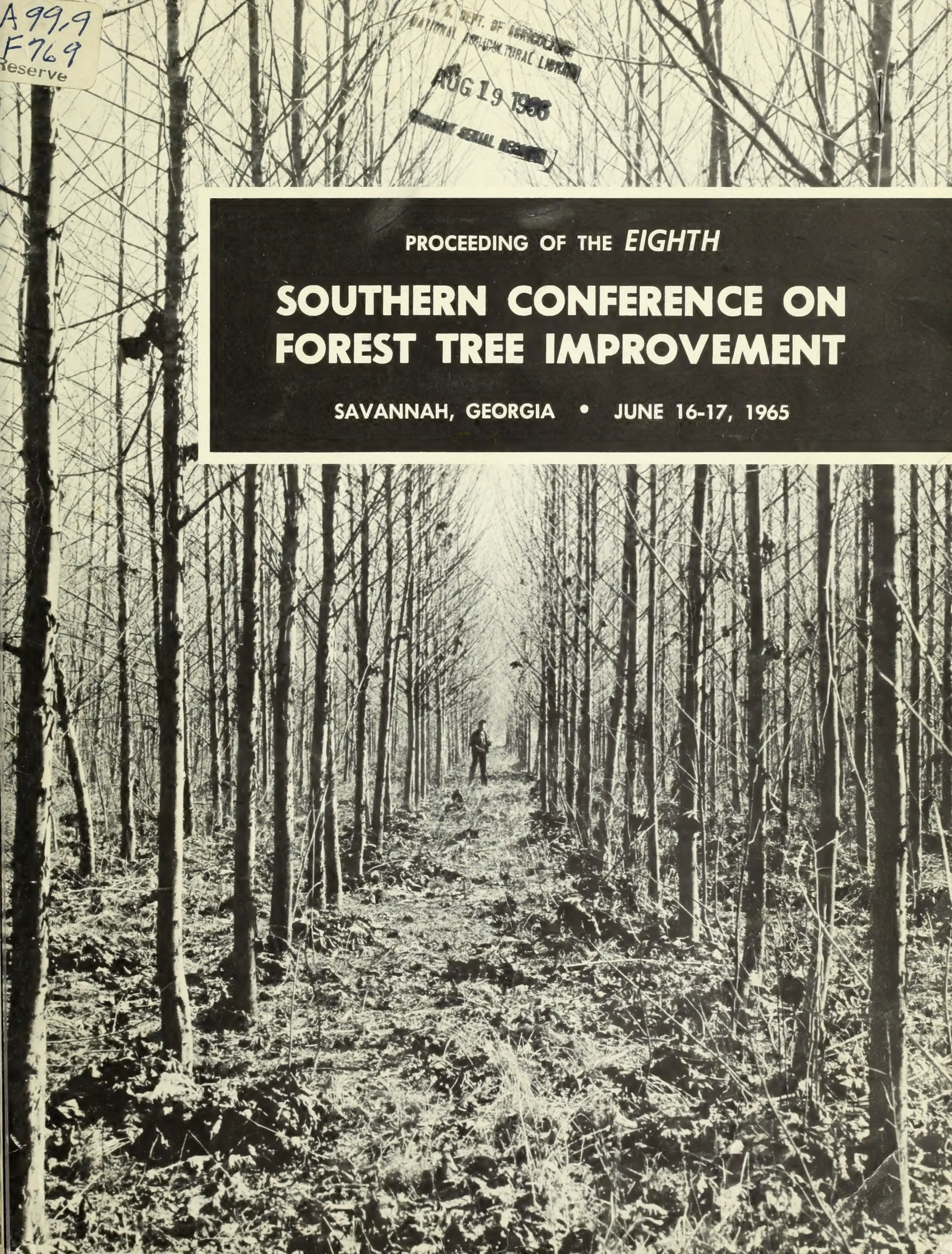

PROCEEDING OF THE *EIGHTH*

SOUTHERN CONFERENCE ON FOREST TREE IMPROVEMENT

SAVANNAH, GEORGIA • JUNE 16-17, 1965

CONFERENCE NOTES

The first day of the Conference was devoted to a General Session with the theme "Hardwoods: A Challenge in Forest Tree Improvement." The participants for this session were selected by the program committee by invitation. *L. N. Thompson, Jr.*, General Manager, Mills and Timber, Georgia-Pacific Corporation gave the keynote address. Moderators for the General Session were *Al Foster, Paul C. Guilkey, J. S. McKnight,* and *Keith Dorman.* Moderators for the Technical Session on the second day of the Conference were *Claud L. Brown, Ray E. Goddard, J. P. van Buijtenen* and *Bruce Zobel.* Papers are in the order of their presentation at the Conference.

