500	3.16	24.4	22.4

Table 5.--Estimates of genetic and phenotypic correlations for "juvenile-mature" relationships between stem dimensions at age four and stem dimensions at earlier ages in sycamore progeny tests in Mississippi

Trait 1	x	Trait 2	Additive Genetic Correlation	Phenotypic Correlations	
				Individual Trees	Family Means
			Rg (±std.dev.)	Rpi (±std.dev.)	Rpf (±std.dev.)
4-Year Stem Volume	x	1-Year Root Collar Class	+.42 (±.251)	+.10 (±.008)	+.21 (±.086)
"	x	1-Year Seedling Height	+.30 (±.221)	+.09 (±.009)	+.12 (±.089)
"	x	2-Year Root Collar Dia.	+.92 (±.093)	+.61 (±.005)	+.69 (±.048)
"	x	2-Year Tree Height	+.75 (±.144)	+.56 (±.006)	+.53 (±.064)
4-Yr.Root Collar Dia.	x	1-Year Root Collar Class	+.55 (±.218)	+.14 (±.008)	+.29 (±.083)
"	x	1-Year Seedling Height	+.19 (±.190)	+.10 (±.010)	+.05 (±.090)
"	x	2-Year Root Collar Dia.	+.91 (±.070)	+.64 (±.005)	+.75 (±.040)
"	x	2-Year Tree Height	+.52 (±.144)	+.54 (±.007)	+.41 (±.075)
4-Year Tree Height	x	1-Year Root Collar Class	+.02 (±.223)	+.12 (±.008)	+.10 (±.090)
"	x	1-Year Seedling Height	+.15 (±.193)	+.14 (±.010)	+.07 (±.090)
"	x	2-Year Root Collar Dia.	+.52 (±.123)	+.53 (±.007)	+.47 (±.070)
"	x	2-Year Tree Height	+.71 (±.124)	+.55 (±.006)	+.56 (±.062)
4-Yr.Root Collar Dia.	x	4-Year Tree Height	+.57 (±.083)	+.76 (±.004)	+.62 (±.054)

(4) $CR_y = .00619i_1 + .01859i_2$.

By comparing equation (4) with equation (1) in Table 4, it is seen that an increase of 16 percent in i_1 and 11 percent in i_2 is needed for selection on root collar diameter at age two to achieve the same gain in four-year volume as obtained from direct selection for that trait. This means that for case (c) in Table 4 one would need to select one tree out of 60, rather than one out of 25, in mass selection and one clone out of five in the progeny test, rather than one out of four. Three hundred trees in total, rather than 100, must be examined for every one that ends up in the rogued orchard, and these calculations are for two traits with a very high genetic correlation (.92). The added number of trees that must be tested to get comparable gains from early selection and direct selection may make the savings in time unjustifiable.

RECOMMENDATIONS

(i) Repeat progeny tests over more than one year of planting when studying genetic variation in traits of trees that are less than four years old.

(ii) Use seed from sources near the Mississippi River in southwestern Mississippi and southeastern Louisiana for planting throughout Mississippi, western Alabama, eastern Louisiana, and eastern Arkansas.

(iii) Use a clonal seed orchard for the production of genetically improved sycamore seed. Select clones from the above-stated optimal seed source zone using a combination of mass selection of trees in the natural stands and progeny tests of the selections. Place heaviest emphasis on progeny test results for selection of these clones.

(iv) Be very cautious of proposals to save two or three years by selection in the nursery or selection after one year in the field to get correlated genetic gains in volume after three field growing seasons. The greatly increased number of trees that must be measured and progeny tested to get gains comparable with those from direct selection may make the savings in time unjustifiable.

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GENETIC VARIATION IN SURVIVAL OF LONGLEAF PINE

R. E. Goddard and Richard Bryant[1/]

Abstract.--Open pollinated progenies of approximately 300 longleaf pines were established in 8 tests across Florida, Georgia and Alabama. Family heritability of survival one year after establishment was 0.35 for bare-root planted seedlings. Phenotypic variance included a large environmental component from the various nurseries, planting crews, and site factors affecting survival.

Heritability of survival of tubelings was lower (0.24). For families planted both as bare-root seedlings and as tubelings, the GxE interaction was low but random error was high. Somewhat different genetic and environmental factors may affect survival of the two seedling types.

Additional keywords: Pinus palustris, genotype x environment interaction.

Although longleaf pine was the dominant species in much of the virgin forestland of the South, it has played a relatively insignificant role in managed forests. Longleaf pine was greatly reduced in second growth forests due to the low frequency of good cone crops, fire protection, and wide use of open range for hogs. Longleaf pine is found even less frequently in the wide scale forest plantation system that has been developed since World War II. Poor survival of planted longleaf was frequently experienced, much more so than with the widely used alternatives, slash and loblolly pines. Additionally, longleaf pine has the "grass stage" habit. Initiation of height growth can be delayed two or three or up to more than 20 years. These two features are certainly not viable for plantation forestry.

The almost uniformly excellent bole form, good growth rate once height growth has started, and, especially, relatively high resistance to fusiform rust have caused renewed interest in longleaf pine. Members of the University of Florida Cooperative Program greatly expanded longleaf pine improvement activities with initial focus on juvenile traits. Testing is underway to determine the extent of genetic variation in planting survival, duration of the grass stage, and rate of early height growth. To the extent that potential for genetic improvement of these traits is indicated, selection will follow.

Earlier studies showed the importance of survival in assessment of families. Snyder (1973) determined that survival was the most critical factor determining 15 year plot volume. Rockwood and Kok (1977) estimated family heritability of initial survival as 0.73.

Certainly, planting survival is subject to many environmental influences. It has long been known that longleaf survival is improved by reduction of nursery

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bed density (Derr, 1955; Scarbrough and Allen, 1954; Shipman, 1960). Lifting, handling, storage, and planting procedures, as well as site factors and weather conditions at time of planting and during following months all influence survival.

The report concerns survival of longleaf pine progenies subjected to a variety of nursery, planting and site factors.

MATERIALS AND METHODS

In the fall of 1977, open-pollinated cones were collected from approximately 300 longleaf pines. These were mostly trees in natural stands but collections from a few seed orchard clones were included. After extraction, seed were divided among 12 cooperators, each receiving seed of up to 200 trees.

Seed were sown in April, 1978, at a spacing of 4" x 4", providing a maximum bed density of 9 per square foot. Beds were undercut once or twice during late summer and fall. There was heavy loss of seed to birds at two locations, but at all other nurseries large, vigorous longleaf pine seedlings were produced. Minor variation in germination percents did not appear to greatly affect seedling size due to the original low density of sowing.

For the planting by International Paper Company in Decatur County, Georgia, containerized seedlings for 150 families were grown in a greenhouse. Ray Leach tubes were filled with a 1:1 mixture of peat and vermiculite to which Osmocote was added. Seed were sown in tubes on October 17, 1978, about six months later than nursery sowing.

Nursery grown seedlings were lifted in January-February, 1979, and, in most cases, planted within one to three days. Tubelings, farily small but actively growing, were outplanted during the last half of March, 1979. Four-tree family plots were randomized within 8-10 blocks per location. In two plantings, seedlings were obtained from three or four different nurseries. In these cases, seedlings from different nurseries (including tubelings) were planted in different blocks.

Survival in all plots was determined as of January, 1980. Plot survival data were subjected to analysis of variance for each planting individually. To determine family x environmental interactions, selected data from 5 locations were analyzed together. Only families common to all five locations and having no missing plots were included. Nursery sources varied but only one nursery source was used per location. Comparable analyses were run for the International Paper Company test (No. 105). In this location, seedlings planted were produced in different nurseries and in containers.

Family heritability for survival was calculated from the analysis of variance tables for individual tests and from the combined tests. For the combined analyses which include GxE interactions, heritability was estimated as:

$$h_f^2 = \frac{\sigma_f^2}{\frac{\sigma_e^2}{BS} + \frac{\sigma_{fxs}^2}{S} + \sigma_f^2}$$

where σ_f^2 = variance among family means

σ_{fxs}^2 = interaction variance of family x site or nursery source

σ_e^2 = residual error variance

B and S = number of blocks or sites, respectively.

RESULTS

Plantings at three locations on very well drained soils suffered drought during the spring after planting. Survival was so poor that these plantings were dropped from further consideration. Excellent initial survival was obtained at a fourth location, but very heavy animal predation of the seedlings destroyed the plantation. The eight plantings retained ranged in survival from 47 to 87 percent (Table 1).

Table 1.--Longleaf pine progeny plantings, including locations, nursery sources of seedlings, survival, and family heritability of survival.

Test No.	Location (County)	Nursery[1/]	No. Families	Survival Mean (%)	Survival Range (%)	Family Heritability
104	Escambia, Ala.	3	87	44	9-81	0.57
		7	105	53	8-83	0.42
		10	106	53	6-88	0.30
105	Decatur, Ga.	3	110	47	0-94	0.77
		4	200	76	25-100	0.26
		9	42	70	25-100	0.64
		11	147	87	56-100	0.24
106	Escambia, Ala.	10	177	74	25-97	0.42
109	Marion, Fla.	7	183	78	47-100	0.58
110	Lafayette, Fla.	8	174	62	20-90	0.65
111	Leon, Fla.	9	196	86	38-100	0.63
112	Hamilton, Fla.	9	188	78	38-100	0.68
113	Nassau, Fla.	5	65	72	40-95	0.70

[1/] Nursery code: 3 - Archer, Fla.; 4 - Bainbridge, Ga.; 5 - Glenville, Ga.; 7 - Chiefland, Fla.; 8 - Day, Fla.; 9 - Capps, Fla.; 10 - Atmore, Ala.; 11 - Tubelings - Bainbridge, Ga.

Family means varied significantly at each planting location. Regardless of mean survival, standard deviations for the individual locations and for nursery sources within locations ranged from 20 to 30 percent. Family heriabilities from the various individual analyses (Table 1) varied considerably but there was no consistent relationship between mean survival and heritability.

For indication of the extent of genetic control of survival with operational planting, an estimate of heritability over a range of environments may be more pertinent than that observed for any single planting. In the analysis of 49 progenies established in five locations, the major effect on survival was due to "locations." This is a complex variable and includes effects on each family of different nurseries, lifting procedures, and planting crews as well as planting sites and local weather. The geographical range was from Escambia County, Alabama, to Marion County, Florida. Family heritability under this very substantial range of environments was 0.35. This is a conservative estimate as the 49 families had a range of survival means about 2/3 as great as the range of all families planted at each location. Family survival was fairly consistent over locations (Table 2) except that occasional families had much higher or lower survival in one test than in the other four. It might be suspected that aberrant low survival of a family at a single location could be due to some unique nursery or handling circumstance.

Test 105 provided comparison of nursery effects on survival at a single location. Analyses utilized data from bare-root seedlings produced in two nurseries and grown in containers (nursery source 11). The combined analysis of 62 families from all three sources indicated significantly higher survival of tubelings than bare-root seedlings. Heritability was much lower than was the estimate from the analysis of families planted in five locations (Table 3). Analysis of survival of bare-root seedlings from two nurseries in Test 105 also indicated significant nursery effects, but heritability was similar to that indicated in the five locations analysis. Finally, data from 119 families in Test 105 produced in nursery 4 and as tubelings were analysed. Methods of seedling production were not significantly different, and there was no significant interaction between family and seedling source. However, error variance was greatly increased with the consequence that heritability was reduced.

DISCUSSION

Survival after planting is obviously subject to many environmental influences. These include those imposed by nursery practices such as spacing, fertilization and watering regimes, etc., seedling handling and storage from lifting through planting, and site and weather conditions at the planting location. However, assuming avoidance of extremes of environmental stress, there appears to be genetic variation in survival.

Because longleaf pine survival is particularly sensitive to nursery and planting treatment, there is possibility of imposing within family common environmental effects. Unique treatments imposed on one or a few families due to

Table 2.--Mean survival of longleaf pine progenies at five locations, ranked by mean survival over sites.

Rank	Family	Survival, Test 106	109	110	111	112	Mean
		%					
		BEST 10 FAMILIES					
1	6378	84	82	80	88	100	87
2	75378	88	96	80	94	75	86
3	6770	91	89	58	88	100	85
4	36278	81	80	83	84	94	84
5	8067	78	80	73	94	97	84
6	1078	69	89	88	91	91	84
7	6165	69	87	80	84	91	82
8	12978	81	80	63	88	91	80
9	6178	56	93	68	91	91	80
10	51278	66	80	78	97	78	80
		POOREST 10 FAMILIES					
40	10978	88	69	58	81	50	69
41	31278	78	58	63	78	66	68
42	30678	78	56	53	81	72	68
43	45778	78	69	43	88	57	67
44	45578	69	64	43	88	69	66
45	72078	72	60	50	69	75	65
46	5170	75	53	28	81	78	63
47	31078	66	47	50	86	66	63
48	31678	59	58	53	91	53	63
49	31578	56	60	60	84	50	62
	mean	75	76	59	85	77	74

non-uniformity in nursery or handling procedures are confounded with genetic effects and lead to exaggerated estimates of heritability. The wide range of heritability estimates from the various individual tests reported here may be, in part, due to such accidentally imposed bias. However, as seedlings for each test were independently grown and planted, the possibility of common environmental effects on a family was eliminated in the combined analyses and differences among families shown would reflect real genetic differences.

Survival is a complex characteristic and may be composed of more discrete traits such as avoidance of excessive dessication during the planting process, ability to rapidly regenerate new roots, or rapid rate of root extension. Whatever the elements of survival, tubelings appear to be responding to somewhat different environmental constraints than nursery grown seedlings. Even with

Table 3.--Proportions of phenotypic variance of longleaf pine survival attributable to family genotypes and genotype x environmental interaction.

Analyses	Major Environmental Effect	No. of Families	Total Phenotypic Variance		
			Family	Family x Environment	Random
			----------%----------		
Analysis 1 Tests 106, 109, 110, 111, 112	Locations[1/]	49	35*	32*	33
Analysis 2 Tests 105, Sources 3, 4, 11	Nurseries[2/]	62	21*	22*	57
Analysis 3 Test 105, Sources 3, 4	Nurseries	69	37*	14	49
Analysis 4 Test 105, Sources 4, 11	Nurseries[2/]	119	22*	7	72

*Significant variance at the .01 level of probablity.

[1/] Includes different nurseries and planting crews as well as site and weather differences.

[2/] Includes bare-root and tubeling seedlings (source 11).

great care, many very fine roots are lost in the lifting, transport, and planting of bare-root seedlings. This loss is avoided in planting tubelings and redevelopment of fine roots is not a factor in their survival. There are no doubt other differences between the seedling types as well as factors that affect them similarly. The interaction of families to microenvironmental differences in blocks within sides led to reduced estimates of heritability that included tubelings.

Goodwin (1976) reported that tubelings survived and grew better than bare-root planted longleaf seedlings in North Carolina. In Test 105, the superior survival of tubelings was confirmed, but, probably due to their superior size, nursery grown seedlings appear to be coming out of the grass much more rapidly than the tubelings.

Family heritability reported here is appropriate for estimation of genetic gain from selection of parent trees or selection of families. Individual tree heritability is not applicable. There can be no direct within-family selection for survival as all surviving trees are of equal value in this respect.

Using the heritability estimate of 0.35 for nursery grown seedlings, selection of one-half of the families with best survival should yield a genetic improvement of 6.5 percentage points. If 70 percent of the families were selected for survival, allowing selection for other traits, genetic gain for survival would be about 4 percentage points. This modest genetic improvement in survival, coupled with proper attention to environmental factors, should provide satisfactory longleaf pine survival under most site conditions.

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SCREENING LOBLOLLY PINE FOR ADAPTABILITY TO DEEP PEAT SITES: A SEEDLING STUDY OF TWO EDAPHIC SEED SOURCES FROM EASTERN NORTH CAROLINA

Claire Williams[1/] and Floyd Bridgwater[2/]

Abstract.--A study has been initiated to screen for adaptability of loblolly pine to excessively wet, deep organic soils in eastern North Carolina and to investigate the use of seedling root characteristics as morpho-physiological indicators in early genetic evaluation. The study consists of 1) field trials to compare a broadly adapted Coastal Plain seed source with a seed source that originated on the deep organic soils in Tyrrell County, North Carolina and 2) a seedling study of the two edaphic seed sources. The results of the seedling study are given. Edaphic seed source differences are slight but considerable variation exists among open-pollinated families from each seed source. Several families exhibited differential genetic response to soil types. An alternative to a separate breeding program for deep organic sites is suggested.

Additional Keywords: Family by soil interaction, Pinus taeda, deep peat and Coastal Plain.

As tree improvement efforts intensify in response to the dwindling land base availability for forestry and to the increasing demands for fiber products adaptability to physiologically difficult sites becomes of critical importance (Bridgwater and Stonecypher 1978). Greater understanding of genetic variation in root response to environmental factors may prove essential to the production of high yield forests on these marginal sites and provide potential physiological indicators for early genetic evaluation (Long 1973, Cannell, et al 1979). The excessively wet areas in the Coastal Plain of North Carolina are an example of marginally productive loblolly pine (Pinue taeda L.) sites.

At present, several companies own forest land in the lower Coastal Plain that include areas of excessively wet, deep peat soils. The flat uniform topography and good growth potential are definite advantages but the excess water and heavy understory vegetation are serious drawbacks to all aspects of intensive forest management (Terry and Hughes 1975). Better logging technology has made harvesting these sites profitable and increased the demand for well-adapted planting stock. Despite improved silvicultural practices, broadly adapted Coastal Plain loblolly often exhibit poor growth, survival and increased susceptibility to windthrow on the deep organic sites (Anonymous 1971, Stonecypher, et al. 1965). In anticipation of a need for genotypes that are adapted to these sites, loblolly pine selections from the Tyrrell County deep peat areas were made in the late 1950's and were grafted into a production seed

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orchard. Since then, two other seed orchards have been established that include these genotypes. These orchards are the principal source of loblolly pine seeds for the deep peat sites in eastern North Carolina. Genetic differences between the Tyrrell County seed source and the more widely planted Coastal Plain seed sources have not been demonstrated.

The objectives of this study were 1) to determine the extent of the genetic differences that may exist between a broadly adapted Coastal Plain seed source and the Tyrrell County deep peat seed source and 2) to screen for seed source(s) or families that are adapted to organic soils.

METHODS

Experimental Materials

The seeds for the study were collected from two rogued first-generation loblolly pine seed (Pinus taeda L.) orchards in North Carolina. The deep peat source came from the first wet-site seed orchard established by Westvaco in 1959. Seeds were collected from eleven clones to represent what is operationally planted on deep peat soils. The Coastal Plain seed source was represented by seeds collected from eleven selected clones in Weyerhaeuser Company's North and South Coastal High (Wood) Density seed orchards. Each of these clones was grafted from select trees that grew on poorly drained mineral soils.

Experimental Procedure

The experiment was conducted in the North Carolin State University phytotron glasshouse at a day/night termperature regime of 26°/18°C. The experimental design was a split-plot with four replications, four soil-water treatment combinations, two seed sources and eleven open-pollinated families within each seed source. There were four seedlings per family-treatment combination in each replication. Watering regimes were the main plots. The soil medium used to simulate the deep organic soils was a 4:1 peat-vermiculite mix. The mineral soil was simulated with a 3:1 river sand-peat mix. Dolomitic lime was added in equal amounts to each medium; soil samples at the time of mixing indicated a pH of 7.00 for sandy soil and 6.2 for the peat. These pH values are not representative of those characteristic of the poorly drained mineral and organic soils of the North Carolina Coastal plain. These sites typically have pH values of 3.0 - 4.0. Higher pH values were maintained to reduce mycorrhizal development, a potential source of uncontrolled variation in this experiment. The bulk densities of the sandy medium and the peaty medium were 1.35 and 0.38 g/cc, respectively. Filled seed were weighed to obtain an estimate of mean seed weight by family. The seeds were soaked in distilled water, stratified for 30 days at 2°C and germinated in a germination chamber at 25°C. We used a priori knowledge of family germination rates to stagger sowing dates so that seeds from all 22 families germinated within a 5-day period in order to minimize age differences at harvest. Each germinant was transplanted into a quart-size milk carton the same day the radicle emerged to avoid damage to the embryonic root. Seedlings were doused weekly with Benomyl®, a broad-spectrum fungicide. A high-phosphate nutrient solution, Plant Starter® (9-15-45), was applied once weekly for three weeks before harvest. Seedlings were watered twice daily until 35 days after germination when the root systems of seedlings designated to receive the waterlogging regime were submerged in water for five days and were watered twice

daily. Seedlings in the "dry" regime were watered once daily until harvest. At age 60 days all seedlings were harvested and their root systems were rinsed free of soil.

Variables

1. Seed weights: Mean seed weights were determined for each family.

2. Total dry weights: Each seedling was dried at 70°C for 24 hours and weighed to the nearest milligram.

3. Number of first-order lateral roots: Each root system was floated in water and all lateral roots longer than 10 mm were counted.

4. Total root length: Total root length was tallied using a grid system (Bohm 1979). A grid with 169 half-inch squares was taped to the bottom of a shallow glass dish filled with water. The root system was spread out in the dish and anchored with glass sides. Each square intersected by a root was counted. Repeatability of the method was highly correlated (0.89) and it was highly correlated (r = 0.89) with total root length.

5. Shoot-root ratios were calculated using logarithms because seedling growth increases exponentially (Russell 1979, Salisbury and Ross 1979). Shoot-root ratios are log (shoot dry weight)/log (root dry weight).

Statistical Analyses

Seed weights were poorly correlated with the other variables (Table 1). Therefore, no adjustment for seed weight was necessary in the analyses that followed. All computations were performed on plot means using Statistical Analysis Systems (SAS Institute 1979).

TABLE 1. Correlation coefficients among mean family seed weight (SW) shoot-root ratio (SRRATIO), total root length (TRL), number of first-order laterals (LAT), and total dry weights (TDW).

	SRRATIO	TRL	LAT	TDW
SW	-.04	.02	-.04	.09
	.27[1]	.59	.14	.004

[1]probability of a greater F value

RESULTS

Response to water regimes was small and statistically nonsignificant for all of the traits except number of lateral roots. Seedling morphological differences were largely due to genetic and edaphic factors (Table 2).

Shoot-root ratio, total dry weight and total root length were highly influenced by soil type; soil constituted the largest single source of

variation. Seed sources, by contrast, were statistically significant at least at the .05 level for shoot-root ratio, total dry weight and first-order lateral roots but accounted for less than 2.5% of the total variation associated with each of the traits. Families within seed sources were statistically significant for all traits measured in the study. Families by soil interaction was a significant source of variation at the 95% confidence level for shoot-root ratio, total dry weight and for total root length. Spearman's rank correlation coefficients were calculated for each of these three traits to determine if the interaction resulted from families rank change on different soils. Only the correlation coefficient for shoot-root ratio ($r_s = 0.45$) was significantly different from zero at the 95% confidence level.

TABLE 2. Means of total dry weight (TDW), number of first-order lateral roots (LAT), shoot-root ratio (SRRATIO) and total root length (TRL).

Source of Variation	TDW (mg)	LAT (number)	SRRATIO (log shoot D.W./ root D.W.)	TRL (score)
Seed Source				
Deep Peat (DP)	267*	25.4*	.58*	64.9
Coastal Plain (CP)	277	26.6	.57	64.6
Soil				
Peat (P)	313	25.9	.59*	74.0*
Sand (S)	229	26.1	.55	55.6
Water				
Wet (W)	277	25.2*	.58	64.0
Dry (D)	266	26.8	.56	65.5
Families				
Maximum Value	331	30	.61	74
Mean	270*	26*	.57*	64*
Minimum Value	216	23	.50	55
Spearman's rank correlation coefficient[1]	.24	--	.45*	.15

*Differences were statistically significant at least at the 95% confidence level.

[1]Spearman's rank correlation coefficient calculated for those traits with significant ($\alpha = .05$) family by soil interaction.

DISCUSSION

Coastal Plain and deep peat seed sources were not genetically distinct in the two test environments. Although the seed source effects were statistically significant for shoot-root ratio, total dry weight and the number of first-order

lateral roots the mean differences accounted for 2.5% or less of the total variation in this study. There was no evidence of interaction between seed source and soil or water regimes. If the seedling traits are reliably correlated with later field trial performance then the seed source differences are of negligible importance in a tree improvement program unless the differences are compounded annually over rotation.

As an alternative, breeding and selection efforts among families should receive more emphasis than seed sources alone since variation among families is considerably greater. Half-sib family blocks or a subset of orchard families which are particularly responsive to the silvicultural and edaphic conditions specific to deep peat sites could be planted instead of bulked seed lots from an edaphic seed source. This approach would allow the tree breeder to capitalize on genotype by site interaction without the expense of a separate breeding program (Bridgwater and Stonecypher 1978) and is under consideration as an operational practice by Weyerhaeuser in North Carolina (R. G. Campbell, pers. comm. 1981). Additional test environments are necessary to examine the full scope of family by soil interaction but the differential genetic response exhibited by several families for the traits total dry weight and total root length warrants a closer look at the opportunities for exploiting adaptability to specific site conditions.

SUMMARY

Differences between Coastal Plain and Tyrrell County deep peat seed sources are small and do not exhibit adaptation to sandy or peaty soil types. Open-pollinated families from both seed sources showed differential genetic response to soil types which could be exploited to provide well-adapted planting stock for the deep organic sites in eastern North Carolina. A separate breeding program is not recommended for the deep organic sites in North Carolina at this time.

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VEGETATIVE PROPAGATION IN FOREST MANAGEMENT OPERATIONS

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Abstract.--A "revolution" involving vegetative propagation is on the new horizon in operational forest regeneration. Although vegetative propagules have been used for operational regeneration programs for many years in a few genera such as Populus in hardwoods or Cryptomeria in conifers, for most forest trees it has generally been considered something for the future. The future is now here and a great deal of progress has been made in the use of vegetative propagation in both hardwoods and conifers.

The appeal of vegetative propagation is in the gains possible through the transferal and utilization of all the genetic variance rather than only the additive portion used in standard sexual propagation programs. This is of special importance for certain growth and adaptability characteristics, and gains will be greatly improved over those that have been achieved using conventional methods.

Dangers are involved when vegetative propagules are used for operational planting, but with proper planning these can be controlled or reduced. The use of large-scale vegetative propagation requires weighing gains against risks and developing a system that results in a balance most beneficial for both short- and long-term objectives.

INTRODUCTION

During the past several years a great interest has developed about possible use of various methods of vegetative propagation in forest regeneration. This method of regeneration has been employed for a long time; there are records in the literature of using rooted cuttings of Cryptomeria japonica for planting during the past century, reported by Ono (1882) and Kanoo (1919). Methods of rooting were developed much earlier and commercial planting of cuttings has been standard for many years. Vegetative propagation has been used successfully for centuries by horticulturists. More recently in forestry its use for research and for seed production in clonal seed orchards has become standard. But aside from a few genera like Populus, Salix and Cryptomeria, vegetative propagation has not been used extensively in operational forest planting programs.

There are many types of vegetative propagation; this paper is not the place to discuss them. Several publications summarize such work; a couple of these are "Vegetative Propagation of Forest Trees--Physiology and Practice" (1977) and "Micropropagation d'Arbres Forestiers" (Anon, 1979b). Work on methodology necessary for use of vegetative propagation is developing well. Primary emphasis in this paper will be on the use of rooted cuttings for operational planting. Grafting is primarily used to preserve trees in clone banks or for seed orchards whose objective is large-scale seed production. The newest aspect of vegetative propagation that has received a great deal of publicity and attention is tissue culture. Although considerable development is still

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necessary to make it operational (Zobel, 1977; Durzan and Campbell, 1974), tissue culture has considerable potential. I will not discuss tissue culture specially in this paper; others in this meeting have that task.

This presentation will emphasize the status, value and use of vegetative propagation in operational forest regeneration programs, not the methodology as such. Great strides are being made with southern pines (van Buijtenen, et al., 1975; Anon, 1979a), with spruce (Birot and Nepven, 1979; Rouland, 1978, Rauter, 1977 and 1979), with radiata pine (Thulin and Faulds, 1968), with Eucalyptus (Campinhos and Ikemori, 1980), and other species. Much of this development has occurred during the past five years so there are many questions related to use of vegetative propagules in applied programs that are still debated. A whole series of papers dealing with aspects of vegetative propagation was published in 1977 by the Institute for Forest Improvement in Uppsala, Sweden.

WHY USE VEGETATIVE PROPAGATION?

What is the special value of vegetative propagation that makes it so appealing to the forest manager? Except for a few genera, it is usually easier to use standard seed regeneration than vegetative propagules, yet the effort toward vegetative propagation is being strongly sponsored (Libby, 1977 and 1979; Thulin, 1969; Fielding, 1963; Campinhos and Ikemori, 1980). Tests are generally inadequate as to the relative performance of vegetative propagules and seedlings (Sweet and Wells, 1974; Sweet, 1972; Rouland, 1978). Fielding (1970) lists a number of interesting similarities and differences.

A complete and technical answer and explanation could be long, detailed and complex. Simply stated, however, the advantage of vegetative propagation is the potential for greater genetic gain and greater uniformity. Genetic variation can be partitioned broadly into additive and nonadditive variance components. When seed regeneration is used, only the additive portion of the genetic variation can be manipulated by the tree improver, unless special efforts such as control-pollination or two-clone orchards are employed; this is not easy to do with potential problems (Libby, 1977). For some characteristics, gains using seed regeneration will be large, but for others that contain significant amounts of nonadditive variance, such as certain growth characteristics, gains through seed production will only be a portion of the potential that would be possible when vegetative propagation is used (Fielding, 1970). In general terms, it is possible to capture and transfer to the new tree all genetic potential through use of vegetative propagation while only part of the additive portion can be captured through seed production. For characteristics such as volume growth that have only low narrow-sense heritabilities, it appears possible to more than double short-term genetic gain by using vegetative propagules rather than seed regeneration.

Another advantage of vegetative propagation is the rapidity with which selected trees can be established from outstanding parents. It is not necessary to wait for seed production before producing vegetative propagules for operational use. Just as soon as a tree has been proven to be a good genotype, it can be used directly for the easy-to-root genera like Populus. In sprouting species such as the eucalypts, where stump sprouts are physiologically juvenile, it takes considerable time to develop a "sprout orchard" which will produce the desired number of cuttings for operational planting. Under the

best of conditions it will take several years to develop enough rootstock from which cuttings can be taken. For more difficult rooters, action must be taken to produce partial or total juvenility or to maintain trees to be rooted in a juvenile stage through methods such as hedging (Libby, 1972; Anon, 1979a, 1979b).

There have been several schemes developed to maintain juvenility while testing the genetic worth of the trees (Pousujja, 1980; Libby, et al., 1972). Methods are being worked on that will cause tissue from mature trees to return to a juvenile stage (Chaperon, 1979) in pine by continued regrafting onto young stock. This methodology has not yet been widely tried but the implications are great; if generally successful it will enable vegetative propagation of trees that are old enough to have proven their genetic worth. A great danger, being ignored by too many persons who are interested in vegetative propagation, is assessment of the worth of a tree at too young an age, especially for growth characteristics. The time frame of such testing should be little different from that of progeny tests. It can be shortened, perhaps, if the clones are selected from families that are already progeny tested. Although there are occasional reports of good juvenile-mature correlations for volume growth, the bulk of the literature for most species indicates that a reliable estimate cannot be obtained until one-half rotation age (Franklin, 1979; Wakeley, 1971). This paper is not the place to argue this most important concept, but those of us who have had widespread experience with a number of species over a long period of time are very worried about bad decisions being made regarding genetic superiority for use in vegetative propagation from too early assessments. There is such an advantage in using physiologically young material that the assumption is too often made that if the tree is superior when young it will still be superior at rotation age.

CONSIDERATIONS WHEN USING VEGETATIVE PROPAGATION OPERATIONALLY

All sorts of problems and advantages could be listed relative to the operational use of vegetative propagation after the actual propagation methods have been developed well enough to use on a mass scale. If one brings all considerations to a common denominator, it adds up to GAIN VS. RISK, i. e., how much gain can be achieved while retaining an acceptable level of risk. The basic questions are widely argued but rarely decided because of differing emphases on the relative risks. It is not important to come to a consensus; what is important is to be aware of the gains and risks and to make a conscious decision as to their relative importance.

The first concept always raised, and of prime importance, is that of the danger of planting large acreages with the same or similar genotypes. This very real problem is a tough one but often is blown out of perspective when it is being argued. On the one hand, some persons cite agriculture and its widespread use of very narrow genetic bases with outstanding success to Society and to the grower. On the other side are those persons who decry planting large acreages of trees of the same species; to them this represents a dangerous monoculture, no matter how variable are the genotypes within the species. The correct position is, of course, somewhere between these extremes. Great care needs to be taken in invoking the horrors of monoculture, but monoculture can be a horror if ignored.

Many agricultural crops can tolerate greater genetic uniformity than forest trees because:

1. The farmer has greater ability to control pests, nutrients, competition and sometimes moisture, while in forest trees such rigid control is less possible or not practical.

2. Short-lived plants are grown only during a part of the year, when conditions are most suitable for growth, so they are relatively uniform.

3. If something goes wrong with an annual-crop variety it can be massively replaced the following year.

Forest trees must survive, grow and reproduce for many years, which will include many differing environments. Weather extremes and pests are numerous, and some are sure to show up during the rotation period of the tree crop; and in order for a tree or group of trees to survive and grow they must be able to tolerate a broad spectrum of conditions.

A common mistake made by laymen and by some foresters is to assume that members of the clone will have little or no adaptability. This is not true; the genotype of a clone can possess a considerable ability for adaptation to differing pests or adverse environments, and we should be able to select clones with greater adaptability than possessed by the average seedling. A forest tree needs this merely to survive and reproduce. The danger arises when the adaptability from the genotype is exceeded by adverse conditions; the result will then be that all trees of a given clone will be subject to attack. But in my opinion it generally takes a much greater change in the destructive agent to destroy a forest tree clone than a true breeding, homozygous agricultural crop. From what I have observed, pathological agents seem to be the ones that can most easily destroy forest trees whose genotypes have produced otherwise good, growing trees in a given environment. Forest trees seem to be less well buffered to attacks by pests than to weather extremes, especially for exotic pests that have come from an area outside the natural range of the tree species.

So the question is--how many clones are necessary for reasonable safety and maximum gain? As usual the standard answer is "It all depends on rotation age, on intensity of forest management, on genetic variability of the species and clones involved and the likely risks and the acceptable loss levels" (Libby, 1981). It is certain that hundreds of clones are not required, as the more cautious advise. I am recommending that 15 clones be used in any one environment for one species with which I work, which is known to be quite variable and which has wide adaptability; this species is grown on short rotations. This is within the range of 7-30 recommended by Libby (1981). Since there are six different environments, two of which are quite distinct, we feel that it is necessary to use about 50 clones in the total operation. However, the number needed cannot be determined until testing has been completed. When the nearly 400 clones that have been chosen and have been tested are ranked, it is evident that double the gain can be obtained if the best 15 clones give double the gain over the best 100 clones. For the species, its variability and short rotations, I have no fear of unusual danger by using the best 15 clones that give large gains.

As a broad generality, I feel that for most species 20 to 25 clones are about the correct number. There are special conditions, such as severe insect or disease attacks, or very severe environments, when very few clones will be justified because only a few are available. This is a short-term and rather risky strategy. Here it becomes a case of using those few that will survive known pests or severe environments such as freezing weather. Generally, however, the more severe the stress a given species or provenance is under (i. e., they are poorly adapted to environment), the greater the number of clones that should be used.

Closely related to the number of clones is their deployment; that is, if 15 clones are used, should they be planted scattered randomly, or should they be planted in small blocks of pure clones? This was argued as early as 1918 by Hirasiro, who felt mixtures of clones were the best. If trees are planted in clonal blocks, then the question arises as to the size of the blocks that are safe. Forest management and logging efficiency and product uniformity all favor large blocks, but the larger the blocks the greater the danger from monoculture, with its attendant risks from pests or adverse environments. It is essential, however, that the blocks meet some minimal operational size if they are to be efficient.

The immediate reaction of most persons is that clones should be planted in mixture. I do not agree with that for the following reasons; furthermore, the analysis of Libby (1981) indicates that mosaics of monoclonal plantings are often the best strategy:

1. Each clone tends to have a different growth curve and developmental pattern. At worst this means that some clones will never be able to develop properly in mixture and might even be severely suppressed by competition from other clones. At the least there will be differences in size and quality, reducing one of the greatest advantages of vegetative propagation, i. e., greater uniformity.

2. Planting and "nursery" operations are much simplified when planting by blocks.

3. Wood uniformity among trees is maximum within a block of trees from the same clone. I foresee the time when trees of different blocks may be used for special products, such as plywood or sawtimber.

4. It is suggested that mixing clones will slow down the spread of pests. This is certainly true for root diseases and for some insects but is less efficient for diseases spread by air-borne spores. I have observed many times that things such as leaf diseases or canker diseases seem to spread about equally rapidly in pure or mixed species stands.

5. If a really serious problem develops within a given clone, a whole block can be harvested and replaced to keep the forest in maximum productivity. Even if it were possible to salvage an individual clone (for example, one of 15), it cannot be replaced when clones are mixed and low stocking results. Generally salvage from mixtures is not economically feasible and often the salvage operation causes more damage to the residuals than the net return from the salvage.

How large should each clonal block be? Again there are all kinds of qualifications based upon species, rotation age and genetic uniformity. For species with reasonable variability and short-rotation ages, I have been recommending pure-clone blocks of 10 to 20 hectares. Many persons feel these are too large but I do not; anything much smaller than 10 hectares becomes inefficient to operate as a unit, and I don't feel the added danger from the larger blocks is that important. With more experience this recommendation may well change, but with what is now known we are going with 10- to 20-hectare blocks.

Another general concept that must be considered is cost of vegetative propagules vs. seedlings. Usually, vegetative propagules are much more expensive to produce and to establish than are seedlings. As methods are developed and experience is gained, costs of vegetative propagules can be reduced greatly (Kleinschmit and Schmidt, 1977) or even be no greater than seedlings (Campinhos and Ikemori, 1980). Direct cost comparisons are really not useful because one must weigh the added gains against the costs. Often a considerable additional cost per planted tree becomes insignificant when assessed on a cost-per-acre basis. For example, just a couple of percentage points of improvement in return from using the better cuttings can often more than justify a doubling or tripling of cost of plant establishment in the field. In my opinion, the cost differential between seedlings and vegetative propagules will continue to diminish as methods are seriously developed for operational scale programs.

Rooting ability varies greatly by clone (Sorenson and Campbell, 1980: Hyun, 1967). In some species, so few parent trees respond well enough to rooting that the broad genetic potential is reduced to an alarming degree. If one selects or develops 100 outstanding trees but only 10 of these root well enough to use operationally, the effectiveness of the program will be greatly limited. Differential rooting appears to be general and has been a serious problem in developing tissue culture methodology in the southern pines. Improved techniques will help some, but losses of large numbers of otherwise excellent genotypes because they have a poor rooting ability may prove to be a serious strain in some species.

OPERATIONAL USE OF VEGETATIVE PROPAGATION-- POTENTIALS FOR THE SOUTH

Little comment is needed on the use of vegetative propagation for species in the genera Populus, Salix, Sequoia, Picea or others. Methods for the first two are known and operational. The major criticism in poplars is not in methodology of regeneration but in lack of hard-hitting, ongoing breeding programs to produce better trees for the regeneration program. Although some organizations have intensive genetic improvement programs combined with their vegetative regeneration, most do not; these latter merely select within natural stands or plantations or produce F_1 hybrids to choose from. Hybrids are often no better than the parents used, and a genetics program to improve the parents before new hybrids are made is essential for long-term gain. Too many persons feel there is something magic about hybrids but they need improvement as do the pure species. Initial gains are large but future gains will be limited without intensive breeding programs.

The vegetative propagation programs in the conifers are just getting started, with the exception of Cryptomeria in Japan. Good gains will be possible by determining outstanding genotypes from current stands but this is not enough and new and improved trees need to be developed. I feel so strongly about

this that I do not recommend that my clients spend a lot of time and money on developing sophisticated vegetative propagation techniques unless there is a parallel intensive genetic improvement program.

Although it is evident to biologists working in this area that a good phenotype may or may not produce a good plant when vegetative propagation is used, many persons assume that a good-looking tree will produce good cuttings. A shockingly large number of organizations do not even test the vegetative propagules and assume that propagules from a good tree will produce good forest trees. Others make the error of assessing the value of cuttings at too young an age. Too early assessment probably is the most serious error being made when vegetative propagation is used operationally; the error is not easily observed, no matter what the rotation age, although it is more evident under long rotation conditions. Libby (1977) addresses the differences in testing philosophy.

Outside of a few species, vegetative propagation is in the developmental stage in the South. Currently, for both rooted cuttings and tissue culture, technique development is of primary importance. Great progress is being made (van Buijtenen, et al., 1975; Pousujja, 1980; Mott, et al., 1976) and I feel it is only a matter of time till both the southern pines and some of the hardwoods will be operationally planted, using vegetative propagules. Methods of developing juvenility (Franclet, 1979) or maintaining juvenility by hedging (Libby, et al., 1972; Thulin and Faulds, 1968; Brix and van Driessche, 1977) are essential to further developments for operational planting of vegetative propagules in the South. Studies of growth and form comparing vegetative propagules to seedlings have been started in the southern pines; I am hopeful we can obtain information such as that by Rouland (1973, 1978) and Birot and Nepven (1979). The tremendous developments in just the past few years in the eucalypts (Campinhos and Ikemori, 1980; Laplace and Quillet, 1980; Franclet, 1963; Chaperon, 1979; Destremau, et al., 1980) show what can be done in a short time. Many questions of proper clone numbers and their allocation are still unanswered but excellent progress is being made. I feel that the progress with the eucalypts may well indicate what might happen in the South.

In my opinion the use of vegetative propagules is special in a forestry operation and they should be used for specific products or needs on the most suitable sites. For example, if a certain kind of wood is desired it can often be supplied by rooted cuttings, even though the genetic base may need to be restricted to fill this special need. For example, many eucalypts have interlocked grain or wood that is under internal stresses that cause splitting when the trees are felled. Occasional trees are straight-grained without internal stress and make fine high-quality plywood or furniture. The few clones with suitable wood can be used to supply the special need for quality. Often, disease-free trees have produced generally disease-free rooted cuttings; a prime example is Diaporthe cubensis on Eucalyptus in Brazil. I can foresee the same special usage of vegetative propagules in the South, i. e., to produce trees with special, uniform or otherwise desirable qualities. I do not foresee the use of vegetative propagules on a wholesale scale in the southern pines in the near future, although a very heavy usage could well occur for some quality hardwoods. Although not generally operational, studies on rooting cuttings have been done on sweetgum (Liquidambar styraciflua) by Brown and McAlpine (1964); on black walnut (Juglans nigra) by Carpenter (1975);

on black cherry (Prunus serotina) by Farmer and Besemann (1975); on sugar maple (Acer saccharum) by Gabriel, et al. (1961); on water oak (Quercus nigra) by Hare (1977); on yellow-poplar (Liriodendron tulipifera) by McAlpine and Kormanik (1972), and on other hardwoods. Several of the authors mentioned feel that vegetative propagation in hardwoods can be developed operationally, and there is no doubt of its value for the species with high-quality woods.

We in the South have a major advantage in that we have ongoing programs for the development of genetically superior stock on which vegetative propagation can be used when the methodology has become more refined. If the South is to stay competitive in the long-term future, we need to take advantage of every possible improvement. Vegetative propagation is the best method to obtain quicker and larger yields of more uniform and desirable wood from genetically improved trees.

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TISSUE CULTURE PROPAGATION OF CONIFERS: CURRENT AND FUTURE

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Abstract -- Tissue culture methods of propagation are already a commercial success for a variety of horticultural crops. These methods are also central to the recent speculative interest in "genetic engineering" applied to plants. On this basis we may be pardoned for being very optimistic about what tissue culture and associated methodologies will do for the forest industry. The question is, when? Technology follows steps in its advancement to commercial use. First, the process is demonstrated in the laboratory, then generalized and broadened to more than one species, then made dependable and more efficient as the product quality is evaluated. Cost effectiveness can then be determined to dictate commercial use. Propagation of small conifer clones (5-20 members) from seedling cotyledons is well advanced along this path to the point where propagule quality is being evaluated. Recent success with recycling propagules, to make more propagules from each, promises to significantly increase the clone members, but the clones must originate from young, unproven seedlings rather than mature elite trees. The methods for elite trees include use of buds (terminal, axillary, fascicle) and plantlet production from stem callus cultures (organogenesis) as well as artificial embryo production from such callus cultures (somatic embryogenesis). Current capability is described for each approach, which is now at or near the initial laboratory demonstration step. We expect substantial application of knowledge from the seedling system to speed development of the other systems. The possible applications of the emerging methods and knowledge to problems other than mass propagation, i.e., selection of disease resistance, protoplast fusion and genetic engineering, are discussed relative to present capabilities.

Additional Keywords: Mass propagation, early selection, genetic engineering

Substantial advances have been made in yield and quality of the forest crop by breeding programs and refined management strategies. Mass vegetative propagation by tissue culture will give us a new dimension, and it is on the door step. The urgent and practical questions concerning the real value of vegetative propagation and its proper deployment for the forest crop are being addressed. We can look to the horticultural industry for a model of tissue culture use in vegetative propagation, but we should also be aware of the emerging methodology of recombinant DNA and gene manipulation in cultured animal and plant cells.

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The technology of test tube genetics offers a more efficient approach to breeding programs, and more efficient methods to map the location and interaction of genes on the chromosomes. This is in addition to the eye-catching accomplishments of engineering bacteria to produce insulin or interferon which have recently made headlines. The potential value of this technology for agricultural crops such as tomato or wheat has sparked an influx of speculative money and new companies almost without precedent. This manifest appraisal of worth for agricultural crops that already have vegetative propagation and rapid breeding programs should not go unnoticed by those of us who seek to improve the conifer crop with its delayed flowering and slow growth to maturity for progeny selection. This paper will attempt to sketch the flow of the emerging technology, then assess the relative position of conifer research in that flow of possibilities.

EMERGING GENERAL TECHNOLOGY

The horticultural industry has recognized that more uniform plants emerge from tissue culture propagation if the cells are not kept too long in culture, and if new shoots are produced directly from existing shoots or leaves rather than from an intervening disorganized callus step (Murashige, 1974). The process is more efficient and less labor-intensive if callus or cell suspensions can be multiplied,then induced to form shoots or embryos. However, variability in the plants so produced can be a problem for many species. Since horticultural crops have high value, the less efficient and more reliable route which avoids callus has received the attention.

Vegetative propagation by tissue culture is preferred commercially for many ferns, foliage plants, woody ornamentals and flower crops. The tissue culture micropropagation methods differ from crop to crop, but they are based on identified general principles (Murashige, 1974). The cultured stocks can be kept for long periods in refrigerators. At the proper season, propagules can be generated in large numbers from these stocks and placed directly in the greenhouse for crop production. The energy and labor-consuming greenhouse space that otherwise would have been used through the year to maintain traditional propagation stock plants is thus released for continuous crop production. With adequate precautions, the tissue culture propagules enter the greenhouse free of viruses and other diseases. Large stocks can be built up quickly from a few select plants, and the uniformity among plants within a tissue culture clone insures that all will be ready for harvest at one time. Greenhouses may thus be emptied on schedule for the next crop. Generalized estimates of required laboratory facilities and costs for commercial clone production have been made (Anderson et al., 1977, Hartman, 1979; Barnes, 1979). Minimal equipment and initial supply costs for a modest production laboratory capable of producing 10,000 plants per week appear to be in the range of $25,000 and the plants produced may cost $0.15 to $0.25 each. Of course these figures depend on expected volume and do not factor in the cost of the research and development of the methodology to be used. Forest clone production, with its stable and continuous market for vast numbers of propagules that must compete with the low cost of seedlings, places strong emphasis on efficiency and economy. This use then departs from the commercial forces that have shaped horticultural clone production. We likely must face the modest but nagging variability problems of callus culture that horticulture could ignore by choosing a different route.

We are not alone, however. Recombinant DNA technology will require callus or cell suspension cultures as the vehicle for new gene insertion into plants. After insertion the callus must regenerate plants which faithfully display their genetic constitution. Others, working along these lines on many different crops, will also focus on understanding and eliminating the small but irritating degree of variability in plants coming from callus cultures. This much effort, on many species, focussed on one problem must surely succeed. The existing variability has even been turned to constructive ends as a source of variant-improved varieties in vegetatively propagated crops such as potato (Shepard et al., 1980). These variants likely represent changes in regulation of existing genes and a new door to useful genetic alteration may have been opened. Time will tell.

The recombinant DNA technology and its logical extensions will serve the forest industry in even more direct ways. Large amounts of particular plant genes can now be manufactured in bacteria. Bacteria contain extra pieces of DNA (plasmids), perhaps viral in origin. Gene sequences from plants can be attached to these pieces and, after they are multiplied within bacteria, one can harvest the bacteria and retrieve many identical copies of the desired plant gene sequence. Now with enough copies, the researcher can set about the task of exposing plant cells to these copies in such a way that the gene sequence becomes incorporated into the permanent genetic composition of the plant cells. If plants are then made from the cells, the cloned plants have the desired gene and thus the new, desirable trait. If the gene imparts disease resistance, the plant now has become a disease resistant variety. Many obstacles exist on the way to commercial application for trees, but the thrust is clear, and the obstacles are being overcome in other crops.

Armed with many copies of a particular gene sequence it is also possible to locate the natural position of that gene on the plant chromosomes. Genetic maps of the chromosomes can be constructed from such test tube manipulation without waiting 6 years for cone and seed production on the tree. Such maps of gene location and linkage with other genes are of great help to the breeder. In addition, when the cell wall is removed from cultured plant cells, the resulting naked protoplasts can be made to fuse. Protoplasts from two plants may thus fuse to produce a hybrid containing the DNA from both parent cells. In principle, we have then accomplished what normally occurs when pollen fertilizes the egg in the pine cone -- but again without the need for pollen or egg. The hybrid plants generated from the cells by way of callus may themselves be useful improvements. Alternatively, as cells divide in callus, most of the chromosomes of one or the other parent may be lost, leaving the chromosomes of one parent with but one chromosome exchanged for its counterpart from the other parent. If desired genes reside in that chromosome, we have made an improvement. Also, since we have only one foreign chromosome, any new traits gained can be attributed to genes on that particular chromosome. Genetic maps can be made by this device as well. Such mapping was conducted effectively for all human chromosomes using hybrid cells between man and mouse. Recent non-technical reviews of this work with human cell cultures (Ruddle and Kucherlapati, 1974) and with gene location on chromosomes (Chambon, 1981) give an appreciation of the possibilities which might be applied to conifers.

Further elaboration of this emerging technology is probably premature, and it is certainly beyond the scope of this paper. It is enough that we recognize that different and powerful capabilities are being developed which will aid tree breeders. Callus and suspension cultures are central to the new technology. Mass vegetative propagation from callus is close at hand. The next and necessary step is to couple this with the advancing technology of genetic manipulation. In this way, rapid breeding programs can generate the new trees that will be worth cloning. I think it appropriate to mention here that it is the business of the forest industry to keep alert to the rules regarding gene-splicing and recombinant DNA now being considered by federal governments. These rules govern whether genetically altered plants and other organisms can be deployed in the field. The forest industry and tree breeders have a stake in the deliberations which will yield the rules.

CONIFER TECHNOLOGY

The technology now exists for the clonal propagation of most conifers from embryonic or seedling materials. Some ten pine species, two spruces, Sequoia, Douglas-fir, Western red cedar, Western hemlock, Cupressus species and others have all shown this potential (Mott, 1981). A specific and detailed step-wise procedure has been developed for loblolly pine (Mott and Amerson, 1981). Seedling cotyledons are used and the method has been tested across many seed families. It extends to other pines including white pine (Mott and Amerson, in press). Clones of 10 or so rooted plants can be expected on the average, but exceptional seedlings can yield much greater numbers approaching 100. Exceptional clones can yield high numbers in radiata pine as well (Aitken et al., 1981), and schemes to recycle and prolong shoot generating cultures show promise to increase numbers with even the less exceptional clones of these species. These sets of propagation methods, applicable to conifers in general, all add up to about what is generally used in the horticultural industry. Clones are produced directly from excised plant parts without intervening callus. The difference is that with conifers, only young seedling materials may be used, not mature trees, and the shoot generation can not yet be prolonged indefinitely. Therefore, the clone numbers are small. Some schemes have been developed (Boulay and Franclet, 1977) which avoid even adventitious buds and relay on axillary bud break to produce new shoots which again produce axillary buds, etc. These schemes of course can be carried on indefinitely to produce large clone numbers which retain juvenility, but the method is labor intensive, and the clones are much too expensive for reforestation.

Small clones of some species have been planted in soil for observation, eg., loblolly pine, radiata pine, Sequoia, Douglas-fir, and Western hemlock. But with the exception of loblolly pine (Kelly, 1978; Leach, 1978, 1979) little public information on performance of the clones in soil is available. It is, therefore, not possible to make confident statements about clonal fidelity in the field for tissue-culture-produced conifer plants. Our research programs at North Carolina State University address this need to carry on through from the lab bench discovery of methods, to production-oriented improvement and ultimately to greenhouse and field testing of the product trees. This program is well underway with clones in the greenhouse being made ready for field plantings. Cooperative support for this work comes from the University and from an increasing number of companies, currently twelve, within the forest industry.

The current technology is thus sufficient for small clone production, and it is being used to research the fidelity and worth of such propagules in the field. Further improvement is likely, such that one can envision shoot production and growth from excised cotyledons using exchangeable liquid medium to reduce handling costs and rooting of the shoots directly in soil as plants grow to planting size under greenhouse conditions. The costs per plant will be reduced accordingly, but the drawback will still be that seedling material must be used when clones from elite mature trees would be far more desirable. Even so, the methodology developed for seedling material will apply to clone production from mature-tree parts when that comes along.

Laboratory demonstrations of clone production from the terminal buds (Arnold and Eriksson, 1979) or from fascicles (Mehra-Palta et al., 1978) of older mature trees have been reported. Adequate surface sterilization of buds and fascicles from the field presents a major problem as does selection at the proper season. In the absence of prolonged shoot generation in culture, the above problems limit clone sizes available by this route, but the clones are from mature trees. Major improvements will be necessary before this avenue is reliably available. Considering the obstacles it is more likely that economical clone production from mature trees will eventually come via intermediate callus obtained from stems or buds. Some shoot production (organogenesis) has been reported from a callus-like culture of Pinus wallichiana initiated from embryos (Konar and Singh, 1980). An imprecise method for early stages of embryogenesis from suspension cultures initiated from Douglas-fir cotyledons was reported as a U. S. Patent No. 4, 217, 730, August 19, 1980. Although both started with embryo or seedling materials they deal with occurrences that have relevance for clone production from mature trees. It will not be long before the discoveries are made which make economical clone production from mature trees a reality. When this occurs, much of the methodology will already have been mastered for handling the shoots or embryos to ensure growth to plantlets ready for the field. We expect the clonal fidelity studies in the field to show faithful clonal traits and consequently we anticipate that mass propagation will faithfully capture for our use the non-additive genetic variance in present tree populations.

Once plantlet regeneration from callus is reliably achieved, whether by organogenesis or embryogenesis, the way is open for genetic manipulations to aid breeding programs. Genetically altered callus can then be made to regenerate genetically altered plants. New and better trees will be generated by current, traditional breeding programs and subsequent mass vegetative propagation will yield second generation capture of non-additive tree improvement. Selection in culture for desirable tree traits will be an important part of mass propagation of these trees, and an even more critical part of in vitro genetic DNA manipulation. If a gene sequence or a chromosome is inserted into a cell, one must be able to recognize its presence in culture by observing the associated trait now acquired by the cell. In this way, the correctly altered cells may be selected for use in subsequent plantlet regeneration. Work must be started now to identify traits which can be recognized at the cellular or callus level in culture. A catalog of these genetic marker traits must be assembled to support the genetic manipulation work to come, if conifers are to take a rightful place in the wave of advancing technology. Foresters and tree breeders should become educated to the nature of markers useful for this purpose, for it is the people who work with the trees

that represent the library from which the catalog must be constructed. Things like albino seedlings, or trees with characteristic terpenes and lignins come to mind.

We have developed procedures for axenic culture of the fusiform rust fungus (Amerson and Mott, 1978) and the blister rust fungus, which are being used to study conifer host resistance to these diseases in culture. This may provide marker traits which can be seen at the cellular level, but it also brings the power of cloned host plus cloned pathogen to bear on the study of the control of disease resistance. It is evident that the emerging tissue culture technology can have practical impact beyond mass propagation. There is potential for impact even with symbiotic organisms. Nitrogen-fixing bacteria were inserted into a conifer mycorrhizal fungus, and the fungus gained the capacity to fix nitrogen (Giles and Whitehead, 1977). Successful mycorrhizal association with pine in the soil and nitrogen fixation beneficial to the pine have yet to be reported, but the example is served.

CONCLUSIONS

Reliable tissue culture propagation for conifers now exists to produce clones of ten to one hundred members from juvenile materials. These clones are being used to develop better methods and to evaluate fidelity in the field. Field performance is promising at this early stage. The economics of reforestation foster a thrust toward plantlet regeneration from an intermediate callus culture. This thrust also fits in with a developing genetic engineering technology which can greatly aid tree breeding programs. Mass clonal propagation from elite mature trees is close at hand and will be aided by preliminary work with clones of juvenile material. As the achievement of mass propagation draws near, the potential of test-tube genetics and test-tube selection for desirable traits stands out and calls for some preliminary action. Conifer tissue culture thus seems poised and ready to move with the leading edge of an emerging technology seemingly without bounds.

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TISSUE CULTURE AND GREENHOUSE PRACTICES FOR THE PRODUCTION OF LOBLOLLY PINE PLANTLETS

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Abstract.--Methodology is presented for tissue culture propagation of Pinus taeda. Pulse stimulation of adventitious shoot production on a cytokinin rich medium, is followed by shoot organization and growth on medium devoid of growth regulators. Rooting is initiated with a high concentration auxin pulse and completed on a medium free of exogenous auxins. When roots are about 5 mm long the plantlets are transferred to a fine textured soil mix of peat, vermiculite, and perlite under intermittent mist in the greenhouse. Leach tubes are used to promote a strong, well developed root system for transfer to the field.

Additional keywords: Pinus taeda, rooting, in vitro, vegetative propagation.

Conifer tissue culture has received great interest in the last 10 years and is now realistically viewed as a potential method for vegetative propagation. Early work on adventitious bud formation in Pinus palustris (Sommer et al. 1975) paved the way for research on many different species (Mott and Amerson 1981). Despite the high level of effort, only about 10 species have produced rooted plantlets which could be carried to soil media (Mott 1981), and detailed greenhouse and field studies have not been reported for any species.

The tissue culture program for loblolly pine (Pinus taeda L.) at N.C. State University was initiated in 1974 and expanded in 1979 to produce and thoroughly evaluate plantlets in the laboratory, greenhouse, and field. Methods developed by Mehra-Palta et al. (1978) and Mott et al. (1977) provided an initial building point for propagation work on about 40 open-pollinated families in an effort to produce several thousand plantlets for evaluation. Early studies by Kelly (1978) and Leach (1978, 1979) served as initial guides for greenhouse and field work. Many changes and improvements have been made from these starting points both in the laboratory and the greenhouse. All phases of the culturing process; shoot initiation, elongation, rooting, plantlet transfer to the soil, and greenhouse growth have developed to the point that plantlets can be routinely obtained from most families. This paper reports these improvements and developments.

TISSUE CULTURE PROCEDURES AND RESULTS

The sequence of steps which constitutes the process used for clonal plantlet production from seed embryos of Pinus taeda as diagrammed by Mott and Amerson (1981) is given in figure 1. This process outlines overall steps, but more importantly it recognizes a number of substeps which must be accomplished

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in the proper sequence via judicious addition and removal of growth regulators (i.e. pulse techniques) (Mott and Amerson 1981). Examination of the process will follow on a step by step basis, with particular emphasis on step 3, rooting of shoots.

Step 1. Explant pretreatment
Partial seed germination, excise cotyledons
↓
Step 2. Shoot initiation and growth
2a: Cell division in peripheral tissues of cultured cotyledons
2b: Adventitious shoot development
2c: Excised shoot stem growth
↓
Step 3. Rooting of shoots
3a: Cell division near vascular tissues at stem base
3b: Root development and growth
↓
Transfer to the soil

Figure 1.--A diagrammatic process for tissue culture propagation of pine from cotyledons of excised embryos.

Examination of the Process

Step 1. Explant pretreatment.--Seeds are scarified at the micropylar end and pretreated in 1% H_2O_2 (changed daily) at 28° to 32°C to stimulate germination (Ching and Parker 1958). After 4 to 5 days of H_2O_2 treatment, the seed coats are removed. Next, the embryos and the female gametophyte tissues are surface sterilized in 15% clorox for 5 minutes and then rinsed 3 times (3-5 minutes per rinse) in sterile distilled water. Following surface sterilization, the embryo is separated from the gametophyte and the cotyledons are excised and placed on a modified GD_1 (Gresshoff and Doy 1) shoot initiation medium (Mehra-Palta et al. 1978, Mott and Amerson 1981) containing 10 mg/l BAP (6-benzylamino-purine) and 0.01 mg/l NAA (α-naphthaleneacetic acid). All media used throughout the process are adjusted to pH 5.5 prior to autoclaving and solidified with 1% agar.

Step 2. Shoot initiation and growth.--There are three substeps necessary for shoot initiation and growth: a. stimulation of cell division, b. shoot development, and c. shoot growth. This tricotomy is necessary since the treatment which stimulates cell division is antagonistic to shoot development and growth.

Substep 2a: Shoot initiation.--The newly excised cotyledons (Step 1) are placed on the shoot initiation medium and maintained at 21±2°C under 1000 to 2000 lux mixed incandescent and fluorescent light. After 2 weeks, numerous cell divisions are visible in the epidermal region, and after 4 to 6 weeks cotyledons are ready for removal from the high cytokinin initiation medium. Cotyledons ready for transfer to substep 2b typically appear swollen, shiny, dark green, and bumpy due to surface divisions (fig. 2a).

Substep 2b: Shoot organization.--Cotyledons entering this substep are placed on half strength GD_1 medium ($GD_{\frac{1}{2}}$) which contains 1% activated charcoal and no added growth regulators. The charcoal facilitates removal of the

regulators used in substep 2a. Cotyledons typically remain on charcoal medium for 4 weeks at 21±2°C under 8000-9000 lux mixed incandescent and fluorescent light. During this period, small shoot apices begin to differentiate. Continued exposure to the charcoal medium is considered detrimental to further development; thus, the cotyledons with newly differentiated shoots are transferred to GD½ without charcoal. Shoots, still attached to the cotyledons, remain on this medium for 4 to 8 weeks (1 or 2 transfers). During this 4 to 8 week period, the developing shoots become crowded on the cotyledons and when shoots are 2-5 mm long they are transfered to substep 2c.

Substep 2c: Shoot growth.--All shoots and developing shoot clusters are excised form the cotyledons and placed individually on GD½ medium. Shoots remain on this medium for 4 to 12 weeks (1 to 3 transfers) in the same environment used in substep 2b to allow for elongation. Individual shoots typically grow well, but shoot clusters often fail to grow or grow slowly. Shoots that reach a total height of 0.5 cm are acceptable for rooting, but those shoots ≥1.5 cm in height (fig. 2b) are better since preparation for the rooting step requires a fresh basal cut of the stem.

With loblolly pine, adherence to the above methods generally results in shoot initiation from more than 80% of the embryos tested. One can expect an average of 35 to 40 shoots per embryo, but embryos producing as few as 1 or as many as 100 shoots are not uncommon. Currently, about 37% of the shoots produced elongate to a height of 0.5 cm or greater, but higher percentages for individual embryos are common.

Step 3: Rooting of shoots.--As with shoot initiation, the rooting process requires substeps, since the treatment which stimulates cell division at the basal end of the stem is antagonistic to further root development.

Substep 3a: Stimulation of cell division.--Shoots which reach a height of 0.5 cm or more may be rooted. These shoots receive a fresh basal cut on the existing stem and are placed on root initiation medium (GD½±BAP 0.1 mg/l and NAA 0.5 mg/l) for 6-13 days. The shoots are maintained at 23±3°C under 1000 to 2000 lux mixed incandescent and warm white fluorescent light. Cell division begins at the stem base within a few days and continues in the presence of auxin. Mott and Amerson (1981) indicated that the shoots were ready for transfer to substep 3b when cell division had progressed to a point where the stem base was swollen, the epidermis was split, and extruded basal callus was evident. That point typically occurred within 10 to 12 days. More recently, we modified our evaluation of substep 3a and no longer seek extruded callus as a signal for passage to substep 3b. The degree of basal swelling and very slight epidermal splitting now sought (fig. 2c) is less than that described by Mott and Amerson (1981) and generally occurs within 8 to 9 days on the above root initiation medium.

Substep 3b: Root formation and growth.--Shoots transferred to substep 3b are placed on GD½ medium devoid of growth regulators, and are maintained under the environmental conditions described in 3a. Root primordia typically emerge from the basal callus pad within 14 to 21 days, but occasionally they appear earlier. Once root primordia are observed, the rooted shoots should be maintained on GD½ medium until roots are at least 3 mm long, and preferably

5 mm or more long (fig. 2d). Plantlets at this stage are suitable for transfer to the soil.

Examination of the Factors Influencing Rooting

Many different parameters and shoot characteristics are emerging as important factors that influence rooting. Shoot age, shoot size, basal medium, growth regulators (types and concentrations), pulse vs. continuous stimulation, previous exposure to rooting trials, and environmental factors such as light quality and quantity all exercise some influence on the rooting efficiency of loblolly pine. All of these factors have been or currently are being evaluated. Two of these factors, shoot size and pulse vs. continuous auxin treatment will be considered here.

Shoot size has an influence on the rooting efficiency of shoots which are pulse treated with GD½ BAP 0.1 mg/l + NAA 0.5 mg/l. Generally, with other parameters equal, larger shoots root better than smaller shoots. This trend has been seen in a number of experiments and table 1, a data set from one experiment, demonstrates the degree of influence. All shoots included in this table were vigorous and of equal age (6.5 months old at the time of rooting). Environmental treatment for all size categories was the same.

Table 1.--Rooting performance by size categories for loblolly pine shoots pulse treated for 9 days with GD½ BAP 0.1 mg/l + NAA 0.5 mg/l

Shoot size	Number Tested	Number Rooted	Percent Rooted[1/]
< 0.5 cm	106	57	54[a]
> 0.5 cm but < 1.5 cm	145	94	65[ab]
> 1.5 cm	14	12	86 [b]

1/ Percentages followed by different letters indicate a significant χ^2 difference at $\alpha = 0.05$.

Comparisons of pulse vs. continuous treatments should consider the rooting percentages obtained, but also should note the time required for rooting. Thus far, the best continuous auxin exposure treatment tested utilized GD½ BAP 0.1 mg/l + NAA 0.1 mg/l medium. This treatment produced an average of 37% rooting in 12 weeks. In contrast, pulse treatments with GD½ BAP 0.1 mg/l + NAA 0.5 mg/l for 6-13 days followed by transfer to GD½ medium routinely produced 60-85% rooting. Rooting via pulse treatments typically is completed 5 to 6 weeks after the pulse, thus the total process requires only 6 to 8 weeks. In comparison to continuous exposure treatments, pulse treatments have given higher rooting percentages in a shorter time period. However, further work is needed before continuous exposure treatments are abolished, since constant exposure treatments were conducted early in the research program before many of the parameters influencing rooting were recognized. In contrast, the pulse treatments were conducted more recently and thus may have some advantage. Experiments are now in progress with shoots of equal quality

in both pulse and continuous treatments to see if continuous treatments can match both the high percentage and rapid rooting obtained with pulse treatments.

GREENHOUSE PRACTICES

There is little published information concerning the growth of tissue cultured conifer plantlets in soil, since few species have been successfully rooted and transferred to soil. Research dealing with transfer of plantlets to the soil has been largely neglected not only for conifers (Thorpe 1977) but also for most crop species (Murashige 1974). However, early studies with loblolly pine by Kelly (1978) and Leach (1978, 1979) indicated that plantlets could be successfully transferred from culture medium to the soil with a reasonable degree of success.

Current Greenhouse Practices

Rooted shoots with total top length (including needles) of 1-2 cm and root length of 3-5 mm or greater are most suitable for transfer to the soil. Plantlets are transplanted directly from the agar medium to soil mix in 164 ml Leach tubes on a greenhouse bench under shade cloth with intermittent mist.

Soil.--The texture of the soil mix is critical for the survival of the small plantlets. A very fine mix of peat, vermiculite, and perlite is necessary since the roots on the plantlets are initially so small that poor soil-root contact results if a coarse mix is used. The fine grades of perlite and vermiculite are used, and the peat is sifted through a 3 mm mesh screen. The pH of the soil is raised to 5.5 by the addition of $Ca(OH)_2$ at approximately 1.5 g/l peat.

Mist.--A Mist-O-Matic® is used to control the amount of mist applied to the plantlets by spraying a fine mist when water droplets evaporate from the control mechanism. This is preferred to an arbitrary misting schedule using time clocks. The mist bench is covered only with 47% shade cloth so that the amount of mist applied fluctuates depending upon temperature and humidity. Plantlets remain in the mist bench until new needle growth is apparent, usually in 10 days to 3 weeks. New needle growth generally indicates that the plantlet's roots are growing and that it is acclimated to greenhouse conditions. The first few weeks of growth in the greenhouse are very critical to survival of the plantlets. Once they are established with well developed root systems (at about 2 months of age) survival to transplanting size is almost assured. The most recent greenhouse experiment started in March, 1981, had a survival of 136 out of 144 plantlets or 94% after two months.

Containerization.--Choice of container is very important for survival and growth of plantlets in the field. Unlike seedlings, tissue culture plantlets do not tend to form a strong taproot. The plantlets usually develop one or two main roots which grow laterally rather than down. If plantlets are grown in conventional pots, the main root circles within the pot and forms a coiled root system (fig. 2e and 2f). Apparently this is a less serious problem for seedlings since the taproot grows straight down and the laterals circle in the pot. Seedling roots can be pot-bound and still grow outward to give support.

The Leach tubes which we are now using force the tissue culture roots to grow downward like a taproot. The ribs in the tube prevent coiling, and the air pruning at the bottom promotes more lateral branching (fig. 2e). The general root configuration of plantlets in tubes is much superior to that in pots.

CONCLUSIONS

Tissue culture and greenhouse procedures for vegetative propagation of loblolly pine have progressed to a point where plantlets are routinely obtained from embryonic material. Pulse application of growth regulators is fundamental to the tissue culture process. Initial greenhouse survival of plantlets is highly dependent upon soil, temperature, and moisture regimes.

Information obtained from and methods developed with plantlets from embryonic origin have experimental value, and value as aids in developing methods for mass propagation of plantlets from callus of mature trees. The steps in callus propagation should be essentailly the same as those from embryonic culture once shoots are obtained. Shoots will be elongated followed by rooting, transfer to soil, and growth in the greenhouse.

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The use of trade names in this manuscript does not imply endorsement of the product named nor criticism of similar products not named.

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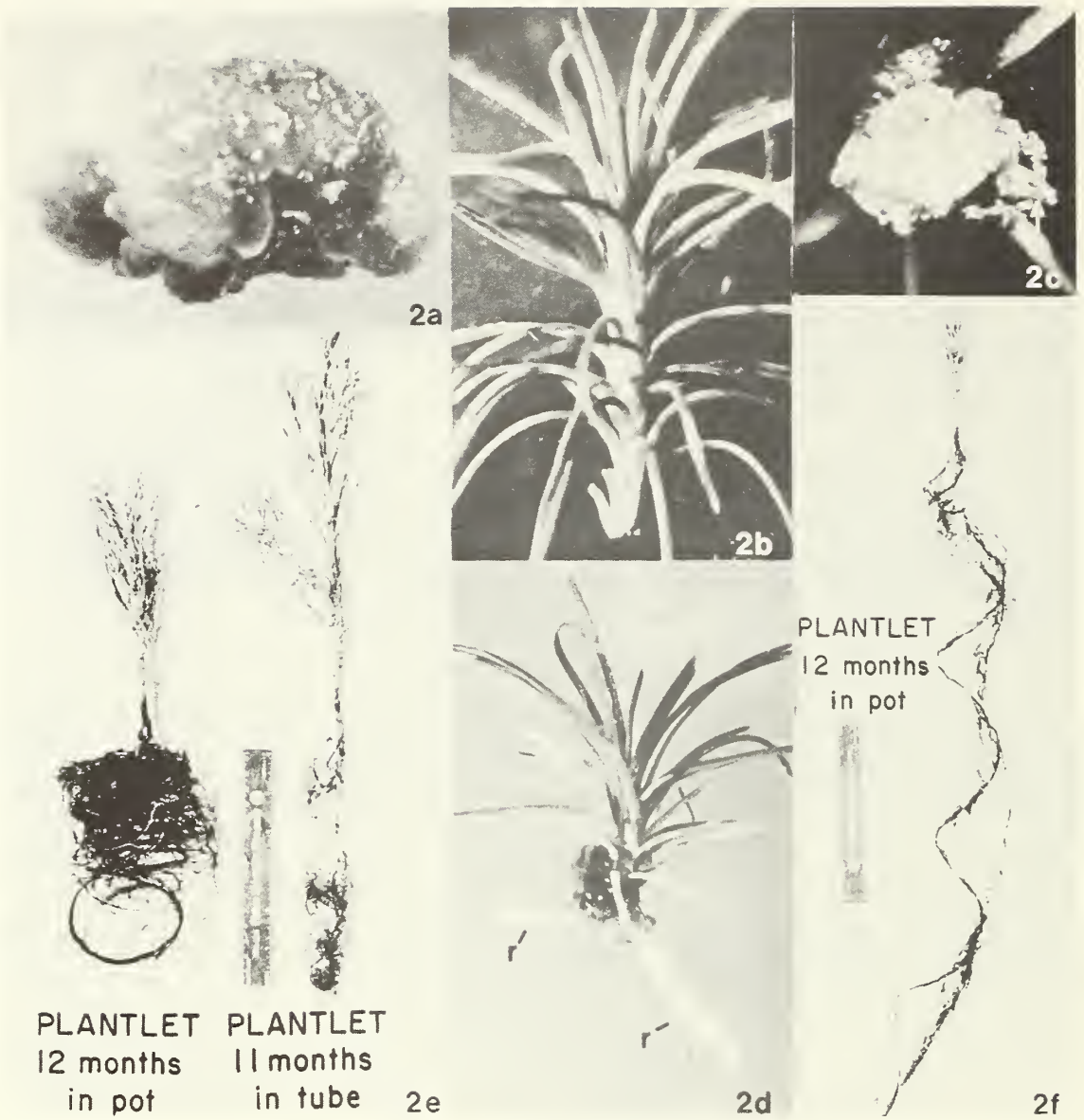

Figure 2.--Various stages of loblolly pine plantlet development.

2a.* Cotyledon ready for transfer to substep 2b. Note shiny, bumpy surface. 13 X

2b.* An adventitious shoot ca. 1.5 cm long. 4X

2c. An end view of a shoot base showing the proper degree of basal swelling (cell division) sought in pulse stimulated rooting. Note: split epidermis (arrow), and intact epidermis (e). 16X

2d.* A rooted propagule ready for transfer to soil medium. 2X

2e. Root systems of a potted plantlet (severely coiled roots) and a tubed plantlet after about one year in soil.

2f. Uncoiled roots of the potted plantlet shown in Figure 2e.

* Pictures from Mott and Amerson 1981.

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ROOTING ABILITY AND VEGETATIVE GROWTH PERFORMANCE OF STEM CUTTINGS FROM ONE- AND FIVE-YEAR-OLD ORTETS OF LOBLOLLY PINE

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Abstract.--Mist provided by nozzles on a gantry boom provide much more even mist than fixed nozzles, which has apparently doubled the percentage of cuttings with roots. Cuttings from 5-year-old ortets rooted significantly better than those from 1-year-old ortets, and rootability varied significantly according to the origin of the cutting in the crown. Cuttings from 1-year-old ortets have grown significantly more than those from 5-year-old ortets after 1 year in the field.

Additional key words: competition, juvenility, Pinus taeda, vegetative propagation.

The purpose of this study is to a) evaluate rooting under a new gantry system; b) compare rooting ability from ortets of loblolly pine aged 1 and 5 years; and c) compare the growth potential of cuttings from these ortets.

Greenwood et al (1980) report that amount of mist fall may explain as much as 75% of the variation observed in rooting loblolly and shortleaf pine stem cuttings. Mist systems with fixed nozzles, which provide an overlapping circular spraying pattern, are bound to provide variable mist fall. Here we report on results obtained with nozzles attached to a moving boom which produce a flat, fan-shapped pattern.

In addition, given the current interest (See Zobel, these Proceedings) in the possibility of mass propagation of select genetic material, we report on the rootability and early growth performance of cuttings from 1- and 5-year-old ortets. One-year-old loblolly pine trees possess a number of traits, both morphological and developmental, which appear to be lost with maturation. Among them are differences in branching and growth characteristics (Greenwood, 1980). There is also a significant decline in the ability of 4-year-old scions to elongate and an increase in ability to flower when compared with 1-year-old scions (Greenwood, 1981). Lambeth (1980) suggests that selections in loblolly pine tests can be made as early as age five with relatively high efficiency in gain per year. Even if families or individual selections can be made at this early age, the consequences of possible loss of juvenile growth characteristics of vegetative propagules must be carefully considered.

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Similar problems in the vegetative propagation of Pinus radiata have already been dealt with extensively (E.G. Sweet, 1973 and Libby, et al, 1972).

METHODS

Plant Material

Cuttings were taken from trees representing five coastal North Carolina half-sib families in two different aged plantings. The older planting was established with containerized seedlings sown on 5-7-73 in 131 ml plastic containers, which were later transplanted into 400 ml plastic cups. The medium consisted of Redi-earth® (W.R. Grace and Co., Cambridge, Mass. 02140) and the seedlings were watered weekly with 5 N Hoagland's solution. The trees were planted north of Hot Springs, Arkansas on 4-1-74, and received complete fertilization (about 200 Kg/ha) in the early spring of 1975 and 1978. During their first three years, tip moth control was applied using either Dursban®, Guthion®, or Disyston® according to the manufacturers recommendation.

The younger planting consisted of trees sown on 6-29-77 in 164 cm^3 plastic tubes, in a medium consisting of peat:vermiculite:perlite (5:5:1 by volume) containing a timed release fertilizer (Osmocote® 18-6-12 at 11.3 g per 4.5 l of medium). The seedlings were kept in a shade house and received 5 N Hoagland's solution weekly until the end of September, 1977. In April, 1978, the seedlings were repotted into 3.8 l pots (medium sand:vermiculite:peat moss, 2:1:1 by volume with Osmocote® added), and placed outdoors. Disyston® (.375 g/pot) was applied to control tip moth.

Thus the older trees were between 5 and 6 years, and the younger between 1 and 2 years from seed when cuttings were taken.

Two rooting experiments were carried out, with cuttings for the first taken on 10-25-78 and the second on 3-5-79. Cuttings were taken from 3 parts of the live crown, as shown in Figures 1 and 2. Twelve trees per family were sampled as 1-year-old ortets, while 6 trees per family were sampled as 5-year-old ortets. Individual ortets identities were not maintained. A single cutting (from the main stem) was removed from each third of the crown of the 1-year-old trees while 2 cuttings were taken from each third of the 5-year-old trees. The cuttings were stored in plastic bags at 4°C for about 24 hours until they were placed in the rooting bench. Prior to sticking, the needles were removed from the base of the cuttings, the base reclipped, wetted, and dipped in 0.5 strength Hare's powder (Greenwood et al, 1980 and Hare, 1974). After trimming the needles to a length of 7-8 cm, the cuttings were stuck 6 cm apart in perlite:vermiculite (1:1 by volume). The average total length of the cuttings was 10 cm for the 5-year-old cuttings and 8 cm for the 1-year-old cuttings. A total of 360 cuttings were stuck in each experiment, with a total of 12 cuttings in each family-age-crown position combination. Each combination was represented by two 6 cutting row plots randomly located in the rooting bench.

Rooting Bench

The rooting bench consisted of a 1.8 x 1.4 x 1.2 m tubular aluminum frame covered with a clear polyvinyl tent. Uniform mist was provided by a gantry boom equipped with 6 nozzles spaced 20 cm apart (#500017, Spraying Systems Co., 4735 Sanford Street, P. O. Box 7278, Metairie, LA). The gantry boom was controlled by a timer (#7994, Veeder-Root Digital Systems Div., Hartford, Conn.) and moved at 2.7 cm/sec. The boom made 2 sweeps 4 times per hour from 7 a.m. to 4 p.m., one time per hour from 4 p.m. to 2 a.m., once per two hours from 2 a.m. to 7 a.m. Overall, the cuttings received between 0.1 and 0.2 mm of mist per hour.

Photoperiod was extended to 20 hours with incandescent lamps, providing an intensity of 2 w/m^2. Bottom heat of 29°C was provided, and an exhaust fan provided cooling when the air temperature in the bench exceeded 26°C. Carbon dioxide levels of 1500-2000 ppm were maintained by timed addition of CO_2. The delivery system was calibrated using an infra-red gas analyzer (Infra-red Industries, Inc., Box 989, Santa Barbara, CA 93102).

The cuttings were sprayed 3 times weekly with 1 N Hoagland's solution and 1 time per week with $AgNO_3$ (250 mg/l). The silver nitrate spray inhibits algae growth. The cuttings in both experiments remained in the bench about 100 days, when all were lifted and scored for rooting. The rooted cuttings from Experiment 1 were potted as described earlier, and kept in the greenhouse until 7-12-79, when they were moved into a shade house where they overwintered. The cuttings from Experiment 2 were potted and kept in the greenhouse until September, 1979, when they were moved into the shade house. About the same number of rooted cuttings resulted from each experiment and the healthiest, straightest plants from both experiments were selected for field planting. Only plants representing cuttings from the terminal shoot from 1-year-old ortets were outplanted, because cuttings not taken from the terminal shoot had several well-developed lateral branches which tended to be plagiotropic. Many cuttings from the 5-year-old ortets have continued to grow plagiotropically. The cuttings have received both weed control and complete fertilization each spring. Plants resulting from both 1- and 5-year-old cuttings from each family were outplanted near Hot Springs on 3-26-80. The planting consists of 5 replications, each containing a single cutting from each age and family. Plant height was measured and total numbers of growth cycles were counted on 3-27-80 and 3-2-81. Analysis of variance was done on rooting results after arc-sin transformation of each row plot rooting percentage. Crowth data were also subjected to analysis of variance.

RESULTS

Rooting by Age and Family

Significant differences in rooting between cuttings from different ortet ages, crown position and half-sib families occurred (see Table 1). In addition, there were some significant two-way interactions. Only one higher order interaction was significant ($p \leq .01$), experiment x year x position, which probably reflects the variation in rooting by crown position in the two experiments for both 1-and 5-year-old ortets (see Figures 1 and 2). The combined means for Experiments 1 and 2 by half-sib family and ortet age

Table 1.--ANOVA for rooting by ortet age, crown position and half sib family

Source of Variation	DF	F	Significance
Experiment 1 vs 2	1	.007	0.935
Ortet Age	1	9.222	0.002
Crown Position	2	4.554	0.011
Family	4	8.033	0.000
Experiment x Age	1	7.336	0.007
Experiment x Position	2	3.422	0.033
Experiment x Family	4	1.539	0.189
Age x Position	2	17.568	0.000
Age x Family	4	1.559	0.183
Position x Family	8	0.899	0.517
Residual	660	0.206	

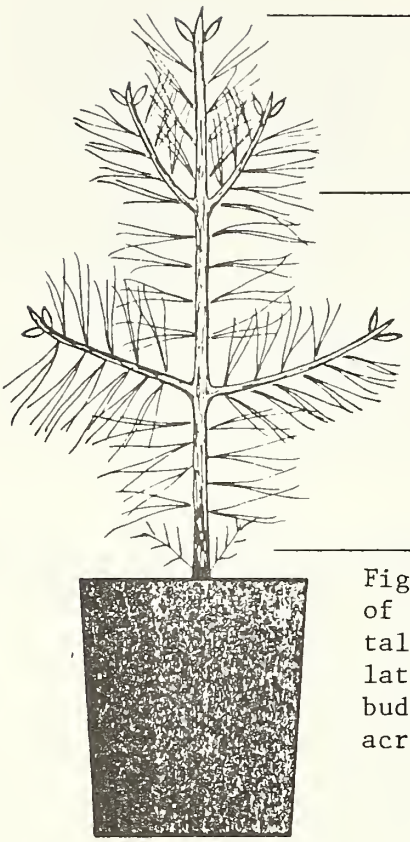
Table 2.--Rooting (%) by Family and Ortet Age. Different letters indicate significant differences at $p < .05$ (Duncan's Test). Overall means are different at $p < .05$.

	ORTET AGE	
FAMILY	1 YR	5 YR
8-59	42 a	40 b
8-86	34 a	44 b
8-66	15 b	22 c
8-76	31 a	40 b
8-01	39 a	60 a
Overall	32	41

Table 3.--Elongation growth and number of cycles produced by field planted cuttings from 1-and 5-year-old ortets in 1979 and 1980 growing seasons. Differences in height and number of cycles by ortet age are significant at $p < .05$.

	ORTET AGE			
	1 YR		5 YR	
	Height	#Cycles	Height	#Cycles
March 27, 1980	41.3 cm	5.4	33.6	4.8
% Change	516	540	336	480
March 2, 1981	80.7	8.0	63.4	7.0
% Change	96	49	89	46

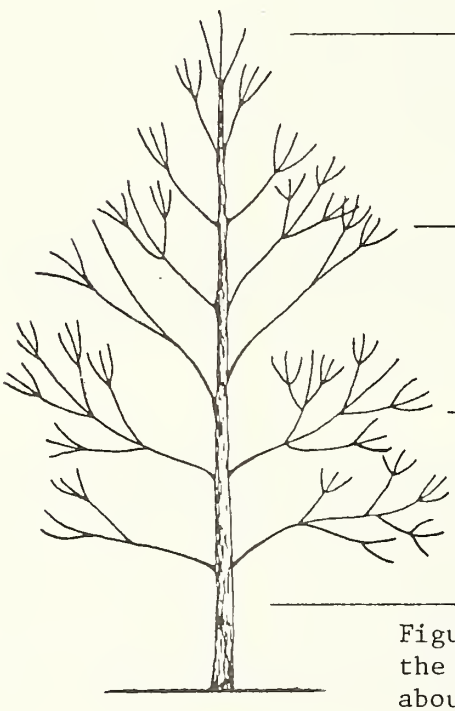
1 YEAR OLD TREES



	ROOTING % (n = 60)	
	Expt. 1	Expt. 2
Upper	33 a	57 a
Middle	28 a	38 b
Lower	22 a	13 c

Figure 1.--Rooting (%) by cuttings from 3 parts of 1-year-old potted trees which were about .5 m tall. Each cutting included either a whorl of lateral branches or lateral buds and the terminal bud at the apical end. Results were combined across all 5 families.

5 YEAR OLD TREES



	ROOTING % (n = 60)	
	Expt. 1	Expt. 2
Upper	30 b	26 b
Middle	68 a	37 b
Lower	37 b	50 a

Figure 2.--Rooting (%) by cuttings from 3 parts of the live crown of 5-year-old trees, which were about 5 m tall. Results were combined across all 5 families.

are shown in Table 2. Family 8-66 is a poor rooter regardless of ortet age, while Families 8-59 and 8-01 rooted relatively well. Variation due to the interaction between ortet age and family was not significant. Overall, cuttings from 5-year-old ortets rooted better ($p \leq .05$) than cuttings from 1-year-old ortets.

The results of rooting by crown position for both experiments are shown in Figure 1 for 1-year-old ortets and Figure 2 for 5-year-old ortets. The cuttings from the upper third of the 1-year-old ortets rooted best in both experiments, but the differences were significant only in Experiment 2. In contrast, cuttings from the upper third of 5-year-old ortets rooted less well in both experiments (note significance of the age x position interaction in Table 1). In Experiment 1, cuttings from the middle third of the crown showed the best rooting, while in Experiment 2 those from the lower third rooted best, which is reflected by the significance of the position by experiment interaction (see Table 1).

Field performance of cuttings

After field planting, survival of the rooted cuttings has been greater than 90%. Height, growth and number of cycles of growth produced during the 1979 and 1980 growing seasons are shown in Table 3. Although the cuttings from the 5-year-old ortets were initially larger and on the whole rooted better than those from 1-year-old ortets, the latter grew significantly more in both growing seasons.

DISCUSSION

Rooting under the gantry system was much improved over previous results that we obtained with fixed nozzles. Overall, rooting of 21% was obtained for loblolly pine using cuttings obtained from the middle to lower part of the crown of 4-year-old trees (Greenwood et al, 1980). Under the gantry system, we obtained 48% rooting with cuttings from the middle to lower crown of 5-year-old loblolly pine (combined results for Experiments 1 and 2, see Figure 2). All cuttings received half strength Hare's powder and supplemental CO_2. Rooting frequency in different parts of the bench did not vary under the gantry system, probably because there was very little variation in mist fall. The results reported here compare favorably with those obtained by Grigsby (1961), who obtained 52% rooting of loblolly pine cuttings in his best experiment. Using similar methods, he was subsequently able to obtain only 23% rooting (Grigsby, 1971).

While the literature abounds with reports of decreased rooting with increased ortet age (E.G. Thimann and Delisle, 1939), we actually obtained better overall rooting on cuttings from 5-year-old ortets than on those from 1-year-old ortets. Grigsby (1961) also obtained better rooting on loblolly pine cuttings from 25-year-old ortets than with cuttings from 6-year-old ortets. However, if rooting is compared only between cuttings from the upper third of the crown, cuttings from 1-year-old ortets appear to root better (see Figures 1 and 2). Thus, comparisons of rooting by ortet age can be confounded by crown position. Nonetheless, rootability of loblolly pine appears to change little between ages 1 and 5.

The growth performance of the cuttings from the two ortet ages is significantly different. Even though the cuttings from the 5-year-old

ortets rooted better, they have grown less than those from 1-year-old ortets (see Table 3). The differences between the two age groups developed in the first growing season when the 1-year-old cuttings grew much more, relative to the original size of the cuttings. In the second growing season, although the total increment was again greater for the 1-year-old cuttings, the percentage change in height growth and number of cycles for cuttings of both ages was about the same. We have obtained closely similar results with grafted scions taken from ortets of different ages (Greenwood, 1981). Scions from 1-year-old trees grew significantly more than those from 4-, 8-, and 12-year-old trees. The decline between ages 4 and 12 is not as great but is still significant. While the plagiotropic behavior of some of the cuttings from 5-year-old ortets may have affected their growth, no plagiotropic behavior was observed on grafted scions at any age. Franklin (1969) also reports an apparent decline in propagule growth due to increased ortet age (ranging from 10 to 30 years) for slash pine. A similar decline has been reported for Pinus radiata (Libby et al, 1972, and Sweet, 1973).

RECOMMENDATION

A successful effort to vegetatively propagate loblolly pine must take into account the effect of ortet age on the growth performance of the resultant propagules. The relatively more vigorous growth of the 1-year-old cuttings probably results from the ability of young trees to grow more rapidly in their first year or two in the field. Without these growth characteristics, propagules from ortets older than 1 year will probably be at a severe disadvantage.

Therefore, any vegetative propagation program for loblolly pine should use propagules from very young ortets as a standard for evaluation of growth performance of propagules from older ortets, or from procedures which are supposed to maintain or restore juvenile growth behavior. To my knowledge, the youngest ortet age tested in other Pinus species is 4 years (Libby, et al, 1972). The use of seedlings for such comparisons is also desirable, but obtaining seedlings and cuttings of comparable size simultaneously is very difficult, and it is impossible to compensate for the effects of origin (seed vs. cutting or plantlet) on subsequent growth. Since we have observed a rapid decline in vegetative growth capability of loblolly pine between ages 1 and 4, we strongly recommend that the standard for juvenile growth characteristics of loblolly pine be propagated from material no older than one year from seed.

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PROPAGATION OF SWEETGUM BY TISSUE CULTURE

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Abstract.--Clones of sweetgum (Liquidambar styraciflua L.) for research purposes are difficult to obtain using conventional means of vegetative propagation, i.e., rooting cuttings. We have developed tissue culture methods for the vegetative propagation of sweetgum using hypocotyl sections as explant tissue. Multiplication rates of 2 to 30X are obtained from 30-75% of the explant sources. Plantlets have been hardened off, transferred to the lathe house and are ready for field planting. The lapse time from culture to planting stock can be 9 months.

Additional keywords: Organogenesis, adventitious buds, plantlets.

It is evident that there is much research to be done on the tissue culture of forest trees and the role of tissue culture in forestry research and operational forestry. Our current primary interest is in the culture of hardwood species, particularly those being tested for use in short rotation coppice plantations in the Southeast. This is a particularly attractive management option to attempt to integrate with tissue culture propagation. The trees are juvenile throughout the rotation, thus phenotypic selections should be readily brought into culture and differentiation obtained. The species used for the study that is reported here is sweetgum (Liquidambar styraciflua). It is difficult to propagate from cuttings. Also problems have been reported with its propagation from seed in the nursery (Kormanik et al., 1977).

METHODS

The general methods used have been described previously (Sommer and Brown 1980, Birchem et al., 1981, and Sommer 1981). Half-sib seedlots, designated as from upland or bottomland sites, from the U.S. Forest Service Falling Creek seed collection area were used for these experiments.

Media used are those of Murashige and Skoog (MS) (1962), Blaydes (BL) (Witham et al., 1971), and modified Risser and White (RW) (1964). Modifications made to these media have been described (Sommer and Brown 1980, Sommer 1981).

1/ Asst. Prof., School of Forest Resources, University of Georgia, Athens, GA 30602. This research was supported by the Agricultural Experiment Station, University of Georgia; Union Carbide Corporation; and DOE. I wish to thank Dr. Paul P. Kormanik, U.S. Forest Service, Athens, GA for providing seeds and Ms. Janet Johnson and Debbie Fortner for technical assistance and Dr. C. L. Brown for his suggestions.

RESULTS

Preliminary Results

While the results reported here were obtained using seedlings, preliminary results indicate some methods are applicable to stump sprouts and young tree explants.

Earlier we have reported on embryogenesis (Sommer and Brown, 1980). The only comment needed at present is that the process is still sporatic. However, we have grown a number of trees to 2-3 feet in height. Some have survived a summer and a winter in the lathe house and leafed out this spring.

Several years previous to the start of the work to be reported here, callus was obtained from some 50 species of hardwoods on a MS media; however, sweetgum did not produce any callus (Brown, unpublished). Likewise during our initial experiments sweetgum explants did not proliferate on MS based media. Since we had seen callus and roots in anther cultures of sweetgum on BL media we switched to BL based media for initial screening experiments.

Using BL basal medium, the concentrations of NAA (α-napthalene acetic acid) and BA (6-benzyl adenine) were varied. After about 6-8 weeks the hypocotyl sections formed a callus. Some calluses differentiated shoots or roots. In general the effect of the hormones on morphogenesis was similar to the classical results from tobacco, a high ratio of NAA to BA favoring root development, while a low ratio favored bud differentiation. At some intermediate ratios no organogenesis was noted. No combination of auxin and cytokinin used caused all calluses on that treatment to produce organs.

Intermediate Results

A series of experiments was then established in an attempt to optimize conditions for organogenesis or embryogenesis. For this experiment seedlings from 3 upland and 3 bottomland half-sib seed lots were used. Medium consisted of one of 2 basal media, BL and modified RW, with one of 20 combinations of NAA and BA for a total of 2,400 cultures. In 4-8 weeks buds differentiated directly on some of the hypocotyl sections. Most of the hypocotyl sections had produced only callus. Upon analysis of the results, we found buds had differentiated on only one of the 40 media used i.e., modified RW with 0.01 ppm NAA and 0.5 ppm BA. Analysis based on seed source revealed that for all bottomland sources, hypocotyl sections had differentiated buds with a frequency of 40-70%, while the sections of only one upland source hypocotyl section had differentiated buds with a frequency of 40%.

Current Research

These results immediately raised two additional questions. Were the cultures that had not produced buds in this experiment capable of producing buds if transferred to either a basal medium or a medium with additional factors favoring bud inititation such as adenine, and if so, can buds be differentiated directly on hypocotyl sections grown under the above conditions? Transfer to basal medium usually led only to the differentiation of roots. The results for

the enriched media have been reported elsewhere (Sommer 1981). Just as an example, when hypocotyl sections were cultured on a medium using 5 ppm 2-iP (2-isopentenyl adenine) as the cytokinin and 1 ppm IAA (indole acetic acid) was also added, in 1 month 75% of the cultured sections had differentiated buds. Thus improvements in yield, speed and synchrony may be possible.

The second question raised was could the buds and shoots formed from bottomland sources on modified RW medium with 0.01 ppm NAA and 0.5 ppm BA be rooted and grown to planting stock size. To answer this question five bottomland seedlots were chosen, and germinated under aseptic conditions.

As before cultures were started from 3 mm hypocotyl sections placed modified RW medium with 0.01 ppm NAA and 0.5 ppm BA. The results are given in Tables IA and IB. It is obvious from the results that the yield of buds varies greatly from seed lot to seed lot. Multiplication rates can be calculated either on total number of seedlings used for explants or only on seedlings that gave buds. In the latter case it gives an idea of potential yield if the shoots from the buds are subcultured. The overall multiplication rate based on buds transferred to RW basal medium for growth was positive. Shoots grown from buds on this medium generally rooted spontaneously. In the case of this experiment no attempt was made to stimulate rooting or shoot growth; the plantlets in the RW medium were transferred to a potting mix and covered with a plastic bag, test tube or beaker. Hardening off to laboratory conditions was done either by gradually cutting away the bag or removing the covering for progressively longer time periods over a week. The relatively low percentage of plantlets recovered (Table IB) was the result of loss due to buds not forming shoots, shoots not rooting, loss during hardening due to uncontrolled relative humidity, and some loss after hardening. However, 94 plantlets have been turned over to Dr. K. Steinbeck and have been planted this spring. Forty-three others are still too small to plant out, so will probably be healed out in the nursery for planting next winter.

Table IA.--Bud differentiation from hypocotyls

Seed lot[a]	# of Seedlings used (A)[b]	# of Hypocotyls forming buds (B)[c]	% Seedling forming buds B/A x 100	Total # of buds (C)	Multiplication rates C/B	C/A
76-1	80	22	28	64	2.9	0.8
76-5	93	52	56	143	2.8	1.5
76-7	50	40	80	156	3.9	3.1
76-10	53	21	40	44	2.1	0.8
78-1	23	6	26	13	2.2	0.6
SUM	299	141	(47)[d]	420	(3.0)[d]	(1.4)[d]

a. All seed lots - half - sibs from bottom landsites.
b. Differences in number of seedlings used due to differences in germination rate.
c. Hypocotyls cut into 3 mm sections and cultured on modified RW with 0.01 ppm NAA, and 0.5 ppm BA.
d. Based on sum of all seed lots.

Table IB.--Plantlets from buds

Seed lot[a]	Total # of buds (C)	# of plantlets[e] (D)	% Plantlets per seedling (D/A x 100)	% Buds yielding plantlets (C/D x 100)
76-1	64	23	29	36
76-5	143	56	60	39
76-7	156	43	86	28
76-10	44	12	23	23
78-1	13	3	13	23
SUM	420	137	(46)[d]	(33)[d]

a-d. See Table IA.
e. See text for details on path from buds to plantlets.

We are currently studying these steps in the culture process using empirical methods. In addition Dr. Hazel Wetzstein is using electron microscopy to follow changes in general anatomy, cuticle and chloroplast development during the hardening off process.

At present we have no data on the survival of sweetgum tissue culture plantlets in the field. However in December 1979, we planted 25 black locust (Robinia pseudoacacia L.) and 46 paulownia (Paulownia tomentosa (Thumb.) Siev. & Zucc. plantlets. This April 96% of the black locust plantlets and 94% of the paulownia had leafed out. However 57% of the paulownia had regenerated from the roots only. No weed control was used and the trees were not watered even during the extremely hot dry summer we had last year.

CONCLUSIONS

Based on the results reported here we can conclude that the regeneration of sweetgum plantlets in tissue culture from juvenile tissue is possible. Field survival of the plantlets is expected.

Our work with tissue cultures from sweetgum seedling is nearly completed except for hardening off and shoot growth studies. The methods developed for culturing are now being applied to explants from stump sprouts and older trees.

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NATURAL VARIATION IN ROOTING ABILITY OF WESTERN PROVENANCES OF SHORTLEAF PINE

G. A. Fancher and C. G. Tauer[1/]

Abstract.--Thirteen trees from each of 22 geographic sources across the five western states of shortleaf pine's range were sampled. Percent of cuttings rooted ranged from 11 for an Oklahoma source to 33 for a Louisiana source. No significant difference was observed for percent rooted among sources, although differences among trees in source were significant. The broad-sense heritability estimate for rooting ability was .26. Four root characteristics, total root weight, total root length, tap root length, and total root number, were studied on the rooted cuttings. No significant differences among sources were found for these traits but differences among trees in source were significant. Root mass per unit root length was significant for sources, suggesting geographic differences in root structure. Results suggest considerable genetic gains in rooting ability are possible through selection, and that origin is probably not important in such a selection program.

Additional keywords: Vegetative propagation, geographic variation, root characteristics, clonal selection, broad-sense heritability, Pinus echinata.

Because of the interest in and usefulness of vegetative propagation as a tool for tree improvement, geographic and clonal variation in rooting ability need to be assessed on a species to species basis. Rooting ability is defined for this paper as the ability of vegetative cuttings to develop roots and is measured as percent rooted. This ability within a species may well be as variable as are the many other traits already described for various tree species. Effective selection for a plant character can be achieved only if genetic variation for that trait exists within the population of interest. If sufficient amounts of either geographic and/or tree to tree variation in rooting ability exists, and if rooting ability is sufficiently heritable, considerable improvement in rooting ability could be achieved through a selection program.

Since environmental conditions in the field are seldom optimum for establishment, favored clones would be those that produce fibrous, spreading root systems, assumed to be highly effective in water and nutrient uptake. In fruit trees it has been found that the unique structure and functioning of the understock of any given genotype has an influence on almost every characteristic of the composite plant (Rogers and Beakbane

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1957). If structural differences in root systems exist and are sufficiently heritable, these differences need to be assessed and procedures for evaluating them incorporated into selection programs.

To evaluate the rooting ability and physical characteristics of the roots of vegetative propagules in shortleaf pine (Pinus echinata Mill.) a study was initiated to examine both the geographic and tree to tree variation in those characteristics.

MATERIALS AND METHODS

Materials for the rooting trial were collected from 22 geographic sources across the five western states of shortleaf pine's natural range (Figure 1). At each location ten cuttings were collected from each of 13 ortets, making a total of 130 observations per source. For collection, cuttings had to be at least six inches long, and the ortet had to be five to eight years old. Collection began June 3 and lasted for 10 days. The stage of development of the first flush was deemed ideal for rooting at this date, as described by Reines and Bamping (1960).

During collection, the cuttings were stored and transported in an upright position in cold storage boxes. The boxes consisted of two horizontally placed, stripped-down refrigerator bodies. The inside of the refrigerators were fitted to support metal trays which held bags of ice four to six inches above the cuttings. Holes were drilled in each box to provide drainage and a six inch layer of perlite and vermiculite (50/50 mix) was added. The ice kept the air temperature around the cuttings near 40 degrees Fahrenheit, and the melting provided moisture for the cuttings.

At the study site the cuttings were placed in a mist room in a completely randomized design using a completely random planting sequence. Prior to potting, each cutting's basal one inch of needles were stripped off and the base was dipped in a rooting hormone (Hormodin 3, 0.8 ppm IBA) mixed with 25 percent by wt. captan powder (50 percent active ingredient). The cuttings were then placed in 2.5 inch square, 4 inch deep pots which contained a 50-50 mix of perlite and vermiculite. The pots were placed on a single large table which had a 2.5 inch layer of the same medium, underlain with heating cables which provided a bottom heat of approximately 79 degrees Fahrenheit. The table was enclosed in a polyethylene covered room which was 15 x 26 feet.

Inside the mist room ten florescent lights (two 40 watt bulbs/light) were used to extend the daylength period to 16 hours. A minimum of 50 foot-candles was provided during the dark hours of the artificial photoperiod.

Cooling was provided by a 12 inch fan located in the center of one of the side walls and an air inlet was located in the center of the opposite wall. Cool air was provided by the greenhouse cooling system.

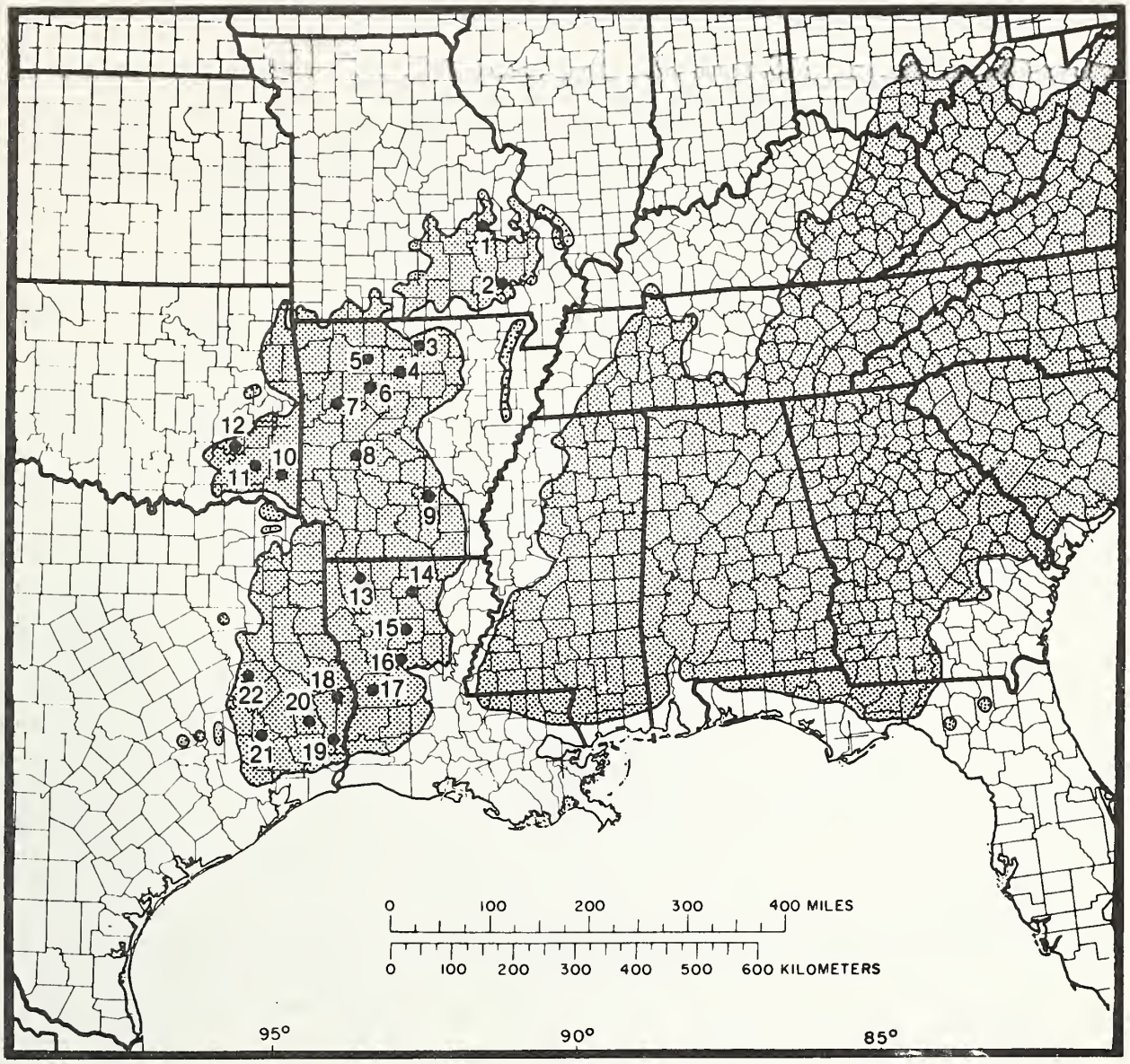

Figure 1.--Geographic location of collection points and western range of shortleaf pine.