Officers of the Committee on Southern Forest Tree Improvement were: *Chairman,* A. A. Foster, Tennessee Valley Authority; *Vice-Chairman,* R. A. Bonninghausen, Florida Forest Service; *Secretary,* Donald E. Cole, Continental Can Company, Inc.

Members of the Program Committee for the Eighth Southern Conference on Forest Tree Improvement were Claud L. Brown, chairman, University of Georgia; Keith Dorman, Southeastern Forest Experiment Station, U. S. Forest Service; and Donald E. Cole, Continental Can Company, Inc.

Officers now serving are: *Chairman,* R. A. Bonninghausen; *Vice-Chairman,* Donald E. Cole; *Secretary,* Keith Dorman.

ACKNOWLEDGEMENT

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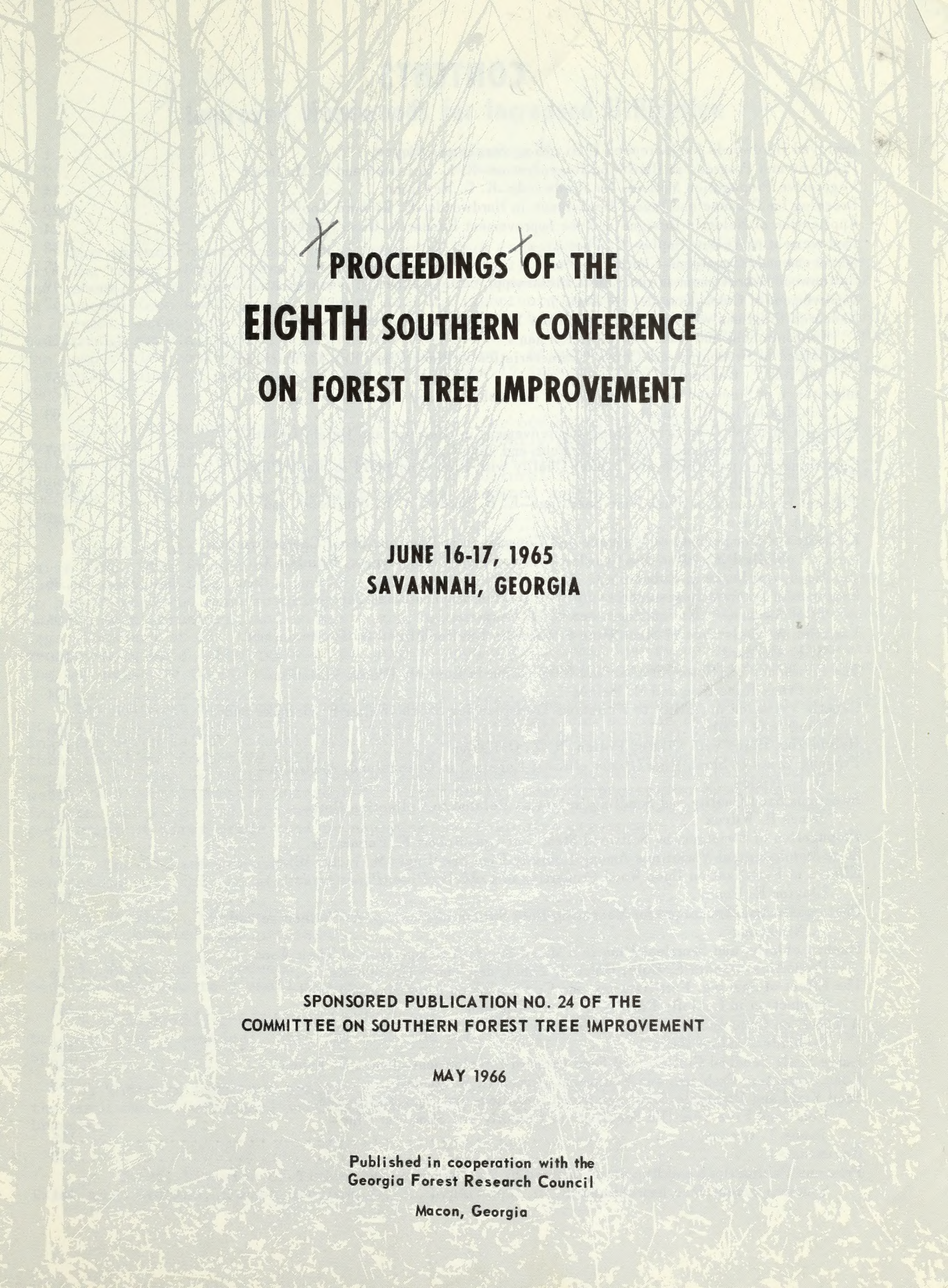

PROCEEDINGS OF THE EIGHTH SOUTHERN CONFERENCE ON FOREST TREE IMPROVEMENT

JUNE 16-17, 1965
SAVANNAH, GEORGIA

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CONTENTS

Improved Hardwoods for Increased Utilization

STEPHEN G. BOYCE[1]

The current low utilization of hardwood logs is primarily due to the small size of existing trees. Small trees can produce only a small amount of the best grades of lumber and veneer. Even under intensive silviculture a preponderance of low-grade material must be expected from small trees. Timber size is important because larger trees are cheaper to harvest, transport, and process, and tend to have higher product value than small trees. Even though many small hardwood logs are being used, larger timber is essential to maintain the competitive position of most forest industries. At present only about 11 percent of the total volume of eastern hardwoods is in trees 19 inches and larger (U.S. Forest Service 1965).