The mist system consisted of 24 0.020 x 1/8 inch foggers. The nozzles were mounted on three lines spaced 47 inches apart, with the nozzles spaced at 32 inch intervals. The lines were suspended 20 inches above the cuttings. The nozzles were activated two ways: (1) When the thermostat turned on the chamber fan, it also activated the time clock that controlled the nozzles. The time clock activated the nozzles six seconds out of every six minutes (2.7 mm water per hour). (2) When the fan did not operate on cool days a separate time clock activated the spray for six seconds every two hours. These conditions provided an average relative humidity of 90 percent and an average daily temperature of 75 degrees Fahrenheit directly around the cuttings. After planting, a modified

Hoagland's solution (van Buijtenen, et al. 1975) was applied as a foliar drench nutrient additive once a day by hand spraying.

The following measurements and information were recorded during the planting phase:

(1) Initial cutting length (measured to nearest 0.1 centimeter)

(2) Initial cutting green weight (measured to nearest 0.1 gram)

(3) Presence of last years growth (yes or no)

(4) Time factor (number of days between collection and first day of planting)

The cuttings remained in the mist room for 106 days (June 14, 1980 to September 29, 1980). Spot checking the border row cuttings after 100 days indicated that the cuttings had been in the mist room long enough to allow sufficient root development for measurement of the characteristics of interest. Van Buijtenen, et al. (1975) reported that rooting percentages increased up to 14 weeks (98 days) then tapered off at an increasing rate.

After 106 days the propagules were lifted in the same order as potted, so as to equalize as best as possible, the number of days each cutting remained in the mist room. It took five days to pot the cuttings and four days to remove them. As each cutting was lifted it was classified according to its physiological state; dead, alive, callused or rooted. Additional data recorded following lifting were:

(5) Total number of roots (each root 0.5 centimeters or longer was tallied)

(6) Tap root length (measured to the nearest 0.1 centimeter)

(7) Total root length (measured to the nearest 0.1 centimeter and including tap root length)

(8) Root dry weight (measured to nearest .001 gram)

(9) Rooted cutting stem dry weight (measured to nearest .001 gram)

Measurements taken on the cuttings prior to planting were used to look for possible relationships between characteristics of the cuttings and percent rooted and root structure. Percent rooted and root characteristics measured were examined by analysis of variance to test for source and ortet in source differences and to estimate the broad-sense heritability of these traits (Table 1).

Table 1.--Method of analysis of variance and heritability estimation for percent rooted and root measurements.

Source of Variation	d.f.	Expected Mean Squares*
Source	$s-1$	$\hat{\sigma}^2_{c/o/s} + K_2\hat{\sigma}^2_{o/s} + K_3\hat{\sigma}^2_{s}$
Ortet in source	$\sum_{i=1}^{s} (o_i-1)$	$\hat{\sigma}^2_{c/o/s} + K_1\hat{\sigma}^2_{o/s}$
Cutting in ortet in source	$\sum_{i=1}^{s} \sum^{i} (n_{ij}-1)$	$\hat{\sigma}^2_{c/o/s}$

$$h^2_{bs} = \frac{\hat{\sigma}^2_{o/s}}{\hat{\sigma}^2_{c/o/s} + \hat{\sigma}^2_{o/s}}$$

*K_1, K_2, K_3 are respective coefficients of the expected mean squares.

RESULTS AND DISCUSSION

Of the 2,860 cuttings planted, 20.5 percent rooted, providing information on all 22 sources. More than half of the 286 ortets produced at least one rooted cutting. Figure 2 presents the percent and number of cuttings observed in each of the four physiological categories recognized at the termination of the study. The analysis of variance for percent of cuttings rooted and percent of ortets rooted showed no significant source differences. However, significant differences occured among ortets within sources for percent of cuttings rooted. Table 2 presents the percent of cuttings and ortets rooted, by source.

For comparison purposes, percent of cuttings rooted by state were computed. The order in which the states ranked, based on percent of cuttings rooted, was Oklahoma 14, Missouri 18.5, Arkansas 19.7, Texas 21, and Louisiana 25.8 percent. The order in which the states ranked based on percent of ortets producing at least one rooted cutting were Oklahoma 30.7, Arkansas 49.4, Missouri 50, Texas 55.5, and Louisiana 64.6. A trend from north to south seems to be evident when looking at these rooting values, but an analysis of rooting ability by state instead of source indicated that these differences were again not significant. One possible reason that this apparent geographic trend in rooting ability was non-significant is the hierarchical structure of the nested procedure of analysis. The important point, however, is that clonal variation in rooting ability is considerable, while source variation is relatively unimportant.

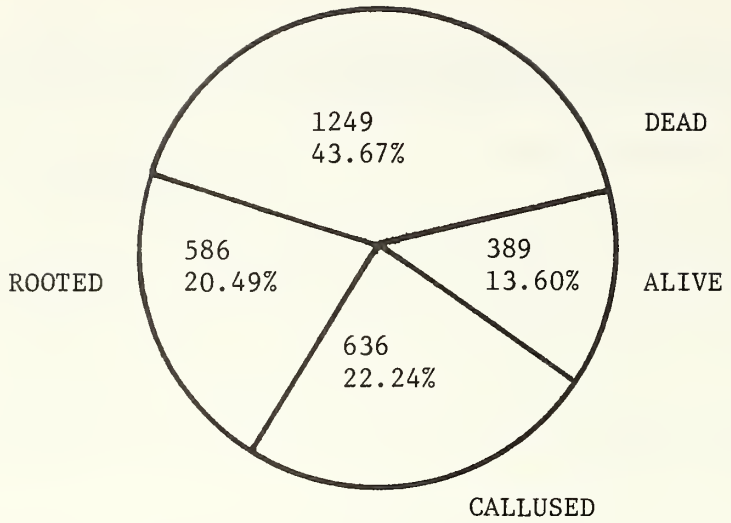

Figure 2.--Physiological state of cuttings at conclusion of study. (Percentages based on a total of 2860 cuttings).

The high proportion of alive and callused but unrooted cuttings (Figure 2) suggest the mist regime or some other unknown factor provided a suboptimal rooting environment. Under optimum rooting conditions, such a large number of living unrooted cuttings might not be expected.

Greenwood et al. (1980) reported, in an article published at the conclusion of this study, that the optimum mist regime for loblolly and shortleaf pine cuttings was .05 to .10 millimeters of water per hour. They reported that the amount of mist applied was the most critical factor of the environment affecting rooting. We applied approximately 2.7 millimeters per hour.

If an optimum environment had been present many of the callused cuttings might have rooted. An analysis of the combined data, cuttings callused plus cuttings rooted, showed that source differences were not significant and that tree in source differences were significant. This is the same conclusion as that reached when examining only the percent rooted data.

Table 3 presents the observed mean squares and F tests for the root characteristics measured. None of the four characteristics measured (tap root length, total root length, total root number, and root dry weight) were significantly different over sources. All four root characteristics were significantly different for ortets in sources. These results suggest that the root system and structure of pine cuttings can be modified through clonal selection for any of the four root characteristics measured.

The four stem characteristics recorded (initial cutting length, initial cutting green weight, presence of old growth, and rooted cutting stem dry weight) were of interest in terms of their relation to the

Table 2.--Percent of cuttings and ortets rooted, by source.

Source	Percent of Cuttings Rooted	Percent of Ortets Rooted
MISSOURI 1	20.8	53.9
MISSOURI 2	16.2	46.2
ARKANSAS 3	13.8	53.9
ARKANSAS 4	16.9	46.2
ARKANSAS 5	17.7	46.2
ARKANSAS 6	13.8	30.8
ARKANSAS 7	18.5	38.5
ARKANSAS 8	29.2	69.2
ARKANSAS 9	28.5	61.5
OKLAHOMA 10	11.5	30.8
OKLAHOMA 11	17.7	38.5
OKLAHOMA 12	12.3	23.1
LOUISIANA 13	16.9	53.9
LOUISIANA 14	20.8	46.2
LOUISIANA 15	33.1	92.3
LOUISIANA 16	26.2	61.5
LOUISIANA 17	31.5	69.2
TEXAS 18	23.1	53.9
TEXAS 19	16.2	38.5
TEXAS 20	20.0	53.9
TEXAS 21	23.1	69.2
TEXAS 22	23.1	61.5
Overall percent rooted	20.5 $\pm$ 3.5	51.8 $\pm$ 13.1

Table 3.--Observed mean squares and F tests for all characters over all sources.

SOURCE	d.f.	TOTAL ROOT LENGTH	F	TOTAL ROOT NUMBER	F	ROOT DRY WEIGHT	F
TOTAL	585	469.42		66.82		0.00248	
SOURCE	21	1505.67	1.39	199.34	1.38	0.00615	1.16
ORTET/SOURCE	127	1076.16	4.45*	144.07	3.79*	0.00528	3.54*
CUTTING/ORTET/SOURCE	437	241.95		37.99		0.00149	

SOURCE	d.f.	TAP ROOT LENGTH	F	ROOT UNIT WEIGHT	F
TOTAL	585	10.35		0.561×10^{-5}	
SOURCE	21	19.41	0.82	0.281×10^{-4}	3.07*
ORTET/SOURCE	127	23.71	3.93*	0.914×10^{-5}	2.60*
CUTTING/ORTET/SOURCE	437	6.03		0.351×10^{-5}	

SOURCE	d.f.	% ROOTING BY STATE	F	SOURCE	d.f.	% ROOTING BY LOCATION	F
TOTAL	2859	0.163		TOTAL	2859	0.163	
STATE	4	0.914	1.72	SOURCE	21	0.489	0.90
ORTET/STATE	281	0.531	4.36*	ORTET/SOURCE	264	0.540	4.44*
CUTTING/ORTET/STATE	2574	0.122		CUTTING/ORTET/SOURCE	2574	0.122	

*Significant at the .05 level of probability of lower.

percent of cuttings rooted and characteristics of the rooted cuttings. All correlations discussed except those including the variables percent rooted or presence of old growth are genetic correlations. Initial cutting green weight was not correlated with percent rooted. Initial cutting length was significantly and positively correlated with percent rooted ($r = 0.59$). Since the southern origins tended to provide longer cuttings, this correlation may explain the apparent slight geographic trend in percent rooted. The correlation also suggests that collection of longer cuttings could increase rooting success.

No significant correlations of initial cutting green weight and rooted cutting stem dry weight with the four root characteristics were found. Initial cutting length had a low but significant negative correlation ($r = -0.15$) with tap root length. Since most research with vegetative propagation utilizes a standardized cutting length that ranges from one to ten centimeters shorter than the cuttings used in this study, and since the correlation was so low, the effects of adjusting cutting length to favor tap root length would be minimal at best. Cutting length was not correlated with any other root characteristic examined.

All correlations between the presence of old growth and the four root characteristics measured were nonsignificant. Old growth was also uncorrelated with percent rooted, indicating that the inclusion of old growth as part of the cutting material was not important.

Seventy three percent of the cuttings that rooted ranged between .22 and .69 g/cm for cutting unit weight (cutting green weight per unit cutting length). The use of cuttings in this weight to length ratio range might facilitate mass production of rooted material.

The root mass per unit root length ratio was computed from total root weight and total root length. The root mass per unit length ratio was found to be significant both for sources and ortets within sources. Since it was apparent the ratio might reflect different developmental stages of the root systems among ortets, an analysis using simple linear regression was applied to the variables to examine the data further. Regression lines of root dry weight on total root length were estimated for each of the 22 sources. Had the slopes of the regression lines for each source been parallel (no significant slope differences), the variable (ratio) would have been interpreted as indicating differences in developmental stages of the roots. However, since significant differences in the slopes of the 22 regression lines were observed, the ratio suggest real source differences in structural characteristics of the roots. Some of the root systems formed tended to have small fibrous roots while others exhibited larger diameter, non-fibrous roots. If these root differences carry over into the field, both geographic and clonal selection might be used to develop clones with more fibrous root systems.

When the percent of rooted cuttings was correlated with the length of time in storage, an unexpected, high possitive correlation ($r = 0.52$)

was observed. Cuttings that were stored longer rooted better, but length of storage may not have been the cause. There may have been phenological differences in the cuttings across the sample range at the time of collection. With the exception of two Oklahoma sources, which had time factor values of one day, the next shortest time factor values (three days to five days) were represented by the two Missouri sources and Arkansas sources three, four, and five, which were also the five northern most sources. Sources one through five would undoubtedly be composed of the least mature cutting material and if lack of maturity resulted in reduced rooting the observed correlation could result. The correlation could also reflect a slight geographic trend in rooting ability, or the relationship between initial cutting length (with a north to south difference) and rooting ability. However, since there is no conclusive data concerning the effects of storage on the rooting of cuttings, the possibility exists that a few days in storage increases rooting percentages.

Broad-sense heritability estimates for all of the root characteristics measured are given in Table 4.

Table 4.--Broad-sense heritability estimates for percent rooted and root characteristics.

TRAIT	ESTIMATE	STANDARD ERROR
Root Mass Per Unit Root Length	.26	±.049
Tap Root Length	.43	±.047
Total Root Length	.46	±.046
Root Dry Weight	.40	±.048
Total Root Number	.41	±.048
Percent Rooted	.26	±.022

All heritability estimates were generally high and it appears that some reasonable gains can be obtained by selecting within populations for more fibrous or spreading root systems. Development of such propagules should result in the production of individuals which have a greater ability to survive and utilize soil nutrients and moisture. The broad-sense heritability estimate for percent rooted was also reasonably high and suggests that rooting ability can be selected for and used as a tool in tree improvement.

CONCLUSIONS

Examination of geographic and clonal variation in percent of stem cuttings rooted of shortleaf pine indicates that genetic improvement in rooting ability is possible through clonal selection, and that origin is probably not important. However, analysis of the mass per unit length ratio of the roots

suggested that there are differences in root structure from one location to the next which might make origin important in terms of root structure. The importance and/or usefulness of these differences has yet to be determined and only through field testing of selected clones can reliable information on the effects of these structural differences on survival be quantified.

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CUSTOMIZE OR COMPROMISE

An Alternative for Loblolly

William T. Gladstone[1/]

Abstract - Within the framework of broad recurrent selection programs, fine-tuning of genotype-site relationships will maximize genetic gain. Interactions evident in progeny, provenance and nursery tests suggest that individual specification of site conditions and cultural practices for many production-scale half-sib families will result in significant growth gains. Segregation of families or groups of families from cone harvest through the regeneration effort can enhance realized genetic gain and, in instances of orchard seed surpluses, permits an after-the-fact roguing of the maternal side of an orchard through preferential planting of the best families. Poorer performers may be used to advantage in other geographic areas, or not harvested.

Additional keywords: Pinus taeda, performance index, family segregation, family performance, non-destructive roguing.

INTRODUCTION

> "The fit are those who fit their existing environment and whose descendants will fit future environments."
>
> Thoday (1958)

It is difficult to say, at any point in time, which of an array of biological populations is the fittest or best adapted for long-term survival and utility, except in retrospect. And then, of course, it could be too late to do anything about it . . . too late to influence the system, to pick the right starting population, or to apply pressure which pushes the population in the direction of long-term fitness.

So, we do the best job we can of anticipating what future environments will be like and act accordingly, regardless of whether we are dealing with tree breeding, with setting long-term corporate policy, or educating our offspring. That we are doing our level best for the future of southern tree improvement is evident from the papers and the discussions of the past two days. But are we devoting enough attention to our current seed crops and their application to the environments of the present? How have we balanced long-range needs for adaptability to diverse and changing environments with short-term desires for specificity and immediate gain? My answer to the latter question is, "Not well enough," and that answer is based on a little evidence and a lot of intuition that we stand to gain a great deal if we make a concerted effort to know, intimately, how our orchard-derived seed and seedling populations behave.

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I anticipate that segments of thoroughly rogued first generation orchards of loblolly pine (Pinus taeda L.) will make useful contributions throughout the lives of their second generation successors, but such contributions will be wholly dependent on intimate knowledge of the performance of orchard-derived populations and on the ability to apply it. Both dependencies can be overcome by the segregation of families or groups of families from cone harvest to plantation. Heed the poet, and . . . ". . . Stick to the devil you know."[2/]

STICKING TO THE DEVIL

Table 1 displays performance and inventory information from a hypothetical loblolly pine orchard, and hints at the flexibility which segregation of orchard families can provide. Without carrying family segregation any further than the seed extraction stage, the orchard manager is much better able to predict the growth gains which can be expected from the whole crop or any part of the crop. The maternal contributions of each orchard clone can be established unequivocally and progeny test information weighted accordingly. For sites which are comparable to the appropriate progeny test sites, a family-weighted prediction of growth should be better than one based on an assumption of equal family contributions to a bulked orchard lot.

Family segregation assists in the roguing of an orchard, both genetically and silviculturally. Accurate records of seed yields by clone help to make the early "silvicultural thinning" decisions and improve later genetic roguing, particularly when several clones have performance records which are close to the orchard's truncation point. For example, in the interest of insuring good overall seed production, Clone 18 or Clone 19 might be retained in our imaginary orchard (Table 1) at the expense of Clone 16. Similarly, the non-productive Clone 4 will doubtless get the axe before Clone 16. Clonal yield histories can result in better roguing decisions.

Extending the family segregation concept to the nursery and regeneration operations can enhance realized gains through preferential planting of the best families. When orchard seed supplies exceed planting requirements, the ability to be selective at the family level amounts to a non-destructive after-the-fact roguing of the maternal side of an orchard. If producing orchards maintain relatively constant per-hectare seed yields through successive roguing cycles, opportunities for such non-destructive roguing will continue to make family segregation attractive, regardless of the physical roguing level. As long as an orchard remains fully stocked from a crown cover standpoint, that condition should prevail.

In a seed surplus situation, family segregation insures that the best genetic material is used first; i.e., seeds of high performance families do not remain in storage in bulked orchard lots while lower performance material proceeds to the plantation. Accountants who deal with inventory finance would label this sytem BIFO, or best in/first out. Applying this procedure to the stock listed in Table 1, it is easy to see that meeting a 1982 sowing requirement of 1500 kilograms with seeds from Clones 1-14 exclusively will best allocate the growth potential of the 1981 seed harvest. If the 1500 kilograms were drawn from

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[2/] Rudyard Kipling. The Gods of the Copybook Headings.

Table 1 - An example of information available to the orchardist who harvests cones and extracts seeds by clone

Clone	Performance Index[a]	1981 Harvest	
		Clonal	Cumulative
		Kilograms of Seed	
1	66	160	160
2	64	95	255
3	63	140	395
4	61	0	395
5	60	65	460
6	58	220	680
7	57	162	842
8	55	143	985
9	54	87	1072
10	54	47	1119
11	54	76	1195
12	53	68	1263
13	53	184	1447
14	52	53	1500
15	51	110	1610
16	51	27	1637
17	50	88	1725
18	50	131	1856
19	50	142	1998
20	49	0	1998
21	47	281	2279
22	47	70	2349
23	46	0	2349
24	44	115	2464
25	44	38	2502
26	42	201	2703
27	37	96	2799
Check	36	-	-
28	35	15	2814
29	33	146	2960
30	33	40	3000

[a] Performance Index is a composite, relative ranking of growth, form and fusiform rust resistance, derived from progeny test information pooled over installation years and sites.

a 3000-kilogram bulked orchard lot, half of the high potential seeds would remain in the freezer. How long they would remain there depends largely on the nature of the long-term orchard supply/nursery demand relationship.

The selection pressure which can be applied in non-destructive roguing is also dependent on this supply/demand relationship. With a long-term surplus of seed, unused families become available for use in other geographic areas or on unusual sites, where genotype/environment interactions may enhance their relative performance. Alternatively, in the early, unrogued life of an orchard, these families may be used for direct seeding or simply not harvested. It should be noted that appreciable flexibility in selective planting can be achieved by handling groups of clones; e.g., by dividing the clones of Table 1 into several sub-groups and maintaining the identity of these, but bulking the families within each group. This is an improvement over orchard bulking, but does not permit the detailed evaluation and optimum allocation of orchard seeds which is provided by complete family segregation.

Not only does family segregation accommodate the best in/first out system, but is also permits the assignment of the best families to the best planting sites available. Thus, sites which demand and receive priority for intensive management treatments can also receive the most intensive genetic treatment. Conversely, the best genetic material has the best opportunity to express its superior productive potential.

GETTING TO KNOW THE DEVIL BETTER

Detailed information on performance accumulates during the orchard, nursery, regeneration and plantation management phases of a family block planting system. Coupled with extending and confirming research, these data continually identify unique and useful family characteristics which would go undetected with the bulked seed system. The identification of a family in Weyerhaeuser's North Carolina orchard program which cannot tolerate early lifting and prolonged cold storage, is a good example of between-family variability which probably would not have been picked up had we not been using the family block system. Ignorance of the need for special handling would have contributed to mortality in plantations established from stored bulked seedlings, mortality which would have gone on the record as "unaccountable." Segregation in the field made the diagnosis possible. Segregation in the nursery provides the remedy, as this high performance family is now lifted and moved to the field with no or minimal storage.

Other examples of useful variability among orchard families are being verified and will be used, ultimately, to tree improvement's benefit through family segregation methods. Dierauf has demonstrated that, although one of five tested families did very well in the field, its tendency to germinate slowly put it at a disadvantage in a random (bulked) nursery sowing pattern (T. A. Dierauf, Virginia Division of Forestry, Charlottesville, Virginia). Early sowing and relatively uniform competition from its half-sibs can insure that this top family does not frequent the cull pile. This can be accomplished, in practical fashion, only be segregating that family.

Provenance tests using identifiable families to represent North Carolina orchard stocks are revealing changes in family ranking on some sites in Arkansas and Oklahoma. These rank changes may provide opportunities to use families which

are fair performers, and which might be relegated to long freezer storage in North Carolina, west of the Mississippi. Again, this refined allocation cannot be made if the orchard output is bulked. Another family ranks among the leaders under fertilized conditions and seems to do almost as well when it's not fertilized . . . its peers do not. If further study verifies this faculty, routine fertilization can be withheld from the blocks containing only that family. Customize!

Some other advantages of the family block system may prove to be:

- Increased crop uniformity at all stages
- Field verification of vulnerability/resistance by family
- Assignment of rust-resistant families to high risk sites
- Earmarking of plantations for specific end products
- Verification of progeny test results on a stand basis

The possibilities are endless and, once started, the system seems to be self-improving. Specificity and identity in commercial plantation units encourage observation, because variability among families provides management alternatives.

CONCLUSION

While I, too, advocate that we proceed rapidly with advanced generation orchards as a means of achieving greater benefits from our tree improvement programs, I am convinced that a more intensive examination and utilization of the material we have in hand is in order. Where practical, the segregation of orchard families permits the fine-tuning of genotype-site relationships which will maximize genetic gains. Interactions evident in progeny, provenance, and nursery tests suggest that individual specification of site conditions and cultural practices for many production scale half-sib families will result in significant improvements in growth and form.

Knowledge of the exact contribution of each family to the seed pool can improve the quality of roguing and of growth predictions. Positive identification of the maternal genotype in plantation parcels can confirm progeny test information in a commercial situation.

Non-destructive roguing after orchard harvest improves the allocation of families to plantations by insuring that the best families are planted on the best sites, that the best families are used first, and that poorer performers are relegated to storage if seed supplies exceed planting requirements. The customizing of nursery, orchard and plantation management practices to take advantage of, or to overcome, special properties of individual families can provide substantial benefits.

We need to learn a great deal more about the potential of our orchard crops, and then "Stick to the devil we know"!

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DESIGN AND LAYOUT OF ADVANCED GENERATION SEED ORCHARDS

A. V. Hatcher and R. J. Weir[1/]

Abstract.--A set of criteria for establishment of advanced generation seed orchards has been developed for The North Carolina State University-Industry Cooperative Tree Improvement Program, based on experiences with first generation seed orchards and a few early blocks of advanced generation orchards. Basic considerations in developing these criteria were to maximize the flexibility for orchard improvement through roguing and to minimize the potential for inbreeding. To achieve these goals, the criteria for orchard layout are: (1) initial stocking of at least 135 trees per acre, (2) the inclusion of thirty to forty clones in each orchard block, (3) a minimum distance of 90' between related ramets, (4) relatively equal clonal frequencies, and (5) avoidance of repetitive neighborhoods.

Additonal keywords: Orchard configuration, clonal composition, inbreeding, panmixis, roguing.

The N. C. State Cooperative Tree Improvement Program has been actively involved in the establishment of clonal seed orchards since the early 1960's. Through the sixties and early seventies, efforts were directed primarily toward the establishment of first generation orchards. In the mid-seventies, attention turned toward establishment of advanced generation seed orchards. As we contemplated this new phase of orchard development and reflected upon our experience with first generation orchards, it became apparent that the choice of orchard configuration and design required re-evaluation. In the first generation a broad range of criteria were used in design selection. The most important criteria were ease of orchard management, the usefulness of a given design for experimental purposes, minimizing selfing, the compatibility of the design with anticipated thinning and maximizing panmixis. The considerations thought to be most important were minimizing selfing and maximizing panmixis (Giertych 1975). All of these criteria were considered for advanced generation orchards. Additionally, several considerations specific to the advanced generation program required evaluation. These included the use of related selections (full-sibs and half-sibs) in the same unit area, and the initiation of orchard development with very young selections. Each of these considerations, old and new, were examined to determine their potential impact on the primary objective of seed orchard establishment--to maximize the genetic quality of seed produced at all times.

ORCHARD ESTABLISHMENT CRITERIA

The primary objective of orchard development is to produce seed of maximum genetic quality for regeneration programs. In this regard, two of the

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considerations previously used for design selection i.e., the suitability of a design for experimental purposes, and the ease of orchard management were concluded not to contribute to the primary objective and were discarded from further consideration in orchard design. The orchard management criterion eliminated concerned the placement of clones in some repeatable and predictable pattern that made it easy to work in the orchard and to locate a specific clone with ease. However, certain mechanical aspects of orchard operation and management provided significant input to decisions relative to the orchard configuration (tree spacing and arrangement).

With the elimination of these considerations, basically only four factors remained for consideration in establishing orchard criteria.

1. Minimizing inbreeding.
2. The compatability of orchard design with anticipated thinning requirements.
3. Maximizing panmixis.
4. Minimizing the impact of selection errors.

The effects of selfing have long been a concern in orchard establishment. As stated earlier, Giertych (1975) reported that minimizing selfing was one of the most frequently mentioned criteria in design selection. With the inclusion of related selections (full-sib and half-sib selections) in the same unit area in advanced generation orchards, the potential for reduced genetic gain as a consequence of inbreeding is substantial. One inbreeding study reported a reduction of 20% in volume alone as a result of half-sib matings (Gansel 1971). Reductions of this magnitude in the genetic quality of seed would negate the expected response to selection. It was concluded, therefore, that minimizing inbreeding is an important criteria in the selection of orchard design and configuration.

The desire to quickly capitalize on the potential gain of advanced generation improvement has resulted in the initiation of orchard development with extremely young selections, often as young as five years of age. As a result of imperfect juvenile-mature correlations, selection at this age is subject to errors (La Farge 1972, Wakeley 1971). Therefore, if the potential gain from advanced generation orchards is to be realized in a timely fashion, consideration must be given to minimizing the impact of the errors likely to occur from the use of young selections. A solution to minimizing the impact of selections subsequently judged unsuitable is to maximize the flexibility to upgrade the orchard through roguing. This can be accomplished by establishing more trees per acre and by using more selections than might otherwise be desired.

The advantages and disadvantages of maximizing panmixis were heavily debated during establishment of first generation orchards. The advantage mentioned most frequently was the desire to maintain maximum genetic variability in the crosses produced. Others believed that maximizing panmixis should be avoided since it eliminated the potential to capitalize on specific combining abilities and thus achieve even greater gain. The latter proposal would be a realistic consideration if information on specific combining abilities was available at the time of orchard establishment. This, however, is rarely the case in advanced generation orchard establishment. The desire to capitalize on potential genetic gain quickly will generally result in the

establishment of production orchards prior to the availability of information from progeny tests of the selection used. Therefore, maximizing panmixis was considered to be a valid concern.

The value of using orchard design restrictions to achieve panmixis has been questioned. For example, van Buijtenen (1971) argued that the design constraints imposed to restrict the occurrence of repetitive neighborhoods were so confounded with factors such as the flowering phenology of clones that the imposed restrictions were likely to have little effect on the genetic variability or the average genetic quality of the seed produced. We agree with van Buijtenen on this point, yet strongly support the argument for the elimination of repetitive neighborhood patterns for other reasons. One of the major frustrations encountered in first generation orchards resulted from the occurrence of repetitive neighborhoods. The negative effect of repeating neighborhoods was recognized when the first genetic thinnings were attempted. Invariably, clusters of good or poor clones occurred. When clusters of good clones were encountered, only two options existed. A clone of good genetic quality could be removed to provide the necessary crown release, or the need for crown release could be ignored and the clone retained with a susbsequent decline in cone production resulting from overcrowding. The second option was obviously incompatible with the objectives of a seed orchard program. A cluster of poor clones required either a "patch clearcut" resulting in a nonproductive area within the orchard, or the continued existence in the orchard of genetically inferior clones. Regardless of the cluster type, a no win situation existed. When such clusters occur in orchards with repetitive neighborhoods, the impact on the genetic quality of the seed produced, as well as the quantity of seed produced, is significant. To minimize the effect of such clusters, nonrepetitive neighborhoods were established as a primary criteria in orchard design selection.

In summarizing the above considerations it became evident that two basic criteria were essential to achieving the primary objective of production seed orchards.

1. Flexibility for the improvement of the genetic quality of the orchard must be maximized.
2. The potential for inbreeding must be minimized.

ORCHARD CONFIGURATION

Maximizing roguing flexibility was the primary objective in determining the orchard configuration, initial ramet spacing and arrangement. Each configuration meeting the primary objective was further evaluated for orchard management and operation.

The first orchard configuration component evaluated was the initial spacing of ramets. To determine the effect of various spacings on the primary objective, some basic assumptions were required relative to the roguing schedule and intensity. Under the prevalent spacing in first generation orchards (15' x 30'), the first thinning required for crown release generally occurred 8-10 years after establishment. By the time of this first thinning, orchards were already producing a significant quantity of seed. Yet at the

time of the first thinning, information on the genetic quality of the clones was generally still insufficient for genetic roguing purposes. Therefore, initial roguings were primarily based on silvicultural and sanitation requirements. Under these circumstances an initial spacing of 15' x 30' was more than adequate to maximize the genetic quality of the orchard through roguing. In advanced generation orchards, information on the genetic quality of selections is available much earlier as a result of analysis of individual and sibling performance in tests from which selections were made. Therefore, the potential to upgrade the genetic quality of the orchard occurs much earlier. Our experience indicates that by the time progeny tests are about age 10 selection errors are minimal, therefore the errors resulting from the use of very young selections could be identified within five years following initial orchard establishment. Since it was considered advantageous to eliminate selection errors as early in the life of the orchard as possible, it was concluded that the initial spacing should provide for a genetic roguing as early as age five. This initial roguing should not, however, decrease the potential for genetic improvement or seed production in the future.

With the prevalent spacing used in first generation orchards (15' x 30'), 97 trees per acre were initially established. This stocking level was sufficient for satisfactory seed yields through the early years of orchard production (up to age 10). To enhance early production, it was determined that the initial spacing should provide for a stocking level of approximately 100 trees per acre following the first roguing at age five. Assuming reasonably equal clonal frequencies within a unit area and a selection error rate of 35% at age 5, an initial stocking level of 135 trees per acre was deemed reasonable to insure adequate production levels in the early years of the orchard. It was anticipated that subsequent roguings would occur at five year intervals with the final roguing occurring at approximately age twenty. In first generation orchards the stocking level following the final roguing is approximately 20 to 30 trees/acre. Assuming the same stocking level in mature advanced generation orchards, an initial stocking level of 135 trees/per acre would provide for the removal of 35% of the ramets at each subsequent roguing. Thus, an initial stocking level of approximately 135 trees/per acre was considered sufficiently flexible to achieve the primary seed orchard objective.

Any number of initial spacings and ramet arrangements exist which result in initial stocking levels of approximately 135 trees/acre. A square arrangement with 18 feet between planting positions would yield 134 trees/acre. A rectangular arrangement of 15' x 20' would yield 145 trees/acre. The modified 15' x 15' configuration proposed by Weir (1973) and illustrated in figure 1 would also yield 145 trees/acre. From the standpoint of initial stocking and orchard management considerations, either of the three configurations were satisfactory. However, the configuration advocated by Weir provided an advantage in crown space since each ramet was surrounded by only three immediate neighbors. For this reason, the modified 15' x 15' is the recommended configuration for use in the establishment of advanced generation seed orchards.

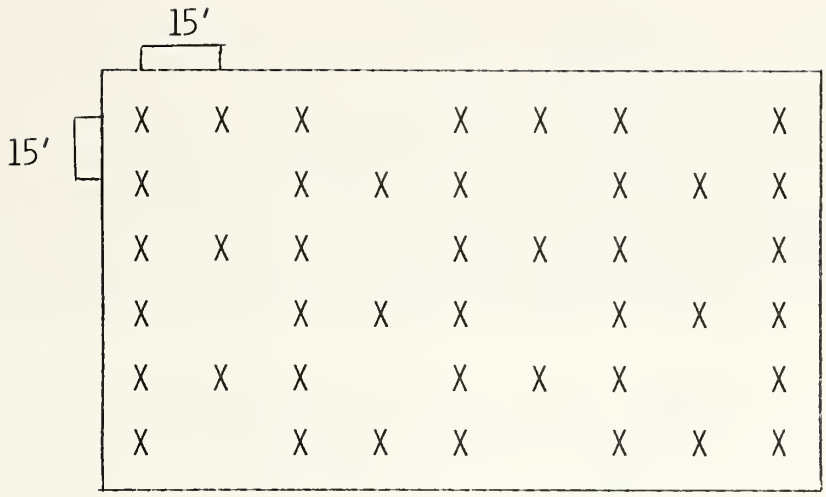

FIGURE 1. MODIFIED 15' x 15' CONFIGURATION. FROM WEIR (1973).

ORCHARD CLONAL COMPOSITION

Both of the primary criteria developed for orchard establishment, maximizing roguing flexibility and minimizing inbreeding, were of significant impact in determining orchard composition. From the standpoint of maximizing roguing flexibility to upgrade the genetic quality of the orchard, it was believed that a sufficient number of clones should be included to allow the lowest 50% of the clones to be rogued. In order to minimize inbreeding, it was determined on the basis of McElwee's (1970) research findings, that the number of clones established must be sufficient to maintain a minimum distance of 90' between ramets of the same or related trees.

Assuming a 35% error rate in selection, an orchard established with 30 to 40 clones would yield 20 to 26 clones following initial roguing for correction of the selection errors. Based on first generation experiences, the orchard would be comprised of the best 10-12 clones following the final roguing. Therefore, an orchard initially established with 30 to 40 clones would allow the removal of the lower 40 to 60 percent of the clones. Thirty to forty clones occurring with relatively equal frequencies would result in three to five ramets of each clone per acre. Roguing down to the best ten to twelve clones would result in a stocking level of 36 to 60 trees per acre. Assuming a final stocking level of 25 trees per acre, the 36 to 60 ramets remaining would provide additional flexibility for selection of specific ramets to achieve a final stand of healthy, vigorous trees appropriately spaced within the orchard with no large gaps or tight spots.

Using the orchard configuration recommended, a minimum of 24 selections is required to maintain the minimum distance of 90' between ramets of the same selection or related selections (full-sibs and half-sibs). Therefore in the total number of selections recommended, there must exist for each selection, a subset of 24 unrelated selections. This means that full-sibs/half-sibs can only be included in the same unit area if the total number of selections recommended exceeds 24. If thirty to forty clones are recommended for an orchard, the recommendations could therefore contain 6 to 16 selections that may be related to each other or to the original set of 24 in some manner. This was considered sufficient flexibility for the inclusion of related selections in the orchard.

Since an orchard composed of less than thirty clones would limit the roguing flexibility and either increase the potential for inbreeding or severely limit the number of full-sibs/half-sibs included, a lower number of clones was not considered. A much larger number of clones within a given unit area was not considered practical from an orchard management standpoint. Exceedingly large numbers of clones will have a negative impact on the genetic gain that can be achieved through the life of the orchard as a result of reduced selection intensity. It was, therefore, concluded that the orchard composition should consist of a minimum of thirty clones and a maximum of forty clones each occurring with approximately equal frequencies.

ORCHARD DESIGN

Based on the primary objective of seed orchards and the resulting criteria, the orchard design selected had to possess three essential elements. First, the design had to be capable of maintaining the minimum distance between ramets of the same or related clones. Second, the design could not create repetitive neighborhood patterns. Third, each clone had to occur with relatively equal frequency.

In first generation orchards the most prevalent design used was a fixed block. To a lesser extent, the shifting-block design (Malac 1962) was used. Neither, however, met the requirements for advanced generation orchards. The fixed block, and the shifting block to a lesser degree, both resulted in repetitive neighborhoods. Both were capable of maintaining minimum distances between ramets of the same clone, but they resulted in extremely unbalanced clonal representations when related selections occurred. Further investigation showed that all systematic designs had similar disadvantages.

Since the use of systematic designs was not desirable, attention turned to random designs. The two considered were randomized complete blocks and the computer-based permutated neighborhood design proposed by La Bastide (1975). The randomized complete block, in its true form, would not provide for separation of ramets of related selections or of the same selection when represented by multiple ramets within an orchard block. For this design to be used in advanced generation orchards, restrictions would be required to provide the minimum separation of related ramets. The permutated neighborhood design of La Bastide's provided for the isolation of ramets of the same clone, the maximization of panmixis and equal clonal frequencies. It did not however provide for the spatial separation of related ramets along the interface of

adjacent blocks. Since advanced generation orchards were generally being established through the installation of adjacent annual blocks, the ability to interface blocks and maintain the minimum separation of related ramets was considered important. Additionally, it would be impossible in advanced generation orchards to retain absolutely equal clonal frequencies as required by La Bastide's design. The degree of relatedness among selections determines the relative frequency with which each can occur in an orchard block. The provision for ramet isolation would also require expansion to include separation of full-sibs and half-sibs. The basic concepts in La Bastide's computer generated designs were compatible with the design requirements in advanced generation orchards but their implementation was too inflexible to handle the problems specific to advanced generation orchards.

This led to consideration of the computer program, COOL, developed by Bell and Fletcher (1978) which was based on the permutated neighborhood design concept. Many of the restrictions imposed by LaBastide's program were eliminated in COOL. The major drawback to this version of the permutated neighborhood design was its inability to handle related selections, specifically the triangular relationships sometimes encountered when using half-sibs, without severely restricting their frequency of occurrence. For this reason, Bell and Fletcher's version was eliminated from consideration.

It was believed, however, that the permutated neighborhood concept could provide the essential elements for advanced generation orchard design. Thus, a relaxed permutated neighborhood design was developed along with a computer program, AGSOL, for Advanced Generation Seed Orchard Layout. This design does not provide the rigid neighborhood control of the previous versions. No specific restrictions are placed on the frequency with which a particular clone can occur with another. In other words, no attempt is made to maximize panmixis. It does, however, through the sequence of ramet establishment, prevent the occurrence of repetitive neighborhoods. A minimum distance of 90' between ramets of related clones is specified. Additionally, a specification exists that clones are to occur with as equal frequency as possible. When conflicts occur between these two specifications, maintaining the required spatial separation of related ramets takes precedence over maintaining equal clonal frequencies. If a position cannot be filled without violating the 90' rule, the clone which will provide the maximimum separation is selected and the violation is noted. Clonal frequencies are equalized to the extent possible given the degree of relatedness among selections. Typically, a selection related to another in the orchard will occur with 60 to 70% of the frequency of a selection which has no relative. A selection related to two others will occur 40% to 50% as frequently as an unrelated selection. AGSOL provides for the generation of layouts for any orchard shape or size. It also provides the capability of expanding orchards without violating ramet separation along the interface.

The design and layouts produced have been used for the past several years for the establishment of advanced generation orchards in the Cooperative. To date, the relaxed permutated neighborhood design has proved suitable for achieving the desired objectives and the layouts produced by AGSOL have proved manageable in orchard establishment and operation.

SUMMARY

Based on the primary objective of seed orchard establishment, the production of seed of maximum genetic quality, two criteria are required for orchard development. The flexibility for improvement of the genetic quality of the orchard through roguing must be maximized. The potential risk for inbreeding must be minimized. To achieve these goals requires a minimum initial stocking level of 135 trees per acre, composed of thirty to forty clones. Each clone should occur with relatively equal frequency provided a minimum distance of 90' is maintained between related ramets. Repetitive neighborhood patterns should be avoided. The requirements necessary to achieve the stated goals can be accomplished through use of a relaxed permutated neighborhood design.

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GENETIC EFFICIENCY IN LOBLOLLY PINE SEED ORCHARDS

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Abstract.--Using seven allozyme loci as genetic markers, gene frequencies in the bulked seed crop of two seed orchards were compared to those expected on the basis of maximum genetic efficiency. Significant deviations from expected values were found for allelic frequencies in embryos as well as in both the ovule and pollen pools which produced the embryos. While contamination from pollen sources in surrounding stands (estimated at 28%) may be important in causing deviations from expectation in the pollen pool, self-fertilization does not appear to be a problem since the proportion of selfed progeny was estimated to be very low (< 1.5%) in these orchards. When seeds were separated by size there was a substantial loss of genetic variability in the ovule pool within a size class. Several other factors which might be responsible for decreased genetic efficiency are considered. Implications of these findings for seed orchard management are discussed.

Additional keywords: Pinus taeda, allozyme variation, seed orchards, self-fertilization, pollen contamination

The purpose of seed orchards is to produce mass quantities of genetically improved seed for reforestation. The efficiency of seed orchards is defined as the degree to which seed crops approach maximal production as well as reflect the genetic superiority and variability present among orchard clones. Factors influencing the efficiency of seed production have received considerable attention in the literature, and techniques for increasing productivity through fertilization regimes, irrigation, insect control, and other cultural treatments have been discussed (see reviews in Faulkner 1975). Genetic efficiency, on the other hand, is difficult to measure, and relatively few studies of factors influencing genetic efficiency have been reported (e.g., Adams and Joly 1980a, Bergmann 1968, Eriksson et al. 1973, Muller-Starck 1978, Squillace 1977).

To achieve maximum genetic efficiency in wind-pollinated seed orchards, the following conditions would need to be met (Woessner and Franklin 1973):

1. Orchard ramets must be more or less completely isolated from surrounding unselected trees.

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2. Natural self-fertilization must occur at insignificant rates.

3. Ramet pollen flight and female flower receptivity must coincide.

4. Ramets must be equally productive of ovules and pollen.

5. Crosses among clones must be equally compatible.

One recent investigation suggests that contamination from background pollen sources could be a serious problem in wind-pollinated seed orchards. Based on monoterpene markers, Squillace and Long (1981) estimated that as much as 80% of the seed in a small slash pine orchard was the result of fertilizations by non-orchard pollen. Selfing, however, may have only a minor effect on genetic efficiency. In a loblolly pine study, the proportion of selfs in the progeny of five seed orchard clones was estimated with the aid of allozyme markers to average only 1.2% (Adams and Joly 1980a). Clonal variation in male and female flower productivity and phenology is well known to orchard managers and has been documented quantitatively in a number of cases (Bergmann 1968, Eriksson et al. 1973, Jonsson et al. 1976). In addition, lack of complete cross-compatibility among clones is suggested by the variable success of two-parent crosses in breeding programs (Woessner and Franklin 1973).

While it is clear that all the conditions above are violated at least to some extent in wind-pollinated seed orchards, it is unclear how these violations ultimately affect genetic efficiency of seed crops. Given a large number of single locus genetic markers, the genetic efficiency of seed orchards can be evaluated (Adams and Joly 1980a). We illustrate the technique in this paper by using seven allozyme loci to analyze genetic efficiency in two loblolly pine seed orchards. We also use allozymes to explore the genetic consequences of seed sizing in seed orchard crops.

MATERIALS AND METHODS

This study was conducted in two loblolly pine seed orchards owned by Champion International Corporation, Newberry, South Carolina. One orchard contains clones selected for high specific gravity wood (HSG); the other, clones selected for low specific gravity wood (LSG). The orchards are each approximately 2 hectares (5 acres) in size, and are separated from each other by a 100-m-wide strip containing a Virginia pine (Pinus virginiana Mill.) seed orchard. This three-orchard complex is surrounded by a 122-m-wide isolation strip comprising a cleared area, a slash pine (Pinus elliottii Engelm.) plantation, and a mixed loblolly-hardwood stand from which all flowering age loblolly pines are periodically removed.

At the time of seed sampling in 1976, orchard grafts were an average of 16 years old and were in full pollen and seed production. A total of 202 ramets of 23 clones were present in the LSG orchard and 183 ramets of 25 clones in the HSG orchard. Numerous roguings had resulted in considerable imbalance of clonal representation in both orchards, with the number of ramets per clone ranging from 1-25.

Beginning in 1975, the seed crops from the two orchards were combined and processed in bulk. Random samples of the bulked seed crops of 1976 and 1978 were obtained by sampling a large number of seeds from each of several storage bins and mixing them together. However, in 1978, the seeds were separated into small (23,000/lb), medium (18,000/lb), and large (13,000/lb) size classes prior to storage. For this year, a random sample of seed was obtained for each size class.

A large number of seeds from the 1976 sample (493) and from each of the 3 size classes in 1978 (221-245) were assayed electrophoretically using the techniques described by Adams and Joly (1980b). The megagametophyte (1N) and embryo (2N) tissues of each seed were analyzed separately and the genotype of each tissue determined at seven allozyme loci: GDH, LAP-1, PGI-2, GOT2, 6PGD, PGM-1, PGM-2. Details of the banding patterns of these allozymes, and analyses of their Mendelian genetics are also found in Adams and Joly (1980b).

Based on the diploid genotypes of the embryos, allelic frequencies at all seven loci were calculated for each of the four seed samples. Since the megagametophyte has the same haploid genotype as the female gamete, the parental origin of the genes in each embryo could be determined. Therefore, allelic frequencies among the female gametes (ovule pool) and among the male gametes (pollen pool) forming the embryos in each seed sample were also calculated.

Utilizing chi-square goodness-of-fit tests, the estimated allelic frequencies in the 1976 seed crop were then compared to those expected on the basis of random mating among the orchard clones. Expected frequencies were first determined separately for each orchard on the basis of the genotypes of the orchard clones. These were known from a previous study (Adams and Joly 1980b). Frequencies expected in the bulked seed crop were then calculated by weighting the LSG frequencies by 0.68, and HSG frequencies by 0.32, the average of each orchard's relative seed production over the five year period from 1970 to 1974. The range of the relative proportion of seed produced by the HSG orchard was relatively small over the five years (0.26 to 0.38); thus, it is unlikely that the weights used are very different from the true relative production in 1976. The calculated frequencies for the bulked seed crop are those expected when all the conditions necessary for maximal genetic efficiency (i.e., full genetic efficiency) are met, including the assumption that all clones produce equal numbers of ovules and pollen grains. However, the large discrepancy in the number of ramets representing each clone in the two orchards likely leads to considerable imbalance in the genetic contribution of each clone to the seed crop. To test the degree to which correction for clonal imbalance in ramet numbers might account for observed frequencies in the 1976 seed crop, expected frequencies were also calculated by first weighting each clonal genotype by the number of ramets with that genotype present during pollination in 1975.

For the 1978 seed crop, it was of interest to determine the degree to which the three seed size classes differed in genetic composition. To test the variation in allelic frequencies over size classes, chi-square tests of heterogeneity were conducted for each of the seven loci.

RESULTS AND DISCUSSION

Significant deviations of observed allelic frequencies in embryos from those expected under full genetic efficiency were found at five of the seven loci investigated in the 1976 seed crop sample (Table 1). Furthermore, significant deviations from expectation occurred in both the ovule and pollen pools, indicating that violation of the conditions for full genetic efficiency involve both male and female gametes. These deviations are not surprising, since the expectations given in Table 1 were formulated on the assumption of an equal number of ramets per clone. Correcting expected frequencies for the actual differences in ramet numbers, however, does little to improve the fit of observed allelic frequencies (Table 2). While only three loci showed significant deviations from expectation in embryos, a total of four loci still showed significant deviations in the ovule pool, and two loci were significant in the pollen pool.

When one considers the wide range in mean flower production per ramet that has been observed among orchard clones (Jonsson et al. 1976, Eriksson et al. 1973, Bergmann 1968), it is understandable why correction for number of ramets alone may not adequately account for seed production differences among clones. For example, in a study of variation in flowering among 15 clones in an 8 year-old loblolly pine orchard, the average number of cones produced per ramet ranged from 1 to 268 among clones, and the average male flower score (i.e., a subjective scale of 0 to 5, where 0 was no flowers and 5, very heavy flower production) ranged from 0.2 to 4.2 (Bergmann 1968). In order to adequately assess the influence of differential flower production among clones on seed orchard efficiency, detailed flowering data would be required. Unfortunately, no such data were recorded for these orchards during the 1975 pollination season.

To explain observed allelic frequencies in the ovule pool, information on variation among clones in relative production of sound seeds would be needed, and data on flowering variation by itself may not be enough. In an earlier study in loblolly pine, strong clonal variation was observed in the total number of seeds per cone; also, variation among clones was found in percent of empty seeds (Bergmann 1968). Factors which may account for differences among clones in sound seed production include intrinsic differences in the number of ovules produced per cone, differences in the proportion of ovules fertilized (which may be related to timing of flowering or incompatibility) and variation in the proportion of fertilized ovules which mature (which may be related to levels of self-fertilization).

In addition to variation in pollen production among clones, deviations from expected allelic frequencies in the pollen pool may result from a high proportion of fertilizations due to selfing and/or due to pollen from non-orchard sources, as well as variations among clones in time of pollen shedding and cross-compatibility. Differences among clones in time of pollen shedding or cross-compatibility are likely to have an effect on allele frequencies only when an allele is unique to a particularly early or late flowering, or extremely incompatible, clone. Thus, the impact of these two factors on overall allelic frequencies is probably not great. However, it is evident that pollen contamination from non-orchard sources is responsible for at least some fertilizations in the 1976 seed crop, based on the presence of allele 6PGD-7 in

the pollen pool sample (Tables 1 and 2). This allele was not found among the orchard clones, but was found in wild loblolly trees sampled within approximately 400 m of the orchards. Using four allozyme markers which were present in the natural stand sample, but could not be produced by the clones in either orchard, the proportion of seed fertilized by non-orchard sources was estimated. The mean for the four markers was 0.28 $\pm$ 0.06. In addition, an estimate of pollen contamination between orchards was obtained with an allozyme marker that was present among the clones in the HSG orchard, but was found in neither the LSG orchard nor the surrounding stands. This estimate was 0.10 $\pm$ 0.02. Thus, pollen contamination from non-orchard sources may be a major reason why allelic frequencies in the pollen pool deviate from expectation.

A high proportion of fertilizations due to selfing, on the other hand, does not appear to be an important factor contributing to deviations from expected frequencies in the pollen pool. To expand an earlier study in these orchards based on seed from five clones in a single year (Adams and Joly 1980a), we estimated the proportion of selfs in the progeny of a much larger sample of clones (7 to 24) in each of three years. Our estimates were never greater than 0.013 for any one year (including 1976) and the pooled estimate (weighted mean) for the 3 years was 0.004 $\pm$ 0.008, in close agreement with the results of the earlier study.

Even though these orchards are apparently far from full genetic efficiency, and their clones probably vary considerably in the relative proportions of male and female gametes they produced, the 1976 bulked seed crop apparently still possesses much genetic diversity. All alleles present among the orchard clones, including seven alleles expected to occur at frequencies of less than 5% (Tables 1 and 2), were found in the ovule pool sample, and the same seven alleles plus an additional non-orchard allele were found in the pollen pool. Thus, based on this very limited sample of loci, no measurable decrease was detected in the level of genetic vaiation in the seed crop relative to that present among the orchard clones.

1978 Seed Crop

Allelic frequencies in embryos were quite variable among the three seed size classes and were significantly heterogeneous at 5 of the 7 loci investigated (Table 3). For example, PGM1-2 varied in frequency from 0.006 in small seed to 0.149 in large seed. An examination of frequencies in the ovule and pollen pools, however, revealed that the heterogeneity among seed size classes was primarily due to variation in the ovule pool (Table 4), as would be expected if clones differ in the average size of seeds they produce. While five of the loci showed significant heterogeneity of allelic frequencies in the ovule pool, only one (PGM1) was significantly heterogeneous ($P < 0.05$) in the pollen pool.

These results indicate that clonal variation in seed size can result in substantial differentiation in the genetic and clonal composition of different seed size classes. Furthermore, there is strong evidence that genetic variability is reduced within seed size classes due to the lack of seeds from individual clones. In five cases (i.e., alleles LAP2-3, PGI2-1, 6PGD-1, PGM1-2, PGM2-1), an allele found in the ovule pool of one size class was not detected in one or more of the other size classes (Table 4). These alleles

are unique to one or a few clones; thus, their absence in a sample indicates that seeds from the clones they mark are at very low frequency, or are not present at all in that seed size class. LAP2-3, for example, is unique to clone 3-40 in the HSG orchard. This allele was found at a frequency of 0.130 in the ovule pool of the small size class seed, 0.037 in medium seed and was not detected in large seed, indicating that seeds from clone 3-40 are small, and are probably completely absent in the large size class. PGI2-1, and PGM2-1 also are unique to individual clones, and 6PGD-1 is unique to two clones. PGM1-2 is found in four clones, and the absence of this allele in the ovule pool sample of small seeds illustrates the significant reduction in clonal representation (at least in the female contribution) that might occur within seedlots as a result of seed sizing.

In addition to the reduction in genetic diversity within seed size classes due to loss of seeds from individual clones, further reduction may occur due to large differences among the remaining clones in relative seed production. For example, since one-half the progeny of clone 3-40 carry the marker LAP2-3, which occurred at an estimated frequency of 0.103 in the ovule pool of the small seed, 20.6% (i.e., 2 x 10.3%) of the small seed can be estimated to have come from ramets of this clone. Similarly, only four clones (3-13, 5-13, 3-16 and 7-45), all heterozygous for allele PGM1-2, were responsible for 46% of the large seed. Because pollen pools were relatively homogeneous over seed sizes, imbalances among clones in total genetic contribution to each size class were not as great as would be indicated from ovule pool frequencies alone. Nevertheless, based on allelic frequencies in embryos (Table 3), 11.2% of the genes in small seeds can be estimated to come from clone 3-40, and 29.8% of the genes in large seed can be estimated to come from the four clones which carried PGM1-2. Thus, some clones appear to be substantially over-represented in the large and small seed sizes, even when contributions of genes through the pollen pool are taken into account.

CONCLUSIONS

Although pollen contamination can lead to increased variability in the seed crop, it may be the single most important factor in reduction of genetic efficiency. Substantial decrease in genetic gains can result from pollen contamination (Squillace 1981). In the two seed orchards studied, it is apparent that the 122-m isolation strip composed of a continuous stand of trees was not effective in preventing undesirable levels of pollen contamination in the 1976 seed crop. Based on the data of Wang, Perry et al. (1960), a cleared isolation strip may be more effective in reducing pollen contamination. Various other methods have been proposed for reducing pollen contamination, including removing orchards from the species area, increasing the size of the orchard or the isolation strip, cooling the orchard to delay flowering relative to flowering in outside stands (Silen and Keane 1969, Fashler and Devitt 1980), and the use of supplemental mass pollination (Woessner and Franklin 1973).

While contamination is important, by itself it does not explain all the deviations in allelic frequencies from those expected. Clonal differences in phenology and numbers of male and female flowers also must be responsible for some of these deviations. However, the relative importance of phenological factors may vary from year to year depending on whether flowering time is condensed or extended. Similarly, the relative importance of clonal deviation in

numbers of flowers may depend on whether it is a generally good or poor flowering year.

Supplemental mass pollination (SMP) is one of the more promising methods suggested as a means to improve genetic efficiency in wind-pollinated seed orchards. SMP could help reduce pollen contamination to an acceptable level. In addition, SMP could increase full seed yield by ensuring that each female flower has sufficient cross pollen applied at the appropriate time to allow maximum seed production per cone. Imbalances in clonal representations which occur in the seed crop due to clonal variation in numbers of male and female flowers and floral phenology could be reduced by appropriately adjusting the pollen mix. Besides the increase in genetic efficiency, selection intensity could be increased in the choice of pollen parents to be included in the mix, and seed crops could be genetically tailored for specific uses (Franklin, 1971). Although the technology may not yet be available to accomplish SMP with dependable results and at a relatively low cost, further research, possibly using allozyme markers (Bridgewater and Trew 1981), may yield effective and practical methods.

Seed sizing could result in a significant loss of variation if seed is culled by size, or if seed from only one seed size is planted in an area. Thus, it is important that seedlings of different seed sizes be mixed for outplanting. These conclusions are in agreement with those of Silen and Osterhaus (1979) who found that in Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco], seed size can vary substantially among wind pollinated families.

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Table 1.--Observed allelic frequencies in the 1976 bulk seed crop, expected frequencies assuming full genetic efficiency, and chi-square values for goodness-of-fit.

Allozyme Locus	Allele	Expected Frequency	Observed: Ovule Pool Frequency	N	χ^2 (df)	Pollen Pool Frequency	N	χ^2 (df)	Embryos Frequency	N	χ^2 (df)
GDH	1	0.900	0.929	492	4.60(1)*	0.909	492	0.44(1)	0.919	984	3.95(1)*
	2	0.100	0.071			0.091			0.081		
LAP2	1	0.509	0.481	483	4.12(2)	0.468	483	4.25(2)	0.475	966	7.89(2)*
	2	0.485	0.507			0.522			0.514		
	3	0.006	0.012			0.010			0.011		
PGI2	2	0.927	0.925	489	3.78(2)	0.956	489	11.62(2)**	0.940	978	2.46(2)
	3	0.053	0.065			0.022			0.044		
	4	0.020	0.010			0.022			0.016		
GOT2	1	0.178	0.103	486	18.68(1)**	0.130	485	7.64(1)**	0.115	971	26.34(1)**
	3	0.822	0.897			0.870			0.885		
6PGD	1	0.029	0.049	493	12.24(4)*	0.043	493	39.57(4)**[1]	0.046	986	19.71(4)**[1]
	2	0.423	0.414			0.349			0.381		
	3	0.035	0.018			0.077			0.048		
	4	0.039	0.049			0.022			0.035		
	5	0.473	0.470			0.505			0.488		
	7	0	0			0.004			0.002		
PGM1	1	0.959	0.925	492	14.47(1)**	0.945	492	2.45(1)	0.935	984	14.42(1)**
	2	0.041	0.075			0.055			0.065		
PGM2	1	0.015	0.020	492	0.83(1)	0.010	492	0.83(1)	0.015	984	0.00(1)
	2	0.985	0.980			0.990			0.985		

[1]Alleles 5 and 7 were bulked prior to calculating the χ^2.

*Significant at 0.05 probability level.

**Significant at 0.01 probability level.

Table 2.--Expected allelic frequencies in the 1976 seed crop when clonal representation is weighted by ramet numbers but full genetic efficiency is otherwise assumed, and chi-square values for goodness-of-fit of observed (shown in Table 1) to expected frequencies.

Allozyme		Expected	χ^2 (df)		
Locus	Allele	Frequency	Ovule Pool	Pollen Pool	Embryos
GDH	1	0.912	1.77(1)	0.06(1)	0.60(1)
	2	0.088			
LAP2	1	0.449	2.02(2)	0.81(2)	2.66(2)
	2	0.539			
	3	0.012			
PGI2	2	0.889	7.43(2)*	26.30(2)**	26.25(2)**
	3	0.087			
	4	0.024			
GOT2	1	0.135	4.49(1)*	0.07(1)	3.33(1)
	3	0.865			
6PGD	1	0.015	49.79(4)**	49.13(4)**[1]	66.68(4)**[1]
	2	0.403			
	3	0.039			
	4	0.032			
	5	0.511			
	7	0			
PGM1	1	0.952	7.85(1)**	0.53(1)	6.22(1)*
	2	0.048			
PGM2	1	0.020	0.00(1)	2.51(1)	1.26(1)
	2	0.980			

[1]Alleles 5 and 7 were bulked prior to calculating the χ^2.

*Significant at 0.05 probability level.

**Significant at 0.01 probability level.

Table 3.--Comparison of allelic frequencies in embryos among three seed size classes (small, medium, large) in the 1978 bulk seed crop.

Allozyme		Small		Medium		Large		Heterogeneity
Locus	Allele	Frequency	N	Frequency	N	Frequency	N	χ^2 (df)
GDH	1	0.888	490	0.890	438	0.898	462	0.29(2)
	2	0.112		0.110		0.102		
LAP2	1	0.401	484	0.454	436	0.454	460	22.00(4)**
	2	0.543		0.521		0.539		
	3	0.056		0.025		0.007		
PGI2	2	0.941	490	0.903	434	0.892	460	18.00(4)**
	3	0.029		0.069		0.091		
	4	0.031		0.028		0.017		
GOT2	1	0.118	484	0.133	436	0.128	454	0.55(2)
	3	0.882		0.867		0.872		
6PGD	1	0.002	490	0	440	0.008	466	19.30(10)*
	2	0.396		0.431		0.363		
	3	0.018		0.039		0.039		
	4	0.024		0.041		0.024		
	5	0.556		0.480		0.560		
	7	0.004		0.009		0.006		
PGM1	1	0.994	490	0.946	442	0.851	442	77.36(2)**
	2	0.006		0.054		0.149		
PGM2	1	0.035	490	0.020	442	0.003	364	10.49(2)**
	2	0.965		0.980		0.997		

*Significant at 0.05 probability level.

**Significant at 0.01 probability level.

Table 4.--Comparison of allelic frequencies in the ovule pool among three seed size classes (small, medium, large) in the 1978 bulk seed crop.

Allozyme		Small		Medium		Large		Heterogeneity
Locus	Allele	Frequency	N	Frequency	N	Frequency	N	χ^2 (df)
GDH	1	0.927	245	0.890	219	0.897	234	2.03(2)
	2	0.073		0.110		0.103		
LAP2	1	0.309	243	0.477	218	0.472	233	39.99(4)**
	2	0.588		0.486		0.528		
	3	0.103		0.037		0		
PGI2	1[1]	0	245	0.037	217	0.121	231	55.31(6)**
	2	0.930		0.848		0.754		
	3	0.037		0.097		0.121		
	4	0.033		0.018		0.004		
GOT2	1	0.127	245	0.142	219	0.103	232	1.70(2)
	3	0.873		0.858		0.897		
6PGD	1	0	245	0	221	0.004	233	23.45(8)**
	2	0.376		0.443		0.309		
	3	0.004		0.014		0.009		
	4	0.004		0.050		0.026		
	5	0.616		0.493		0.652		
PGM1	1	1.00	245	0.950	221	0.769	221	81.87(2)**
	2	0		0.050		0.231		
PGM2	1	0.053	245	0.018	221	0	182	12.38(2)**
	2	0.947		0.982		1.00		

[1]PGI2-1 is detectable in megagametophytes only.

*Significant at 0.05 probability level.

**Significant at 0.01 probability level.

GENETIC AND ECONOMIC CONSEQUENCES OF POLLEN CONTAMINATION IN SEED ORCHARDS

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Abstract. -- Pollen contamination can be a serious obstacle to achieving maximum genetic gains from seed orchards. In the future, the problem will be greater as early-flowering techniques speed up the generation turnover time and advanced-generation seed orchards come into full production. This will lead to a larger gene frequency differential between orchard and nonorchard clones than occurs in first-generation seed orchards. Economic analyses indicate that the corrective measures available depend upon the number of acres an organization will be planting, the amount of pollen contamination and the gene frequency differential between advanced-generation orchards and the source of pollen contamination. More research is needed to determine how much pollen contamination occurs in seed orchards and the effectiveness of various corrective measures.

Additional keywords: Pollen dilution zone, advanced-generation seed orchards.

INTRODUCTION

The objective of seed orchards is to produce sufficient seed of good genetic quality to meet all of an organization's regeneration needs. Most members of the North Carolina State University - Industry Tree Improvement Cooperative are now meeting this need with their genetically rogued first-generation seed orchards. In addition, Cooperative members have established or are in the process of establishing second-generation orchards.

Predicted gains in volume from loblolly pine plantations established from seed orchard seed over nonimproved plantations is 15 percent from rogued first-generation orchards and 35 percent from second-generation orchards (Weir 1977). However, this expected gain will be achieved only if several assumptions hold. Two major assumptions are that self-fertilization is not great and that the amount of contamination by nonorchard pollen is not significant.

Recent evidence indicates that the proportion of progeny arising from self-fertilization in loblolly pine seed orchards is probably less than 2 percent (Adams and July 1980, Freidman and Adams 1981). Thus, it will not be discussed further in this paper.

Empirical estimates of the amount of wild pollen fertilizing ovules in seed orchards is scarce. In a recent review, Squillace and Long (1981) indicated

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that -- based upon pollen flight patterns, measurements of background pollen, and other factors -- pollen contamination may be extensive in some cases.

To minimize pollen contamination, the policy of the NCSU-Industry Tree Improvement Cooperative is to recommend that each seed orchard have at least a 400-foot pollen dilution zone surrounding it. This dilution zone is expected to significantly reduce pollen contamination in seed orchards.

Until recently, only a few Cooperative members were obtaining sufficient seed to meet their annual regeneration needs. Therefore, seed orchard management practices emphasized increasing the overall yield of cones rather than assuring that the seed obtained was of the best genetic constitution (Woessner and Franklin 1973). Now that many orchards are meeting or exceeding their regeneration needs, emphasis can be shifted to improving the genetic quality of the seed obtained.

DISCUSSION AND ANALYSES

Genetic Consequences and Considerations

Maximum expected genetic gain from plantations established with seed orchard seed can only be obtained if there is no pollen contamination. The clones selected for use in a seed orchard have undergone intensive selection for several traits. Through selection and establishment of seed orchards, tree breeders are creating new populations where the average frequency of favorable alleles for the traits under selection is higher than in the base population from which the trees were selected.

It is this increase in the frequency of favorable alleles that is responsible for the realized genetic gains observed in plantations and progeny tests. This gain can be a maximum only if there is no migration of pollen into the orchard. If migration occurs, the frequency of the favorable allele(s) in the seed orchard progeny is reduced. The change in average allele frequency in progenies from seed orchards due to pollen contamination, Δp_o, is

$$\Delta p_o = m(p_o - p_f) \qquad \text{(Wright 1976)}$$

where

m = ratio of outside pollen / (2) (outside + orchard) pollen
p_f = frequency of an allele "a" in the pollen coming from outside the orchard
p_0 = frequency of the same allele "a" in the seed orchard

It can be seen from this formula that both the amount of migration and the gene frequency differential between the two populations influence how much the expected gain will be diminished. The effects of pollen contamination on gene frequencies is illustrated in Table 1. For example, with a differential gene frequency between a seed orchard and source of contamination of .10 and 40 percent pollen contamination, the effective gain in frequency of a favorable allele is .08 versus .10 when there is no pollen contamination.

Table 1. Effective gain in frequency of a favorable allele ($\Delta p'$) in progeny of seed orchards with varying amounts of migration (%) and initial gene frequency differentials, Δp.

% pollen migration (m)	Δp 0	.01	.05	.10	.30	.50	.70	.90	.95	.99	1.0
0	0	.01	.05	.10	.30	.50	.70	.90	.95	.99	1.0
20	0	.009	.045	.09	.27	.45	.63	.81	.855	.841	0.9
40	0	.008	.041	.08	.24	.40	.56	.72	.760	.792	0.8
60	0	.007	.035	.07	.21	.35	.49	.63	.665	.693	0.7
80	0	.006	.030	.06	.18	.30	.42	.54	.570	.594	0.6
100	0	.005	.025	.05	.15	.25	.35	.45	.475	.495	0.5

$\Delta p = p_o - p_f$ = differential gene frequency between seed orchard and source of contamination.
m = donor/ 2 (donor + recipient) pollen because the pollen supplies only 1/2 the genes of the tree.
$\Delta p' = \Delta p - \Delta p_o$
$\Delta p_o = m(p_o - p_f)$

Several important points can be noted in Table 1. If there is no pollen contamination then the maximum achievable genetic gain can be realized from the seed orchard. Also, if there is 100 percent pollen contamination the maximum achievable gain in the frequency of the favorable allele is one half of that expected with no pollen contamination. Assuming a completely additive genetic model, this will correspond to an actual gain of one-half of the expected gain. From a practical standpoint, there will always be some contamination unless the seed orchard is located ourside the range of the species or some method is used to speed up or delay the time of flowering in the seed orchard.

A second point illustrated in Table 1 is that pollen contamination has an effect only if there is a difference in average gene frequency, Δp between the seed orchard and the source of contamination. Since the clones included in seed orchards will have undergone very intensive selection, a gene frequency differential should always exist between the two sources.

If the seed orchard is surrounded by stands or plantations of poorer genetic quality than the base population from which the clones were selected, the consequences of pollen contamination will be more severe than previously expected. One instance where this will be the case is with advanced-generation orchards. With the emphasis on quick turnover of breeding generations, it is conceivable to have a fourth-generation seed orchard surrounded by plantations originating from genetically nonimproved seeds or seeds from first-generation orchards. Advanced-generation seed orchards will have a larger gene frequency differential between orchard and nonorchard clones than first-generation seed orchards. This means the reduction in expected genetic gains resulting from pollen contamination will be greater than in the first-generation seed orchards. This is illustrated in Table 2, where the

average frequency of the favorable allele is .15, .10 and .05 in the seed orchard, in the base population from which the clones in the seed orchard were selected and in the population that is responsible for the pollen contamination, respectively. In this case, the effect of 100 percent pollen contamination from population A would be to reduce the effective gene fre-

Table 2. Influence of percent pollen contamination and source of contamination on effective gene frequency of seed orchard progeny. Assume orchard frequency of allele is p = .15 (see text for explanation).

Pollen Contamination (%)	Population A Base population for clonal selections (p = .10)	Population B Nonbase population (p = .05)
0	.15	.15
20	.145	.140
80	.130	.110
100	.125	.100

quency of seed orchard progeny from .15 to .125 (halfway between the frequency of the allele in the seed orchard and the base population). If in fact the pollen contamination is 100 percent and originates from population B, then the effective gene frequency of the seed orchard progeny would only be .10; or in this example the same as in the base population from which the clones for the seed orchard were selected (population A). Thus, the expected gain due to selection would be nullified and the genetic quality of the seed would be about the same as that expected from the seed orchard of the previous generation in which there was no pollen contamination.

Economic Consequences and Considerations

Pollen contamination reduces the expected genetic gain. Whether or not action can be taken to reduce contamination depends on the cost of the corrective measure and the benefits obtained.

No satisfactory estimates of the amount of pollen contamination occurring are available, and it probably varies by orchard and year from less than 5 percent to 20 percent or more. The total cost that would be incurred to reduce pollen contamination will vary depending on whether corrective measures are undertaken each year that the orchard is flowering (e.g. supplemental mass pollination) or whether it is a one-time action, such as increasing initial orchard size or increasing the size of the dilution zone.

In the case where some action would be taken in each year the orchard flowers, the net present value (NPV) of the loss in gain due to one trait such as volume growth is given by the formula:

$$NPV_x = V_n / (1+i)^n \qquad \text{(Duerr 1960)}$$

where

x = age at which treatment is applied
i = interest rate
n = time from treatment until end of rotation (years)
V_n = s x b x r x g" x a = value at rotation age of loss in volume due to pollen contamination
s = stumpage value ($/cord at time of harvest)
b = base growth rate (cords/acre/year)
a = number of acres planted per year
r = number of years in rotation
$g'' = (g-g') = g(\frac{m}{2})$ = loss in volume gain due to pollen contamination
g = expected gain in volume with no contamination (%)
g' = expected gain in volume with m amount of contamination (%)

The NPV for several levels of genetic gain, stumpage value and base growth when the level of pollen contamination is only 10 percent is shown in Table 3. For a projected gain in volume of 15 percent over nonimproved seed, an interest rate of 8 percent, a rotation age of 25 years, and a base growth rate of 1.0 cord/acre/year a company that plants 15,000 acres per year could spend up to $3,521 each year to reduce pollen contamination by 10 percent even at a moderate stumpage price of $10/cord. This amount increases as the interest rate decreases and as the stumpage value, base growth rate, number of acres planted per year, amount of pollen contamination or expected genetic gain increases. For example, the expected genetic gain in volume from second-generation seed orchards is 35 percent. Under the same conditions as first generation orchards, the amount that can be spent to reduce the level of pollen contamination by 10 percent is more than doubled (Table 3). The NPV in Table 3 represents the break-even cost that could be incurred each year to reduce contamination.

If it proves simpler or more efficient to reduce pollen contamination through a one-time operation such as increasing the size of the isolation zone, then the amount that could be spent can be estimated from the following formulae:

$$NPV_y = V_n \frac{(1+i)^p - 1}{i\,(1+i)^p} \qquad \text{Duerr 1960)}$$

$$NPV_o = \frac{NPV_y}{(1+i)^y}$$

where

NPV_y = value at the year before the first plantation is harvested of volume loss due to pollen contamination of all plantations originating from seed of that orchard.

y = number of years from orchard treatment until one year before the first plantation is harvested.

NPV_o = value at time of orchard establishment of volume loss due to pollen contamination of all plantations originating from seed of that orchard.

V_n = value at harvest time of loss in volume due to pollen contamination

p = number of years of full production of seed orchard

i = interest rate

The NPV at time of orchard establishment for the same conditions given in Table 3 is shown in Table 4. An additional condition, in this example, is that a seed orchard begins to produce enough seed to plant 15,000 acres per year at age 12 and continues to do so for 20 years. The figures in Table 4 represent the amount that could be spent at the time of orchard establishment to reduce pollen contamination by 10 percent under the conditions stated.

Both Table 3 and Table 4 consider volume gain only. If the added value of improvement in straightness, wood quality and other traits were considered, then it will be more profitable to reduce pollen contamination.

Table 3. Present value (at time of yearly treatment) of taking measures aimed at lessening the amount of pollen contamination occurring during a given year for the conditions given. 1/

	Case 1		Case 2	
Expected genetic gain	15%		35%	
Stumpage Value $/cord at time of harvest)	Base Growth (cords/ac/yr) 1.0	2.0	Base Growth (cords/ac/yr) 1.0	2.0
6	$ 2,112	$ 4,225	$ 4,929	$ 9,858
10	3,521	7,042	8,215	16,431
15	5,281	10,563	12,323	24,646
20	7,042	14,084	16,431	32,862
30	10,563	21,125	24,646	49,293

1/ Based on 25 year rotation, 8% interest rate, 10% pollen contamination and 15,000 acres planted per year.

Table 4. Present value (at time of seed orchard establishment) of reducing the amount of pollen contamination occurring over the productive life of the orchard for the conditions stated. 1/

	Case 1		Case 2	
Expected genetic gain	15%		35%	
Stumpage Value ($/cord at time of harvest)	Base Growth (cords/ac/yr) 1.0	2.0	Base Growth (cords/ac/yr) 1.0	2.0
6	$10,376	$20,752	$24,210	$48,421
10	17,293	34,586	40,351	80,701
15	25,940	51,879	60,526	121,052
20	34,586	68,172	80,701	161,403
30	51,879	103,759	121,052	242,104

1/ Based on 25 year rotation, 8% interest rate, 10% pollen contamination, 15,000 acres planted per year and a productive life of 20 years for the seed orchard.

The use of pollen dilution zones is the primary method of reducing pollen contamination in most seed orchards. To be effective, the dilution zone requires a large amount of land be taken out of timber production. Therefore, maintaining a pollen dilution zone around a seed orchard can be very expensive. However, even a moderate reduction in pollen contamination is sufficient to justify the expense. For example, a 35 acre second-generation seed orchard might require an additional 80 acres to ensure a 500-foot pollen dilution zone. Assuming a land cost of $1,200 per acre, a base growth rate of 1.5 cord/acre/year, a stumpage value at the time of harvest of $15/cord, and an interest rate of 8 percent, the cost of including a 500-foot dilution zone would be about $107,000. To offset this cost (for a second-generation seed orchard) the dilution zone need reduce pollen contamination by less than 20 percent, assuming a base growth rate of 1.0 cord/acre/year, a stumpage value of $15 per cord, and the conditions stated in Table 4. That is, a 20 percent reduction in pollen contamination would give an increased stumpage value of $121,052 for a company that planted 15,000 acres per year.

In most cases, the actual cost of the pollen dilution zone will be much less than stated. When the seed orchard is on prime agricultural land (as assumed above) the land can often be leased to farmers for row or forage crops. When the seed orchard is not located on prime agricultural land, the land cost will be much lower than in the above example.

CONCLUSIONS AND RECOMMENDATIONS

Both the genetic and economic cost of contamination may be high and will be greater in the future. Each organization must determine how much pollen contamination it is faced with and must decide on what corrective measures, if any, it wishes to take. Among the options are (Squillace and Long 1981):

1. Increasing the size of the pollen dilution zone.

2. Increasing orchard size.

3. Use of only clones whose flowering times are known to be fairly synchronous.

4. Use of management practices to increase pollen production.

5. Increasing scrutiny to seed orchard site selection. Among the variables to consider are abundance and genetic quality of surrounding stands or plantations. The ideal situation would be to locate an orchard outside the species range or in an area where the flower phenology of the orchard trees would be out-of-phase with those contributing the background pollen.

6. Modification of the environment of the seed orchard so that the trees are out-of-phase with those in the surrounding area.

7. Use of supplemental mass pollination techniques (SMP) to increase the relative level of orchard pollen present at crucial times (Bridgwater and Trew 1981, Woessner and Franklin 1973).

All of the above options have some merit. If it is not possible to locate an orchard in an area with no background pollen, the best choice would probably be to use a combination of several of the options listed.

Use of pollen dilution zones is a standard practice for members of the N. C. State - Industry Tree Improvement Cooperative. The dilution zones are no doubt effective in reducing the level of pollen contamination. However, the precise effectiveness of these dilution zones is really unknown. The two estimates of pollen contamination presently available are 28% in one case and greater than 80% in another case (Friedman and Adams 1981, Squillace and Long 1981, respectively). Both of these studies used small orchards, so the estimates of pollen contamination obtained may be higher than expected in a typical seed orchard. The genetic and economic consequences of pollen contamination will continue to increase as more advanced-generation seed orchards are established. Therefore, more information is needed on the amount of pollen contamination occurring in seed orchards to determine if it is severe enough to warrant additional attention.

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PITCH CANKER IN SEED ORCHARDS

L. D. Dwinell and Jane Barrows-Broaddus [1/]

Abstract.--Pitch canker, caused by Fusarium moniliforme var. subglutinans, is a serious disease of pines in southern seed orchards. The disease has been confirmed in over 30 seed orchards from North Carolina to east Texas on a wide range of economically important pine species. Symptoms include branch and bole cankers, and shoot dieback. Wounds are readily infected by the pitch canker fungus. Within pine species, individual clones vary markedly in their susceptibility to infection and incidence of disease is frequently related to the geographic source of seed. This fungus also causes conelet abortion, mortality of maturing cones, and seed deterioration. Control strategies and current research initiatives are presented.

Additional keywords: Fusarium lateritium f. sp. pini, tree shakers, Arthrobacter sp., biological control, systemic fungicides.

As management of commerical forests in the Southern United States becomes more intensive, greater reliance will be placed on seed orchards to supply genetically improved seed for regenerating cut-over lands. Pitch canker, caused by Fusarium moniliforme Sheld. var. subglutinans Wr. & Reink. (Dwinell 1978; Kuhlman et al. 1978), is one of the diseases that is rapidly increasing in importance in seed orchards across the Southeast. Disease impacts are increasing in spite of and sometimes because of the specialized maintenance practices used to force seed production and to harvest the crop. Shoot dieback, known by seed orchard managers for at least 20 years, waxed and waned, and attempts to determine the causal agent were limited. However, in 1975 the disease suddenly became severe in two loblolly seed orchards in separate regions of the South (Dwinell et al. 1977). Since then, pitch canker has been confirmed in over 30 seed orchards.

SYMPTOMS

Two types of symptoms are associated with this disease. The classic symptom as described by Hepting and Roth (1946) is the resinous cankers on the trunks and larger branches which commonly develop at injuries. These cankers are usually sunken, and the underlying wood is soaked with pitch, often to the center of the stem. These cankers are perennial, and frequently girdle the tree (Blakeslee et al. 1980; Dwinell and Phelps 1977).

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A second type of symptom is shoot or crown dieback, which occurs when cankers form on the current year's shoot, girdling them before the next growing season. In the fall, needles on recently killed shoots turn yellow to reddish brown; they later turn greyish brown to dark grey. The summer growth flushes appear to be the most frequently attacked, with the terminal usually showing symptoms first. Infected twigs and branches are often soaked with resin. Shoot dieback markedly thins the crown, and cankers often kill shoots soon after they develop the following spring. Intensification of shoot dieback symptoms may result in the loss of a year's crop because cone-bearing branches in the crown are killed to the tip. In succeeding years, however, the trees may recover and resume full production (Blakeslee et al. 1980; Dwinell and Phelps 1977; Phelps and Chellman 1976).

DISTRIBUTION AND HOSTS

Disease surveys conducted in the past 5 years have confirmed pitch canker incidence in approximately 30 seed orchards in North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, and east Texas. Shoot dieback is most severe on slash (Pinus elliottii Engelm. var. elliottii) pine in Florida, and loblolly (P. taeda L.) and shortleaf (P. echinata Mill.) pines elsewhere in the South. Bole and branch cankers are common on slash, shortleaf, longleaf (P. palustris Mill.), and Virginia (P. virginiana Mill.) pines. The incidence and symptoms of pitch canker are highly variable and depend on the inherent susceptibility of the pine species and the environment in which the trees are growing.

TREE SHAKER WOUNDS

Most canker-producing organisms, including F. moniliforme var. subglutinans, require a wound as an infection court. In slash pine seed orchards, bole cankers often develop through injuries caused by mechanical shakers used in cone collection. The most obvious damage caused by tree shakers is the actual removal of bark at the point where the pads grasp the bole. However, cankers may develop at grasp sites where there is no obvious bark removal. Furthermore, pitch cankers frequently develop on the upper portion of the bole where the vibration (or whiplash) of the main stem is most vigorous.

A study conducted during 1980 in two Georgia Forestry Commission seed orchards determined the location of bole cankers on slash pines in relation to areas of tree shaker contact. The 80 trees sampled at the Arrowhead and Horseshoe Seed Orchards averaged two cankers per tree (Table 1). Approximately three-fourths of the trees had cankers at the point of tree shaker contact (near breast height). Some two-thirds of the trees had cankers on the middle third of the stem (15-30 ft). Dissection of 10 slash pines at the Arrowhead Seed Orchard revealed that many of these cankers were initiated by infection through branch stubs and fusiform rust galls on the bole. These cankers were commonly the site of breakage during severe weather.

Table 1.--Location of bole cankers on slash pines in two Georgia Forestry Commission seed orchards that have been mechanically shaken for several years

Seed orchard	Tree age (years)	No. trees sampled	Tree DBH (mean)	Tree height (mean)	Position of cankers on bole[a]				
					Shaker wound	Lower third	Middle third	Upper third	Canker/tree (mean)
Arrowhead	23	30	12 in.	42 ft.	80%	63%[b]	53%	13%	2.1
Horseshoe	18	50	13 in.	51 ft.	66%	26%	82%	16%	1.9

[a] % trees with cankers

[b] The % trees with cankers above or below the point where the trees are grasped by the tree shaker

In 1978 and 1979, tree shaker pads were sampled during regular slash pine cone harvesting operations at the Arrowhead Seed Orchard to determine if the pitch canker fungus and other related fusaria were being spread from tree to tree on the pads. The pads were sampled after every five trees were shaken. The sampling procedure consisted of dispensing 20 ml sterile deionized water at the center top of the pad and collecting the water at the bottom of the pad in a sterile glass bottle. The shaker pads were cleaned with 70% ETOH before and between samples. In 1978, a total of 10 samples representing 50 trees was collected, and in 1979, a total of 20 samples representing 100 was collected. The samples were diluted and a 1-ml aliquot was spread evenly on petri plates containing a medium selective for fusaria (Agrawal et al. 1973). Although eight species of Fusarium were isolated; F. moniliforme var. subglutinans occurred infrequently (3-4%) (Table 2). Also, pathogenicity tests of these isolates indicated that only 50% of them were virulent, qualifying them as the pitch canker strain. Both sampling dates occurred during an extended drought, and under these environmental conditions, it appeared that the risk of spreading the causal fungus on shaker pads was low. The population levels of F. moniliforme var. subglutinans may increase significantly during periods of rainy weather, and given these environmental conditions, the spread on tree shaker pads may be markedly increased. Sporodochia, commonly observed in slash pine plantations in Florida (Blakeslee et al. 1978b) were not observed on active bole cankers in the seed orchards.

Table 2.--Isolations of fusaria from tree shaker pads during slash pine cone harvest at the Arrowhead Seed Orchard. September 1978 and 1979

Year	No. Samples	No. per sample	Fusarium species (%)[b]							
			Fms	Fm	Fre	Frs	Fl	Fo	Ft	Fs
1978	10	38	4	7	4	80	0	1	4	0
1979	20	45	3	21	0	42	2	30	1	1

[a] Each sample represents a sequence of 5 trees

[b]
Fms = F. moniliforme var. subglutinans
Fm = F. moniliforme
Fre = F. roseum 'equiseti'
Frs = F. roseum 'semitectum'
Fl = F. lateritium
Fo = F. oxysporum
Ft = F. tricinctum
Fs = F. solani

OTHER WOUNDS

Any wound, regardless of cause or location, provides an infection court for the pathogen. Routine seed orchard management practices such as branch pruning, mowing, and, in the case of loblolly pine, tearing cones from the branches, create wounds for the pathogen to invade. Weather-related injuries such as those from wind and hail may also serve as entry points. Hurricanes and tornados in recent years have caused intensification of pitch canker in at least two seed orchards, one shortleaf and the other Virginia pine, in Alabama. The role of insect damage in the disease complex has not been completely elucidated, but the deodar weevil (Pissodes nemorensis Germar.), the subtropical pine tip moth (Rhyaciona subtropica Miller), and the needle midge (Contarinia sp.) have been linked to the disease (Blakeslee et al. 1978b; Matthews 1962; Overgaard et al. 1976).

HOST VARIATION

Within pine species, the incidence of pitch canker is frequently related to the geographic source or provenance of the host (Dwinell et al., 1977). In three loblolly pine seed orchards on the Coastal Plain, for example, incidence of pitch canker on loblolly pine was higher on Piedmont than on Coastal Plain seed sources (unpublished data). In Florida, Blakeslee and Rockwood (1978) found that slash pine clones from central Florida were more resistant than clones from other geographic areas.

Individual clones within species also vary greatly in their susceptibility to infection by F. moniliforme var. subglutinans (Dwinell et al. 1977; Phelps and Chellman 1976). This phenomenon has been noted for loblolly, slash,

longleaf, shortleaf, and Virginia pines grown in southern seed orchards. In a Virginia pine progeny test, Barnett and Thor (1978) also found clonal variation in the incidence of pitch canker.

CONELETS, CONES AND SEED

Fusarium moniliforme var. subglutinans does not limit its activities to causing cankers. Miller and Bramlett (1978) demonstrated that the fungus can cause the abortion of female strobili and conelets and mortality of maturing cones of slash pine. They also found that the fungus is carried in seeds and causes deterioration in stored seedlots. Fusarium moniliforme Sheldon is known to cause damping-off of coniferous seedlings (Spaulding 1914) and Barnard and Blakeslee (1980) reported pitch canker on seedlings in forest tree nurseries in Florida. However, linkages between these various host-parasite interactions and disease situations have yet to be demonstrated.

CONTROL

Although pitch canker was first described over 35 years ago (Hepting and Roth 1946), the current lack of information on the inoculum source and other aspects of the disease cycle precludes many control measures. Because wounds are known to be a prerequiste for disease initiation, control recommendations are limited to altering management practices to reduce wounding, especially during periods of high disease risk, primarily in the fall and winter. Tree shakers should be properly adjusted and operated by trained personnel. Loblolly pine cones should be harvested by clipping rather than tearing to reduce stripping of the bark. Mower damage to the tree stem and anchor roots should be avoided (Blakeslee et al. 1980).

Because seed orchard trees have high monetary value, chemical control of the disease is economically feasible. Systemic fungicides of the benzimidazole group have demonstrated effective inhibition of F. moniliforme var. subglutinans in vitro (unpublished data). Several promising fungicides applied by injector are being evaluated for control of the disease in seed orchards.

Presently, a soil bacterium, Arthrobacter sp., is being evaluated as a biological control agent of the pitch canker fungus (Barrows-Broaddus and Kerr 1981). Studies are underway involving the colonization of artificially created wounds on slash pine boles with Arthrobacter and other antagonists and to monitor not only development of pitch canker in inoculated and noninoculated trees, but also to evaluate persistance of introduced microflora and host response to colonization by the pathogen and/or antagonists of the pathogen. The ultimate goal of this research is to determine how to manipulate the bark environment in order to aid the tree's own defense responses against invasion by F. moniliforme var. subglutinans.

Since seed orchard management practices may contribute to the incidence of pitch canker, two simulated slash pine seed orchards have been established in cooperation with the Georgia Forestry Commission. These disease research seed

orchards are being used to study the effects of balanced fertilizer application in the spring, ammonium nitrate application in late summer, and tree shaker useage on the development of the disease. One seed orchard, at the Baldwin State Forest, is also being used to study systemic fungicides, biological control, and wounding in an effort to develop sound control strategies.

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EARLY LOBLOLLY PINE CONE COLLECTION IN A SOUTH CAROLINA SEED ORCHARD

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Abstract.--In the fall of 1978 and 1979, loblolly pine cones were collected from 14 seed orchard clones at the South Carolina State Commission of Forestry's seed orchard located near Sumter, South Carolina. Cones were collected on September 6, 12, 20, and 26 in both years. On each date, the collected cones were subject to the following five treatments: (1) shade with burlap cover and sprinkled, (2) shade without cover and sprinkled, (3) cones sealed in plastic bags and refrigerated at 38-40° F., (4) cones placed in burlap bags and airdried in sunlight, and (5) cones placed in burlap bags and airdried under 50% shade. Seeds were then extracted and cones were rated for degree of opening. No single treatment or date of collection clearly yielded the highest germination or greatest degree of cone opening. However, treatments 1 and 5 gave the best results throughout and more importantly, were the best treatments on the earliest collection dates giving nearly complete cone opening and germination averaging over 80%. It was concluded that loblolly seed orchard cones given the proper treatment may be collected up to 4 weeks earlier than the normal cone ripening period with good to excellent seed yield and germiation.

Additional keywords: Pinus taeda, cone opening, seed yield, seed germination.

Loblolly pine (Pinus taeda L.) is one of the most important reforestation species in the Southeast. Hundreds of millions of seedlings are produced annually and this figure is increasing yearly. All loblolly pine seed is currently collected by hand because no mechanical means of collection has been perfected.

Optimum cone collection time for loblolly pine has been found to occur from the first to about mid-October for a period of 15 to 20 days (Wakeley 1954). This short collection period has proven to be a serious problem for the seed orchard manager, especially when large amounts of seed are desired. Currently, cone collection is very expensive because a large concentration of equipment and manpower must be made available in one short period.

Extending the cone collection period by early collection (10 to 14 days) would allow more seed to be harvested and reduce the amount of labor and equipment needed. This would also reduce overall cost and allow for a more orderly procedure in preparing cones for drying and seed extraction. This paper reports the results of an early cone collection study and five after-ripening treatments on seed production and quality under field conditions.

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METHODS

Two loblolly pine seed orchards were selected from the Fulton B. Creech Seed Orchard complex located near Sumter, South Carolina. Three clones were selected from the Piedmont orchard and 11 clones were selected from the Coastal orchard. The Piedmont clones were selected on the basis of previous outstanding performances regarding cone production and seed germination. The Coastal orchard has a history of highly variable cone yields among individual clones; consequently, a larger sample of clones were selected. Both orchards range in age from 14 to 16 years old and have been producing seed for about 10 years. In each orchard, several ramets of each clone were selected but no distinction between ramets was made at the time of collection.

Cones were collected from each clone on September 6, 12, 20, and 26 in 1978 and 1979. In 1978, 50 cones were collected from each clone on each date. Due to a poor cone crop and to facilitate the experiment, only 25 cones were collected from each clone on each date in 1979. The 1978 cones were randomly divided into groups of 10, and the 1979 cones were randomly divided into groups of five cones each. The following treatments were applied to each of the five groups:

1. "Shade-with cover" - Cones were placed under lath shade, covered with burlap, and sprinkled with water intermittently (every 3 days).

2. "Shade-no cover" - Cones were placed under lath shade without burlap cover and sprinkled with water intermittently (every 3 days).

3. "Cold" - cones were placed in sealed plastic bags and refrigerated at 38-40^{o} F.

4. "Sun" - Cones were placed in burlap bags and airdried in sunlight.

5. "Orchard" - Cones were placed in burlap bags and airdried under 50% shade.

Four weeks after the last collection date, the treatments were ended. The cones were placed in paper bags and put into a forced air-dry kiln for a period of five days at 120^{o} F. When the cones were removed, each cone was individually "bumped" so that all available seed was extracted. No attempt was made to remove seed by cone dissection or any other forceable manner. The cones were inspected for degree of openness and a numeric value of one through five was assigned to each cone. A value of one was considered to be fully closed, and a value of five was considered to be fully open. All 1979 seed samples were weighed and germination tests were begun immediately. Two samples of 50 seeds each were drawn and stratified for three weeks at 40^{o} F. Germination procedures were followed as suggested in Seeds of Woody Plants of the United States (1974).

RESULTS

Germination

The orchard treatment produced the highest overall germination mean for the 1979 Coastal orchard (table 1), but the plot of germination by date illustrates that the orchard treatment did not prove to be superior for all collection dates (fig. 1). In general, all treatments produced poor germination.

The cold treatment for the 1979 Piedmont orchard averaged only 65.0% germination for all dates while all other treatments averaged 80.5% or greater (table 2). A plot of mean germination by date for each treatment illustrates several important trends (fig. 2). The sun, cold, and shade-no cover treatments had the lowest germination on the first collection date. However, the sun treatment had the highest germination on the second and last collection date.

Degree of cone opening

Clearly, the orchard treatment had the best overall mean and proved to be superior on all dates for degree of cone opening for the 1979 Coastal orchard. It should be noted that good results were obtained on the first collection date using the orchard, shade-no cover, and shade with cover treatments (table 3 and fig. 3).

The orchard treatment and the shade with cover treatments had the highest overall means for degree of cone opening for the 1979 Piedmont orchard. Excellent results were obtained using these treatments and the shade-no cover treatment on the first collection date (table 4 and fig. 4). For this publication, only 1979 data are presented. The data for 1978 are available upon request.

DISCUSSION

No single treatment or date clearly proved to yield the highest germination or greatest degree of cone opening for either orchard for either year. However, there are several trends that can be noted. In 1979, the orchard treatment gave excellent results on the first collection day and had the highest overall mean for degree of cone opening for both orchards. Also, the orchard treatment had the highest germination mean for the 1979 Piedmont orchard on the first collection day and had the highest overall germination mean for the Coastal orchard. The sun treatment tended to give good results for germination from the second collection date until the last; however, it did not prove to do well for cone opening. In 1978, the shade-with cover treatment performed the best overall dates for both orchards for degree of cone opening. The shade-with cover treatment also gave good results in the 1979 Piedmont orchard.

Obviously, different treatments performed better for each variable on different dates. However, on all dates for both orchards in both years, the shade-with cover treatment gave slightly higher germination results (80%) than the orchard treatment (76.5%) and resulted in a slightly lower degree of cone opening (4.56) than the orchard treatment (4.84). Depending on facilities, one of these two treatments would have to be considered the most advantageous for application.

Table 1. Mean germination values for 1979 Coastal orchard.

	DATE				
TREATMENT	9/6	9/12	9/20	9/26	MEAN
Cold	31.4	47.6	36.8	44.2	40.8
Orchard	62.3	75.6	62.5	73.8	68.8
Shade-no cover	60.3	71.2	55.1	53.7	60.9
Shade-with cover	64.6	63.1	66.8	63.1	64.3
Sun	50.1	77.4	65.0	72.8	66.8
MEAN	57.3	69.5	57.4	61.5	60.3

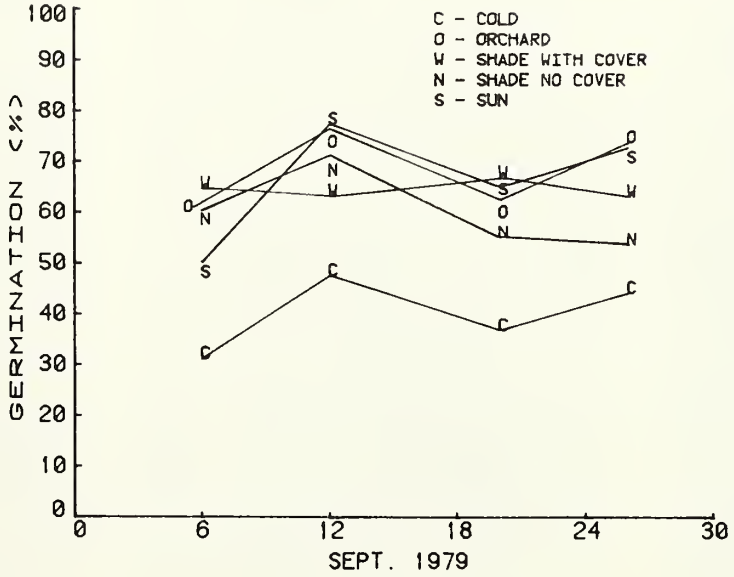

Figure 1. Germination by date for all treatments for 1979 Coastal orchard.

Table 2. Mean germination values for 1979 Piedmont orchard.

	DATE				
Treatment	9/6	9/12	9/20	9/26	MEAN
Cold	70.8	49.0	65.7	75.6	65.0
Orchard	85.3	90.0	72.7	89.0	84.3
Shade-no cover	70.6	84.0	83.3	85.3	80.5
Shade-with cover	81.3	86.0	85.3	93.6	83.5
Sun	71.0	96.0	83.3	93.7	86.0
MEAN	76.0	80.8	78.1	85.0	79.9

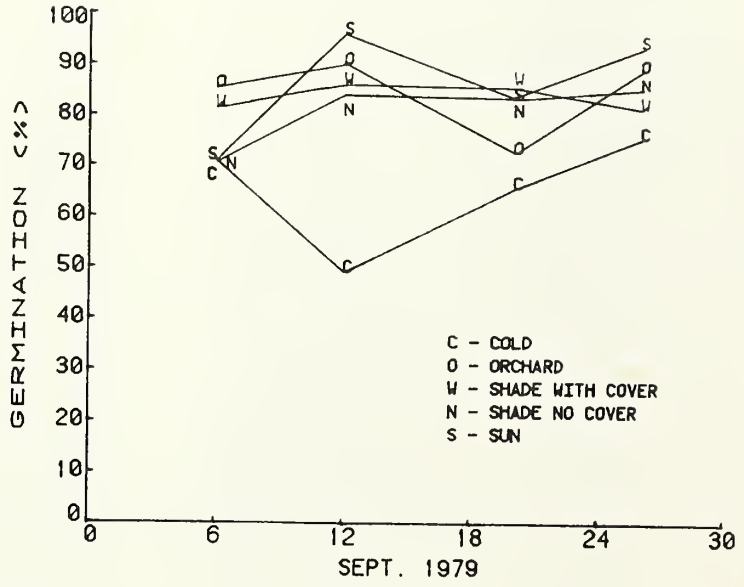

Figure 2. Germination by date for all treatments for 1979 Piedmont orchard.

Table 3. Mean degree of cone opening values for 1979 Coastal orchard.

	DATE				
TREATMENT	9/6	9/12	9/20	9/26	MEAN
Cold	1.49	1.85	2.76	3.78	2.47
Orchard	4.96	4.74	4.58	4.43	4.68
Shade-no cover	4.81	3.96	2.45	3.10	3.58
Shade-with cover	4.72	4.10	3.40	3.58	3.95
Sun	3.09	3.96	3.07	2.87	3.25
MEAN	3.81	3.72	3.25	3.55	3.58

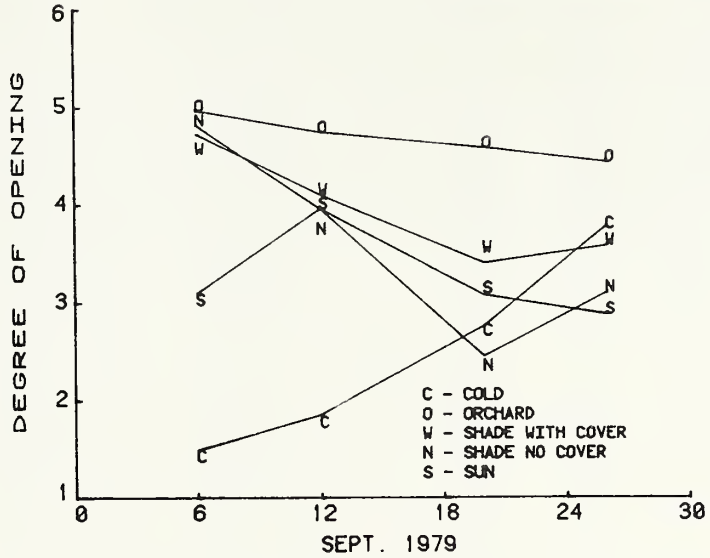

Figure 3. Degree of cone opening by date for all treatments for 1979 Coastal orchard.

Table 4. Mean degree of cone opening values for 1979 Piedmont orchard.

	DATE				
TREATMENT	9/6	9/12	9/20	9/26	MEAN
Cold	2.46	2.40	4.53	5.00	3.60
Orchard	5.00	5.00	5.00	5.00	5.00
Shade-no cover	5.00	4.33	4.80	4.86	4.74
Shade-with cover	5.00	4.93	5.00	5.00	4.98
Sun	4.66	4.80	4.73	4.86	4.76
MEAN	4.42	4.29	4.81	4.94	4.61

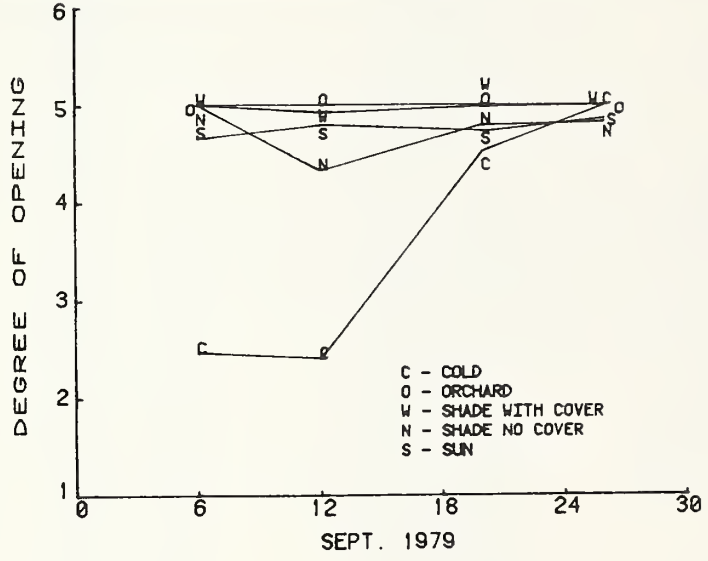

Figure 4. Degree of cone opening by date for all treatments for 1979 Piedmont orchard.

It appears that the shade and moisture treatments performed the best on the earliest collection dates. This is evidenced by the fact that no other treatment exceeded the performance of the orchard or shade-with cover treatments on the first collection day.

CONCLUSION

The results of this study definitely show that Piedmont loblolly pine cones may be collected up to 4 weeks earlier than normal with excellent seed yield and germination. Additional work investigating the Coastal clones is needed due to the variability among individual clones in this orchard. However, it appears appreciable progress toward earlier collection dates can be made with certain individual clones.

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TRICKLE IRRIGATION AND SYSTEMIC INSECTICIDES FOR CONTROLLING TIP MOTH IN YOUNG SEED ORCHARDS

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E. P. Merkel and C. M. Gallegos[1/]

Abstract.--Initial investigations indicate that liquid formulation, systemic insecticides can be successfully applied through trickle irrigation systems for pine tip moth control. Furadan and Di-Syston are the favored chemicals. Trickle irrigation system design is an important consideration when planning insecticide applications.

Additional keywords: Rhyacionia spp., carbofuran, disulfoton, irrigation design.

Trickle irrigation has proven to be a cost-effective approach to the application of water and certain fertilizers in seed orchards (O'Loughlin 1979) Additionally, various other agricultural chemicals have been applied through irrigation systems in various agronomic crops (Anonymous 1979). Insecticide application through trickle irrigation systems is attractive for several reasons including:

1. Tractors, associated labor and equipment are not required for application.

2. Lack of soil moisture that could prevent root uptake of soil-applied insecticides is not a concern.

3. Heavy single applications with accompanying hazards to man and wildlife are avoided.

4. Lower levels of the insecticides can be applied periodically as required for tree protection.

5. Fading insect control late in the growing season, associated with a single early-season insecticide application, is avoided.

6. Savings in chemical costs by a potential reduction in the amount of insecticide required.

Pine tip moths (Rhyacionia spp.) cause a significant growth reduction in young seed orchard trees. International Paper Company has a number of trickle irrigation systems established in their orchards and, in an effort to utilize these systems to their best advantage, investigations into insecticide application through these trickle systems were begun.

1/ Manager-Orchards & Nurseries, Supervisor-Tree Improvement, Forest Entomology Consultant and Sr. Research Forester, respectively, for International Paper Company. The authors express their appreciation to R. H. Smeltzer and C. R. Mayfield of IP's Natchez Forest Research Center for the chromatograph analysis of the various irrigation samples.

Since a successful insecticide application through a trickle system would be similar to a soil drench application, various systemic liquid-formulation chemicals that held promise of effective soil drench application were field tested. Several questions had to be resolved regarding the feasibility of this approach.

1. Would any of the potential insecticides be harmful to various trickle irrigation components?

2. Would a trickle irrigation pattern of water placement (7.5' x 20' grid) and timing of application prove adequate for root uptake and insect protection?

3. Which insecticides and rates of application would be most effective in controlling tip moth?

4. Could the insecticides be successfully metered into the trickle system and uniformly applied to the trees?

METHODS

The six chemicals that were field tested in 1979 (Table 1) were evaluated for irrigation component deterioration by soaking various plastic components in a 1:1 mixture of each liquid insecticide and water for 48 hours at room temperature.

Table 1.--Liquid Formulation Insecticide Rates (1979)

Chemical	Pounds Active Ingredient/Gal.	Annual Application Rate (Pounds Active Ingredient) Per Tree	Annual Application Rate (Pounds Active Ingredient) Per Inch Basal Diameter
Furadan (carbofuran)	4.00	0.050	0.020
Di-Syston (disulfoton)	6.00	0.046	0.018
Systox (demeton)	2.00	0.040	0.016
Bidrin (dicrotophos)	8.00	0.012	0.005
Cygon (dimethoate)	2.67	0.040	0.016
Metasystox-R (oxydemeton-methyl)	2.00	0.100	0.040

Various insecticides and rates of application were evaluated during the springs of 1979 and 1980 on loblolly pine (Pinus taeda L.) grafts at the Bellamy Seed Orchard located near Marianna, Florida. Tree spacing is 15 x 20 feet. Soils on this orchard are well drained, moderately fertile Orangeburg loamy sand and Red Bay fine sandy loam which were previously under cultivation. Subsoil, beginning at 6 to 18 inches, is a sandy clay loam. The 1979 insecticide applications (Table 1) were begun in early April on vigorous young grafts beginning their third growing season in the orchard. Tree diameter at the ground line was 2 to 3 inches and tree height was 4 to 6 feet. Each treatment plot consisted of five trees and was replicated three times. Tip moth infestation was evaluated in June and September by determining the proportion of the 10 uppermost shoots attacked per tree. Insecticide (diluted with an equal

volume of water) in one experiment was applied as a single dose at the beginning of the season (early April) and, in another experiment, was split into eight smaller applications evenly distributed over the growing season. The total amount of active insecticide in the eight smaller applications was equivalent to the single April application. A total of 210 trees were included in the studies. The insecticide for a particular tree was applied to the soil in a very small area (<10 sq. in.) immediately adjacent to the two 1/4-inch water delivery tubes, each located about 3.5 feet opposite the bole in a N-S orientation. The irrigation system was run normally throughout the growing season, thus a trickle system application was simulated.

The 1980 evaluations were primarily rate tests. The first phase (late May) was a shadehouse evaluation of phytotoxicity in potted (1 gallon nominal) rootstock plants 18 to 24 inches tall that were somewhat rootbound. Each insecticide rate was diluted in a half gallon of water and applied as a soil drench on four potted seedlings. A mid-June evaluation was completed.

The second phase of the 1980 evaluations involved a single soil drench around vigorous, well-established young orchard grafts that were beginning their second growing season in the orchard. Tree height was 2 to 3 feet and ground diameter was 1 to 1-1/2 inches. The June insecticide application (Table 2) involved five trees/treatment in each of three replicates for a total of 225 grafts. September shoot infestation was evaluated according to the previously-mentioned method. Unlike the 1979 test, the insecticides were diluted in one quart of water and the soil was drenched within the 4 square feet immediately around the tree. Irrigation continued normally throughout the growing season. The trees in this test were irrigated with both water delivery tubes at the immediate base of the tree, which is the standard orchard practice on these size trees.

Table 2.--Liquid Formulation Insecticide Rates (1980)*

		Annual Application Rate (Pounds Active Ingredient)			
		Low Rate		High Rate	
Chemical	Ingredient/Gal.	Per Tree	Per Inch of Basal Diameter	Per Tree	Per Inch of Basal Diameter
Furadan	4.00	0.013(½x)	0.010	0.025(½x)	0.020
Di-Syston	6.00	0.138(3x)	0.110	0.276(6x)	0.221
Systox	2.00	0.120(3x)	0.096	0.240(6x)	0.192
Bidrin	8.00	0.036(3x)	0.029	0.072(6x)	0.058
Orthene (acephate)	0.75/Pound of Wettable Powder	0.055	0.044	0.110	0.088

*Chemical rates are noted as multiples of the 1979 per tree test rates (x).

One of the chemicals that performed successfully in the above evaluations (Furadan) was actually metered into the irrigation system and discharge samples taken at various tree locations within a subsection of the orchard. Twelve locations were selected (two sample stations 20 feet apart/location) to give a selection of the various distances the insecticide would be carried within the irrigation piping system. An initial run indicated that, to bracket the application curve for each location, a 30-minute injection cycle required a minimum of six samples (per location) at the following times (zero minutes = start of the injection cycle): 10, 20, 30, 45, 60 and 75 minutes. A total of 144

samples were analyzed from these stations. Using the ppm (parts per million by weight) analyzed in each sample and multiplying this by the number of minutes the sample represented (ppm minutes), the total amount of chemical sampled can quickly be compared with an expected value.

Prior to injection, liquid Furadan was mixed with water in a 1:11 ratio, and was continuously agitated during the 30-minute injection cycle. After the discharge samples were collected, the irrigation was continued for 24 operating hours, then the system was flushed. The water that was pumped through the system during the flush was also sampled at various flush ports 1, 4 and 8 minutes from the beginning of the flow cycle. Six of the sample points were located on submain flushing ports, and 12 of the sample points on lateral flushing ports. A total of 54 flush samples were taken. If any of the chemical settled in the irrigation piping system during the injection cycle, the high water velocity of the flush cycle would have picked it up along with any other sediment.

A high pressure liquid chromatograph analyzed the samples for the insecticide by light absorption at 274.3 micrometers. Detection limit of the analysis was one part/million by weight.

RESULTS AND DISCUSSION

The 1979 tip moth population was relatively low and the June evaluation showed very little infestation. The lack of data from the June evaluation prevented an estimate of the initial protection provided by the various treatments. Counts from the September evaluation were transformed by $\sqrt{X+1}$ and ANOVA's indicated that treatments were different at the .05 level. The September evaluation (Table 3) indicates that a trickle irrigation application

Table 3.--Mean Percentages of Terminal Buds Attacked by Tip Moth September 17, 1979

Treatment	%Infestation	
	Single Application	Multiple Split Application
Control	33	29
Furadan	0**	0**
Di-Syston	22	16*
Systox	40	15*
Bidrin	19*	17*
Cygon	22	17*
Metasystox-R	25	23

*Significant at .05 level for Dunnett's test for comparisons involving a control mean when actual counts are transformed by $\sqrt{X+1}$.
**Significant at .01 level for Dunnett's test for comparisons involving a control mean when actual counts are transformed by $\sqrt{X+1}$.

(localization of the chemicals in two spots near the tree) worked exceptionally well with Furadan in both types of applications. A lower application rate would have been effective. Of the other chemicals tested, only Bidrin provided significant response compared with the control in the single application. In

the split application, Di-Syston, Systox, Cygon and Bidrin were significantly different from the control. Thus, it seems that a split application tends to decrease the severity of fading insect control late in the growing season, when compared to single early-season applications. The split application technique, when viewed for all chemicals, was significantly different from the single applications when compared by a Wilcoxon sign rank test at the .05 level. Since a multiple split application approach would allow less chemical to be utilized if infestation remained low during part of the season, and since late season fading of control can be reduced, this is the preferred method. In this particular case, for instance, only seven of the planned eight applications were actually applied demonstrating the potential effectiveness of a lower annual rate with multiple applications. No insecticide phytotoxicity was noted in any trees.

The 1980 test was based on information gained from the 1979 test and on information developed regarding the effect of the chemicals on irrigation components. It was determined that none of the chemicals harmed polyethelene (PE) components, but Metasystox-R and, to a lesser degree, Cygon, were damaging to polyvinyl chloride (PVC) pipe. Thus, these two chemicals were eliminated from further evaluations. The rates of the remaining chemicals were varied upward in the 1980 test with the exception of Furadan which was decreased (Table 2). Since the trees in the 1979 location had grown well, they were judged as being too tall for the 1980 test and younger trees in an adjacent part of the orchard were utilized. It was also felt that the smaller trees would be more representative of the tree size that is usually given tip moth protection in a seed orchard. Although the split application approach was determined to be the best operational method, a single application was utilized in order to simplify the test and more strenuously evaluate the residual effect of the chemicals. Since these smaller trees were not large enough for the previous configuration of the trickle system to be most effective, both water delivery tubes were placed near the base of the tree as is standard practice in the orchard. Thus, a drench application was made at the base of the study trees to simulate a trickle application.

As a pilot evaluation of the potential phytotoxicity of the chemicals involved in the 1980 test, high rates were applied to potted rootstock. The results (Table 4) show that Systox killed all seedlings and Orthene burned needle tips.

Table 4.--Insecticide Rates and Phytotoxicity on Potted Pine Stock (1 Gallon Container)

Chemical	Application Rates Pounds/Active Ingredient/Pot In 1/2 Gallon of Water	Tree Response 30 Days After Application
Di-Syston	0.068	No Noticeable Effect
	0.136	No Noticeable Effect
Systox	0.060	All Seedlings Died
	0.120	All Seedlings Died
Bidrin	0.018	No Noticeable Effect
	0.036	No Noticeable Effect
Orthene	0.026	Needle Tip Burn on All Trees
	0.052	Needle Tip Burn on All Trees
Control	0.000	No Noticeable Effect
	0.000	No Noticeable Effect

Table 5.--Mean Percentages of Terminal Buds Attacked by Tip Moth October 2, 1980

Treatment	% Infestation		
	Zero Rate	Low Rate	High Rate
Furadan	74	33*	17*
Di-Syston	66	1*	6*
Systox	62	23*	21*
Bidrin	60	62	56
Orthene	67	67	52*

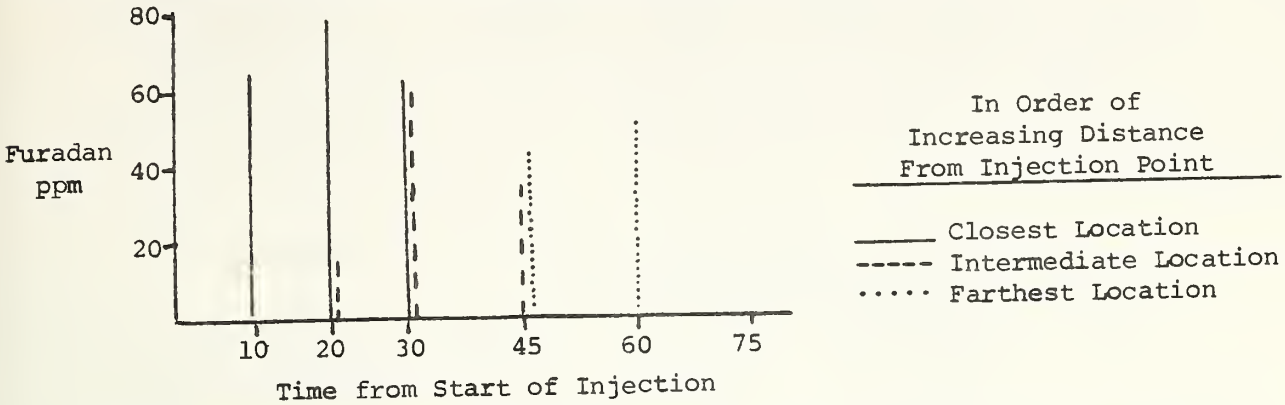
*Significant at the .01 level for Dunnett's test for comparisons involving a control mean.

Results of the 1980 field test (Table 5) indicate that the tip moth population was at a normal level. Analysis of variance for infestation percentage indicated that treatments (and blocks) were different at the .01 level. Dunnett's test was utilized to compare the zero rate of each treatment to the low and high rates. June applications of Orthene and Bidrin, for all practical purposes, were ineffective in controlling tip moth during September. Furadan and Systox were effective. Di-Syston was extremely effective at the tested rates. Some slight needle tip burn was noted on about half the trees treated with Systox (6x) and Furadan (.5x). The experience in these 1980 evaluations was that Di-Syston is the only effective chemical that did not cause any phytotoxic symptoms. It is interesting to note that, although the higher rate of Furadan caused some needle burn, it had begun to fade in its effectiveness three months after application. A multiple application of the high rate Furadan would have helped avoid the needle burn. With Furadan, the higher rate was more effective in this single application. For Di-Syston and Systox, the low rate was as effective as the high rate for all practical purposes. Based on the 1979 test experience, splitting the lower rates of the three effective chemicals into several applications, with the last one nearer September, would likely have decreased the incidence of infestation.

Of the three chemicals that are good potential candidates for the control of tip moth through a trickle irrigation system (Furadan, Di-Syston, Systox), there was some question as to whether Furadan would stay in suspension long enough to be successfully piped through the irrigation system (McCalley 1978). The Furadan detected in the samples taken at various tree locations indicated that the chemical usually took 10 to 45 minutes from the start of the injection cycle until the chemical was first registered, depending on the piping distance from the injection point. The Furadan detected indicated that the chemical would still be in the system 30 to 45 minutes after the end of the injection cycle. The time of peak concentration at locations nearest the injection station (via the piping system) tended to be between 20 and 30 minutes from the start of the injection cycle, and 45 minutes for locations farthest from the injection station. There seems to be a tendency for higher peaks to be reached by locations adjacent to the submains when compared to those farther down the lateral line (Figure 1). The standard deviation (670 ppm-minutes) of the detected chemical rate delivered per location was approximately 45% of the mean (1,467 ppm-minutes), thus the rate of application per tree can be controlled only within broad boundaries (although it is within the boundaries

indicated by the range of rates encountered in granular applications). The expected mean for the injection was estimated between 2,000 and 2,600 ppm-minutes. Inexact estimates of the amount of water pumped through the system, the small number of sample locations, the non-random placement of sample points, and the relatively long-time interval between samples at a location, prevent a close accounting of the Furadan injected into the system during this trial run.

Figure 1.--Furadan Detected in Water Samples at Three Locations



Water samples that were obtained when the system was flushed after 24 hours of operation (since the beginning of the injection cycle) revealed no traces of Furadan. Thus all the injected Furadan passed through the system during normal operation. Based on this data, Furadan should work well when piped through this trickle system.

Trickle irrigation systems that have very low water velocities in the lateral lines could possibly have problems with settling of the Furadan within the pipes. The Bellamy irrigation system utilized 1/2-inch PVC lateral lines with emitted junctions every 15 feet that deliver water to the surface at 4 to 5 GPH (gallons per hour). Lateral lines are located every 20 feet on the tapered submains and tap from the submain approximately 4 gallons of water per minute. Submains are headed by a pressure regulator and are tied to a 6-inch main.

When any pesticide is injected into an irrigation system, backflow-preventing devices should be installed in the main lines. This will avoid the possible seepage of the chemical into the water supply (pond, river, aquifer, etc.). The Bellamy system has three backflow-prevention devices on the main line: two check valves in the pump and filter sections and a foot valve on the suction line. Also each pressure regulator on the submains is of the backflow-prevention type.

Based on the test results to-date, the effective rates for the liquid formulation of Furadan, Di-Syston and Systox can be estimated (Table 6).

Table 6.--Tentative Rate Recommendation Regarding Trickle Irrigation Application of Liquid Formulation Systemic Insecticide for Control of Tip Moth

Chemical	Per Tree Rate/Application Pounds Active Ingredient/Inch Basal Diameter	No. of Applications Per Year
Furadan	0.005	2 to 5
Di-Syston	0.015	2 to 5
Systox	0.030	2 to 5

These rates are generally equivalent to annual rates utilized in other types of applications. A comparison of chemical cost for controlling tip moth on vigorously growing small orchard grafts in a year of normal tip moth activity (Table 7) indicates Systox is too costly for practical consideration. The other alternatives are roughly equivalent with granular Di-Syston being the most economical. The practical advantages gained by the liquid formulations of Furadan or Di-Syston over a granular application are due to three considerations: (1) the liquid formulation would allow smaller incremental investments in the early portion of the control program and later applications could be applied or deleted depending on insect activity, (2) the cost of application (not including chemical cost) would be less with a liquid formulation applied through the trickle system when compared with a soil incorporation granular application, (3) the trickle application would be immediately available to the plant, whereas the granular application would depend on a soaking rain for good root uptake.

Table 7.--Annual Chemical Cost of Controlling Tip Moth on 1,000 Trees (Basal Diameter 1→1½ Inches) in an Orchard with Trickle Irrigation

Chemical	Rate Application Pounds Active Ingredient/Tree	No. of Applications	$ Cost/Pound Active Ingredient	1981 Annual Chemical Cost ($)
Liquid Furadan	0.005	4	$11.00	$ 220
Liquid Di-Syston	0.015	4	6.06	362
Liquid Systox	0.030	4	11.90	1,428
Granular Furadan	0.013	2	9.50	247
Granular Di-Syston	0.019	2	7.33	139

CONCLUSIONS

Although the liquid formulations of Furadan and Di-Syston are currently not specifically registered for this type of application, these chemicals hold much promise for improving the techniques of controlling tip moth in young seed orchards that have trickle irrigation systems. Lower rates per application (compared to soil-incorporated granular applications) are desirable and convenient when utilizing this technique. A reduction in the total amount of insecticide applied annually is also possible with this new technique. Successful metering of Furadan through a trickle irrigation system was demonstrated, with no residuals remaining in the piping. Chemical application rates per tree vary significantly when applied through the trickle system but remain within the range of generally utilized granular rates. International Paper Company is continuing its evaluation of these techniques for the control of various orchard insects.

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SCREENING CLONAL ROOTSTOCKS OF SLASH AND LOBLOLLY PINE

Ralph C. Bower[1/]

Abstract.--Two clones of loblolly pine which had shown high rates of graft incompatibility in previous usage, were grafted to ramets of thirteen rootstock clones which had been propagated by rooting.

Significant differences were observed in both scion survival and scion growth among the rootstock clones. Scion survival ranged from 93 percent to 17 percent on the thirteen rootstock clones while mean scion growth ranged from 29 cm to 7 cm.

The results indicate that the first year survival and growth of the scion can be significantly influenced by the rootstock to which it is grafted.

Additional keywords: Pinus taeda, Pinus elliottii, grafting, stock-scion relationships, graft incompatibility

Horticulturists use special rootstocks to control the growth rate and final size of grafts, and to induce early and prolific flowering in many fruit trees. Specific rootstocks have also been used to develop resistance to certain diseases, insects or nematodes or tolerance to certain adverse weather or soil conditions.

The grafting of scion material from difficult-to-graft varieties to highly compatible rootstocks has long been used in horticulture. This has been possible because many rootstocks used for horticultural species are relatively easy to propagate vegetatively. Until recently it has not been possible to root sufficient numbers of loblolly and slash pine cuttings to make screening of clonal rootstocks worthwhile.

Techniques have been developed at the Texas Forest Service Genetics Laboratory to produce rooted cuttings of loblolly (Pinus taeda L.) and slash pine (Pinus elliottii Engelm.) in large enough quantities to begin a screening processing (van Buijtenen and others 1975).

This paper will discuss the first year results of a continuing study in the use of clonal rootstocks in forestry research. The first phase involves the grafting of difficult-to-graft clones onto clonal rootstocks.

[1/]Forest Geneticist, MacMillan Bloedel Limited, Woodlands Services Division, Nanaimo, B.C. This work was accomplished while the author was a graduate student at Texas A&M University. Provision of assistance and facilities by the Weyerhaeuser Company and the Texas Forest Service is gratefully acknowledged.

The primary objective of the study is to find one or more rootstock clones which show a high degree of compatibility. The secondary objectives, as the grafts reach maturity, are to select rootstocks which increase flower production and/or have a dwarfing effect on the composite tree.

METHODS AND MATERIALS

The rootstocks used in this study were all rooted cuttings of slash and loblolly pine. All material was rooted during 1974 and 1975 at the Forest Genetics Laboratory at College Station, Texas, using the procedures described by van Buijtenen and others (1975). The age from propagation of the rootstock ranged from nine to eighteen months.

Table 1 is a listing of the rootstock clones used in this study. The first twelve clones were slash pines. Clones R7 through R42 were all half sibs. They were first rooted in 1969 from six-week old seedlings. Clones R74 through R90 were all full sibs, having been rooted in 1970 from six-week old seedlings. Clone R324 is unrelated to any of the other clones and was first rooted as a ten-week old seedling in 1972. Clone R343 is an open pollinated loblolly pine that was originally rooted in 1972 when it was six years from seed.

Table 1.--Listing of clonal rootstocks and number of each used in a particular scion rootstock combination

Rootstock clone	Species	Number of grafts per scion clone
R7[a/]	slash pine	6
R15[a/]	slash pine	6
R18[a/]	slash pine	8
R20[a/]	slash pine	5
R27[a/]	slash pine	7
R38[a/]	slash pine	10
R42[a/]	slash pine	7
R74[b/]	slash pine	7
R85[b/]	slash pine	5
R88[b/]	slash pine	10
R90[b/]	slash pine	5
R324	slash pine	7
R343	loblolly pine	5
Total		88

[a/] Related as half-sibs

[b/] Related as full-sibs

The rootstocks were transported to the Weyerhaeuser Company's Craig seed orchard near Broken Bow, Oklahoma in January 1976. As scion material Weyerhaeuser chose two loblolly pine clones which had shown a high rate of incompatibility in previous usage. The number of grafts made of a particular scion-rootstock combination varied according to rootstock availability (Table 1). It has been shown that the performance of loblolly pine scion material grafted to slash pine rootstocks is equal to or better than the performance on loblolly rootstocks (Schmidtling 1973, McKinley 1975).

All grafts were made using a side graft and were performed over a two-day period in March 1976 by the same grafter. The grafts were maintained in a shadehouse and received irrigation as needed. None of the grafts received fertilization.

Final survival and height measurements were made in October 1976. The surviving grafts were then outplanted to be kept under observation until they had reached full flower production so that growth rate and form, incompatibility and seed production, could be more fully evaluated.

RESULTS AND DISCUSSION

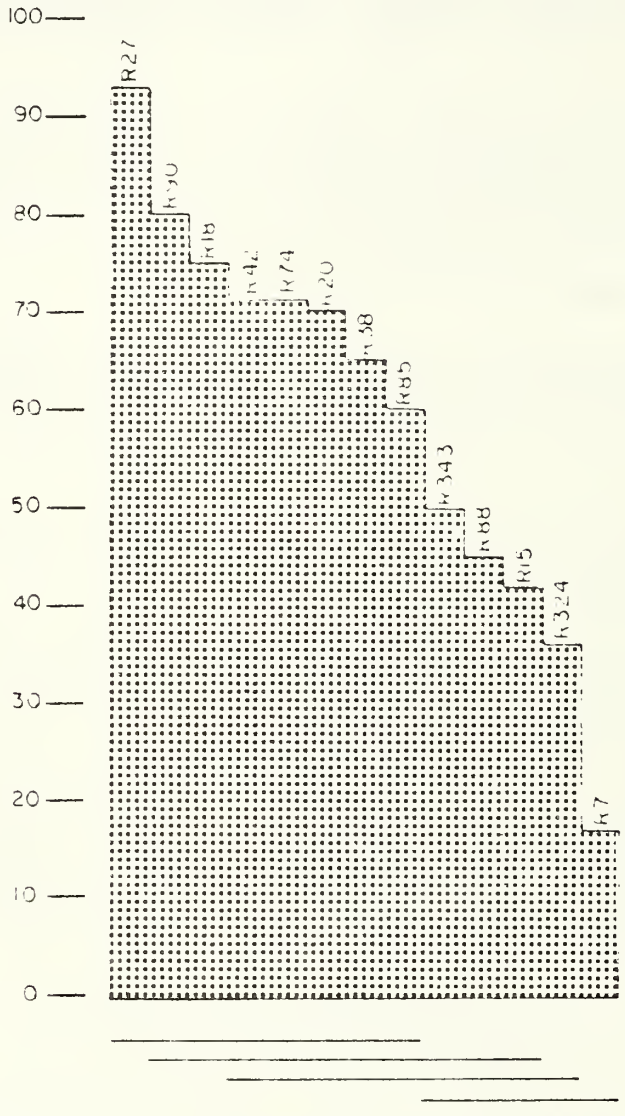
Scion A had an overall survival of 51 percent while scion B had an overall survival of 68 percent. The mean survival for both scion clones grafted to each rootstock ranged from 93 to 17 percent. F values for scions and rootstocks were both significant at the 0.05 level of probability.

Duncan's Multiple Range test was performed on the rootstock means (Figure 1). It is evident that significant gains in first year scion survival can be obtained by selecting the proper rootstock clone.

Scion growth was calculated as the difference between initial height and final height. Analysis of variance showed significant (.05) differences among rootstock clones, but no significant differences between the two scion clones. The mean growth for both scion clones grafted to each roostock clone is presented in Figure 2. Duncan's Multiple Range test was performed on these means, the results of which are also presented in Figure 2. If the variation in growth rate shown by these first year results continued to maturity it would be possible to select rootstocks which would increase or decrease average scion growth. The use of dwarfing rootstocks would have very practical importance in seed orchard management because small trees would facilitate cone collection.

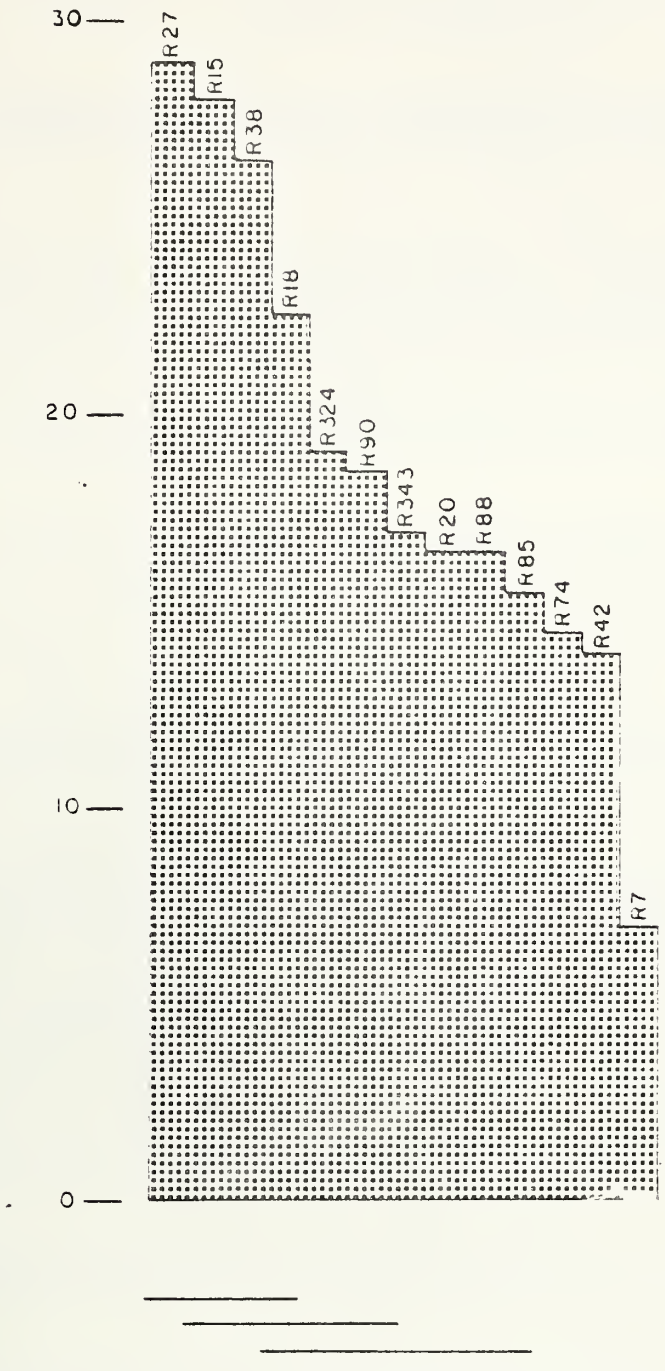
Much variation in scion growth was observed among replications of the same scion-rootstock combination. As an example, the six replications of A on R38 had a range in scion growth of 10 cm to 52 cm with a mean of 30 cm. This gave a coefficient of variation of 57 percent. Since these were clonal scions grafted onto clonal rootstocks, the expectation would be for much more similarity in performance. Personal observation has shown that there is considerable variation in the size of root systems developed by individual ramets of the same clone, thus there is variation in the amount of water and nutrient absorption possible. This variation in water and nutrient uptake is one possible explanation for the large amount of variation in scion growth observed among grafts of identical genotypes.

FIGURE 1. MEAN SURVIVAL FOR BOTH SCIONS GRAFTED TO EACH ROOTSTOCK



ROOTSTOCKS NOT CONNECTED BY A LINE ARE DIFFERENT AT THE .05 LEVEL USING DUNCAN'S NEW MULTIPLE RANGE TEST.

FIGURE 2. MEAN SCION GROWTH FOR BOTH SCIONS GRAFTED TO EACH ROOTSTOCK



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CONCLUSIONS

There were significant differences in graft survival among rootstock clones. The range in survival was from 93 percent to 17 percent. Therefore, obtaining a highly graftable rootstock by screening clonal rootstocks shows promise.

Significant differences in scion growth rate were obtained on the rootstocks used. If these differences continue to exist through to maturity, it will be possible to select rootstocks that can increase or decrease scion growth.

Considerable differences exist in scion growth among replications of the same scion-rootstock combinations. Since both scion and rootstock are of clonal origin a similar response would be expected from all replications of a specific scion-rootstock combination, unless environmental factors were different among the replications. A possible explanation for this variation is the difference in size of the root systems among ramets of a rootstock clone causing differential nutrient and water availability to the scions. Further research is needed to elucidate the role of these environmental factors.

No conclusions can presently be made about the effect of any of these thirteen rootstocks on incompatibility or flower production. For this reason the grafts have been planted in an experimental seed orchard to undergo further evaluation.

LITERATURE CITED

McKinley, C.R. 1975. Growth of loblolly scion material of known genetic origin. Thirteenth Southern Forest Tree Improvement Conf. Proc. 1975: 230-233.

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SCREENING CLONAL ROOTSTOCKS OF SLASH AND LOBLOLLY PINE

Ralph C. Bower[1/]

Abstract.--Two clones of loblolly pine which had shown high rates of graft incompatibility in previous usage, were grafted to ramets of thirteen rootstock clones which had been propagated by rooting.

Significant differences were observed in both scion survival and scion growth among the rootstock clones. Scion survival ranged from 93 percent to 17 percent on the thirteen rootstock clones while mean scion growth ranged from 29 cm to 7 cm.

The results indicate that the first year survival and growth of the scion can be significantly influenced by the rootstock to which it is grafted.

Additional keywords: Pinus taeda, Pinus elliottii, grafting, stock-scion relationships, graft incompatibility

Horticulturists use special rootstocks to control the growth rate and final size of grafts, and to induce early and prolific flowering in many fruit trees. Specific rootstocks have also been used to develop resistance to certain diseases, insects or nematodes or tolerance to certain adverse weather or soil conditions.

The grafting of scion material from difficult-to-graft varieties to highly compatible rootstocks has long been used in horticulture. This has been possible because many rootstocks used for horticultural species are relatively easy to propagate vegetatively. Until recently it has not been possible to root sufficient numbers of loblolly and slash pine cuttings to make screening of clonal rootstocks worthwhile.

Techniques have been developed at the Texas Forest Service Genetics Laboratory to produce rooted cuttings of loblolly (Pinus taeda L.) and slash pine (Pinus elliottii Engelm.) in large enough quantities to begin a screening processing (van Buijtenen and others 1975).

This paper will discuss the first year results of a continuing study in the use of clonal rootstocks in forestry research. The first phase involves the grafting of difficult-to-graft clones onto clonal rootstocks.

[1/] Forest Geneticist, MacMillan Bloedel Limited, Woodlands Services Division, Nanaimo, B.C. This work was accomplished while the author was a graduate student at Texas A&M University. Provision of assistance and facilities by the Weyerhaeuser Company and the Texas Forest Service is gratefully acknowledged.

The primary objective of the study is to find one or more rootstock clones which show a high degree of compatibility. The secondary objectives, as the grafts reach maturity, are to select rootstocks which increase flower production and/or have a dwarfing effect on the composite tree.

METHODS AND MATERIALS

The rootstocks used in this study were all rooted cuttings of slash and loblolly pine. All material was rooted during 1974 and 1975 at the Forest Genetics Laboratory at College Station, Texas, using the procedures described by van Buijtenen and others (1975). The age from propagation of the rootstock ranged from nine to eighteen months.

Table 1 is a listing of the rootstock clones used in this study. The first twelve clones were slash pines. Clones R7 through R42 were all half sibs. They were first rooted in 1969 from six-week old seedlings. Clones R74 through R90 were all full sibs, having been rooted in 1970 from six-week old seedlings. Clone R324 is unrelated to any of the other clones and was first rooted as a ten-week old seedling in 1972. Clone R343 is an open pollinated loblolly pine that was originally rooted in 1972 when it was six years from seed.

Table 1.--Listing of clonal rootstocks and number of each used in a particular scion rootstock combination

Rootstock clone	Species	Number of grafts per scion clone
R7[a/]	slash pine	6
R15[a/]	slash pine	6
R18[a/]	slash pine	8
R20[a/]	slash pine	5
R27[a/]	slash pine	7
R38[a/]	slash pine	10
R42[a/]	slash pine	7
R74[b/]	slash pine	7
R85[b/]	slash pine	5
R88[b/]	slash pine	10
R90[b/]	slash pine	5
R324	slash pine	7
R343	loblolly pine	5
Total		88

[a/] Related as half-sibs

[b/] Related as full-sibs

The rootstocks were transported to the Weyerhaeuser Company's Craig seed orchard near Broken Bow, Oklahoma in January 1976. As scion material Weyerhaeuser chose two loblolly pine clones which had shown a high rate of incompatibility in previous usage. The number of grafts made of a particular scion-rootstock combination varied according to rootstock availability (Table 1). It has been shown that the performance of loblolly pine scion material grafted to slash pine rootstocks is equal to or better than the performance on loblolly rootstocks (Schmidtling 1973, McKinley 1975).

All grafts were made using a side graft and were performed over a two-day period in March 1976 by the same grafter. The grafts were maintained in a shadehouse and received irrigation as needed. None of the grafts received fertilization.

Final survival and height measurements were made in October 1976. The surviving grafts were then outplanted to be kept under observation until they had reached full flower production so that growth rate and form, incompatibility and seed production, could be more fully evaluated.

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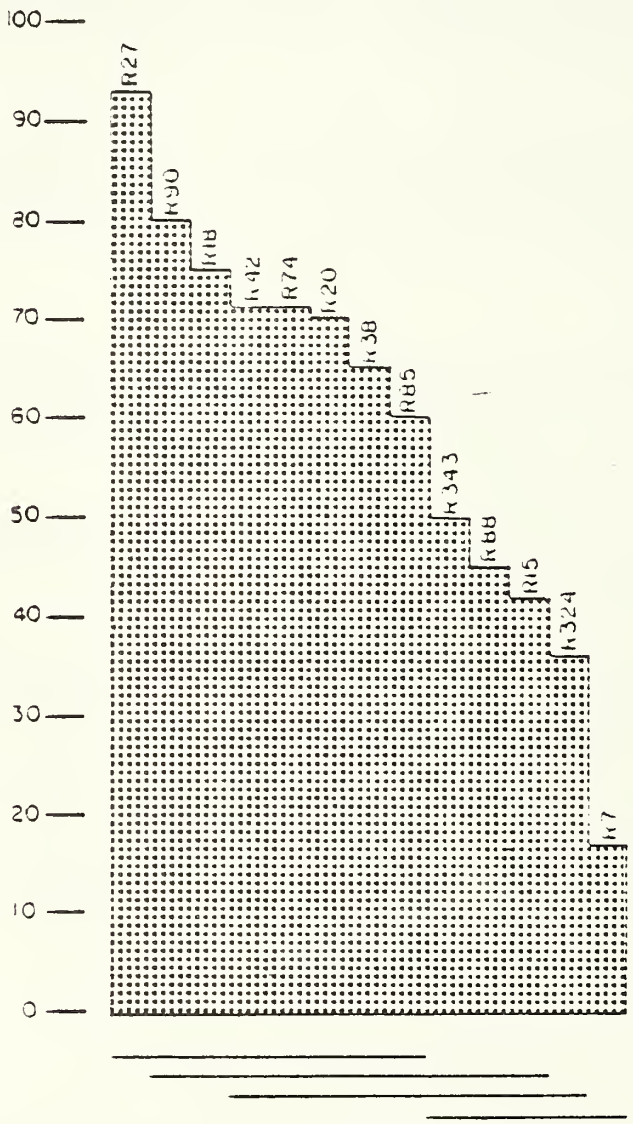

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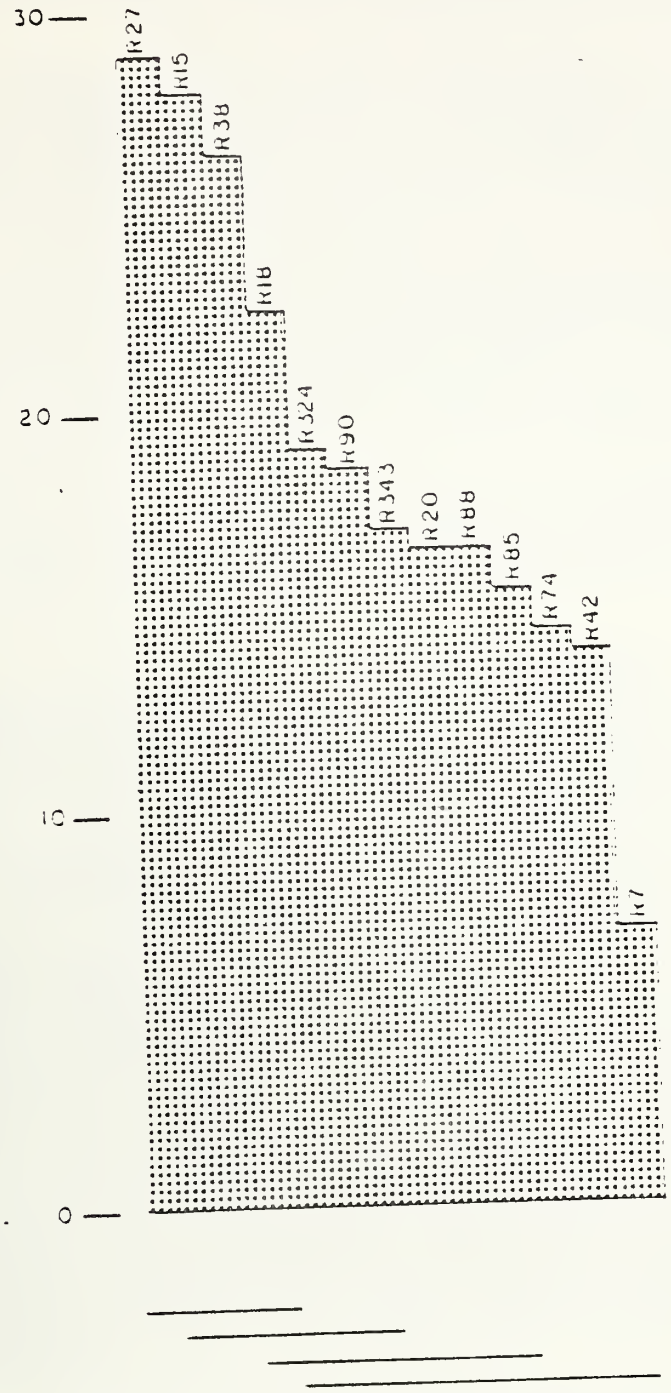

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POLLINATION, POLLEN TUBE DEVELOPMENT AND ORCHARD NURTRIENT STATUS EFFECTS ON CONELET ABORTION IN OPEN POLLINATED LONGLEAF PINE

Early Y. McCall and Robert C. Kellison[1/]

Abstract.--Possible causes investigated for the 60-90% abortion rate of longleaf pine conelets at the North Carolina Forest Service longleaf clonal seed orchard at Bladen Lakes State Forest were: (1) the absence of pollen or its failure to germinate and (2) possible nutrient deficiencies or excess.

Ovule sections were examined histologically for the presence of pollen, pollen germination, and overall ovule condition. Of the 284 ovules observed, 72% had pollen present in the micropyle. Pollen germination within the micropyle was not inhibited as 78% of those ovules with pollen present had germinated pollen. Thirteen percent of the ovules with germinated pollen were aborted and the incidences significantly increased over time (.01 level using the log-likelihood ratio test). In every instance where aborted ovules were observed the pollen tube appeared normal. Therefore the abortion of conelets of these ovules was apparently not related to lack of pollen or failure of the pollen to germinate.

The possibility of a nutrient problem was investigated by analyzing Bladen Lakes longleaf orchard soil and tissue samples and comparing to standards and symptom descriptions for longleaf and other pine species. Boron was found at deficient levels at the seed orchard and descriptions of fruit drop caused by B deficiency for other species of pine and for fruit and nut trees closely resemble those found at the longleaf orchard.

Keywords: Pinus palustris, conelet drop, ovule, ovule abortion, seed orchard management, mineral nutrition.

From 1971 to 1975 about 80 percent of the potential cone crop from the longleaf pine seed orchard of N. C. Forest Service Bladen Lakes State Forest was lost from "conelet abortion". Conelet abortion results from inherent or environmental disorders present within the conelet, tree, or site on which the tree exists. In longleaf pine aborting conelets may appear normal for several weeks after pollination, but internal necrosis develops at the base of the conelet and spreads through the axis toward the apical end. The conelet eventually dessicates and either drops from the tree or may be retained in place for as long as a year. Conelet abortion usually begins about 6 weeks after pollination and is greatest for a short period thereafter, tapering off as the conelet growing season progresses.

The cause of conelet abortion may encompass several different factors in any one orchard or species. Other attempts to define the causes of high conelet

1/ The authors are respectively; Tree Improvement Forester, ITT Rayonier Inc., Fernandina Beach, Florida and Director, Hardwood Research Program, School of Forest Resources, N. C. State University, Raleigh, N. C. Manuscript based on research conducted by the senior author in partial fulfillment of the Master of Science degree.

abortion at this orchard include controlled pollination studies (White, 1975), biochemical studies (White, 1975), and fertilization studies (Summerville, et al., 1979). Based on their work with radiata pine (Pinus radiata) and the work of Sarvas (1962) with Scotch pine (P. sylvestris), Sweet and Bollman (1970) concluded that both pollination levels and competition for nutrients and carbohydrates between the shoot and conelet are important factors causing conelet abortion. In this report, pollination levels and macro and micronutrient levels are investigated as potential causal agents of conelet abortion of longleaf pine (P. palustris) at the Bladen Lakes seed orchard.

METHODS AND MATERIALS

The orchard was grafted in 1965 on trees of an existing longleaf plantation situated on a Lakeland soil. The soil is characterized by deep sands with poor nutrient holding capacity, excessive drainage, and low pH.

In 1973, the orchard was split into two sections to study the effect of varying amounts of fertilizer and irrigation on male and female strobilus initiation and retention (Summerville et al., 1979). In each section, three treatments were administered annually: 1) control--nonfertilized, 2) medium rate--400 lbs./acre of 0-20-20 in November, 150 lbs./acre of NH_4NO_3 in February, and 250 lbs./acre of NH_4NO_3 in July, and 3) heavy rate--500 lbs./acre of 10-10-10 in November, 300 lbs./acre of NH_4NO_3 in February, and 300 lbs./acre of NH_4NO_3 in July. Equipment failures prevented application of the irrigation treatments. These fertilizer treatments were used to study the effect of nutrient status of orchard trees on conelet abortion and the effect of fertilization on pollen tube development.

Pollination Studies

Three ramets from each of four clones were chosen for conelet sampling from each of the three fertilizer treatments. Two apparently healthy conelets were sampled from east and west aspects of each tree at the fifth, seventh, ninth and eleventh weeks after pollination occurred during the second week of March in 1976. Each conelet was sectioned for preparation of slides from which two ovules were microscopically observed for the presence of pollen, pollen tubes and an evaluation of ovule health after pollen tube growth (McCall, 1980). Each ovule was classified as follows:

Pollination Class I - no pollen present in the micropyle
Pollination Class II - pollen present but not germinated
Pollination Class III- pollen present and germinated but ovule aborting
Pollination Class IV - germinated pollen present and ovule apparently healthy

Shortage of conelets at latter sampling dates permitted only 187 of the originally planned 192 conelets to be sampled for a total of 374 ovules. Data were analyzed using the log-likelihood ratio test (G-statistic) which demonstrated the strength of association between sampling parameters and pollination classes. The advantages of using the log-likelihood test of independence over the conventional chi-squared (X^2) test are: (1) the computations are less tedious than for X^2, (2) it more accurately follows the x^2 distribution than does the X^2 statistic, and (3) it allows for testing of more than two rows and columns (Sokal and Rohlf, 1969).

Aborting conelets containing some live ovules were also collected. Serial sections were made of two ovules per conelet and pollination classes were compared with sections from apparently healthy conelets to see if lack of pollen might have caused the conelet's ultimate demise.

Nutrient Status Studies

Three ramets of six clones in each of the three fertilizer treatments were randomly selected for conelet counts. Counts were done separately in the two sections of the fertilizer study and were treated as replications for a total of 108 trees. These counts helped to identify the impact of fertilizer treatments on conelet abortion. Initial counts of female strobili were made in March, 1977 before conelet abortion started, and retained conelets were tallied in October, 1977.

Foliage, conelet, and soil samples were collected and analyzed for dry weight nutrient concentration by the Agronomic Division of the North Carolina Department of Agriculture to determine the nutrient status of the orchard trees. Three ramets were chosen at random from three clones within each of the three existing fertilizer treatments for a total of nine sample trees. Conelet samples were taken in the sixth week after pollination when signs of conelet abortion were becoming apparent and subsequently in the seventh, eighth and tenth weeks. Foliage samples were collected from these same nine trees only in the tenth week after pollination to avoid competition imbalances that may have occurred from removal of foliage before conelet sampling was completed (Sweet and Bollman, 1970).

RESULTS

Pollination Studies

For all parameters, except time, no significant association between each parameter and pollination class could be demonstrated. The number of ovules falling into the various pollination classes changed significantly (.01 level) from the fifth to the eleventh week after pollination (Table 1).

Table 1.--Number of ovules of longleaf pine by pollination class at four sampling dates from Bladen Lakes seed orchard.

Sample Date (weeks after pollination)	Pollination Class[a/]			
	I	II	III	IV
Fifth week	25	23	1	23
Seventh week	20	13	1	38
Ninth week	16	4	6	46
Eleventh week	20	6	13	31

a/ Pollination Class I - no pollen present in the micropyle
Pollination Class II - pollen present but not germinated
Pollination Class III - pollen present and germinated but ovule aborting
Pollination Class IV - germinated pollen present and ovule is apparently healthy

As expected, Class I did not change significantly because the number of ovules containing pollen was fixed at the time of pollination. Of all of the ovules assigned to Class I only 21 percent were aborted. Decrease in Class II shows that the pollen grains were still germinating from the fifth through the eleventh weeks. Partitioning of the pollination classes using the log-likelihood analysis showed that increase in germinated pollen grains over time (Class I and II X Class III and IV dependence) was significant (.01 level). Increase in Class III in the ninth and eleventh weeks demonstrated that even though pollen had germinated, incidence of ovule abortion increased. Class IV remained fairly constant although there was a decrease in the number of healthy ovules containing germinated pollen from the ninth to the eleventh week.

When ovules from 42 aborting conelets were compared to those from 187 apparently healthy conelets, 72 percent of the ovules from nonaborted conelets and 59 percent from aborted conelets had at least one pollen grain (Classes II, III, and IV). The difference between aborting and healthy conelets could have been a reflection of the sample size difference, although 42 aborting conelets should have rendered a fair comparison. Only a few pollinated ovules are needed for normal maturation of reproductive structures in shortleaf pine (Bramlett, 1972) and in slash pine, controlled pollinations may produce apparently normal cones with only a few viable seeds.

There also seemed to be adequate germination of pollen, even in aborting conelets (Class III). It appears, therefore, that something other than failure of the pollen to germinate caused the conelets to abort. It also appears that ovule abortion did not directly affect conelet abortion since there was not a large number of aborted ovules in conelets appearing normal even though conelets were collected during the period of maximum conelet abortion.

Conelet Loss Determination within Fertilizer Treatments

Counts of open pollinated female strobili and subsequent conelet abortion from 1971 to 1975 by the N. C. Forest Service showed abortion rates of 26, 96, 88, 100, and 89 percent, respectively. Conelet losses from counts done for this study in 1977 were 56 percent.

Percent retention of conelets in the two replications of this study were best in the nonfertilized plots, although differences among fertilizer treatments are not significant using a covariance analysis. Investigators thus far have found that increased flowering and greater cone and seed yield are obtained from increased fertilization (Shoulders, 1967; Shoulders, 1968; Sweet and Bollman, 1970; Sarvas, 1962; Barns and Bengtson, 1968). However, these results are for species other than longleaf pine. Heavy applications of fertilizers in this longleaf orchard could be causing an adverse effect on conelet retention (Table 2).

Table 2.--Percent of longleaf pine female "flowers"[a/] counted at Bladen Lakes seed orchard in March, 1977, retained as conelets in October, 1977, by fertilizer treatment.

	Nonfertilized	Normal Fertilization	Heavy Fertilization
	% female flowers retained[b/]		
Section I	35	25	34
Section II	37	24	24

a/ Only "flowers" judged to be healthy were scored.

b/ Each percentage figure represents 18 trees. Flowers and conelets were counted on the southeast quadrant of each tree. Branches counted in March were identified with spray paint to minimize errors in the subsequent October conelet count.

Nutrient Concentration by Fertilizer Treatments

Although P and K had been added to the normal and heavy rate treatments by way of inorganic fertilizers there was no difference in conelet or needle nutrient concentration between the fertilized plots and the controls (Table 3). At the time of this study, fertilizer had been withheld from the control plots for four years. Soil samples from these plots showed that the amount of elemental P and K in the normally fertilized plots was higher than that in the heavily fertilized plots but values of both exceeded the control. This was expected as more fertilizer P and K was actually added to the normally fertilized plots than to the heavily fertilized plots. There was no difference in conelet or needle P and K among treatment plots despite the fact that these nutrients are considered highly mobile within trees (Greulach, 1973).

Table 3.--Nutrient analysis of collections made at four sampling dates by fertilizer treatment at Bladen Lakes longleaf seed orchard.

	Mean concentration in conelets by dry weight										
	%						ppm				
Treatment	N	P	K	Ca	Mg	Na	Fe	Mn	Zn	Cu	B
Heavy Fertilization	1.93	.24	.80	.13	.13	.04	21	78	61	5	19
Normal Fertilization	1.80	.24	.85	.12	.14	.02	21	82	56	6	15
Control (nonfertilized)	1.57	.23	.83	.17	.14	.03	18	97	66	6	14

(Table 3 continued)

Treatment	Mean concentration in needles by dry weight										
	%						ppm				
	N	P	K	Ca	Mg	Na	Fe	Mn	Zn	Cu	B
Heavy Fertilization	1.52	.09	.44	.30	.10	.03	50	79	25	4	10
Normal Fertilization	1.24	.08	.40	.30	.11	.04	53	56	25	4	7
Control (nonfertilized)	1.07	.10	.40	.33	.12	.03	49	55	37	4	6

Treatment	Mean nutrient levels in soil samples							
		lbs./acre[a/]				ppm		
	pH	P	K	Ca	Mg	Mn	Zn	Cu
Heavy Fertilization	5.0	18	36	559	73	1.7	1.1	.07
Normal Fertilization	5.6	34	43	720	162	1.9	1.2	.22
Control (nonfertilized)	5.3	13	16	501	121	1.7	1.5	.15

a/ lbs./ac. values are equivalent to kg./ha.

Nutrient Sufficiency Levels

Nitrogen levels in conelets and needles were directly related to the amount of N applied. Copper and manganese were found at low levels and boron was found at deficient levels in needles collected from the first flush of the previous year's growth (Table 3). Deficiency symptoms usually occur in Pinus spp. when needle levels of Cu and Mn drop below approximately 2 and 40 ppm, respectively, and when B levels drop below 10-15 ppm (Stone, 1967).

Low Mn and Cu are not thought to hinder the retention of reproductive structures (Epstein, 1972; Kozlowski, 1971) however, B deficiency in apples (Malus spp.) and walnuts (Juglans regia) cause visual symptoms and subsequent fruit abortion quite similiar to that at Bladen Lakes seed orchard. Vegetative growth may also be affected by B deficiency in pines, but usually only after reproductive growth is inhibited or abortion occurs (Sprague, 1964). Levels of B were also deficient (mean of 6 ppm) in needle samples collected from a collaborative study involving 30 trees in the Bladen Lakes seed orchard in February, 1977.

Boron may be held unavailable to plants by high levels of K, N, and especially Ca (Epstein, 1972; Chapman, 1966). Calcium has been applied heavily in the form of lime to the Bladen Lakes Orchard especially in the early years of its establishment. Heavy liming has been found to result in B deficiency (Brady, 1974) on deep acid sands such as those found at this orchard. In naturally acid soils B is available largely in a soluble form (H_3BO_3) which may be easily leached. Soils in the area surrounding the Bladen Lakes orchard had an average pH of 3.9, therefore much of the soil's B may have been depleted before orchard establishment in 1965. Additions of Ca in the form of lime would help to complex more B. A study was established in 1978 to determine the effect of B on conelet abortion at the Bladen Lakes orchard, but frost damage and limited flowering prevented its completion.

CONCLUSIONS

Change in pollination classes over time was caused by two factors: 1) increased occurrence of germinated pollen and 2) increased ovule abortion among ovules with germinated pollen. Even though ovules with nongerminated pollen decreased, germination seemed to have been delayed as pollen was still germinating even in the eleventh week of collection. Possibly some growth substance supplied by germinating pollen is produced too late to prevent ovules from aborting. Some investigators have found growth substances being expelled from germinating pollen which are believed to have a role in ovule development and survival (Sweet, 1973; Sweet and Lewis, 1969; Sweet and Lewis, 1971). Sarvas (1962) found that Scotch pine ovules gradually deteriorate after the third week past strobilus receptivity if they are not pollinated. Pollen associated growth substances should be identified and research done to determine if they are produced in time to prevent conelet abortion. Inhibitors and nutrient deficiencies may also cause the pollen to be late in germinating. Boron deficiency has been found to cause poor pollen germination (Stanley and Linskins, 1974), but further studies should be conducted to determine if the pollination delay is caused by B shortage at Bladen Lakes longleaf orchard.

Increased ovule abortion among ovules with germinated pollen was observed during the sample period. In every instance, even where aborted ovules were observed, the pollen tube appeared normal suggesting the ovules would have aborted regardless of the presence or absence of germinated pollen. When ovules within aborting and nonaborting conelets were compared, very few aborted ovules were found in apparently normal conelets, therefore ovule abortion appears to be secondary to conelet abortion. Since most of the conelets were collected before or during the period of maximum conelet loss, conelets with the potential to abort should have been identified by a large number of aborted ovules if ovule deterioration occurred before conelets aborted.

Lack of pollen or failure of pollen to germinate was ruled out as a direct cause of abortion based on the high occurrence of pollen and germinated pollen within ovules. Upon microscopic examination, no mycelial growth was found inside conelets or ovules, also eliminating fungus contamination as a possible cause of abortion.

High doses of NPK fertilizer may have a damaging effect on cone crops, especially in highly leachable soils. A balanced fertilizer, preferably containing a slow release micronutrient mix, should be applied to these sites and foliage nutrient levels monitored to make sure orchards are being supplied with all essential nutrients.

More research is needed on effect of competition for carbohydrates between vegetative and reproductive structures in longleaf pine. Conelet abortion begins and is heaviest for a short period of time after the sixth week past the point of maximum flower receptivity. This period of time coincides with occurrence of the second flush of needle growth which is quite demanding on available carbohydrates. By removing needles which would otherwise compete with conelets for these available carbohydrates, Sweet & Bollman (1970) concluded that conelet abortion was reduced. This same approach could be taken to study competion effects at the Bladen Lakes orchard.

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LOBLOLLY PINE POLLEN GRAIN COUNTS BY OVULE DISSECTION

Fred R. Matthews and Tony E. Blalock [1/]

Abstract.--A procedure for counting pollen grains on the nucellar tissue of loblolly pine conelets after ovule dissection is described. The technique involves harvest of conelets 2 weeks after maximum pollen receptivity and the removal of individual ovule-bearing scales. After the integument is excised, the nucellus with adhering pollen grains is placed in a drop of stain on a microscope slide and the pollen grains counted. Conelets may be frozen in water for dissection later. The technique can be used to evaluate efficiency of controlled pollinations or supplemental pollination, and in studies involving flower receptivity and pollen quantity and quality.

Additional keywords: *Pinus taeda*, pollination, ovulate strobilus

The number of pollen grains that enter individual ovules in conifer conelets is of concern to tree breeders. The success of pollination of an ovulate strobilus depends upon the number of pollen grains entrapped in the pollen chamber of each fertile ovule. Theoretically, the more viable pollen grains within the chamber, the better the chance of subsequent fertilization and development of viable seed. In wind-pollinated conelets, multiple pollen grains per ovule can reduce the impact of self pollination and increase the chances for genetic outbreeding. The absence of pollen in the pine ovule, resulting from inadequate pollen supply or failure of the pollen to reach the nucellus, has been shown to cause first-year ovule abortion which is a major factor in reduction of seed yields (Sarvas 1962, McWilliam 1959).

Pollen grains in conifer ovules traditionally have been counted by standard histological procedures which involve paraffin embedding of the detached ovule, serial sectioning, staining, and microscopic examination (Sarvas 1962, Bramlett and Johnson 1975). This process requires considerable time and equipment, difficulties occur in recognizing individual grains in the serial sections, and grains may be lost during the procedure. A method in which pollen grains within the pollen chambers of fresh ovules could be quickly and accurately counted would overcome the limitations inherent in the histological procedures. Lill (1974) presented data on total pollen counts in and around the micropyles of fresh ovules of *Pinus radiata* D. Don, and Brown (1971) counted the number of pollen grains within the ovules of *P. sylvestris* L. However, no details of the procedures used were presented in these reports.

During the development and evaluation of a new pollinator (Matthews and Bramlett 1981) and in studies involving pollen quantities in controlled pollinations, it was apparent that there was a need for a practical method to determine the number of pollen grains in a large number of loblolly pine (*P. taeda* L.) ovules. This paper reports details on such a method.

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METHODS

Open and control-pollinated loblolly pine conelets were collected from one ramet of each of three clones located at the Arrowhead Seed Orchard in Pulaski County, Georgia. The conelets were collected 2, 4, and 6 weeks after maximum strobilus receptibity and were stored either in plastic bags at 3C or - 15C, or in water-filled plastic tubes at - 15C until use.

Conelets were dissected on the stage of a dissecting microscope equipped with cool (fiber-optics) illumination. Basal infertile scales were removed with a micro-scalpel until the first course of fertile scales appeared. Fertile scales were recognized by the presence of normal-appearing ovules and remnants of attached micropylar arms. Beginning at a point one-two scales above the first recognizable fertile scale, 10 sample scales were randomly selected to represent the entire fertile portion of the conelet. Each sample scale was removed from the conelet axis by a basal incision with the micro-scalpel. The detached scale was then held by self-closing forceps, and an L - shaped incision was made in the top of the ovule integument with the micro-scalpel. The loose flap of integument was folded back to expose the underlying nucellus and the pollen chamber. The nucellus and the adhering pollen grains on its tip were excised from the underlying ovular tissue with a hooked micro teasing needle. Both ovules on each sample scale were dissected.

The nucellus was then placed in a drop of 0.5% acid fuchsin in saturated chloral hydrate on a microscope slide. A cover slip was placed over the specimen and pressed lightly to separate the pollen grains and to enhance microscopic examination. Acid fuchsin stained the pollen germ tube red, while the chloral hydrate dissolved the resinous material in which the pollen grains adhere to the nucellar tip. The periphery of the nucellus and the walls of the pollen grain were also stained slightly. Both nucelli from the scale may be placed in the same drop of stain if they are kept separated.

The specimen was then examined at 100 X magnification on a compound microscope and the number of grains counted. Approximately 20 ovules per hour can be dissected and the grains counted by an experienced technician.

RESULTS AND DISCUSSION

Pollen grain counts in 100 ovules of each of the three clones of wind-pollinated loblolly pine showed a mean of 4.0 grains per ovule with a range of 0-7. Germination of these grains was 82%. The counts were influenced by the relative positions of the 10 sample scales on the conelet. The two lower-most and two upper-most fertile scales averaged about 30% fewer pollen grains than did scales from the middle of the conelet. Lill (1974) reported that micropylar (pollen chamber) capacity of P. radiata limited the amount of pollen that reached the nucellus, with the capacity being smaller on the basal scales. Although no measurements were made, it appeared that the ovules of loblolly pine were smaller in the apical region than those in the middle and basal regions of the conelet. Lower grain counts in the basal ovules may be caused by a shortened exposure to pollen due to the developmental progression of strobilus receptivity.

Conelet collections made 2 weeks after maximum strobilus receptivity were superior to those made 4 or 6 weeks after receptivity. In collections at 2

weeks, the pollen grains were more easily separated from the resinous deposit on the nucellar tip than in the 4 and 6 week collections in which the grains adhered tightly to the nucellus possibly due to germ tube penetration. It should be noted, however, that macroscopic evidence of the beginning stages of ovule abortion due to lack of pollen was apparent only in conelets collected 6 weeks after maximum receptivity.

Freshly collected conelets may be frozen in water if long-term storage is required. Conelets have been stored in this manner for up to 1 year with no detrimental effect on the dissection and grain counting procedures. Dry freezing or storage at 3-5C in plastic bags will suffice for periods up to 1 week.

This technique has applicability for evaluating: (1) the efficiency of controlled pollinations, (2) the effect of supplemental pollination, (3) flower receptivity, and (4) pollen quality and quantity.

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GENETIC ASPECTS OF NURSERY MANAGEMENT FOR SWEETGUM SEEDLING UNIFORMITY

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Abstract

Several experiments were designed to evaluate various genetic and environmental aspects of sweetgum (Liquidambar styraciflua L.) seedling production. Open-pollinated seed lots of 12 clones were sorted into three density classes. Family and seed density class affected early seedling height but became unimportant by mid-summer. Removal of a particular density class from a bulked seed lot altered the genetic composition of the lot. Year of collection also affected growth and uniformity of the seedling crops. Experimentation further revealed that (1) sweetgum seedlings require elemental soil phosphorus levels greater than 50 kg/ha in sandy soils, (2) amendments of soluble phosphates or mycorrhizal inocula to fumigated nursery soils have greatest impact early in the growing season, (3) mycorrhizal inoculation is not a substitute for good soil fertility, (4) family-by mycorrhiza interaction is nonsignificant, and (5) elemental phosphorus levels as high as 130 kg/ha do not inhibit mycorrhizal development.

Additional keywords: seed sizing, mycorrhizae, Liquidambar styraciflua L., seedling growth.

INTRODUCTION

Successful establishment of sweetgum plantations requires uniformly tall, large calipered seedlings. Unfortunately, nursery managers have had difficulty in consistently producing seedling crops of acceptable quality. Traditional factors at the disposal of nursery managers to improve seedling crops are seed quality and soil fertility. Important components of seed quality include seed size, seed year, and genetic composition. Soil fertility management traditionally includes maintenance of macro-and micronutrients and their combination at specified levels for good seedling growth. Use of mycorrhizae has recently been determined to have the same type of beneficial effect on seedling growth as fertilizer supplements. This paper summarizes several studies conducted by the Hardwood Research Cooperative at North Carolina State University to evaluate potential nursery practices which would improve seedling uniformity and quality in sweetgum.

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EFFECT OF SEED SIZE

In a study of seed size by year of collection bulked seed lots were collected from Weyerhaeuser Company's select sweetgum seed orchard in Washington, N. C. in 1975 and 1976. Seeds from each collection year were separated into four density classes using a gravity feed table in a manner described by Bonner (1979) for sycamore. Seed fractions were sown in a greenhouse using a replicated complete block design in July, 1978. Each treatment plot of nine square dm contained ten seedlings after the last thinning was completed in October, 1978. The December 1978 measurements reflected a trend (not statistically significant) of larger seedlings corresponding to heavier seeds (Table 1). Year of collection significantly affected height growth, but not root collar diameter (RCD).

Table 1. Effect of seed density and year of collection on seedling height and root-collar diameter

HEIGHT

Collection Year	Seed Density 1 (lightest)	2	3	4 (heaviest)	$\bar{X}$
	cm				
1975	25.4	26.6	26.8	29.4	27.0
1976	27.5	29.6	30.5	30.0	29.4
$\bar{X}$	26.5	28.1	28.6	29.7	28.2

ROOT COLLAR DIAMETER

Collection Year	Seed Density 1 (lightest)	2	3	4 (heaviest)	$\bar{X}$
	mm				
1975	2.9	2.9	3.0	3.3	3.0
1976	3.0	3.0	3.3	3.0	3.1
$\bar{X}$	3.0	3.0	3.1	3.1	3.1

In a study of seed size by half-sib family (HSF), seed lots were collected from twelve clones in Weyerhaeuser's orchard in the fall, 1978. The seeds from each lot were extracted, floated to remove debris and unsound seeds, and stored in a cold room until spring, 1979. Each lot was then separated by placing it in water and adding sodium tartrate (an inert salt) until the density caused one-third of the seeds to float. After these seeds were removed and rinsed, more salt was added to the solution to separate the remaining seeds in half. A portion of each seed lot was left unsorted. To prevent differences in water absorption rates from influencing density, seed lots were soaked in water for three days prior to separation.

All lots were sown in April, 1979 in the Federal Paperboard Company Nursery at Lumberton, N. C. Plots were 30 cm by 140 cm, the bed width, and were separated by pieces of heavy plastic-covered cardboard buried 13 cm deep to restrict lateral root competition among plots. The nursery bed was fumigated two weeks before planting and was fertilized before and after planting to maintain soil nutrients at specified levels. Final thinning brought the spacing to 1.1 seedling per square dm.

Analysis of seedling height measured in June, at 12 weeks of age, revealed seedling size was significantly affected by both HSF and seed density within HSF (Table 2). Heavier seed density classes generally produced larger seedlings. Family and seed size within family accounted for 40% of the variation in plot means.

Table 2. Mean height of sweetgum seedlings by clone and seed density class in June at 12 weeks of age

Clone	Seed Density			$\bar{X}$	Unsorted
	Light	Medium	Heavy		
	cm				
1	8.6	7.9	10.9	9.13	11.3
2	10.1	10.4	10.9	10.47	10.6
3	8.6	9.6	10.9	9.67	9.9
4	8.5	10.2	10.1	9.57	12.8
7	8.3	7.8	9.0	8.38	9.2
9	9.7	14.1	12.3	12.04	13.4
10	10.5	7.9	9.5	9.29	11.0
13	10.7	9.8	9.0	9.82	10.0
23	8.9	9.1	10.0	9.33	11.6
29	8.8	8.7	10.9	9.46	7.5
39	10.7	11.4	10.2	10.76	9.5
42	8.7	10.4	10.5	9.89	8.0
$\bar{X}$	9.33	9.78	10.35	9.82	10.40

By August neither HSF nor seed density within HSF had a significant effect on seedling height growth. Only two families still showed a consistent trend of larger seedlings being produced from heavier seeds. By October, two families showed larger seedlings being produced from heavier seeds, but these were not the same two families. The mean height of seedlings grown from non-sorted seed was not significantly different than the mean of those from the sized seed lots, indicating no competitive advantage by growing seeds from sized seed lots. Root collar diameter was also not significantly affected by HSF or density within HSF, further suggesting that the nursery environment and seed to seed variation were more influential in affecting seedling size than were the effects of HSF or density class.

These findings were also supported by a study to determine whether seedlings grew better when sown by family or by density class (Johnson, 1980). No height growth advantage was obtained in segregating seeds by family or by density class.

The density distribution of seeds within families was subsequently examined. Fifty seeds were selected from each of the non-sorted seed lots and floated using known concentrations of sodium chloride (Table 3). Both the mean density and degree of variability required to float seeds differed among families. Such variation alters the genetic composition of bulked seed lots when they are density sorted. The heavier families remain in larger proportions after removal of the lighter seeds. This same effect has been found in white spruce (Hellum, 1976) and Douglas-fir (Silen and Osterhaus, 1979).

Table 3. Sweetgum seed density distribution by clone

Density	Clone											NaCl per 100 ml water
	1	2	3	4	7	9	10	13	23	29	39	
g/cc	Percent of seeds that float											gm
1.084	0	0	0	2	0	2	0	0	4	2	2	12
1.098	0	0	0	2	2	2	2	4	4	2	2	14
1.112	0	6	2	2	2	4	6	4	4	2	2	16
1.126	0	6	4	4	6	4	8	4	6	4	2	18
1.140	2	6	4	6	6	10	10	4	12	16	4	20
1.154	6	6	4	6	14	28	16	4	24	38	20	22
1.168	32	20	8	16	40	32	28	8	50	80	64	24
1.182	32	60	22	44	66	61	54	26	72	96	84	26
1.196	62	88	38	88	94	80	74	50	88	100	96	28
1.210	94	94	62	90	100	82	90	66	90	100	100	30
1.224	100	100	90	100	100	86	100	76	100	100	100	32

EFFECT OF PHOSPHORUS AND MYCORRHIZAE ON SEEDLING SIZE

Since sorting sweetgum seed by density class and family did not improve growth or uniformity, emphasis was shifted to nursery soil fertility factors. Conventional wisdom implies that the presence of mycorrhizal fungi, as well as minimum nutrient levels, must be maintained for the genetic potentials of seeds to be expressed.

Since sweetgum is reported to be an obligate endomycorrhizal species (i.e. it does not grow past the primary leaf stage without endomycorrhizae), the use of methyl bromide fumigation could contribute to inconsistent seedling crops (Kormanik et al. 1977). In an experiment evaluating one endomycorrhizal fungus, Glomus fasciculatus, and three open pollinated sweetgum

families collected in 1974 from the Weyerhaeuser orchard, Paschke et al. (1979), found that: (1) sweetgum seedling height was negatively affected by fumigation, (2) amendments of mycorrhizal inocula or water-soluble phosphates (surface broadcast) equally increased seedling heights, (3) family effect was significant but the family by mycorrhizal interaction was always nonsignificant, and (4) background soil phosphorus determined the significance of the mycorrhizal effect, i.e., when elemental soil phosphorus (P) was above 50 kg/ha, the mycorrhizal effect was barely significant, whereas the mycorrhizal effect was highly significant when soil phosphorus was below 50 kg/ha.

To better evaluate the phosphorus fertility, mycorrhizal, and family relationships, three mycorrhizal fungi (Glomus etinucatus, Glomus fasciculatus, and Gigaspora margarita) plus a control, and six randomly selected families from the 1978 seed collection were chosen for further investigation. A standardized inoculum density of 110 spores per square decimeter was applied. Two replications were planted in soil with an elemental soil P content, as determined by the double acid extractant, of 30 kg/ha (low P), and the remaining two replications were planted into a soil having 67 kg/ha of P (high P). The soils were fumigated with over 600 kg/ha of methyl bromide (MC2) before planting, and seedling density by the fourth month was reduced to 1.1 per sq. dm.

The combined analysis utilized data from both fertility levels (Table 4). Mycorrhizal and family effects were significant for seedling height at all measurement times and RCD measured at month seven. Foliage dry weight was not affected by either family or mycorrhizal inoculation, although control seedling means were significantly smaller than inoculated seedling means for height and RCD. No statistical differences existed among the mycorrhizal fungi. Family mean rankings changed over time but only family 7 made any important rank change after the fifth month. The family by mycorrhizae interaction was nonsignificant for all measured traits regardless of soil P content.

The high P replications exceeded the soil P level of 50 kg/ha recommended for hardwood seedlings (Davey, 1980). In this case the mycorrhizal effect on seedling height was significant for months three and four but became nonsignificant after month five (Table 4). By the seventh month the control seedlings, though still the shortest, were not significantly different from the inoculated seedlings. Seedling RCD was affected by the fungal treatments. Seedlings inoculated with Glomus etinucatus and Gigaspora margarita were significantly larger than seedlings treated with Glomus fasciculatis, and all inoculated seedlings were significantly larger in RCD than the control seedlings. Under high P conditions no family differences were observed.

For seedlings grown with low soil P, the mycorrhizal effect for seedling height was significant at the ten percent level for months three, four and five (Table 4). For these months control seedlings were significantly shorter than the inoculated seedlings, though no differences developed

Table 4. Rankings of height over time, root collar diameter, and foliage dry weight means for mycorrhizae and family effects by Duncan's Multiple Range Test, and Analysis of Variance significances

			Combined		Low P		High P	
Main Effect	Trait	Measurement Time	ANOVA Significance	Mean Rankings	ANOVA Significance	Mean Rankings	ANOVA Significance	Mean Rankings
Mycorrhizae								
	Height	3 months	**	1,2,3,4	+	1,2,3,4	*	3,2,1,4
		4 months	**	1,2,3,4	+	1,2,3,4	*	3,2,1,4
		5 months	*	2,1,3,4	+	2,1,3,4	NS	2,3,1,4
		7 months	*	2,1,3,4	+	2,1,3,4	NS	3,2,1,4
	Root Collar Diameter	7 Months	*	2,3,1,4	*	2,1,3,4	**	2,3,1,4
	Foliage Dry Wt.	7 months	NS	2,3,1,4	**	2,1,3,4	NS	3,4,1,2
Family	Height	3 months	**	9,13,28,20,24,7	**	9,13,28,24,7,20	**	13,9,28,20,24,7
		4 months	*	9,13,28,24,7,20	+	9,28,24,7,13,20	+	13,9,28,20,24,7
		5 months	*	28,13,7,9,24,20	**	28,7,9,24,13,20	NS	13,24,9,28,7,20
		7 months	**	28,13,9,24,7,20	**	28,7,9,24,13,20	+	13,28,24,9,7,20
	Root Collar Diameter	7 months	NS	13,28,9,24,7,20	NS	28,9,24,7,13,20	NS	13,9,28,24,7,20
	Foliage Dry Wt.	7 months	NS	28,13,24,9,7,20	**	28,24,9,7,13,20	NS	13,28,24,9,7,20

a) Mycorrhizal Treatments:

1= Glomus etinucatus
2= Glomus fasciculatus
3= Gigaspora margarita
4= control

Any two mean rankings with the same line in common are not significantly different by Duncan's multiple range test procedure which used the ANOVA significance as the probability level.

and + means significant at 10 percent probability level.
* means significant at 5 percent probability level.
** means significant at 1 percent probability level.

among the fungal treatments. At seven months, the mycorrhizal effect upon height had increased in significance to the five percent level with Glomus species superior to Gigaspora. Foliage dry weights were highly significant with the control plots being inferior to the amended plots. Ranking of the fungi was the same for height and foliage dry weight. Mycorrhizal effects on RCD were significant at the ten percent level. Control seedlings were again significantly smaller than the inoculated seedlings. No family differences were found for RCD in low P, but the family effect for height was highly significant at months three, five and seven. Foliage dry weight also had a highly significant family effect. Family mean rankings for height stabilized after month five with ranking of foliage dry weight mirroring these results.

Soil P content had a major impact upon the significance of the mycorrhizal treatments. Yet, the practical outcome of this experiment was that mycorrhizal inoculation was not a substitute for good soil fertility because the shortest seedlings in the high P replications were larger than the tallest seedlings in the low P replications. The diminished significance caused by the high soil P level can be explained by the effect mycorrhizal fungi have upon root absorption area of developing seedlings. Bieleski (1973) calculated that four connections per mm of root, each extending 20 mm from the root surface, could increase phosphorus uptake from ten times if uptake were proportional to root surface area to about 60 times if diffusion were limiting.

Considering the small root system of developing seedlings, the additional root absorption area caused by mycorrhizal infections can explain observed significant effects. Eventually, even the non-inoculated seedlings would become mycorrhizal as the root systems extended beyond the fumigation zone, although this development would be delayed by low P levels. Infection and subsequent improved growth of control seedlings reduced the significance of the inoculation treatments in the high P soil. Seedlings in low P soil could not grow until a mycorrhizal relationship was established supporting findings of Kormanik et al. (1977).

Family differences were also influenced by soil P fertility with differences evident under high P exaggerated by low P conditions. Family 13 was most sensitive to the P fertility differences moving from next last rank when P was limiting to second best under high P.

Since most nursery soils contain soil P levels above 50 kg/ha, the relatively uniform family results reported for high P are more likely consistent with nursery expectations as well as with the seed size trial mentioned earlier. Other sweetgum studies have found the family component to be highly significant (Weir and Sprague, 1975, Kormanik et al. 1979). Since the families for the reported studies were collected from a seed orchard, the uniformity could have been caused by panmixia. Seed year has played a role in family differences because the 1974 seed collection (Paschke et al. 1979) had highly significant family differences. Nevertheless, the uniform family growth would be desired by nurserymen and plantation establishers.

CONCLUSIONS

Sowing seeds by density class or family should not increase sweetgum seedling growth or uniformity since family and seed density did not affect seedling size after three months. However, removal of a particular density class from bulked seed lots will affect the genetic composition. Year of collection affects both growth and uniformity of a seedling crop. Seed orchard seed appeared to produce seedlings superior to natural stand collections.

Mycorrhizal inoculation in fumigated nursery soils has its greatest effect early in the growing season because of the small root absorption area of the seedling. Mycorrhizal inoculation was not found to be a substitute for soil fertility. Soil P levels significantly affected seedling growth and should be maintained above 50 kg/ha. Amendments of mycorrhizal inoculation or soluble phosphates (surface broadcast, 5-10 kg/ha) were found to equally increase sweetgum seedling height. Family differences for the 1978 seed year were masked by soil P fertility above 50 kg/ha but the family by mycorrhizae interaction was always unimportant. RCD was increased by inoculation and differences among the fungi existed at the high P level. This may prove important after further evaluation. Soil P levels as high as 130 kg/ha did not inhibit mycorrhizal development but could affect uptake of other important nutrients.

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VARIATION IN SEEDLING GROWTH RATES: THEIR GENETIC AND PHYSIOLOGICAL BASES

Thomas O. Perry and William L. Hafley

Abstract.--Studies of 45 progenies of loblolly pine (Pinus taeda L.) reveal that seed coat thickness, seed weight, condition of the embryo, seed treatment, and rate of germination can account for some 20% of the variation in initial seedling size and growth rates. These and other seed properties are affected by the genotype and environment of the mother tree and can affect progeny test results as well as having a strong influence on the results of nursery management practices.

Additional keywords: Seed properties, genetics, Pinus taeda L., growth rate.

INTRODUCTION

There has been a great deal of effort expended on attempts to reduce the generation time for tree improvement programs--particularly through the use of infrared gas analyzers and seedling selection on the basis of greenhouse and nursery performance. These attempts were largely unsuccessful. This lack of success, we believe, was due in part to the confounding effects that the genotype of the mother tree, year-to-year variation in the environment, and other factors have on early germination and growth of tree seedlings.

The studies reported here are part of an effort to quantify and separate these confounding factors from the effects of the genetic characteristics of the zygote on the growth and yield potential of the seedlings under field conditions. These efforts have been only partly successful. Nonetheless, the results have important implications for tree planters, managers of forest nurseries and workers in the field of Tree Improvement.

Previous findings

Simple correlations between seedling size in the nursery and size at increasing ages decrease systematically and are particularly poor when the seedlings used for the correlation are less than 3 years of age (Lambeth 1980). This concept is well developed in discussions of changes in heritability with time (Franklin 1979, Namkoong and Conkle 1976, Namkoong et al. 1972).

Seed weight, seed coat thickness, polyembryony, seed stratification requirements, number of days required to germinate, and a number of other seed and seedling characteristics affect initial growth rates and seedling size (Righter 1965, Nanson 1965, 1967, 1969, Perry 1976). These characteristics

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are often determined by the genotype of the mother tree and the nursery environment. They have little to do with the genotype of the zygote and can be considerably modified from year to year (Silen and Osterhaus 1979, Perry 1976). Often the differences in seedling size generated by these seed and early germination phenomena persist for 15 or more years but the intrinsic growth rate of the seedlings is not altered (see for example Overton and Ching 1978, Sluder 1979, and Wakeley 1963).

Large seedlings can suppress small seedlings growing in the nursery bed and exaggerate initial differences in seedling size. Hence arrangement of plants in the nursery and arrangement of plants after they are out planted can considerably bias progeny test results (unpublished data of Adams et al. 1973, Dierauf).

Accurate prediction of future growth on the basis of early progeny performance requires that the various factors, genetic and environmental, that regulate early germination and growth be taken into account. Two recent attempts to do this with progenies of loblolly pine (P. taeda L.) have been relatively successful (Cannell et al. 1978, Robinson and van Buijtenen 1979).

Cannell et al. (1978) have made correlations between seedling growth rates and progeny performance under field conditions. They achieved their results by delaying the measurements of the seedlings of the 16 loblolly pine progenies they studied until they were 140 mm tall ("when the effects of seed size no longer affected daily growth rates") and by growing the progenies under varying conditions of water stress (the major variable of the field environment). There was an interaction between progeny and water stress such that those progenies that grew best under conditions of low water availability had daily growth rates that were correlated with the results of 8-year-old tests of the same progenies on upland sites and those progenies that grew most rapidly in well watered nursery conditions had growth rates that correlated positively with the results of 8-year-old tests on dry sites. There were appropriate differences in the root-shoot ratios of the progenies that corresponded well with the interaction with water stress and with differences in performance under field conditions. The literature review on early progeny testing for this excellent paper is probably one of the most comprehensive in the forestry literature.

Robinson and van Buijtenen (1979), in a study of seed weight, percent of seedlings of a progeny with distinct terminal buds, and percent of seedlings of a progeny without basal branches showed a positive correlation with 5, 10, and 15-year volumes for a loblolly pine progeny test in Texas.

Studies of diallel crosses with white pine (P. strobus L.), Sitka Spruce (Picae sitchensis (Bong.) Carr.), and Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. menziesii) indicate that a large proportion of the variation in size among progenies is attributable to differences among mother trees (Campbell 1971, Kriebel et al. 1972, Samuel et al. 1972). Reciprocal crosses with slash pine (P. elliottii Engelm. var. elliottii) showed 30% differences in volume and gum yield at age 11. There were significant differences in growth rates of 4 and 7 pairs of reciprocal crosses with slash pine at age 3 (Susan Kossuth, personal communication, U. S. Forest Service).

Progeny tests with loblolly pine conducted by the North Carolina Tree Improvement Cooperative indicated that maternal determination of seed size may be one of the variables related to early progeny performance (Table 1 and Figure 1, Perry 1976). The correlation between seed weight and early progeny performance is often poor and other seed variables affect early seedling size and growth rates. These variables include polyembryony, seed coat thickness and ability to shed seed coats promptly.

Table 1.--Relative weights of open-pollinated seed taken from selected and unselected trees of loblolly pine (Federal Paper Board Co., North Carolina). Commercial check = seed from trees selected at random in natural stands. Rogued clones = seed from mediocre clones which have been rejected in the tree improvement program. Select clones = seed from outstanding trees. Some of the difference between commercial check and seed orchard trees is attributable to the superior cultural circumstances of the trees in the orchards and some is a reflection of genetic differences in ability to produce seed among the different categories of trees.

Classification	Seed Weight (mg seed^{-1})	% of Commercial Check	% of Rogued Check
Commercial check	23.2	---	90
Rogued clones	26.8	116	---
Select clones	36.5	157	137

MATERIALS AND METHODS

Open-pollinated seed from 40 loblolly pine clones of the North Carolina Forest Tree Improvement Program (North and South Coastal clones of the Weyerhaeuser Company) were used in the studies reported here.

One hundred seed of each progeny were weighed individually to the nearest .1 milligram and then mounted so that X-ray images of their internal structure could be prepared. The seed were classified into 5 categories on the basis of their X-ray images:

1. Seed apparently sound.
2. Embryo defective: image fuzzy, not opaque, not fully developed, distorted, cracked, other.
3. Gametophyte defective: criteria as above.
4. Both embryo and gametophyte defective: same criteria as above plus: seed empty and seed with indistinct residue of embryo and gametophyte (a ghost image).
5. Seed polyembryonic.

The relative thickness of the seed coats of a given progeny was estimated in thousandths of an inch by using a graduated air-photo-dot scale and placing it

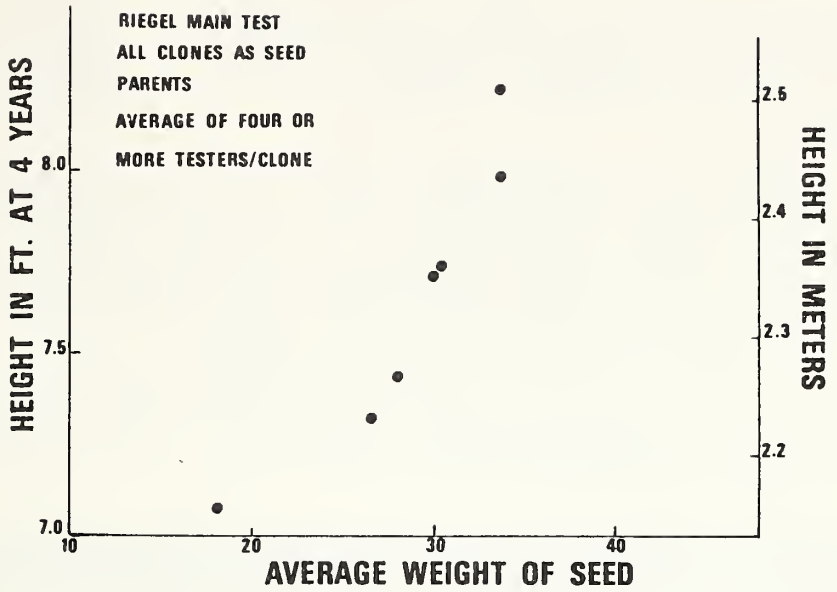

Figure 1.--Effects of seed weight of maternal parent on progeny performance when pollen from a single parent is used (loblolly pine data age 4, Federal Paper Board Company). Differences among female parents accounted for 88 percent of the variation in seed weight while differences among males only accounted for 12 percent of the variation (Perry 1976).

over the X-ray image of the seed. The averaged value of measurements from 10 seeds was used in subsequent statistical analyses.

Each seed was then planted in an individual container and daily records of its early germination and growth were kept. The nominal dimensions of the containers used to grow each seedling were 3" x 2" x 9" deep. "Pro Root", a calcined clay equivalent to "Sorbolite" or "Kitty Litter" screened to an average particle size of 2 mm was used as the growth medium. The containers were then used in two separate experiments. For the first experiment reported, they were placed in the 26° day, 22° night of the Phytotron at N. C. State University. The watering schedules and nutrient solutions and general care of the plants represented the standard practices of the N. C. facility (Downs and Bonaminio 1976). For the second experiment, they were placed in a typical greenhouse with the thermostat set for 23° during the day and 17° at night. Incandescent lights were used to interrupt the dark period in both the phytotron and the greenhouse.

For the first experiment, 20 seeds of each progeny (still kept individually), were placed in a pipette washer with 10^{o} to 13^{o} water flooding over them and changing every 5 minutes for 96 hours before they were planted in the phytotron.

For the second experiment, 10 seeds of each progeny were planted without treatment in the greenhouse in the same type of containers and soil medium. They were watered by a mist system for 5 minutes twice a day. They were fertilized twice a month with fertilizer solution in accord with the recommendations of the manufacturer.

Records of germination and growth were taken daily in the phytotron for 86 days (i.e., when germination was complete). The plants were then moved to a test plot at our School Nursery where they have been measured once a week during the active growing season and at least once a month during January and February. There were 1350 seed at the beginning of the phytotron study. Some 1050± seedlings from these studies are still being measured.

Records of germination and growth were taken daily in the greenhouse for 201 days (in order to allow time for complete germination). The seedlings from this study have been discarded.

The data from these studies were stored on magnetic disc drives of the IBM 370 at the Research Triangle Computing Center and the Statistical Analysis System (SAS) was used for the subsequent analyses.

RESULTS

The results are illustrated in Figures 2-11. Statistical analyses reveal that there were significant differences among progenies in all characteristics measured: seed coat thickness, seed weight, number of days required to germinate, number of days required to shed seed coats and the average size of progenies on all dates measured.

Multiple regressions of seed weight, seed coat thickness, number of days required to germinate and number of days between germination and seed coat shed reveal that variation in the number of days required to shed seed coats is the best single predictor of initial seedling size and accounts for 13% of the variation in seedling size at day 86. The best multiple regression equation for predicting initial seedling size only accounted for 20% of the variation in initial seedling size and included the variables of number of days required for seed coat shed, seed weight and seed coat thickness. Appropriately, seed coat thickness was negatively correlated with initial seedling size.

Surprisingly, the frequency distribution of seed sizes for several of the progenies was discontinuous and at least bimodal. This plus the observed relationship between seed coat thickness and seed weight may explain in part why average seed weight can sometimes be such an inadequate predictor of seedling size and subsequent growth.

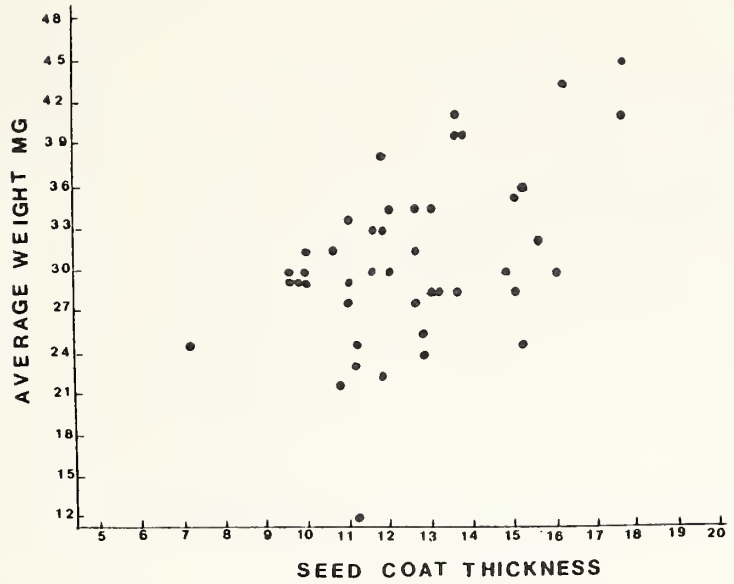

Figure 2.--Average weight vs. seed coat thickness. The seed coat is maternal tissue and its thickness and weight affect early growth and progeny performance. Seed weight = 13 + 1.36 (seed coat thickness), r^2 = .26. Weight is in milligrams. Seed coat thickness and other variables confound the direct relationship between seed weight and initial seedling size and growth rate.

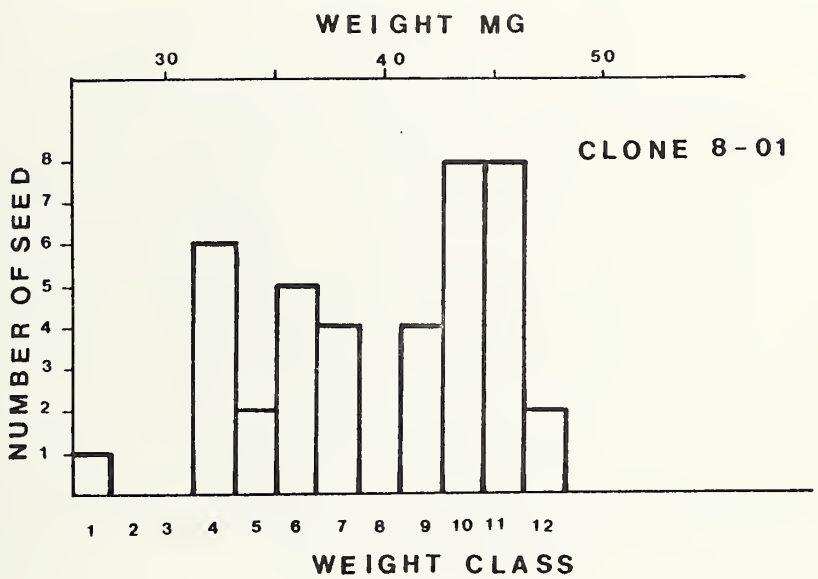

Figure 3.--Frequency distribution of seed weights for clone 8-10. Several progenies had seed weights which yielded discontinuous frequency distributions of the type observed here. Could the seed have come from different ramets in the orchard? Peculiar frequency distributions of the type observed here could be one of the reasons why the relationship between initial size and seed weight is so poor.

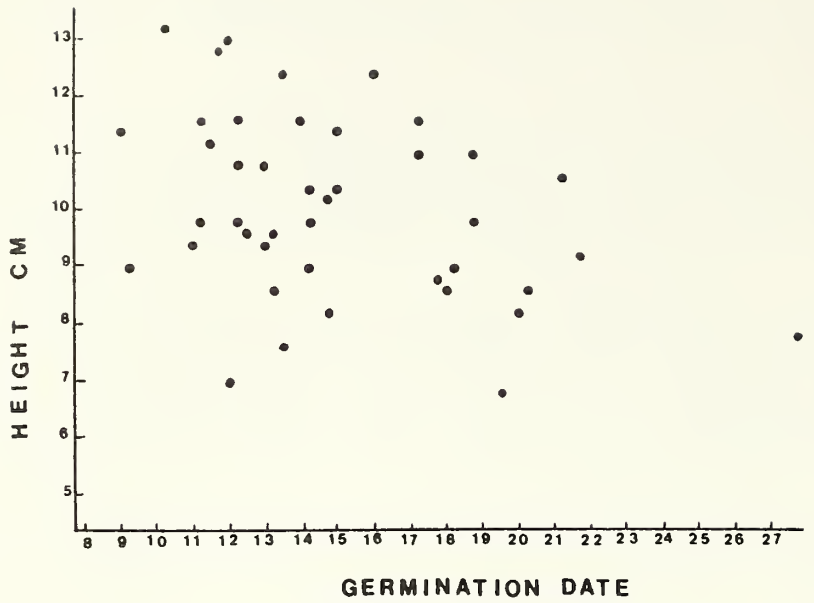

Figure 4.--Height of seedlings in the phytotron at day 86 vs. germination date. These seed were cold soaked in well oxygenated running water for 96 hours prior to planting. The slowest family to germinate required an average of 28 days. This contrasts markedly with the studies of the same seedlot germinated without treatment in a greenhouse. See Figure 8.

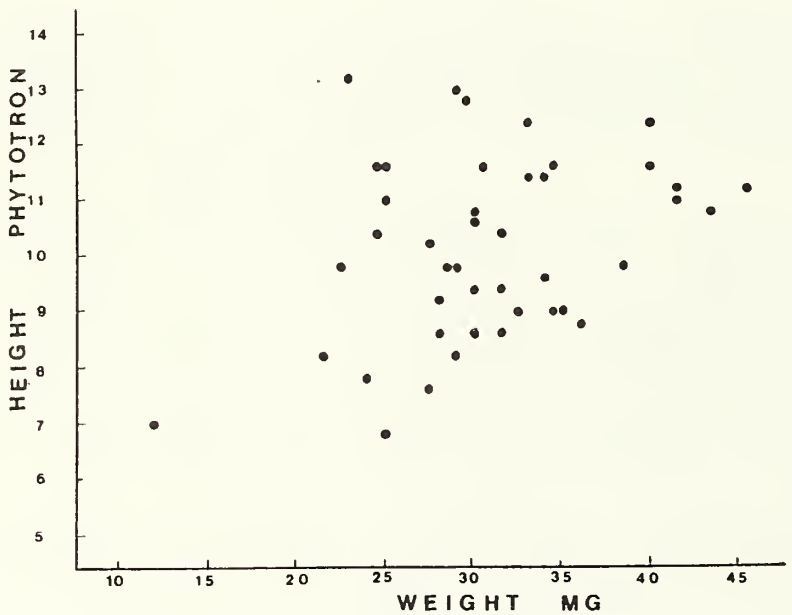

Figure 5.--Height in the phytotron (day 86) vs. seed weight in milligrams. With the exception of 5 families, there is a fair trend. Contrast these results with those obtained in the greenhouse (Figure 9).

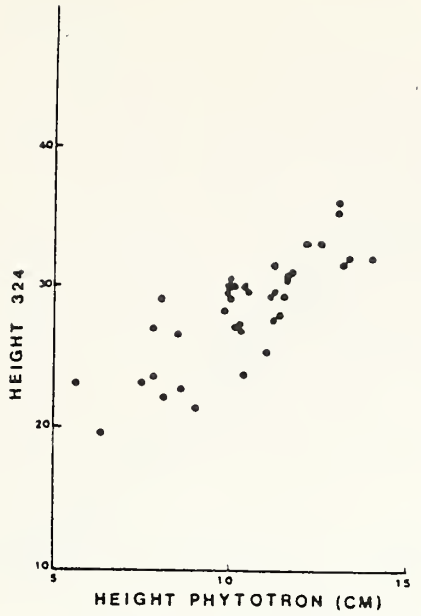

Figure 6.--Height on day 324 in the field vs. height on day 86 in the phytotron. At the end of the first year in the field the relative sizes of the progenies did not change materially.

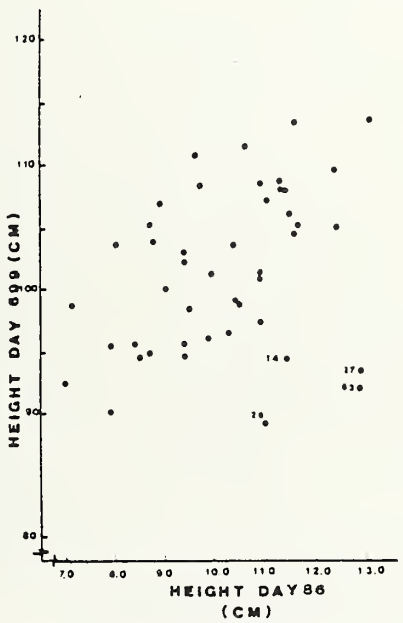

Figure 7.--Height day 699 in the field vs. height day 86 in the phytotron. Only four families have made major changes in rank relative to their sizes at day 86 in the phytotron. The effects of initial plant size are still apparent.

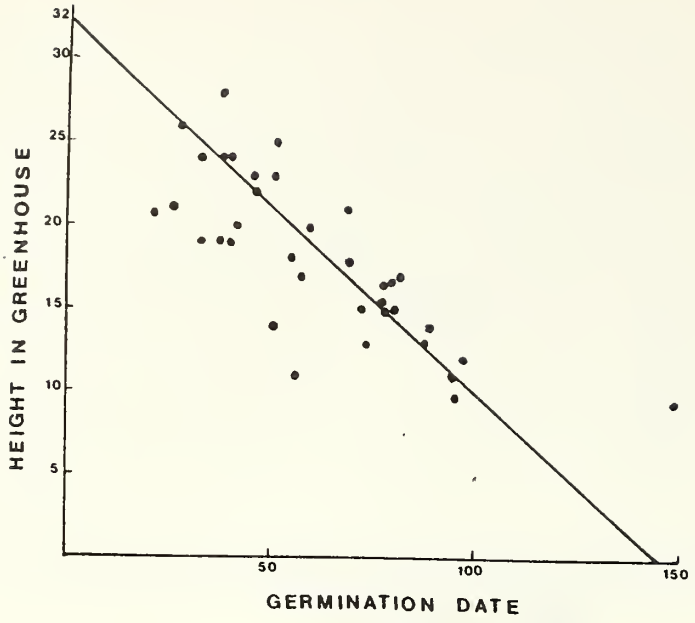

Figure 8.--Height in the greenhouse, day 201 from planting vs. germination date. In this experiment, the seeds were planted with no pretreatment. Germination date had a major effect on the initial height of the seedlings. The results contrast markedly with those observed with partially stratified seed in the phytotron. (r^2 = 0.61. Other variables not significantly correlated with initial height: seed weight, seed coat thickness, weight x thickness.) Compare with Figure 4.

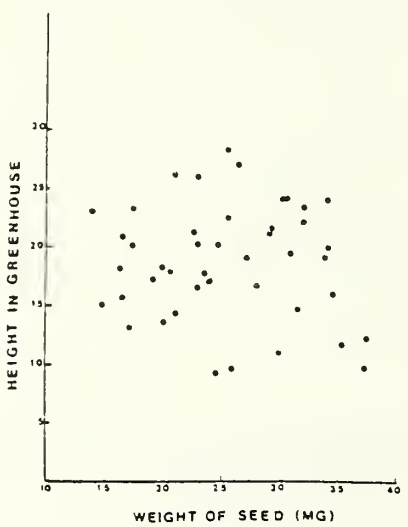

Figure 9.--Weight of seed in the greenhouse vs. height in the greenhouse at day 201. There is no detectable correlation. This contrasts with the phytotron results. See Figure 8.

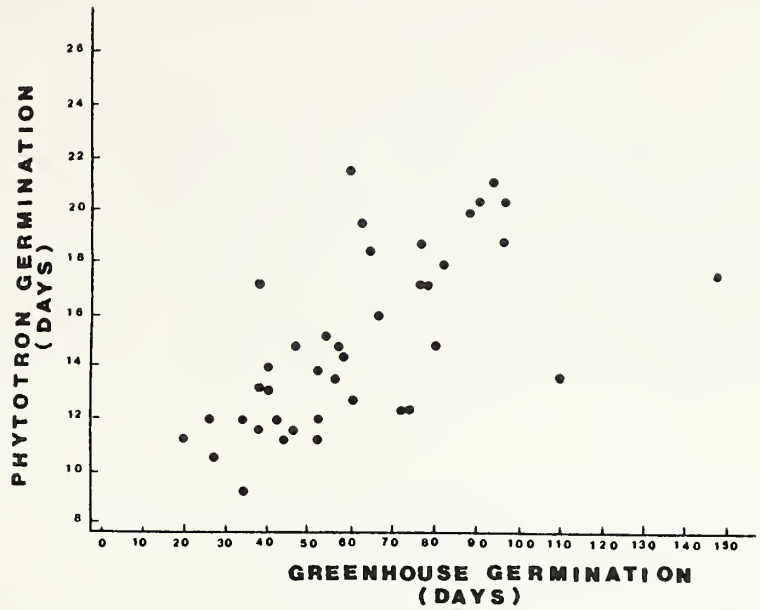

Figure 10.--Correlation between the number of days required to germinate in the phytotron and the number of days required to germinate in the greenhouse. There was a definite correlation in spite of the differences in seed treatment (r^2 = .35).

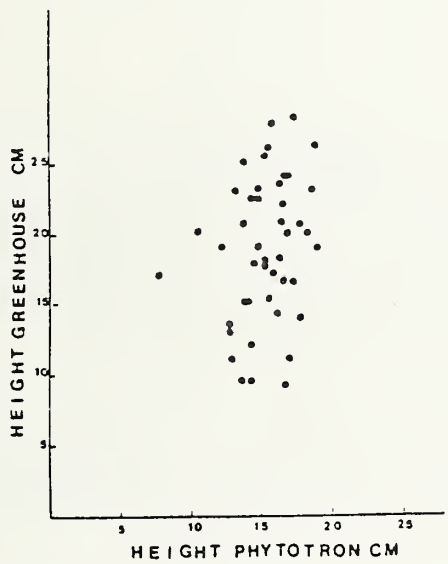

Figure 11.--Height in the greenhouse vs. height in the phytotron. There may be some weak correlation. The greater spread of the greenhouse heights is a reflection of the lack of pretreatment of the greenhouse seeds. Seed handling, treatment, and nursery environments can alter the variability of progeny test results.

Examination of individual seedlings and progenies during the entire study reveals factors that affect initial size and growth rates. One of these is the characteristic of some progenies to have their cotyledons trapped for long periods. Over 80% of the seedlings of one progeny had their cotyledons trapped by the seed coat for 77 days after planting. Initial growth of these seedlings was stunted and crooked.

The results of attempting to relate initial size and growth performance with condition of the seed and gametophyte as estimated from examining their X-ray images were not consistent. Sometimes seed classified as sound did not perform any better than seed with embryos or gametophytes which were classified as fuzzy or defective. For some progenies there were distinct differences in the growth performance of seeds that were classified as sound or defective; while for others, the defective seeds of a progeny were as likely to give a superior performance as were the sound ones. Seeds with obvious defects (category 5) either did not germinate or produced weak plants that did not survive in the phytotron.

There was no correlation between seed weight and number of days required to germinate. Nor was there between seed coat thickness and number of days required to germinate or to shed seed coats.

Comparison of the results in the phytotron and in the greenhouse (Figures 4, 5, 8, 9, 10, 11) reveal that seed handling and rearing conditions can considerably alter the relative importance of seed variables in determining initial size and growth rates. Seed weight and seed coat thickness were significant variables in determining initial size and growth rates when seed were prewashed in well oxygenated cold water for 96 hours and grown in the phytotron. The number of days required to germinate masked the effects of other seed variables in determining initial seedling size and growth rates when seeds were not pretreated (the greenhouse study).

SUMMARY AND DISCUSSION

Non-destructive measurements of seed properties (seed coat thickness and seed weight) plus variation in the number of days required to shed seed coats accounted for only 20 percent of the variation in the size of seedlings 86 days after planting. Number of days required to shed seed coats was a better predictor than number of days required to germinate (show any sign of emerging radicle) in accounting for variation in size at day 86. These variables could only account for 7 percent of the variation in size after two years of growth in a test planting.

Attempts to account for early differences in seedling size on the basis of examination of X-ray images of the seeds prior to planting gave inconsistent results. Identification of partially developed seeds with obviously defective embryos and gametophytes was relatively easy. However, it was not possible to consistently rate other seed on the basis of X-ray images that were distinct or indistinct, as being sound or defective, or to correlate these classifications with early seedling size and growth.

The trapping of cotyledons by seed coats and various unknown seed characteristics may account for part of the residual 80% of the variation in initial seedling size. Some of the variation may be due to differences in the properties of the zygote.

Changes in seed stratification and other nursery management practices, such as root and top pruning can radically alter the importance of seed and seed germination characteristics on initial seedling size.

Frequent measurements during two years since outplanting reveal that progenies with seedlings that were initially large or small tend to remain relatively large or small. There were no significant differences in the duration of seasonal growth, or in K, the specific rate of growth ($(dH/H)/dT = k$, H = height, T = time) that could account for the variation in progeny sizes after two years of measurements. The correlation between initial size and current size decreased with time. However, only 4 of the 45 original progenies have made height growth radically different than would have been predicted on the basis of their initial size.

In many of our progeny tests, we are not separating the effects of genetic variation of the zygote from genetic and environmentally determined attributes of the seed and the seedling environment. The seed coats and gametophytic tissue of a conifer seed commonly amount to 80% or more of the weight of the seed and are determined by the genotype of the mother tree.

Seed size and seed quality increase as the ramets of a seed orchard increase in age and vigor. Seeds from orchards which are fertilized, irrigated, and protected from insects are going to be larger and of better quality than "commercial check" seed which was gathered from random trees in the forest.

Changes in the environment during a particular year of seed maturation and changes in nursery practice can further alter the size and relative performance of a progeny.

These non-genetic effects can account for a large portion of the variation in the size of progenies at age 4. These non-genetic effects decrease with time but continue to confound interpretation of progeny test results for 20 years or more. They seriously alter estimates of additive and non-additive genetic variance and can lead to exaggerated estimates of the amount of gain in vigor or growth that can be attributed to altering the genotype.

The array of genetic and environmental factors that combine to effect the size and condition of seeds is complex. No single measurement, such as seed weight, seed coat thickness, or condition of the embryo is sufficient to account for all of the variation observed. Even with careful stratification, and sorting of seed by size, there are unpredictable variations in the average size of seedlings produced from a given ramet in a given year.

In the nursery, large seedlings of one progeny interact to suppress the smaller seedlings of another progeny. Hence potential differences in individual seedling size and average size of a progeny can be greatly exaggerated by random or mixed plantings in the nursery.

The literature reviewed in this paper (Campbell 1971, Kriebel et al. 1972, Perry 1976, Samuel et al. 1972) indicate that the factors shown to be of influence in these studies of initial size and growth rates are affected by the genotype and environment of the mother tree and may have a strong influence on the early years of seedling development. Seed from reciprocal crosses, from different ramets of the same clone, and from different year classes may vary markedly in their potential for germination and growth. Mixture of seed of these different categories could confound experimental and practical results of tree improvement programs when decisions are made at early ages.

We recommend that both research and commerical collections of seed from a given mother tree be kept separate, receive custom treatment, and be planted separately in the nursery.

Seeds of progenies with a long stratification requirement or a low germinative energy or germinative capacity should receive special seed stratification treatments and be planted earlier in the nursery and at different seed bed densities than seedlings with contrasting characteristics.

The simple act of managing the seeds of different progenies and different year-classes separately will increase the yields of plantable seedling per hectare of nursery, reduce the magnitude of variability among seedlings, and yield a more uniform and vigorous plantation in the field.

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COMPARISONS OF PROGENY OF A LOBLOLLY PINE SEED PRODUCTION AREA WITH PROGENY OF PLUS TREE SELECTIONS

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Abstract.--Four progeny tests compared performances of progeny of Georgia Forestry Commission (GFC) seed orchard clones; a seedlot from a seed production area (SPA) in Warren County, Georgia, established by the Continental Can Company; and several commercial check lots. The clonal progenies consistently outranked the SPA lot and the commercial check lots for crown/height ratio at age 5 and for height, d.b.h., stem volume and stem straightness at age 15. There were few consistent differences for number of galls/tree at age 5 or plot volume, percentage of rust-free trees, and survival at age 15. When all traits were considered, clonal progenies performed best as a group. Differences between the SPA lot and the commercial checks were not significant.

Additional keywords: Commercial check lot, phenotype, nonparametric, *Pinus taeda, Cronartium quercuum.*

One of the early efforts to improve the genetic quality of forest nursery stock was to set aside and manage certain stands as seed production areas. Removal of all but the selected seed crop trees was based only on phenotypic characteristics. There has been little empirical evidence that progeny of seed production areas possessed any potential for genetic gain. Four progeny test plantations of loblolly pine (*Pinus taeda* L.), established in 1965, contain progeny of a seed production area along with progenies of plus tree selections represented in two clonal seed orchards and several commercial check lots. Though designed to test progenies of seed orchard clones, these plantations offer a means of evaluating the genetic potential of the seed production area. Nine important traits were compared among three main progeny groups, and these results are the subject of this paper.

MATERIALS AND METHODS

The four plantations in which the data for this study were collected were designed to test polycross progenies of clones in two Georgia Forestry Commission (GFC) seed orchards (the Arrowhead Seed Orchard in Pulaski County and the Horseshoe Bend Seed Orchard in Wheeler County) and to compare them with several controls.

In this paper we compare three groups using progeny test data: Group 1, progeny of plus tree selections used to establish clonal seed orchards, hereafter referred to as clonal progenies; Group 2, a seedlot collected from a seed production area (SPA) in Warren County, Georgia, established by the Continental Can Company; and Group 3, commercial check lots supplied by the GFC as nursery run controls in the progeny test plantations.

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The four plantations, numbered 69, 75, 76 and 77, contain 22, 8, 22 and 17 clonal progenies, respectively. Because some progenies are common to two or more plantations, the total number of different clonal progenies is 53. Three commercial check lots were used, but no more than two in any plantation, and only one in Plantation 76.

All plantings were in randomized complete blocks, with the numbers of replications varying from 5 to 8. Plantations 69 and 76 contained 25-tree square plots; Plantations 75 and 77 had 5-tree row plots. Plantations 69, 76 and 77 are in Bleckley County in the Upper Coastal Plain, and Plantation 75 is in Jasper County in the Lower Piedmont.

Since numbers of clonal progenies in the three groups of interest varied considerably, a one-way analysis of variance with unequal subclass numbers was used to analyze most traits. In two plantations the nature of the data for two traits permitted a 2-way analysis of variance with unequal but proportional subclass numbers (Snedecor, 1956, Sokal and Rohlf 1969). However, this method produced a gain in efficiency in only one trait in one plantation.

The traits analyzed in this study are: (1) height, (2) d.b.h., (3) tree volume, (4) plot volume, (5) number of fusiform rust galls/tree (*Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*), (6) percentage of trees free of rust, (7) straightness, (8) crown/height ratio, and (9) percentage survival. Galls/tree and crown/height ratio were measured at age 5, all other traits at age 15. The growth traits were measured in metric units. The number of galls/tree was transformed to $\sqrt{X + .5}$, and the percentages of rust-free trees and survival were transformed to the arcsin $\sqrt{\text{percent}}$. Straightness was indexed by ocular estimation from 1 = straight through 6 = very crooked and transformed to $\sqrt{X + .5}$ for the analyses.

Analyses of variance and Duncan's Multiple Range Tests were performed on data for all 9 traits, except that the data for the percentage of rust-free trees in Plantations 75 and 77 had to be omitted; in these tests all or nearly all trees were infected, so that meaningful comparisons could not be made.

In addition to these analyses, the group means were ranked for each trait and two nonparametric methods were used to interpret results. The first method involved an interaction chi-square test for goodness of fit. The ranks of all traits were summed for each group in each plantation. The second method, which utilized the same ranked data, was Friedman's test, which is a chi-square approach to a randomized complete-block design (Steel and Torrie 1960). In this case the four plantations were considered to be replicates of the three groups. In this application each method became a form of nonparametric multivariate analysis, since all traits were combined into one variable, rank.

RESULTS AND DISCUSSION

Since nine traits were analyzed in Plantations 69 and 76 and 8 traits in the remaining two progeny tests, 34 analyses were performed in all. Only seven of these 34 tests produced significant variance analyses (table 1), and only six tests resulted in significant Duncan's multiple range tests (table 2). However, inspection of the group means in each plantation revealed that the clonal progenies appeared to rank first much more frequently than would seem to result from chance alone (table 3). Hence, two nonparametric analytical methods were applied to the ranked data.

The first method is a test for goodness of it. Ranks (1,2 or 3) of each group in each plantation were summed for all eight or nine traits, and these sums are listed as the "observed" data in the top row for each group in table 4. The expected values are listed in the second row for each group in table 4. Each expected value = rank x number of traits; e.g., for clonal progenies, Group 1, in Plantation 69, the expected value is 1 x 9 = 9.

We expect Group 1, the clonal progenies, to rank first for each trait because their ortets were selected in natural stands or plantations on the basis of greater size and better form than the surrounding trees and on the basis of absence of fusiform rust galls. In theory, each ortet was selected as the best of a sufficient number of trees in its stand, so that the selection differential is at least one standard deviation above the mean.

The SPA lot, Group 2, also represents some theoretical increment of genetic gain, since the dominant trees remaining in the area for seed production should be superior phenotypes compared to those which were rogued. However, because of the number of trees which must be left for seed production, selection intensity is limited, so that the selection differential is necessarily something less than one standard deviation above the mean. Hence, we expect a second rank for the SPA lot, and its expected value in Plantation 69 is 2 x 9 = 18.

The commercial check lots, which represent nursery run stock, have in theory a selection differential of zero. Since they are ranked third, the expected value in Plantation 69 is 3 x 9 = 27.

Only one chi-square, that of the clonal progenies in Plantation 69, indicated a significant difference between the observed and expected rank sums (table 4). However, chi-square for the goodness of fit test of all observations, taken as a whole, is 15.12 at 8 degrees of freedom and is not significant at the .05 level. The chi-squares for each group are also not significant (at 3 degrees of freedom for each group). The high observed rank sum for Group 1 in Plantation 69 probably results from the very poor performances of the clonal progenies in both rust resistance traits and in survival (table 3). The clonal progenies do not rank third for any other trait in any other plantation. Finally, the heterogeneity chi-square for each group is not significant. This means that the relative ratios of observed rank sums among the three groups are homogenous from one plantation to another.

Table 1.--*Degrees of freedom (d.f.), mean squares (MS), and significances of differences among groups for nine traits in four loblolly pine progeny test plantations in Georgia*

Source	Plantation 69		75		76		77	
	d.f.	*MS*	*d.f.*	*MS*	*d.f.*	*MS*	*d.f.*	*MS*
				HEIGHT				
Among groups	2	0.193	2	1.065	2	1.664	2	2.649
Error	136	.288	58	1.830	132	.668	95	1.480
				DBH				
Among groups	2	2.07	2	24.72	2	.46	2	5.59
Error	136	2.12	59	605.97	132	2.94	95	7.98
				TREE VOLUME				
Among groups	2	.001	2	.010*	2	.001	2	.004
Error	136	.001	59	.003	132	.002	95	.002
				PLOT VOLUME				
Among groups	2	.158	4[a]	.247*	2	.068	2	.032
Error	136	.392	65	.067	132	.471	97	.044
				GALLS/TREE				
Among groups	2	.059	2	1.76*	2	.065	2	.387
Error	136	.075	71	.42	132	.213	97	.292
				TREES RUST-FREE				
Among groups	2	89.15*	--[b]	--	2	5.74	--[b]	--
Error	136	25.21	--	--	132	22.55	--	--
				STRAIGHTNESS INDEX				
Among groups	2	.880**	2	.123	2	.672*	2	.793
Error	136	.095	59	.532	132	.158	95	.467
				CROWN/HEIGHT RATIO				
Among groups	2	31.54**	2	52.86	2	3.77	2	31.61
Error	136	4.58	70	31.69	132	17.37	97	22.56
				SURVIVAL				
Among groups	2	75.03	2	596.69	2	16.50	2	79.82
Error	136	295.14	85	328.55	132	110.23	97	330.26

[a] The mean squares and degrees of freedom were synthesized by means of the Satterthwaite-Cochran approximation in a 2-way ANOVA with unequal but proportional subclass numbers (Snedecor 1956).

[b] No comparisons due to very high infection.

* Difference is statistically significant at the .05 level.

** Difference is statistically significant at the .01 level.

Table 2.--*Duncan's multiple range tests comparing means of three groups for nine traits in four loblolly pine progeny test plantations in Georgia*

Group	Plantation 69	75	76	77
		HEIGHT, m		
Clonal progenies	14.3 a[a/]	13.6 a	15.0 a	14.8 a
Seed production area lot	14.2 a	13.0 a	14.7 a	14.8 ab
Commercial check lots	14.1 a	13.3 a	14.4 a	14.0 b
		DBH, cm		
Clonal progenies	21.3 a	23.7 a	20.2 a	19.3 a
Seed production area lot	20.5 a	21.3 a	19.8 a	19.8 a
Commercial check lots	21.2 a	23.5 a	20.0 a	18.3 a
		TREE VOLUME, m^3		
Clonal progenies	0.21 a	0.21 a	0.18 a	0.16 a
Seed production area lot	.19 a	.15 b	.16 a	.16 a
Commercial check lots	.20 a	.20 ab	.16 a	.13 a
		PLOT VOLUME, m^3		
Clonal progenies	2.54 a	0.34 a	2.24 a	0.46 a
Seed production area lot	2.39 a	.17 a	2.28 a	.41 a
Commercial check lots	2.66 a	.20 a	2.09 a	.39 a
		GALLS/TREE, $\sqrt{X + .5}$		
Clonal progenies	2.1 a	2.1 b	2.4 a	2.8 a
Seed production area lot	2.0 a	1.5 a	2.5 a	3.1 a
Commercial check lots	2.1 a	2.4 b	2.4 a	3.0 a
		TREES RUST-FREE, ARCSIN $\sqrt{\text{percent}}$		
Clonal progenies	8.8 a	--	9.1 a	--
Seed production area lot	14.3 a	--	7.9 a	--
Commercial check lots	9.8 a	--	5.7 a	--
		STRAIGHTNESS INDEX		
Clonal progenies	2.8 a	3.4 a	3.4 a	3.2 a
Seed production area lot	3.0 ab	3.7 a	3.8 b	3.5 a
Commercial check lots	3.2 b	3.4 a	3.6 ab	3.5 a
		CROWN/HEIGHT RATIO		
Clonal progenies	52.6 a	44.1 a	52.7 a	56.6 a
Seed production area lot	55.1 b	44.7 a	53.8 a	59.7 a
Commercial check lots	54.2 b	47.7 a	53.1 a	58.2 a
		SURVIVAL, ARCSIN $\sqrt{\text{percent}}$		
Clonal progenies	58.5 a	34.7 a	46.9 a	51.5 a
Seed production area lot	62.0 a	27.6 a	49.0 a	46.2 a
Commercial check lots	61.3 a	25.9 a	45.8 a	52.8 a

[a/] Within plantations, group means followed by the same letter are not significantly different at the .05 level.

Table 3.--*Rank comparisons (1 = best) of three groups for nine traits in four loblolly pine progeny test plantations in Georgia*

Group	Plantation 69	75	76	77
		HEIGHT		
Clonal progenies	1	1	1	1
Seed production area lot	2	3	2	2
Commercial check lots	3	2	3	3
		DBH		
Clonal progenies	1	1	1	2
Seed production area lot	3	3	3	1
Commercial check lots	2	2	2	3
		TREE VOLUME		
Clonal progenies	1	1	1	1
Seed production area lot	3	3	3	2
Commercial check lot	2	2	2	3
		PLOT VOLUME		
Clonal progenies	2	1	2	1
Seed production area lot	3	3	1	2
Commercial check lots	1	2	3	3
		GALLS/TREE		
Clonal progenies	3	2	2	1
Seed production area lot	1	1	3	3
Commercial check lots	2	3	1	2
		TREES FREE OF RUST		
Clonal progenies	3	--	1	--
Seed production area lot	1	--	2	--
Commercial check lots	2	--	3	--
		STRAIGHTNESS		
Clonal progenies	1	2	1	1
Seed production area lot	2	3	3	2
Commercial check lots	3	1	2	3
		CROWN/HEIGHT RATIO		
Clonal progenies	1	1	1	1
Seed production area lot	3	2	3	3
Commercial check lots	2	3	2	2
		SURVIVAL		
Clonal progenies	3	1	2	2
Seed production area lot	1	2	1	3
Commercial check lots	2	3	3	1

Table 4.--*Sums of ranks, their expected values, deviations from expected and Chi-squares for each group in each of four plantations in an interaction Chi-square test for goodness of fit* [a/]

Group	69	75	76	77	Totals	d.f.
1. Clonal progenies:						
Observed	16	10	12	10	48	
Expected	9	8	9	8	34	
Deviations	+7	+2	+3	+2	+14	
Chi-square	5.44*	.50	1.00	.50	7.44ns	3
Heterogeneity χ^2					1.68ns	2
2. Seed production area lot:						
Observed	19	20	21	18	78	
Expected	18	16	18	16	68	
Deviations	+1	+4	+3	+2	+10	
Chi-square	.06	1.00	.50	.25	1.81ns	3
Heterogeneity χ^2					.34ns	2
3. Check lots:						
Observed	19	18	21	20	78	
Expected	27	24	27	24	102	
Deviations	-8	-6	-6	-4	-24	
Chi-square	2.37	1.50	1.33	.67	5.87ns	3
Heterogeneity χ^2					.22ns	2
Totals:						
Observed	54	48	54	48	204	
Expected	54	48	54	48	204	

[a/] Total Chi-square = 15.12ns at 4(3-1) = 8 d.f.

* Difference is statistically significant at the 0.05 level.

ns Difference is not statistically significant at the 0.05 level.

The means of all trait ranks for each group in each plantation are listed in Table 5. These averages are then themselves ranked for the three groups in each plantation; these ranks are listed in parentheses. There are ties in Plantations 69 and 76 for the second and third ranks. This non-parametric 2-way ANOVA of ranks obtained a Chi-square = 6.00, which is significant at the .05 level with 2 degrees of freedom. This method, called Friedman's procedure, is a randomized complete-block design in which we have treated the four plantations as replications. Since the rank totals for Groups 1, 2 and 3 are 4.0, 10.0 and 10.0 respectively, it seems legitimate to conclude that the clonal progenies perform better for most traits than do the SPA or commercial check lots. We may also conclude that we can find no significant difference between the SPA lot and the commercial checks.

We should caution that Group 2, the SPA lot, is the least well replicated group in each plantation. If these tests had been planned to detect real differences among groups, more than one SPA lot would have been included, together with controls from stands adjacent to each SPA lot. One SPA lot can not sample the stand variation which has been shown to exist in Georgia (La Farge 1974).

The relative performances of the three groups for specific traits are also of interest. Group 1, the clonal progenies, performs most predictably for the growth traits (height, dbh and tree volume), and least predictably for traits measuring incidence of fusiform rust (galls/tree, percentage of trees free of rust). Survival is also unpredictable because in these tests it is largely a function of incidence of rust. Similarly, plot volume seems less consistent in its rankings than tree volume because it is partly a function of survival. Generally, the progeny testing of GFC clones has not shown the selection of rust-free phenotypes in natural stands to be very successful. Probably many of the ortets scored as rust-free had in fact lost branch galls through natural pruning.

The results in this study are consistent with those of the Texas Forest Service Tree Improvement Program (1962), in which the SPA seedlings had poorer height and diameter growth than the commercial control. However, they do not agree with results reported by Easley (1963), in which the SPA lot dramatically outgrew the nursery run stock on both clay and sandy sites. Since this study did not compare the SPA lot with any controls from stands adjacent to the seed production area, our results are not comparable with those of Gansel (1967), who reported slight but nonsignificant gains of a seed production area over an adjacent stand control.

CONCLUSIONS

The results of this study have very limited application. They tell us more about the selection of superior phenotypes for clonal seed orchards than they do about SPA selections. They suggest limited but acceptable gains for selection of plus trees in natural stands for inclusion in clonal seed orchards. However, they do not prove, nor do they disprove, the potential genetic gains obtainable in seed production areas. More sensitive field tests are needed to make such evaluations. Until then, seed production areas represent good forestry practice.

Table 5.--*Means of ranks in all traits of each group in each plantation, and ranks of the means in each plantation (in parentheses), Friedman's test for differences among groups* [a/]

Group	Plantation 69	75	76	77	Rank totals
1. Clonal progenies	1.78 (1.0)	1.25 (1.0)	1.33 (1.0)	1.25 (1.0)	5.61 (4.0)
2. Seed production area lot	2.11 (2.5)	2.50 (3.0)	2.33 (2.5)	2.25 (2.0)	9.19 (10.0)
3. Check lots	2.11 (2.5)	2.25 (2.0)	2.33 (2.5)	2.50 (3.0)	9.19 (10.0)

a/ Chi-square = $\frac{(12(4.0^2 + 10.0^2 + 10.0^2)) - 4x3(3 + 1)}{4x3(3 + 1)}$

= 6.00* at 2 d.f.

* Difference is statistically significant at the 0.05 level.

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MASS VEGETATIVE PROPAGATION OF LOBLOLLY PINE -- A REEVALUATION OF DIRECTION

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Abstract.--The problems that will be encountered in producing plantable seedlings from vegetative cultures promise to be significant. At best, systems to handle this material from tissue cultures to rooting medium to seedling nursery (or greenhouse) will be expensive.

Rooted cuttings offer an alternative method of vegetative propagation for which we envision a system of production that would require little new technology. "Cutting orchards" also compare favorably with seed orchards on a propagule per acre basis, and may be less costly to operate.

The promise of a system for economically producing operational numbers of vegetative propagules justifies a more intensive effort in trying to develop a reliable technique for rooting loblolly pine cuttings.

INTRODUCTION

The potential for increased genetic gains through the use of vegetative propagation has been demonstrated for many forest tree species. Bypassing sexual recombination allows both general and specific combining ability to be "captured" in production plantings. For loblolly pine (*Pinus taeda* L.), in particular, an additional 5% to 10% gain in growth could probably be made if mass production of superior genotypes via vegetative propagation was possible.

Historically, most emphasis in vegetative propagation has been placed on rooted cuttings. To date, there has been very limited success with rooting southern pine cuttings (Hare 1974, van Buijtenen *et al.* 1975, Greenwood *et al.* 1980). Only juvenile material (usually less than 4-6 years old) has been rooted with a reasonably high degree of success. Research emphasis has shifted to tissue culture because some researchers feel this may avoid problems of decreased rooting and growth potential related to vegetative propagation of more mature tissues in meristems. There is little doubt that tissue culture of loblolly pine will soon be possible. However, providing the large numbers of plants needed for forest regeneration will require more than the ability to do vegetative propagation. Efficient systems for producing and growing vegetative propagules must also be developed. Considerable time and effort will probably be required to research and develop systems that will produce large numbers of tissue culture plantlets economically. It may be possible to develop a system to produce large numbers of rooted loblolly pine cuttings much sooner. If so, it should be implemented to provide vegetative propagules for forest regeneration until economical tissue culture systems can be developed.

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STATUS OF TISSUE CULTURE RESEARCH

Tissue culture methodology for production of loblolly pine planting stock is still in its infancy. Research to achieve mass propagation of loblolly pine has been in progress for several years, but operational use of tissue culture is still in the future. Three basic methods of multiplication *in vitro* have been proposed for forest trees and some horticultural crops (Murashige 1977, Minocha 1980):

1. Somatic cell embryogenesis -Somatic embryos are organized structures which are essentially identical to embryos from zygotes. They will germinate in culture and develop into seedling-sized plants.

2. Adventitious shoots and buds -Organogenesis of shoots and buds can develop from excised plant parts or from callus cultures. When shoots form, they can then be rooted.

3. Enhancing axillary and apical buds to produce shoots. Miniature branches are excised from plants *in vitro* and are later rooted. This is often called micropropagation.

There are certain advantages to each of the three methods. Embryogenesis and organogenesis have been proposed as the most likely methods to use for mass production of trees. Virtually unlimited numbers of trees could be propagated in a very small area in a short period of time. For example, with embryogenesis in cultures of carrots, yields of 500 embryos per gram of callus per month have been achieved (Murashige 1977).

Micropropagation (best described as miniature rooted cuttings) has the broadest applicability among most plant genera. Virtually all commercial applications of tissue culture technology in horticultural crop species employ micropropagation (Boxus and Druart 1980, Murashige 1978). The greatest success has been commercial propagation of orchids through apical and axillary shoot cultures (Murashige 1974). Some researchers (Thompson and Gordon 1977, Minocha 1980, Banga 1974) have proposed microprogation as a technique for large-scale production of forest trees.

The basic problem with micropropagation methods for reforestation is their inefficiency. Micropropagation is very labor intensive, requiring a great deal of handling at each stage of plantlet development. Only species which have a relatively high per plant value such as orchids, ferns, and fruit trees have potential for use in this method. For most forest species, the initial value of an individual seedling is a few cents.

Many people who are not familiar with tissue culture techniques suggest using horticultural tissue culture methods as models for plantlet production systems of forest trees. Unfortunately, forest regeneration requires that millions of trees, not just a few thousand, be produced each year. Micropropagation currently appears to be feasible only on a relatively small scale to mass produce vegetative propagules of forest trees.

Callus and cell suspension cultures which utilize embryogenesis or organogenesis as a propagation method are the most feasible tissue culture methods for forest trees. Growing trees from single cells or small groups of

cells allows for very large-scale production. The critical limitation of this technology will be the development of radically different engineering systems for producing propagules so that producing plantlets in very large numbers will not be extremely labor-intensive. Innovative laboratory, greenhouse, and nursery procedures must be developed before tissue culture propagation of large numbers of trees becomes a reality.

STATUS OF ROOTED CUTTING RESEARCH

Experimental techniques for rooting southern pine cuttings with rigorous environmental control (Hare 1974) have been adapted to root relatively large numbers of loblolly pine stem cuttings with considerable consistency. Cuttings from 1-year-old loblolly and slash pine (Pinus elliotti var. elliotti) have consistently been rooted with about 50% success (van Buijtenen et al. 1975). Furthermore, rigorous control of the rooting environment promises to improve the success of rooting larger numbers of cuttings. The amount of mist applied was a critical factor in rooting cuttings from 4-year-old loblolly pine in one experiment where the best treatment had 64% rooted cuttings (Greenwood et al. 1980).

Unfortunately, the rooting success and subsequent growth rate of loblolly pines declines with increasing age of ortet (McAlpine and Jackson 1959, and Greenwood 1981). This is an important problem since the optimum genetic selection age for loblolly pine seems to be greater than ages at which loblolly pine cuttings can be rooted with consistency. For example, the optimum genetic selection ages for rotation ages of 30 and 40 years was 6 and 8 years, respectively (Lambeth 1980). If selection is at an age when rooting success and growth have declined, the benefits from vegetative propagation may be lost. Fortunately, work with other species of pines has shown that the decline in rootability and growth of propagules can be arrested, i.e. juvenility can be maintained. Hedging Pinus radiata D. Don. slows the maturation effects on rootability (Libby et al. 1972). Micropropagation of brachyblasts (short shoots of needle fascicles) that are just beginning to elongate "rejuvenates" Pinus pinaster Ait. (Franclet 1979). The most important priority for rooted cutting research with loblolly pine is to test these techniques to determine whether they will arrest maturation or "rejuvenate" mature genotypes.

Genetic variation in rooting ability of loblolly pine must be considered in developing a vegetative propagation system. Rooting percentages of clones from 4-year-old loblolly pines ranged from 0 to 100 percent (Foster 1978). Selection for rooting ability could be combined with selection for growth to choose clones which are superior for both traits.

Rooting loblolly pine is possible now. If systems are developed to "rejuvenate" or slow the maturation of older material, and if efficient systems for producing large numbers of propagules are developed, the use of rooted cuttings may be a practical method of operational vegetative propagation.

Producing rooted cuttings for field planting can be broken down into two phases: 1) producing cuttings, and 2) rooting and growing cuttings to a plantable size. We conceived a model for a cutting orchard to see if large numbers of cuttings could be produced on a reasonable land area and compared our model to a mature seed orchard to get an idea of comparative efficiency.

Operational procedures for rooting and growing Norway Spruce (Picea abies (L.) Karst.) cuttings were used as a model for the second phase.

A Model for a Loblolly Pine Cutting Orchard

Dimensions of hedges and numbers of cuttings per hedge were determined from six ornamental hedges of loblolly pine growing in a yard in Hot Springs, Arkansas (Foster and Bridgwater 1978). The trees were 11-years-old and had been pruned annually in June for the previous nine years. This treatment produced hedges that averaged 1.60 meters (m) tall with a somewhat circular and flat top, averaging 1.64 m^2 in area (Table 1). In May, 1977, the total number of stem tips was counted on each hedge. Since the optimum size for a loblolly cutting had not been determined, every branch tip at least 2.5 cm long was counted. An average of 653 stem tips were growing on the top surface of each hedge or 413 stem tips per square meter of hedge top (Table 1). The numbers of potential cuttings growing from the sides of the hedges were neglible and therefore, not counted.

Table 1.--Tree dimensions and numbers of stem tips on 6 ornamental hedges of loblolly pine

Variable	Average of 6 hedges	Minimum	Maximum
Total Height	1.63 (m)	1.50	1.75
Diameter of Top	1.42 (m)	0.93	1.73
Surface Area of Top	1.64 (m^2)	0.68	2.35
Number of Stem Tips			
$\geq$ 2.5 cm on the Top	653	309	1253
Number of Stem Tips			
per M^2	413	259	623

(After Foster and Bridgwater 1978)

One acre (0.41 ha) section of cutting orchard, illustrated in Figure 1, can be extended to any number of hectares or clones. Our illustration has 18 rows of continuous hedges, each with 63 plants whose tops are about 1 m wide. Thus, there are 1144.8 m^2 hedges per acre (0.41 ha) of cutting orchard in our model. The tops of adjacent plants will join to give one continuous surface for each row; and would be maintained at a height to faciliate management. This configuration would seem to lend itself to the development of mechanical

and harvesting systems. A distance of 2.5 m (just over 8 ft.) was left between rows of hedges for the passage of equipment.

We assumed that 300 stem tips (75% of the 400 average) would be suitable for rooting. Even this reduced number may be optimistic since loblolly pine cuttings 10 to 15 cm (4 to 6 in) long are used by van Buijtenen et al. (1975). Only 129 acceptable cuttings were produced per square meter of hedge after hedging P. radiata for 3 years (Libby et al. 1972). However, the number of cuttings suitable for rooting may be increased by cultural treatments such as fertilization and irrigation and if more than one crop of cuttings can be harvested per year.

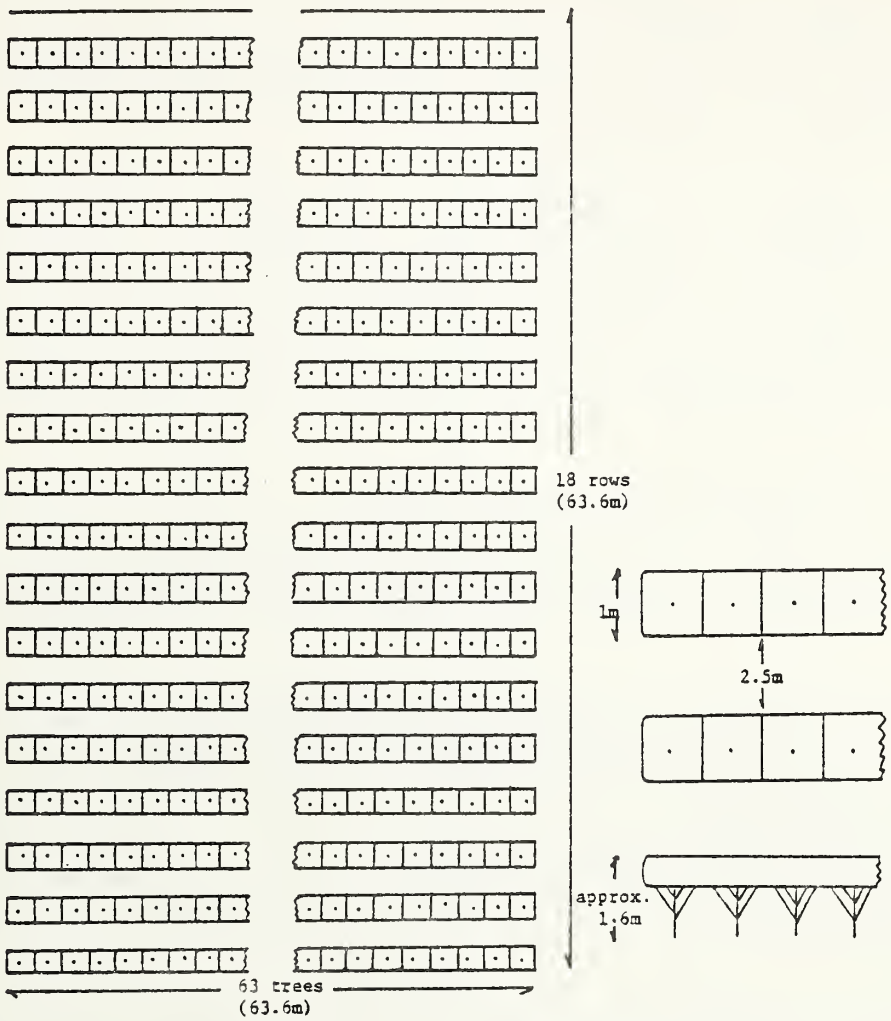

Figure 1.--Diagram of a 1 acre (0.41 ha) section of a cutting orchard to mass produce stem cuttings of loblolly pine. (after Foster and Bridgwater 1978)

We assumed that at least 64% rooting, the best reported by Greenwood et al. (1980), can be consistently achieved. Experience from other of our rooting trials with loblolly pine has shown that about 85% of cuttings which rooted will survive through their hardening-off period until they are outplanted.

The number of plantable cuttings per acre (0.41 ha) of orchard is the product of:

1) The area of hedges per acre (1144.8 m^2);
2) The number of suitable cuttings per square meter of hedge (300);
3) Rooting success (64%);
4) Survival after a hardening-off period (85%).

Over 186,000 propagules per acre of orchard will be produced if our assumptions are met. This is about the same as a loblolly pine seed orchard producing 30 lbs. (13.5 kg.) of seed per acre (0.41 ha) from which 6,200 plantable seedlings are realized per pound (0.45 kg.) of seed.

Yield estimates for both seed orchards and cutting orchards are conservative. But we believe our examples show that cutting orchards can compete favorably with seed orchards on the basis of the number of outplants produced per hectare. Furthermore, cutting orchards may be more economical to operate than seed orchards since they will not require working in lift-buckets as in mature loblolly pine seed orchards, and will better lend themselves to mechanization, should require a shorter time to reach full production, and should have less annual fluctuation in numbers of propagules.

Rooting and Growing Large Numbers of Cuttings

Developing systems to produce large numbers of rooted cuttings for outplanting will mean "scaling-up" the system for producing a few thousand propagules described by van Buijtenen et al. (1975). This system includes:

1) treating cuttings with hormones (usually IBA) to enhance rooting,
2) extending natural daylengths with artifical lighting,
3) controlling ambient air temperatures within 20°-25° C,
4) bottom heating,
5) carbon dioxide enrichment,
6) humidity control (usually by misting),
7) a "hardening-off" period before field planting to reduce planting shock.

Similar systems employing plastic greenhouses for environmental control have been used to produce large numbers of rooted cuttings of Norway Spruce for operational outplanting in Germany for the last decade (Kleinschmit and Schmidt 1977) and in Finland since the mid-1970's (Lepisto 1974). Trials should be initiated to adapt available techniques to systems for producing large numbers of loblolly pine rooted cuttings.

COST CONSIDERATIONS

Loblolly pine seed orchard and nursery management has been refined to the extent that high-quality seedlings can be reliably produced at a low cost per plant. Systems for vegetative propagation are not well developed and undoubtedly will be more costly than for seedlings. These costs must be minimized so they do not negate the returns from increased genetic gains from vegetatively produced stands of selected genotypes. Estimating the costs for producing large numbers of vegetative propagules will require more specific information about systems than is available at present. Therefore, we estimated the amount that might be spent on vegetative propagation under different sets of assumptions (Table 2).

Table 2. Present value of genetic gains from vegetative propagation under different set of assumptions.[1/]

Stumpage Price and Rotation	Planting Density[2/] in trees/acre	10% Discount Rate Improved Growth Rate 10%	15%	25%	5% Discount Rate Improved Growth Rate 10%	15%	25%
	681	0.5¢	0.8¢	1.3¢	1.6¢	2.4¢	4.1¢
$10/cord @ 25 years[3/]	538	0.6	1.0	1.6	2.1	3.1	5.1
	436	0.8	1.2	2.0	2.5	3.8	6.4
	681	1.3¢	2.0¢	3.3¢	5.4¢	8.0¢	13.4¢
$35/cord @ 30 years[3/]	538	1.7	2.5	4.2	6.8	10.2	16.9
	436	2.1	3.1	5.2	8.4	12.5	20.9
	681	2.5¢	3.8¢	6.3¢	10.2¢	15.3¢	25.5¢
$50/cord @ 30 years[4/]	538	3.2	4.8	8.0	12.9	19.4	32.3
for S.I. 90+ land	436	3.9	5.9	10.0	15.9	23.9	39.8

[1/] Value indicates how much additional can be spent for a single plantable propagule to realize the indicated genetic gain and realize a given rate of return on the investment over and above inflation.

[2/] Spacing levels are: 8' x 8' = 681 trees per acre
9' x 9' = 538 trees per acre
10' x 10' = 436 trees per acre

[3/] Assumes unimproved growth rate of 1.5 cords/acre/year

[4/] Assumes unimproved growth rate of 2.0 cords/acre/year (only for best sites of Site Index 90+). (After McKeand 1981).

The per plant present value of genetic gains realized at harvest varied from 0.5¢ to almost 40¢ per tree with different assumptions. These values apply to vegetative propagules derived from tissue culture or rooting cuttings. Loblolly pine seedlings can be purchased in the southeastern U. S. for about 1.5 ¢ each ($15/M). If costs for mass vegetative propagation are 3 times that for seedlings as for Norway spruce (Kleinschmit and Schmidt 1977) then the present value in Table 2 must exceed 3.0¢ per plant to recoup this additional cost of vegetative propagation. Present values exceeding 3.0¢ require higher stumpage prices to make vegetative propagation profitable, particularly for lower levels of genetic gain and a 10% discount rate. Unless the cost differential between seedlings and vegetative propagules is less than 3.0¢ per tree then vegetative propagules will probably be used only to regenerate high site index lands and for rotation lengths that will produce larger, more valuable trees.

SUMMARY

Techniques for vegetative propagation of loblolly pine by tissue culture are not known. Once known, innovative techniques for producing the very large numbers required for operational regeneration will take additional time to develop. Techniques for rooting loblolly pine stem cuttings are known, but need refinement and "scaling-up" to produce the numbers required. A model for a loblolly pine cutting orchard was proposed which compared favorably to a mature seed orchard with regard to the number of outplants produced per hectare of orchard.

The development of systems to produce large numbers of rooted cuttings of loblolly pine should receive more emphasis. Rooted cuttings offer a way to realize the benefits from vegetative propagation until tissue culture systems are perfected.

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SPECIFIC GRAVITY AS A SELECTION CRITERION IN SYCAMORE

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Abstract.--Specific gravity, fiber length, and fiber, vessel and ray volumes were measured at DBH in the second growth ring of coppiced sycamore (Platanus occidentalis L.) from a progeny test in the Georgia Piedmont. From these measurements, the means, phenotypic standard deviations, heritabilities and genetic correlations were determined to estimate the effects of selection for high specific gravity on sycamore wood properties. Results indicate that substantial gain in specific gravity could be made by mass selection in the progeny test accompanied by increases in ray and fiber content and decreases in vessel content. Changes in tissue proportions are probably too small to seriously affect pulping characteristics of the wood. Fiber length would be virtually unchanged by selection for specific gravity.

Additional keywords: Platanus occidentalis, heritability, genetic correlation, fiber length, fiber volume, vessel volume, ray volume.

INTRODUCTION

In recent years there has been an upsurge in the planting of hardwoods for utilization as pulp and as a possible source of fuel. Sycamore is one species being given considerable attention because of its fast growth rate and coppicing ability.

With large scale planting genetic improvement for biomass production becomes justified. Results from a Georgia Piedmont indicate that moderate genetic gains are possible by selecting for volume and high specific gravity. (Webb et. al., 1973).

Selection for specific gravity may be accompanied by changes in the anatomical characteristics of wood. In hardwoods, this is because the major tissues of the wood, rays, vessels and fibers differ greatly in their specific gravities (Taylor, 1969a). Increases in ray and fiber volumes and decreases in vessel volume are associated with increases in specific gravity. (Taylor, 1969b; Taylor and Wooten, 1973). On a phenotypic basis, variation in sycamore specific gravity is due more to differences in relative tissue volumes than thickness of fiber walls. This is in contrast to southern pines where increases in specific gravity are associated with increases in tracheid wall thickness (Van Buijtenen et. al., 1968).

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If the relationship between specific gravity and tissue proportions is inherited, selection for specific gravity will result in greater ray and fiber and lesser vessel proportions. And, if these changes are large, high specific gravity selections may produce poor quality paper since a high volume of rays and a low volume of vessels may be detrimental (Horn, 1978; Marton and Agarwal, 1969).

It is the purpose of this study to determine what changes in wood properties can be expected from selection for high specific gravity in sycamore, and, if these changes are likely to affect paper properties.

MATERIALS AND METHODS

Plantation Site, Design, and Treatment.--The progeny test used in this experiment is located on the Oconee River bottom near Scull Shoals in Greene County in the Georgia Piedmont. It consists of 64 wind-pollinated families of sycamore from the Greene and adjacent, Clarke and Oglethorpe Counties. Plantation design was randomized complete block with six replicates and four-tree square plots. Spacing was 1.25m x 1.25m (4 x 4 feet).

The trees were planted as 1-0 seedlings in March, 1968, and the shoots harvested in the winter of 1971 (Webb et. al., 1973). Samples for this research were taken from the subsequent coppice growth.

Sample Selection.--Twenty-four families were chosen at random from the forty-six in which at least two trees survived in each replication. Two trees were then randomly selected within each. Since multiple sprouts were often present, the sprout displaying height dominance was selected for sampling.

Measurements.--The wood samples were stem segments taken at a height of 4.5 ft. The second growth ring of each segment was used for all measurements of proportionate tissue volumes, fiber length, and specific gravity. Proportionate tissue volume was estimated utilizing a Leitz six-spindle integrating stage according to the method outlined by Smith (1967) and percentage volumes for rays, fibers, and vessels were calculated. Fiber length was measured by projecting macerated fiber onto a sampling grid. Specific gravity was determined as oven dry weight divided by green volume determined by immersion.

Statistical Analysis

Each trait was subjected to analysis of variance to determine if family effects were significant and to estimate variance components for heritability calculations. Analysis of the randomized complete block design indicated no replicate effects. The data was then reanalyzed using the completely randomized model:

$$\text{measured character} = \text{mean} + \text{family effect} + \text{error}.$$

An analysis of covariance was performed according to Becker (1975) in order to estimate genetic correlation between each pair of traits.

Phenotypic correlations were also calculated.

RESULTS AND DISCUSSION

Phenotypic and genetic parameters.--The phenotypic population parameters of wood properties measured in the Scull Shoals progeny test are presented in Table 1. In general the mean values are similar to those reported from other populations. For specific gravity the average of 0.40 compares favorably to 0.41 in wood of similar age from natural Mississippi stands (Schmitt and Wilcox, 1968) and another Georgia Piedmont stand (Saucier and Ike, 1969). Likewise at a comparable height and age similar fiber lengths were found in Mississippi trees (Taylor and Wooten, 1973) and the Schull Shoals trees.

Table 1.--Means, phenotypic standard deviations and coefficients of variation (CV) of wood properties from Scull Shoals progeny test.

Trait[1/]	$\bar{X}$	σ_P	CV
Specific Gravity	.40	.02	.05
Ray Volume (%)	11.1	1.55	.14
Vessel Volume (%)	32.2	3.29	.10
Fiber Volume (%)	53.4	3.34	.06
Fiber Length (MM)	1.55	.05	.03

[1/] Volumes are percent of total wood volume.

Ray, vessel and fiber volumes reported in Table 1 are precent of total wood volume. The sum of these volumes averages 96.7%. The remainder is primarily axial parenchyma. Other studies of wood tissue volumes have shown somewhat higher proportions of ray volumes than our 11.1%; Saucier and Ike (1969) reported 25%, Taylor (1976) 19%, and Myer (1922) 19%. These higher values may be attributed, in part, to inclusion of axial parenchyma in their ray volume fractions. Vessel and fiber volumes were similar between this and the other studies.

Variability for each wood trait is presented in terms of phenotypic standard deviation and coefficient of variation. By either expression it is apparent that wood tissue volumes exhibit a large amount of variation compared to specific gravity or fiber length. Schmitt and Wilcox (1969) concluded that selection for fiber length was not merited because of insufficient variation. On the other hand, they and Lee (1972) suggested that selection for specific gravity might be profitable.

Although specific gravity and fiber length were less variable than the tissue volumes, they were more highly heritable (Table 2). In fact, the calculated heritabilities for specific gravity and fiber length were greater than one. This may be due to the fact that individuals in a family could be more closely related than half-sibs as was assumed in the calculation. This is probable since families represent open pollinated collections from mother trees in several natural stands. The high heritabilities may also occur because of imprecise variance estimates. This is indicated by the widths of the 95% confidence intervals

(Table 2). Confidence intervals presented here have been truncated at 1.00 and 0.00 since we have no confidence that heritabilities fall outside this range. All traits are considered to have a significant genetic component ($h^2 > 0$) since family means were statistically significantly different for each trait (Table 3).

Table 2.--Single tree heritabilities for wood properties.

Trait[1/]	H^2	H^2 95% CI
Specific Gravity	1.10	.59-1.00
Ray Volume	.67	.29-1.00
Vessel Volume	.35	.07- .86
Fiber Volume	.21	.00- .66
Fiber Length	1.40	.87-1.00

1/ Volumes are percent of total wood volume.

Table 3.--Family F values for wood properties.

Traits	"F" ratios for families
Ray Volume	3.42**
Fiber Volume	1.67*
Vessel Volume	2.14**
Specific Gravity	5.41**
Fiber Length	7.66**

* significant at $\alpha = .05$
** significant at $\alpha = .01$

Ray and fiber volumes have strong positive correlations and should increase with selection for high specific gravity. Conversely, vessel volume is negatively correlated and will decrease with selection for high specific gravity. Fiber length is poorly correlated with specific gravity (Table 4).

Table 4.--Genetic correlations between specific gravity and other wood properties.

Trait[1/]	Correlation Coefficient[2/]
Ray Volume	+.50
Vessel Volume	-.87
Fiber Volume	+.52
Fiber Length	+.06

1/ Volumes are percent of total wood volume.

2/ Standard errors of the genetic correlations range between .20 and .30.

Selection for high specific gravity.--The progress made by mass selection for high specific gravity in the Scull Shoals progeny test is given by gain = $i\sigma_p h_I^2$ (i = intensity of selection, σ_p = standard deviation of trees in the progeny test and h_I^2 = individual tree heritability calculated in the progeny test). By selecting the thirty trees with the greatest specific gravity from those 1224 surviving individuals, i = 2.4 (Becker, 1975). The genetic gain would be 0.05, or an increase of 12% (Table 5). For this calculation a heritability of 1.00 was assumed.

Table 5.--Response of wood properties to phenotypic selection of the 30 densest trees out of 1224 (I = 2.4).

Trait[1/]	Change from mean	
	Absolute Units	%
Specific Gravity	+.05	+12.0
Ray Volume	+1.52	+13.5
Vessel Volume	-4.06	-12.5
Fiber Volume	+1.91	+ 4.0
Fiber Length (MM)	+0.01	+ 0.5

1/ Volumes are in percent of total wood volume.

In selecting for high specific gravity changes in the tissue volumes are also expected because of their strong genetic correlations with specific gravity (designated r_A). However, the amount of that change is also determined by other factors including selection intensity (i), phenotypic standard deviation of the correlated trait (σ_{py}), square root of the specific gravity heritability (h_x) and square root of the correlated trait heritability (h_y). Together the change in the correlated trait (CR_y) = $i\sigma_{py}h_x h_y r_A$. Selecting 30 trees with the

densest wood would result in increases of ray and fiber volumes by 1.52 and 1.91 percent of wood volume, respectively, at the expense of vessels which drop by 4.06 percent of wood volume. In other terms progeny of the selected trees would have 4% greater fiber volume, 13.5% greater ray volume and 12.5% lesser vessel volume (Table 4).

Fiber length is little affected by genetic selection for specific gravity.

Practical significance.--On the basis of phenotypic variation Schmitt and Wilcox (1969) and Lee (1972) have suggested selection for specific gravity in sycamore, presumably to increase the yield of pulp per unit volume of wood. From our heritability estimates, and those of Webb et. al. (1973), it indeed appears that significant increases in specific gravity and hence pulp yield, could be made by mass selection. (Because of the high heritability family selection has little utility).

Such phenotypic selection would concomitantly result in greater proportions of rays and fibers and less vessel elements. Fiber length would be virtually unaffected, and, unlike pine, it is probable that fiber wall thickness would not be altered since it is poorly correlated with specific gravity. (Taylor, 1976).

Genetic variation in specific gravity, thus, appears to result largely from different proportions of the wood tissue types. The relative proportion of these has been shown to affect the pulping properties of angiospermous wood. Horn (1978) demonstrated that hardwood rays contribute to the fines and that a high percentage of these is detrimental to bursting and tensile strength. In Quercus alba, Betula papyrifera and Populus fibers were shown to make stronger paper than vessels, but whole pulp produced the best result (Marton and Agarwal, 1965). As yet there is too little information to completely define the relationships between tissue volumes and paper properties, but it does not appear that even very strong selection for specific gravity (selection of the best 0.1% of the population) will result in tissue volume changes (ray volume: + 2.1, fiber volume: + 2.7, vessel volume: -5.8 on a % of wood volume basis) that will greatly alter paper properties (Horn, per. comm.).

Maximizing pulp yield from sycamore plantations depends on increasing volume production as well as specific gravity. Heritabilities for growth variables were about 0.3 from four year old trees in this same progeny test (Webb et. al., 1973), indicating that moderate gains can be expected from selection for volume. However, the genetic correlations between growth parameters and specific gravity were negative, about -0.2. Selection for volume or specific gravity alone would result in losses in the other. The most rapid improvement would be made by joint selection or by selection for stem biomass directly. However selection for stem biomass first requires the development of weight yield tables.

Selection for biomass has taken on a new significance with the current interest in sycamore as potential source of fuel. Here, too, producing maximum dry weight per acre is desirable. The same selected genotypes may therefore serve for energy or fiber production.

Limitations of the results.--Strictly speaking this data and the conclusions drawn from them apply only to wood in the second growth ring of once coppiced

sycamore growing in the Scull Shoals progeny test. In addition the heritabilities and hence the predicted gains from selection in this progeny test are somewhat overestimated since the test occurs at only one location (genotype x environment interaction being ignored) and because individuals in a family are more closely related than half-sibs. The results found in this study should be tested in other populations.

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THE EFFECT OF SHADING AND AGE ON THE DRY MATTER DISTRIBUTION IN CLONES AND SEEDLINGS OF AMERICAN SYCAMORE (PLATANUS OCCIDENTALIS L.)

Michael E. McVay and Stanley B. Carpenter

Abstract.-- Half-sib seedlings and cloned seedlings of three genotypes were grown outdoors in shade frames at the University of Kentucky's forest in eastern Kentucky. Shade frames were covered with green shade cloth to provide lighting levels corresponding to 0, 47, 73, and 93% reduction from full sun. Periodically, during the growing season, trees were destructively sampled to determine differences in dry matter distribution. Allometric analysis indicated that as the level of shading increased shoot growth relative to root growth. There were differences in the balance of shoot growth as well as how the balance was attained between clones, age classes of clones, and between cuttings and seedlings.

American sycamore (Platanus occidentalis L.) is one of the largest trees of the eastern deciduous forest biome. It occurs in early seral to climax forest communities (Fowells 1965). In recent years the need for increased biomass and fiber production by various cultural practices (Steinbeck et al. 1972, Steinbeck and Nwoboshi 1980, and Wood et al. 1976) has created interest in this species. In spite of this increased interest there have been few studies of a physiological nature on sycamore to develop criteria for selection and propagation.

Utilization of hardwood cuttings can offer several advantages over planting seedlings. Cuttings lend themselves more readily to machine planting than do setting seedlings. Cuttings can be custom grown to desired sizes, and clonal lines can be multiplied in relatively short time, leading to faster field testing and use of genetically improved stock (Steinbeck and McAlpine 1973).

American sycamore is readily propagated vegetatively by cuttings obtained from young sprouts (Nelson and Martindale 1957). The rapid establishment of a root system is a necessity for the growth of seedlings (Parker 1968) and the need for a rapidly expanding root system is even more crucial for cuttings. The roots must absorb and transport water to meet the high transpirational demands induced by large leaf areas, intense radiation, and substantial vapor density gradients (Pallardy and Kozlowski 1979). This suggests the need for

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a balance between shoot and root growth. Ledig et al. (1970) suggest that this balance is important in understanding the mechanism by which plants adapt to their habitat, and perhaps in explaining variation in dry matter production.

One way to study the balance between shoot and root growth is through an empirical technique known as allometric analysis, which was used extensively by Huxley (1932). According to this mathematical relationship, all genotypes in a given environment grow exponentially during the early stage of development. Therefore, the change in weight of plant per unit time is equal to a constant times the initial weight of the plant. Similarly, a change in weight of any given organ per unit time is equal to a constant times the initial weight of the organ (Ledig and Perry 1965).

Recent attempts have been made to assess the relative growth rates of shoot and root provenances of Populus trichocarpa, Picea sitchensis, and Pinus contorta (Cannell and Willet 1976), Populus deltoides (Drew and Bazzaz 1978), different sources of Pinus taeda (Ledig and Perry 1965, Ledig et al. 1970), different sources of Populus clones (Pallardy and Kozlowski 1979), and different sources of Quercus rubra and Quercus prinus (Immel et al. 1978). The results of these studies indicated little genotypic variation in the balance between shoot and root growth and that the allometric coefficient for shoot and root growth is stable, even over successive years.

In our study, techniques of allometric analysis were employed to study dry matter distribution in half-sib seedlings and 3 clones of American sycamore grown in different levels of shade.

METHODS

Seeds were collected from a single open-pollinated American sycamore tree in late January 1980. During the last week of March 1980, the seeds were germinated and transplanted to 19-liter pots and transferred to the greenhouse on the University of Kentucky campus, where they were watered and fertilized until the first week of May 1980.

Cuttings were obtained from one-year-old coppice sprouts of 3 clones of American sycamore from a previously established clonal bed growing near Noble, Kentucky, on the University of Kentucky's Robinson Forest. Cuttings were taken during the dormant season in early March 1979 and 1980 for 2-year-old and one-year-old clones, respectively. Each cutting, approximately 40 cm long, was treated with a rooting hormone containing IBA and planted in 19-liter pots with at least 1 node above the soil surface. The potted cuttings were then transferred to a misting bed for 1 month. After the mist bed, the cuttings were transferred to a lath-house for 1 month.

During the first week of May 1980, half-sib seedlings and cuttings in their second growing season were transferred to shade frames at the University forest. The shade frames were covered with green saran shade fabric with relative reductions of 47, 73, and 93 percent of full sunlight. One shade frame was left uncovered for a 0 percent reduction of full sunlight. Cuttings in their first growing season remained in full sun for the duration of the study.

The potting medium for seedlings and cuttings was the same and consisted of a 1:1:1 mixture of sand, peat moss, and vermiculite. During the growing season the trees were irrigated regularly to maintain moisture at optimum levels. Fertility levels were maintained by the use of 3-gram 14-4-6 Agriform^{R} container tablets, and approximately once a month a foliar application of iron was applied to each tree.

Three times during the growing season, starting in the first week of June 1980 and at 4 week intervals thereafter, trees were destructively sampled for allometric analysis. The procedure consisted of sampling 3 cuttings of each clone and 3 half-sib seedlings per light treatment per sample date for a total of 57 trees. The trees were divided into leaves, roots, current year's growth, 1-year-old growth, and the original stem. The component parts were oven-dried at 65°C to obtain dry weight production.

A general linear regression model was used to generate the allometric coefficients (slopes and intercepts) and the level of significance for the several models tested. The slope of the regression line was taken to be representative of the balance between shoot and root growth. An analysis of covariance (ANCOVA) was used to test significance of slopes between treatments and clones/seedlings.

RESULTS

Allometric analysis of shoot and root development as influenced by the level of shading revealed little effect on the relative growth between shoot and root (Table 1). Each treatment yielded highly significant linear regressions, including significant slopes and intercepts. The analysis of covariance indicated that only Treatment 3 (47% reduction) with a slope of 0.586 was significantly different from Treatment 5 (93% reduction) with a slope of 0.764 ($P<0.05$). Treatment 1 which represents cuttings in their first growing season grown in full sun (0% reduction) had a slope of 0.439. Although this balance between shoot and root growth is not significantly different from other treatments which include cuttings in their second growing season, and half-sib seedlings exclusively, there was a trend for younger cuttings to partition less dry matter to shoots relative to roots.

A further analysis of shoot development under different levels of shade suggested that it was not increased dry matter allocation to leaf growth that was of primary importance for the observed balance between shoot and root growth. Instead, it seems that increased allocation to stem growth was a more important factor as indicated by the relative magnitude of the slopes for each model tested. For example, Treatment 3 (47% reduction) has a slope of 0.401 for the model $\text{LnLEAF} = \beta_0+\beta_1\text{LnROOT}$ and a slope of 0.948 for the model $\text{LnSTEM0} = \beta_0+\beta_1\text{LnROOT}$. Therefore, for Treatment 3 (47% reduction) a slope of 0.948 which is relatively greater in magnitude than a slope of 0.401 indicates that the balance between shoot and root growth was primarily affected by increased allocation to stem growth. LnLEAF and LnSTEM0 refer to the natural log of leaf dry weight and the natural log of the dry weight of current year's stem growth, respectively. For the model of LnLEAF versus LnROOT analysis of covariance

Table 1. Slopes (β_1) and intercepts (β_0) of several allometric relationships as influenced by light intensity.[1]

Treatment[1]	Age/shade level[2]	LnSHOOT=β_0+β_1LnROOT		LnLEAF=β_0+β_1LnROOT		LnSTEM0=β_0+β_1LnROOT	
		β_0	β_1	β_0	β_1	β_0	β_1
	1st growing season						
1	0%	1.487	0.439	1.272	0.428	-0.273N.S.	0.486
	2nd growing season						
2	0%	1.467	0.690	1.162	0.578	-0.949	1.130
3	47%	1.835	0.586	1.447	0.401	-0.084N.S.	0.948
4	73%	1.813	0.598	1.342	0.498	0.029N.S.	0.830
5	93%	1.384	0.764	0.873	0.725	-0.598	1.169

[1]Regression coefficients for each treatment were significant at the 0.05 level unless followed by N.S.

[2]Percentages correspond to percentage reduction from full sun.

indicated significant differences between slopes for Treatment 2 (0% reduction) and Treatment 3 (47% reduction) and 5 (93% reduction) as well as significant differences between Treatments 3 (47% reduction) and 4 (73% reduction) ($P<0.05$). Significant differences between slopes were also noted for the LnSTEM0 versus LnROOT model. For this model slopes for Treatments 2 (0% reduction and 4 (73% reduction) and Treatment 4 (73% reduction) and 5 (93% reduction) were significantly different ($P<0.05$).

There was some genotypic variation in the relative growth between shoot and root as well as differences that were attributable to differences in age (Table 2). Significant differences between slopes were noted between half-sib seedlings with a slope of 0.756 and clone 2 which had a slope of 0.998. There was also a significant difference between the slope of clone 2 and the slopes of clones 104 and 109 ($P<0.05$).

The effect of age of the cutting on the relative growth between shoot and root is seen as a relative increase in the rate of shoot growth compared to root growth as the cutting ages. Clones 25, 1045, and 1095 are of the same respective genotypes as Clones 2, 104, and 109, and therefore differ only in age. The increase in the relative rate of shoot growth was significant only for Clone 2 which has a slope of 0.328 during its first year of growth and a slope of 0.998 in its second year of growth ($P<005$). Although age differences were not significant for Clones 104 and 109 they exhibited a similar trend when compared to their younger counterparts. A further breakdown of shoot development indicated that for half-sib seedlings and clones in their second growing season the primary factor contributing to the balance of shoot and root growth was increased dry matter allocation to stem growth. For the younger cuttings of Clones 2 and 104 (Clones 25 and 1045, respectively) it appears that increased partitioning of dry matter into stem growth is more important. Clone 1095 followed the same trend as older cuttings and seedlings.

DISCUSSION

Ledig (1976) suggested that a better understanding of what constitutes optimum partitioning of dry matter among plant parts is one of the most important aspects of plant physiology. This requires a more intensive analysis than can be achieved by measuring height or diameter alone. Through more intensive analysis, a better understanding of how various environmental and cultural regimes alter the allocation of dry matter to various plant parts can be achieved. This more intensive analysis is not without problems. In trees, the partitioning of dry matter among various plant parts is difficult due to their large size, which creates sampling problems and impairs the ability to extrapolate from single trees to stands of trees (Kramer and Kozlowski 1979).

When both roots and shoots are growing, the proportion of photosynthate retained by the shoots and translocated to the roots depends on the relative strengths of each of these sinks and their proximity to a carbohydrate source (Kramer and Kozlowski 1979). Environmental factors and cultural practices can shift the balance of dry matter allocation (Lyr and Hoffmann 1967). The vegetative propagation of a woody species requires the rapid development of a large and ramifying root system. In terms of selection and propagation of clonal material, it would be ideal to create an environment that would optimize root growth and then select for rapid root growth.

Table 2. Slopes (β_1) and intercepts (β_0) of several allometric relationships for clones and seedlings of American sycamore.[1]

Plant Type[2]	LnSHOOT=β_0+β_1LnROOT		LnLEAF=β_0+β_1LnROOT		LnSTEMO=β_0+β_1LnROOT	
	β_0	β_1	β_0	β_1	β_0	β_1
SEEDLINGS	1.227	0.756	0.808	0.606	0.239N.S.	0.878
CLONES 2	1.270	0.998	0.993	0.858	-1.200	1.435
104	1.402	0.780	0.802	0.772	-0.654	0.889
109	1.712	0.744	1.192	0.739	-0.182N.S.	0.971
25	1.608	0.328N.S.	1.464	0.353	-0.566N.S.	0.183N.S.
1045	1.706	0.692	1.442	0.639	0.236N.S.	0.99N.S.
1095	1.424	0.564	1.119	0.496	0.123N.S.	0.866

[1]Regression coefficients for each clone were significant at the 0.05 level unless followed by N.S.

[2]Clone numbers ending in 5 refer to cuttings in their first growing season grown in full sun.

Our results indicate that some level of shading is required to get the desired partitioning of dry matter between shoots and roots of American sycamore. The data indicate that a 47 percent reduction in light from full sun (Treatment 3) provided the most favorable balance of growth for optimizing root growth.

The effect of age of the cutting on the allocation of dry matter between shoots and roots can be seen as a relative decrease in the allocation of dry matter to roots (Table 2). So, a young cutting is expending more of its metabolic energy into root growth and, as the cutting ages, there is a shift towards increased allocation of dry matter to shoot growth. This shift in the relative growth of shoot and root probably reflects a move towards a more balanced relationship between absorbing and transpiring surfaces as the tree ages. For seedlings, this shift occurs much earlier in their developmental process as compared to cuttings. This delay in a shift between the relative growth of shoots and roots for cuttings is not unexpected, since initially they have no roots at all whereas seedlings emerge from the seed with differentiated root tissue ready to grow and develop. This ontogenetic sequence is an adaptation (Ledig et al. 1970) which serves to control plant proportions. Of course, there are other adaptations occurring such as leaf morphology and other leaf characteristics which change as the tree grows and develops.

CONCLUSIONS

There seems to be some genetic variability in the balance of shoot and root growth of American sycamore. Furthermore this balance of growth is altered by the level of shading and the age of the cutting. The genetic variability and the relative balance of shoot and root growth afforded by the level of shading can be utilized for successful vegetative propagation and in a selection program. Differences in the balance of shoot and root growth between seedlings and cuttings are a result of the amount and types of differentiated tissue each have at the time of propagation.

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DELINEATING SEED COLLECTION ZONE BASED ON MULTI-PLANTATION PROVENANCE TESTS

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Abstract.-- In a white ash provenance test, height and survival at age three were found to be correlated with the latitude of the seed source. Regression curves can be useful in delineating the seed collection zone for each plantation. Local seed source was the best for Ohio. Southern seed sources grew taller and survived better in Wisconsin. In Illinois, the southern seed sources grew taller but the northern seed source survived better. The contour plot was useful to project suitable seed collection zone over a broad region. Illustrative examples are given in this paper.

Additional keywords: Height growth, survival, white ash, regression, response surface.

The choice of seed sources is one of the most important factors affecting the establishment and productivity of the tree plantation. Provenance studies can be helpful in making the best choice. In the practice of silviculture we either make generalized planting recommendations or specify a certain stand, based upon the results from the progeny test. If the geographic variation is predominantly clinal, generalized seed sources are recommended. For example, Bey (1973) found that using seed sources two hundred miles south of the planting sites to be most desirable. On the other hand, if the geographic variation is predominantly ecotypic, then a specific seed source is recommended. For example, Wright (1976) preferred the Spanish variety of Scotch pine for high quality Christmas trees.

Besides the pattern of geographic variation, another factor that influences the seed source recommendation is the significance of the provenance x plantation interaction. In the absence of this interaction a few superior genotypes may be recommended over a broad area. Conversely, if the interaction is significant, one would select from each test plantation the best seed source for each corresponding planting site.

Other problems related to seed source recommendations are multiple-trait evaluation and general projections from the multiple-plantation provenance test. In this paper I will use a white ash geographic study to illustrate these problems.

MATERIALS AND METHODS

The material used in this paper is part of a provenance/progeny test of white ash initiated in 1975 by the North Central Forest Experiment Station at Carbondale, Illinois. Seed was collected in 1975 and seedlings were grown in a southern Illinois nursery for one year. A total of 22 plantations were established but only four of them with a balanced complete design were used here (table 1).

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Table 1.--White ash outplanting summary

No.	State	County	Lat.	Long.	Cooperator
1	LA	St. Landry	30.4	92.0	John Toliver
7	IL	Union	37.5	89.3	Fan Kung
11	OH	Muskingum	40.0	82.0	Dan Houston
19	WI	Oneida	46.6	89.5	Hans Nienstaedt

Height and survival at age three were recorded. Plantation means of each stand in four plantations were presented in table 2. Results from the analysis of variance (table 3) indicated a strong seed source x plantation interaction. Thus, no single seed source should be recommended for all plantations. In other words, the best seed source should be selected individually for each plantation.

Table 2.--Performance of nineteen stands in four outplantings

Seed source			Height in plantation					Survival in plantation				
State	Stand no.	Lat. deg.	LA	IL	OH (cm)	WI	Mean	LA	IL	OH (%)	WI	Mean
TX	6768	30.3	82	184	151	24	110	91	92	69	18	68
LA	6738	30.5	76	153	117	13	90	67	61	22	20	43
MS	6737	30.8	57	173	130	30	98	66	76	67	40	67
MS	6740	33.4	63	196	131	37	107	83	91	58	31	66
AL	6733	34.5	51	135	134	33	88	76	78	41	56	63
TN	6728	35.3	48	153	157	30	97	95	100	83	65	86
TN	6871	35.5	50	168	143	29	97	88	100	68	72	82
KY	6734	36.9	38	167	162	29	99	81	100	75	60	79
KY	6792	37.3	34	145	183	32	98	84	94	90	80	87
IL	6721	37.7	47	155	182	34	105	89	99	85	71	86
IN	6795	38.3	35	144	180	37	99	84	97	92	85	90
WV	6778	38.9	42	67	157	34	75	61	92	77	60	73
IL	6771	39.0	52	126	214	49	111	96	100	97	96	97
CT	6794	41.3	46	88	155	36	81	71	96	77	85	82
ME	6785	44.9	43	70	125	37	69	84	95	57	73	77
MI	6779	45.2	40	70	147	37	73	68	88	60	64	70
VT	6782	45.4	50	73	187	38	87	56	92	76	68	73
WI	6723	45.7	51	75	164	45	84	64	100	80	88	83
MI	6736	46.6	43	70	141	37	73	63	96	72	73	76
Plantation Ave.			50	127	156	34		78	92	71	63	
Population Ave.							92					76

Table 3.--Analysis of variance for height and survival

Source	df	Height MSQ	Height VC	Height %	Survival MSQ	Survival VC	Survival %
Plantation	3	715805**	3362	72.3	21663**	95	16.1
Seed source	188	11423*	97	2.1	4050**	52	8.8
Interaction	54	7158**	591	12.7	1741**	129	21.9
Residual	768	597	597	12.9	314	314	53.2
Total	843		4647	100.0		590	100.0

*,**, significant at 5% and 1% level, respectively

Since the data in table 2 suggests that clinal variation more appropriately describes the pattern of growth than ecotypic variation, a second degree regression curve based on seed source latitude is used to predict survival and height growth in each of the four plantations.

SEED SOURCE RECOMMENDATION FOR OHIO

In the Ohio plantation the height growth (Ht) and the survival percentage (Su) of the various seed sources can be expressed as a function of the latitude of the seed source (Lat).

Ht = -644.58 + 40.90 Lat - 0.513 Lat*Lat, with r = .60

Su = -506.57 + 29.40 Lat - 0.367 Lat*Lat, with r = .61

The regression curves were plotted in figure 1. Since the peak for height growth and the peak for survival rate coincide with the latitude of the plantation (i.e. 40 degrees north), the seed source recommendation would be simply selection for the local race.

From the shape of the curve it can be seen that using a seed source within two degrees of the latitude of the plantation does not seriously impair the performance. In other words, it is safe to use seed within a 60 mile range of the plantation and still obtain less than a two percent reduction in performance as compared to the local seed source.

SEED SOURCE RECOMMENDATION FOR WISCONSIN

The regression models for height growth and survival based on the latitude of the seed source are Ht = -129.69 + 7.65 Lat - 0.087 Lat*Lat, with r = 0.73, and Su = -736.46 + 39.27 Lat - 0.471 Lat*Lat, with r = 0.88. From these regression curves (figure 2) we find the peak of survival at 42 degrees north while the peak of height growth is at 44 degrees north; both of which are south of the plantation (46.6 degrees north). So for the seed source recommendation in Wisconsin, stands 100 to 150 miles to the south of the plantation offer the greatest growth and survival.

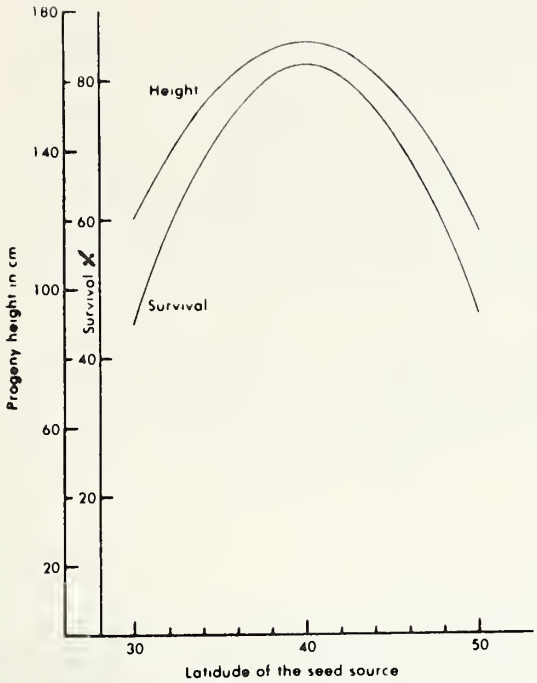

Figure 1. Regression curve for the Ohio plantation

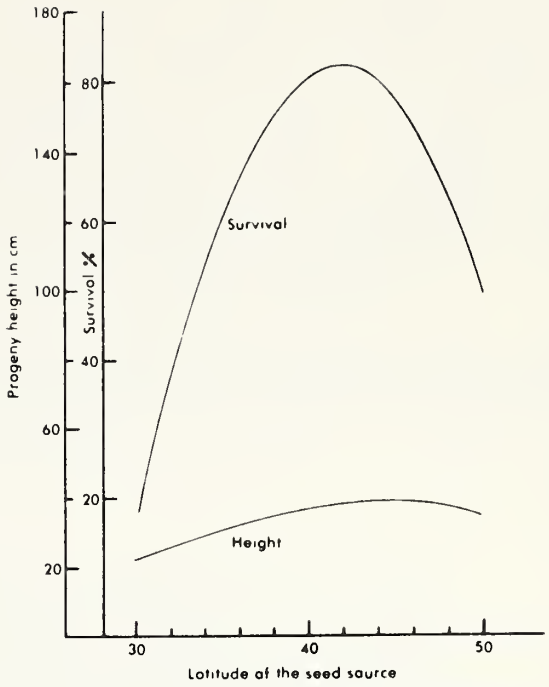

Figure 2 Regression curve for the Wisconsin plantation

SEED SOURCE RECOMMENDATION FOR ILLINOIS

The regression curves for height and survival in the Illinois plantation are Ht = 148.21 + 6.45 Lat - 0.180 Lat*Lat, with r = 0.89, and Su = -235.50 + 16.36 Lat - 0.200 Lat*Lat, with r = 0.69. The peak of survival is at 41 degrees north latitude but the peak of height growth is out of the range in figure 3. Therefore, we can define the best seed source for survival but not for height growth. For survival we can recommend local seed or seed from stands up to 200 miles to the north of the plantation. For height growth it would become a laughing matter if one would recommend the stands at 18 degrees north as the best seed source based on the maximum of the regression formula. No white ash stand has been known to grow at that latitude.

SEED SOURCE RECOMMENDATION FOR LOUISIANA

The regression models for the Louisiana plantation are Ht = 533.45 - 24.07 Lat + 0.293 Lat*Lat, with r = 0.85, and Su = -108.43 + 11.08 Lat - 0.159 Lat*Lat with r = 0.63. While the survival curve is similar to the previous three plantations, the height growth curve has taken an unusual turn. It turns upside-down. Thus, for survival we can recommend local seed or seed from stands up to 250 miles to the north of the plantation. We cannot recommend the best seed source for height. However, from the curve we can see where to avoid seed collection. Trees from 40 degrees north grow slower than others.

MULTI-TRAIT CONSIDERATIONS

When we consider only one trait at a time, a regression curve can be a

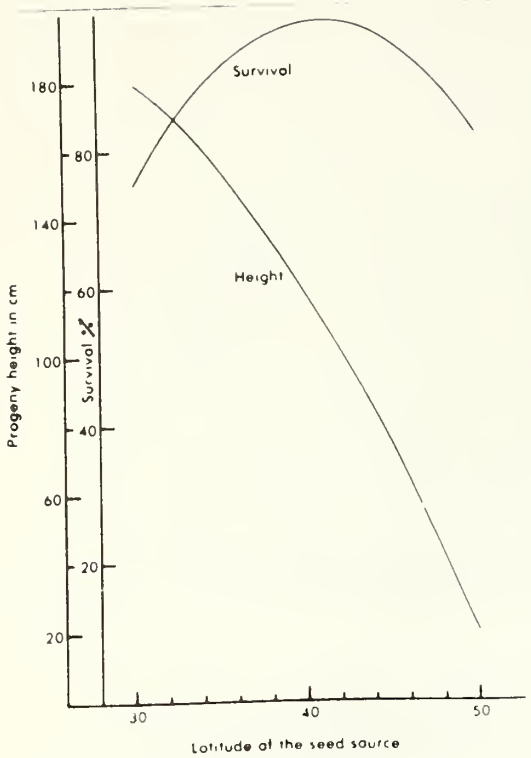

Figure 3 Regression curve for the Illinois plantation

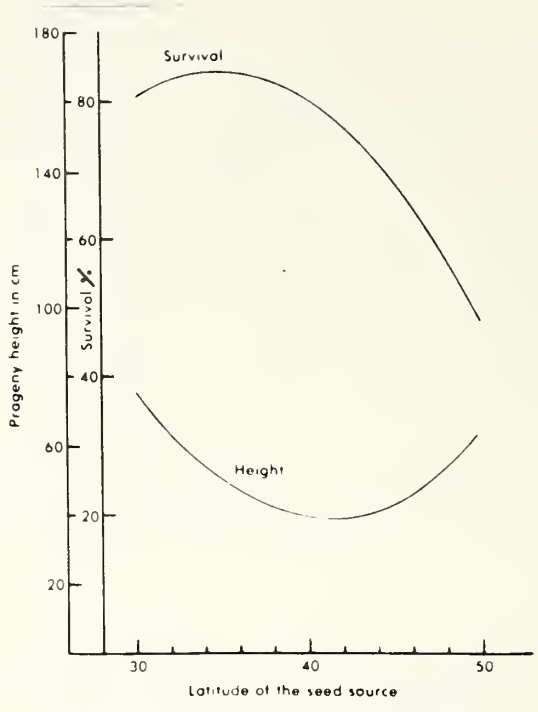

Figure 4 Regression curve for the Louisiana plantation

useful tool to set the range of suitable seed source. If the peak can be found within a reasonable range, such as all the curves for the survival data in this paper, we can define the best seed source or the range of the best seed source. But if the projected peak is out of the natural range of the species, or the curve has a minimum but no maximum, the regression curve would be worthless. Therefore, if we consider several traits simultaneously, each trait must have a usable peak so that the peak of the multivariate observations can become meaningful.

In the case of the Ohio plantation, where the peak for height growth and the peak for survival coincide, the problem of defining seed source for two traits can be reduced simply to that for a single trait. In the case of the Wisconsin plantation where the two peaks differ in location, a single peak can be found by combining two regression formulas into one: W = X(-129.69 + 7.65 Lat - 0.087 Lat*Lat) + Y(-736.46 + 39.27 Lat - 0.471 Lat*Lat), where W is the combined worth of the two trait selection, X is the weight assigned to height growth regression model, and Y is the weight assigned to the survival model. Depending on the value given to X and Y, the peak for W should fall between the peak for X and the peak for Y. Therefore, if we expand this combining method to cover many traits the composite peak must fall within the range of the individual peak for each trait.

PROJECTION OVER A BROAD REGION

As we compared the peaks from the survival curves in the four plantations, we found that the local seed source survived best in Ohio, while the peak shifted to the south in Wisconsin and moved to the north in the Illinois and the

Louisiana plantations. Can we make a general projection of which latitude of seed source can effect the best survival in which latitude of the planting site? I found it to be extremely helpful to use the contour plot techniques (SAS 1979) to study the latitudinal effect of the seed source and that of the planting site. Figure 6 was plotted using the following response surface model: $W = aXX + bXY + cYY + dX + eY + f$, where W = survival percentage, X = latitude of the seed source, Y = latitude of the planting site, and a,b,c,d,e, and f = regression coefficients. The contour plot is constructed in such a way that the darker the area, the higher the survival percentage. It can be easily seen from the contour plot which seed sources are the best for which planting site, and how wide a range of superior seed sources can be used for a given plantation.

For example in figure 5, the seed sources which would give the best survival percentage for a plantation located at 31 degrees of latitude are those from 35 to 39 degrees. As another example, seed sources from 35 to 43 degrees north should be planted between 30 to 41 degrees north.

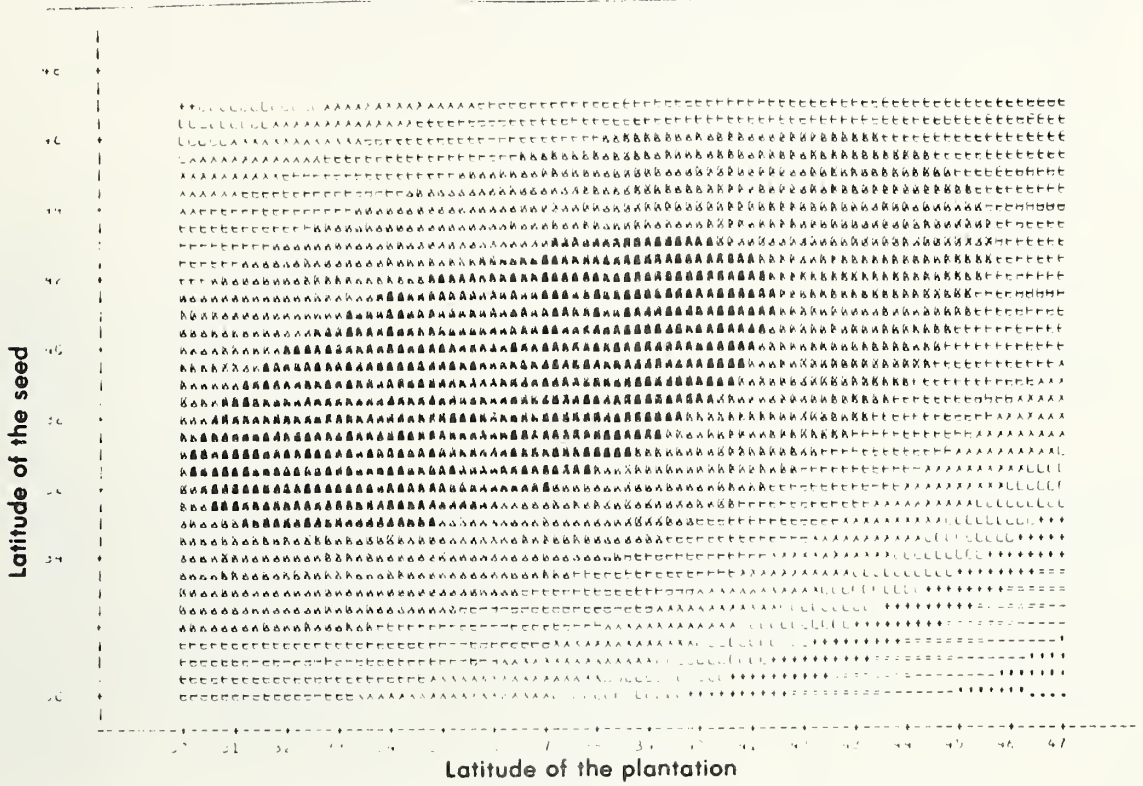

Figure 5. Contour plot for the white ash survival percentage

DISCUSSION

The second degree regression curve is useful to indicate the peak and the range of latitude of the seed source suitable for a specific plantation. The response surface model shows a general view of the seed collection zone over a broad planting range. Although the given examples deal with the latitudinal zoning for white ash, other limiting factors such as longitude, elevation, temperature or moisture zoning may be more suitable for some other species. The primal contribution of this paper is to introduce the readers to the use of regression curve or response surface in seed zone delineation. Since the validity

of the model depends on the nature of the data used, the readers are urged to explore all possible alternative variables in the process and discard the unreasonable model.

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PROSPECTS FOR INTEGRATED PEST MANAGEMENT IN SOUTHERN PINE SEED ORCHARDS

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Abstract.--The concept of Integrated Pest Management (IPM) for southern pine seed orchards is based upon the use of all suitable techniques in an organized way to reduce and maintain cone and seed insect populations at levels low enough so that any seed losses which occur can be tolerated. The prospects for developing such a system based upon traditional methods of chemical and biological control are good. Short-range IPM objectives should be aimed at reducing the frequency, rates, and costs of insecticide use through timing and efficiency of applications and by minimizing the impact of insecticides on beneficial insects. Long-range objectives require the development of better methods of monitoring, as well as the acquisition of the basic information needed to adequately understand the population dynamics of the cone and seed insects found in seed orchards.

Additional keywords: cone and seed insects, *Leptoglossus*, *Dioryctria*

Seed orchards are small areas of extremely valuable forest real estate; they are intensively managed for a single purpose--to produce adequate supplies of genetically improved tree seeds. The prevention of seed losses caused by insects has greatly improved seedling production. It is essential to insure a continued increase. In this paper, I argue that Integrated Pest Management (IPM) offers a rational approach to the prevention of unacceptable losses to insects in seed orchards.

IPM for our purposes can be defined as the utilization of all suitable techniques in an organized way, to reduce pest populations and maintain them at levels low enough so that losses can be tolerated. A conceptual model can be used to show the interactions of various components (fig. 1). In my opinion, IPM is also a common sense approach to pest control, whereby the strengths of various tactics are emphasized, and precautions are taken to avoid any repercussions due to weaknesses. Forest entomologists have promoted this idea for years, but the emphasis on a systems approach where a number of techniques are utilized in an organized manner is new.

BACKGROUND

More than 10,000 acres of grafted trees have been established in the South during the past 30 years (Lantz 1979). Eight state forestry organizations, 36 forest industries, and one forest tree seed company belong to three active tree improvement cooperatives--the North Carolina State University-Industry Cooperative, the University of Florida Forest Tree Improvement Cooperative, and the Western Gulf Forest Tree Improvement Cooperative. Five other state forestry organizations, Region 8 of the U.S. Forest Service, and TVA have tree

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improvement programs. The South's seed orchards produced more than 60 tons of genetically improved seed in 1977. Annual nursery production has reached 1 billion seedlings, and 370 million or 41 percent of the seedlings grown in 1978 were genetically improved trees.

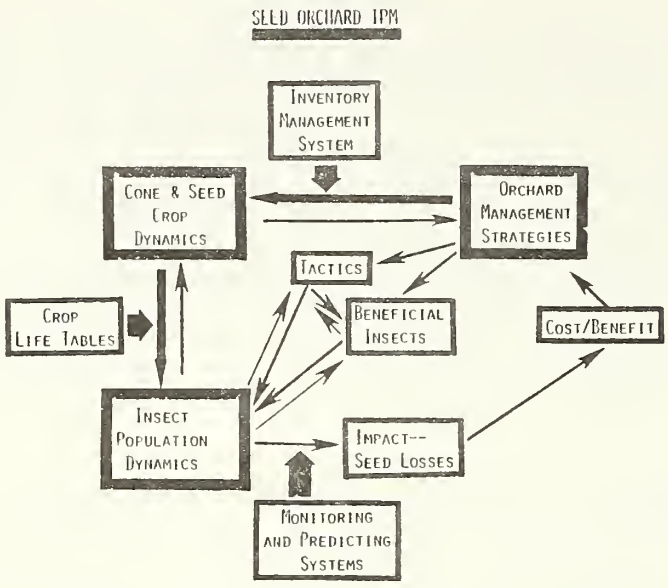

Figure 1.--A conceptual model of a pest management system for southern pine seed orchards (adapted from Waters and Cowling 1976).

Loblolly pine, *Pinus taeda* L., is the most important species and occupies the most orchard acreage. Others include slash pine, *P. elliottii* Engelm. var. *elliottii*; shortleaf pine, *P. echinata* Mill.; longleaf pine, *P. palustris* Mill.; Virginia pine, *P. virginiana* Mill.; and eastern white pine, *P. strobus* L. When an orchard is established, about 100 trees are planted per acre. By age 20, an orchard has been rogued several times and may have only 12-15 trees per acre. Orchards are routinely mowed, fertilized, subsoiled and treated with insecticides.

Seed orchards are usually isolated from other pine stands in order to minimize the influx of wind-blown pollen. This practice tends to insulate the orchards, for a short time, from the large reservoirs of both pests (Goldman 1977) and beneficial insects indigenous to natural stands. At about age 10, cone production starts to increase rapidly, and shortly thereafter so does insect depredation.

Several 'key' pests usually occur in a seed orchard. Key pests are the perennially occurring species that must be controlled to prevent intolerable seed losses. One or two species of cone and seed insects predominate in any seed orchard, but in years of good cone crops secondary insect species often become more abundant (table 1). Inter-specific competition is one of the major factors limiting cone and seed insect populations (Mattson 1978). Both intra- and inter-specific competition occurs when cone crops are poor, and often insect survival and fecundity are reduced.

Table 1.--Key cone and seed insect pests of loblolly pine, slash pine, and eastern white pine seed orchards

Host	Key pest	Secondary pest
Loblolly pine	*Dioryctria amatella* (Hulst)	Cecidomyiidae
	Leptoglossus corculus (Say)	*Dioryctria clarioralis* (Walker)
		Dioryctria disclusa Heinrich
		Dioryctria merkeli Mutuura & Munroe
		Eucosma cocana Kearfott
		Laspeyresia ingens Heinrich
		Laspeyresia toreuta (Grote)
		Nepytia semiclusaria (Walker)
		Rhyacionia frustrana (Comstock)
		Tetyra bipunctata (H.-S.)
Slash pine	*Dioryctria amatella* (Hulst)	*Cecidomyia bisetosa* Gagné
	Leptoglossus corculus (Say)	*Dioryctria clarioralis* (Walker)
	Gnophothrips fuscus (Morgan)	*Dioryctria ebeli* Mutuura & Munroe
		Dioryctria merkeli Mutuura & Munroe
		Laspeyresia anaranjada Miller
		Tetyra bipunctata (H.-S.)
Eastern white pine	*Conophthorus coniperda* (Schwarz)	*Eucosma tocullionana* Heinrich
	Leptoglossus corculus (Say)	*Tetyra bipunctata* (H.-S.)
		Megastigmus atedius (Walker)

Flower initiation and seed potential per cone are strongly linked to the genetics of each clonal selection (Bramlett 1974). The greatest losses of potential seed production occur during the first and last few months of strobili development. Flower, conelet, and first-year ovule mortality usually exceeds cone and seed losses (DeBarr and Barber 1975, Yates and Ebel 1978, Fatzinger *et al.* 1980). Yields from unprotected seed orchards are only a fraction of the potential represented by initial flower crops (Godbee *et al.* 1977); insects cause the major loss.

In natural stands, cone and seed insect population densities are related to annual fluctuations in cone crop size (Mattson 1978). Low infestations usually occur in years of heavy production, if the cone crop was small the previous year. Conversely, when a poor cone crop follows several years of good cone crops, insect-caused losses usually are heavy because of a delayed density-dependent relationship.

The goal of intensive management in seed orchards is to maximize annual cone crops. Large recurring cone crops will tend to favor the build-up of cone and seed insect populations, unless control is an integral part of orchard management. Annual cone yields have increased dramatically during the past several years (fig. 2). Improved seed is so valuable that the economics of insect control are easy to justify. Porterfield (1979) described the direct and proportional relationship that exists between seed production and profitability as follows:

"Within the orchard, genetic gain is largely fixed. This means that insect and disease control in the orchard...are of the utmost importance. Allowing a 20 percent loss in seed yield means a 20 percent decline in that year's net present value from tree improvement."

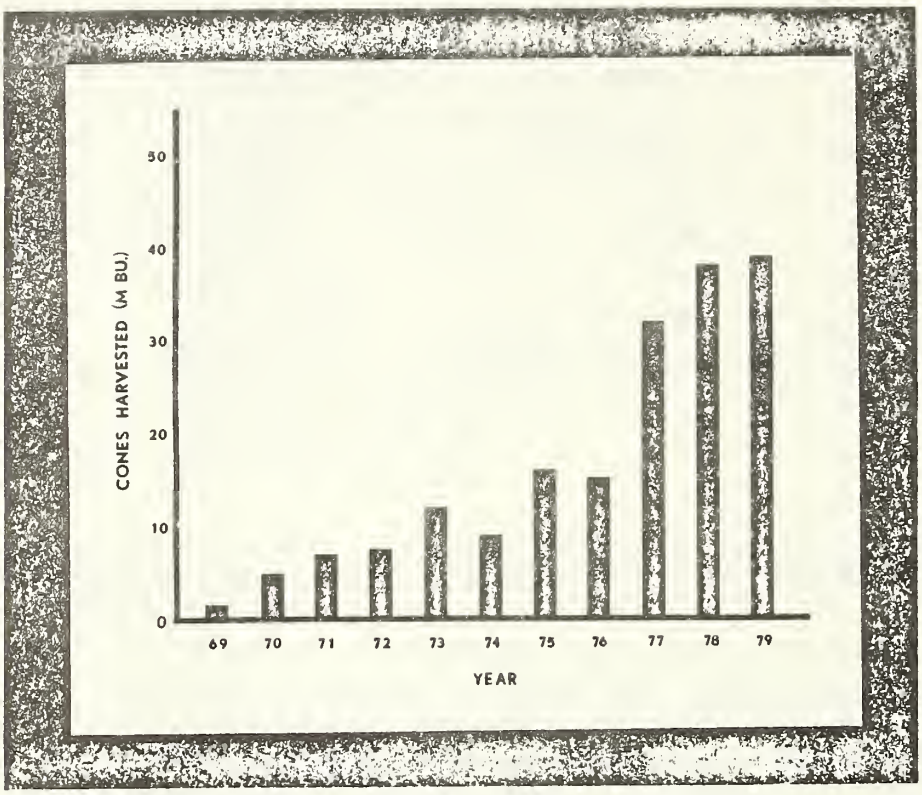

Figure 2.--Cone yields from the N. C. State University-Industry Tree Improvement Cooperative seed orchards, 1969-1979 (Anon. 1980).

NEED FOR IPM

Orchard managers may ask us why it is necessary to spend additional time, money, and effort to develop an IPM system when we already have several effective insecticides that can be used for control. The answer, of course, is that total reliance on chemicals for the suppression of cone and seed insect pests has several serious drawbacks. These include the selection for resistance, outbreaks of secondary pests, resurgence of key pests, hazards to personnel, environmental contamination from residues, and possible legal problems. In addition, broad-spectrum insecticides, such as azinphosmethyl (Guthion®), may limit the role beneficial insects can play in regulating pest populations in orchards. Finally, the use of insecticides represents a direct and ever-continuing expense for labor, equipment, and materials. And, these costs are escalating because the pesticide industry is highly dependent upon petroleum products.

An IPM system for seed orchards most likely will depend heavily upon traditional chemical and biological control. Insecticide application is the only practical method for reducing insect-caused seed losses to a tolerable level in operational orchards. Their use has greatly increased the availability of seed. This in turn has resulted in the establishment of plantations of improved pines capable of yielding additional wood and fiber worth millions of dollars.

Thus, despite the drawbacks, heavy reliance on insecticides is likely to continue for some time. Our long-range goal, however, should be to use insecticides to suppress rather than prevent outbreaks as we do now.

Unnecessary use of an insecticide occurs when the need to control or suppress the pest insect has not been established. Preventive insecticide applications are common in seed orchards. For example, carbofuran (Furadan®) is routinely applied in February as "insurance" against seed losses caused by seedbugs (DeBarr 1978). Guthion® is applied up to five times per year on schedules based upon the calendar instead of actual need to control *Dioryctria* (Merkel *et al.* 1976). These applications might be avoided, costs reduced, and a substantial quantity of insecticide eliminated from the orchard environment if we were able to provide the orchard manager with some method of predicting the need for such tactics.

IMPROVING EFFICIENCY

In the short run, there is plenty of room for improving the efficiency with which insecticides are used. Increased costs, along with trends toward low-volume applications and concern about pollution make it imperative that we apply insecticide on target. In seed orchards, as in other areas where pesticides are used, only a small amount of the insecticide applied acts to kill the target pests. Typical losses between the spray nozzle and site of toxic action for a ground spray or aerial application are shown in fig. 3. Up to one-third of the insecticide applied may be lost as drift or misapplication. In the target area, principal losses include volatilization, leaching or surface transport, and deposition on nontarget surfaces such as the ground. In most cases, only about half is found as toxic residue on the tree. Something less than 1 percent is near the cones or target insect. An even smaller fraction is absorbed by the insect, and only an infinitesimal amount ever reaches the site of toxic action inside the insect. For example, the LD_{90} for Guthion® topically applied to adult seedbugs is about 2 micrograms/g of insect body weight (J. C. Nord and G. L. DeBarr--unpublished data). One gram of Guthion® A.I. is enough to kill 5 million seedbugs. Each time an orchard manager sprays an acre of seed orchard at the registered rate, he applies about 2 kilograms of Guthion®, or enough to kill 10 billion seedbugs.

Obviously, the potential for increasing the efficiency of insecticide applications is enormous. New technology or simple changes in present application methods can reduce costs and environmental contamination, without sacrificing benefits. For example, as seed orchards reach 20-25 years of age, it becomes increasingly difficult and expensive to apply insecticide with ground equipment on trees 60-70 feet in height. Aerial applications are more efficient.

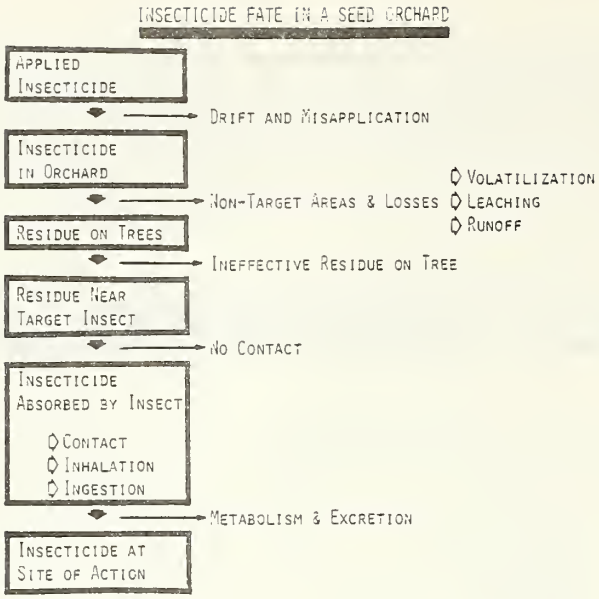

Figure 3.--A conceptual model of the fate of insecticides in southern pine seed orchards (adapted from von Rümker and Kelso 1975).

BIOLOGICAL CONTROLS

There is one outstanding example of cultural control of a seed pest, but entomologists cannot take the credit for it. Seedworms, *Laspeyresia* spp., overwinter in the cone axis and are inadvertently removed with each year's harvest. The result has been a low incidence of seedworm damage in loblolly pine orchards (G. L. DeBarr--unpublished data). Because cone collection is so difficult and costly, several other alternatives for collecting seed, such as the use of nets, have been proposed. If this particular technique becomes widely accepted, and cones are left in the orchards, seedworms will likely become much more common in orchards.

Chemicals used in seed orchards undoubtedly kill some beneficial insects, but a greater effect may occur because of reduced host availability. Compared with populations of many other forest pests, the numbers of cone and seed insects present on seed orchard trees are quite low. Often they are most abundant at the time of cone ripening, but even then they are scattered over a large canopy of orchard tree crowns. Host finding by natural enemies is likely to be more difficult for these pests than for those of agronomic crops. There, population levels are usually much higher and more concentrated. Following the application of insecticides in seed orchards, the numbers of cone and seed insects may be too low to adequately support beneficial insects. Thus, successful biological control will depend upon our ability to modify parasite-host or predator-host ratios and to maintain favorable ratios when pest populations in orchards are low.

Chant (1966) described conservation, augmentation, and introduction as the three basic kinds of biological control using parasites. "Conservation" is the enhancement of the effectiveness of natural enemies by changing their environment. A simple application of the conservation approach might be a change in concentration, time of application, or kind of insecticide used to control a cone or seed insect pest.

For years we have speculated that systemic insecticides applied to the soil or implanted directly into the tree might be less detrimental to the complex of parasites found in seed orchards. Recently, Belmont (1979) found comparative levels of control by several species of *Dioryctria* spp. parasites in Furadan®-treated and untreated areas of a slash pine orchard in Florida. Guthion®, which remains active on the foliage for long periods after sprays and has a broad spectrum of toxicity, would almost certainly destroy many of these parasites. Therefore, if our primary target pests are seedbugs, it appears there may be an advantage in using Furadan® instead of Guthion® to conserve the effectiveness of *Dioryctria* spp. parasites.

A more complex example of conservation in seed orchards is enhancement of the effectiveness of natural enemies of seedbugs by planting some agricultural crop in or near an orchard. This crop might serve as an insectary for populations of alternate host insects. This strategy is based upon our observation that the predator-parasite complex attacking *Leptoglossus corculus* (Say) and *Tetyra bipunctata* (H.-S.) is composed of many of the same species associated with other common coreid and pentatomid bugs (G. L. DeBarr and G. F. Fedde--unpublished data).

Just as the lack of ecological diversity in agronomic crops disrupts the predatory-prey relationships in favor of pests (DeBach 1964), the pine monoculture of seed orchards undoubtedly has the same adverse effect upon the natural enemies of seedbugs. Monocultures tend to favor development of "exploding" pest populations (Hagen and Hale 1974).

It seems likely that populations of beneficial insects in seed orchards are disrupted by the lack of nearby vegetation in which to overwinter; alternate food supplies such as pollens, nectars or honeydews; and alternate host-prey for food. Cover crops or patch plantings could be used to attract alternate host insects. In turn, the presence of these insects would serve to attract and concentrate indigenous populations or inoculative releases of beneficial insects in the orchard. These plots would also serve as havens for them once the seedbug populations had been diminished.

Studies under way at the Forestry Sciences Laboratory, Athens, Georgia, are aimed at determining the potential of three species of egg parasites, *Anastatus reduvii* (Howard), *Gryon pennsylvanicus* (Ashmead), and *Ooencyrtus trinidadensis* Crawford, in a biological control strategy for seedbugs. The idea of using a diversity of plants to enhance the effectiveness of these parasites as part of an IPM system for southern pine seed orchards is also being evaluated.

"Augmentation" or the mass rearing and periodic release of sufficient numbers of a natural enemy to overwhelm a pest population is a promising strategy. Orchards vary in size from 10 to 400 acres. It might be feasible to use parasites in a manner similar to chemical insecticides but without the associated problems of environmental hazard and safety, and with the added possibility of recurring control. Developing mass rearing techniques, producing a strain of parasites competitive in the field, and timing the production and release to coincide with host vulnerability are all problems unique to this particular approach. Inundative releases of egg parasites for the pine seedbugs or *Trichogramma* spp. for *Dioryctria* spp. control appear to have the greatest potential.

Introduction of natural enemies not already present in the United States also may have potential. Research in Europe and Asia sponsored by the PL-480 grant programs has revealed the existence of several natural enemies of *Dioryctria* spp. that might be introduced as components of our seed orchard IPM system.

INTEGRATED PLANNING

How successful we become in applying the concept of integrated control to seed orchards in the future will depend to a large extent upon our commitment to develop plans to:

1. Identify and answer critical questions related to the dynamics of cone and seed insects and develop predictive models.

2. Standardize methods for collecting, analyzing, and evaluating data.

3. Lay out long-range strategies and short-range tactics, and continually evaluate the progress and potential of each in the context of an IPM system.

In the past, specific plans to carry research from the laboratory to small-scale field tests and finally pilot tests to demonstrate efficacy have often been lacking or incomplete. The planning and cooperation involved in our efforts to test and register insecticides for use in seed orchards clearly demonstrate how a diversity of individual talents and resources can be brought together to fulfill a common goal (DeBarr 1976, van Buijtenen 1981). These experiences should be equally valuable in the development and implementation of other components of an IPM system.

Campbell and McFadden (1979) emphasized that the key to attaining the goals of any pest management research and development program is accountability. If goals are not clearly defined, individuals often hold themselves accountable only for their own self-imposed objectives. Their efforts may contribute new knowledge, but fail to answer questions relevant to the development of an integrated pest management system. Therefore, to make real progress, each research study and pilot test needs to be critically questioned as to its contribution toward an IPM system for seed orchards.

TRANSFERRING TECHNOLOGY

Coordination of successive phases of technology development from research through implementation is far better for seed orchard pest problems than for most other forest pests. There is a general coordination of effort by U.S. Forest Service Research and State and Private Forestry personnel working through the Southern Forest Insect Work Conference, the Southern Forest Tree Improvement Conference, the Tree Improvement Cooperatives, and the Southern Regional Cone and Seed Insect Project (S-118). Our users are a group of about 200 highly committed and enthusiastic forest managers. We know most of them personally. Getting them to implement a new control tactic is usually not as big a problem as talking them out of using it before it has been proven effective. Many of the usual barriers to technology transfer do not exist.

The willingness and rapidity with which orchard managers are going to accept new ideas and alternatives is closely linked to the nature of each particular innovation. Muth and Hendee (1980) listed five characteristics that influence the chances that a new innovation will be quickly accepted by the user--relative advantage, compatibility, complexity, trialability, and observability. These five factors should be kept in mind when we propose components for a seed orchard IPM system.

A new alternative control tactic must possess some relative advantage over any other options currently available. This advantage is often one of economics, but there are also other criteria. As an example, prior to 1974 there were no insecticides registered for cone and seed insect control in loblolly pine seed orchards. When Guthion® was registered its relative advantage was purely economic (van Buijtenen 1981). The alternative was to do nothing and suffer intolerable seed losses.

When Furadan® was registered in 1976, it quickly replaced Guthion® for seedbug control, even though both chemicals are about equal in efficacy and costs. This time the relative advantage was safety. Granular Furadan® has a dermal toxicity greater than 10,000 mg/kg compared to about 200 mg/kg for Guthion®. Only a single application of Furadan® is required for season-long control (DeBarr 1978), while multiple applications of Guthion® are necessary (Merkel *et al.* 1976). The relative advantage of Furadan® was reduced hazard to personnel.

Compatibility is the degree to which an alternative control tactic fits in with other orchard management strategies or the values and needs of the orchard manager. As an example, the development of varieties of plants resistant to pests is an important part of IPM for many agronomic crops. Although clones in pine seed orchards vary widely in susceptibility to almost all the key pests (DeBarr *et al.* 1972), this approach has little potential for seed orchards. Resistance to cone and seed insects is not a trait of primary concern once the trees have been established in plantations, and forest geneticists believe that only primary traits should be included in the selection process. They say that if a tree has good characteristics, such as growth and form, the problem of susceptibility to cone and seed insects should be overcome by more intensive orchard management. Thus, breeding trees for resistance to cone and seed insects is incompatible with current views.

Complexity is the relative ease with which an innovation can be understood and implemented. Blacklights have been very useful to researchers in monitoring the seasonal occurrence of various species of *Dioryctria* (Merkel and Fatzinger 1971, Yates and Ebel 1975). However, very few orchard managers have used them, primarily because of the difficulty in separating and identifying the moths of *Dioryctria* species. In contrast, disposable sticky traps, baited with female sex pheromone are cheap, easy to deploy, and species-specific, catching only *Dioryctria* moths (DeBarr and Berisford 1981). Although the identification and development of synthetic pheromones to bait the traps requires some rather sophisticated research techniques, practical application is simple.

Trialability is the extent to which an innovation can be tested and evaluated by the orchard manager. And finally, observability is the ease with which an innovation or its effect can be seen. The quick knockdown effect that the

pyrethroid insecticides have on seedbugs is easily observed (DeBarr and Nord 1978), but the more subtle effect of egg parasites is not nearly as dramatic. This difference in observability is likely to influence how quickly each of these alternatives is accepted.

Several years ago, the research director for a large forest industry wrote the following in the Journal of Forestry:

> "The most far-out, test-tube, bench-oriented scientist needs to know, understand, and really have a positive conviction that the results of his research will proceed to applied research, to development, to application, to profit or to the good of society. There should be pressure to get research into operation--the research job is not finished until the new information is in use." (Stabler 1975).

Interestingly, a loblolly pine orchard owned and intensively managed by this company was one of the first to produce an average of 200 bushels of cones/acre and 2 lbs. of seed/bushel--yields thought to be impossible only a few years before. This same company also now does most of its control crosses of loblolly pine on small potted trees in greenhouses using an advanced breeding technology made possible by the rapid implementation of basic research on early flower initiation. These are both fine examples of good accountability, technology transfer and rapid implementation.

SUMMARY

Short-range IPM objectives should be aimed at reducing the frequency, rates, and costs of insecticide use through improved timing and efficiency of applications. We also need to develop better methods of monitoring insect activity, whereby orchard managers can decide to use insecticides only when the threat of damage is real, rather than anticipated or imagined. Finally, we need to find ways to minimize the impact of insecticides on beneficial insects.

The full potential of IPM for seed orchards can only be achieved by a carefully designed, organized effort to identify areas where additional information and understanding are required. There are thousands of variables associated with orchard management and the complex of insects found there. Our challenge is to discover those that we can use to understand the dynamics of this particular biological system.

For the foreseeable future, insecticides will continue to be major components of this sytem. However, we should remain alert to their many shortcomings. I believe that through creative and innovative research we can exploit a variety of biological, chemical and cultural alternatives. At best, this integrated approach to the control of cone and seed insects will minimize outbreaks and the need for a crisis-response. Control will not be absolute. However, the opportunities for developing an IPM system for the South's forest tree seed orchards are so varied and unique that our success is almost a certainty.

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