One way to increase utilization is to wait for our trees to grow larger. But, this may not occur soon enough to meet our needs. Currently recommended cultural treatments applied to natural stands can increase growth and utilization in a reasonable time (Roach 1965). But we also need more intensive cultural and genetic techniques that greatly increase the utilization of the most valuable hardwood species in the shortest possible time.

Increased utilization requires trees with a number of characteristics other than large size. The structure of the wood must permit minimum waste in manufacturing. Knots must be confined to a small center core. And uniform wood structure among logs is needed to permit repeated manufacturing of uniform products. Large size, cylindrical shape, uniform wood structure, and no knots are features that increase the usefulness of hardwood logs (Lockhard et al. 1963). Apparently the most usable hardwood log for lumber and veneer would be a large cylinder of uniform wood with a small knotty core. This theoretical log may never be grown but it can serve as a goal for developing some improvement concepts.

The quickest improvements for increased utilization can be made by applying cultural practices in immature stands. But the greatest progress can be made by improving the inherent potential of valuable species and by using the best cultural practices to grow these trees on productive soils. To do this we must plant vigorous seedlings of inherently superior strains on soils with good physical properties. We must completely eliminate weeds; add fertilizers to nutrient-deficient soils; provide protection from diseases, insects, and fire; and irrigate when necessary. In addition, we can grow the maximum percentage of first-grade wood by applying the following concepts:

1. The highest percentage of first-grade lumber and veneer can be produced by concentrating cultural and genetic practices on the butt log.

2. Straight, vertical stems have uniform wood structure and can be efficiently harvested, handled, and processed.

3. Waste can be reduced and manufacturing efficiency can be increased by confining buds and branches to a small centered core of the butt log.

4. A uniformly growing cylindrical bole requires a symmetrical crown centered and balanced over a vertical, straight stem and provided with a continously increasing growing space.

5. The most important genetic qualities for increased utilization are adaptation to the environment, straight, vertical stems, and early abscission of suppressed buds and branches.

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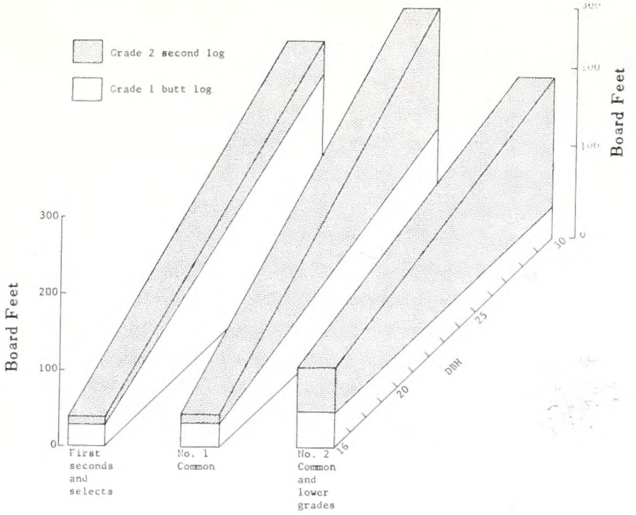

Figure 1 -- A grade 1 butt log has a large amount of first-grade lumber. A grade 2 second log adds large amounts of poorer grades. This diagram shows the expected recovery of Factory Grade lumber from 1- and 2-log black oaks 16 to 30 inches d.b.h.

THE BUTT LOG

The butt log is the most valuable part of the stem. Between 40 and 100 percent of the merchantable volume of most hardwood trees is in the first 16-foot log. And, the best lumber and veneer are made from butt logs. This log has the best chance of qualifying for grade 1, either for factory lumber or for veneer, while the second and third 16-foot logs usually are grade 2 or lower. A grade 2 second log adds a small amount of high-grade lumber and a large amount of low-grade lumber (fig. 1). For black oak from 16 to 30 inches d.b.h. a grade 2 second log adds only 13 to 18 percent more top-grade lumber but 120 to 300 percent more low-grade lumber. Similar ratios exist for other hardwoods (Wollin et al. 1949).

The butt log is generally considered to be 16 feet long. Cultural practices can be extended to a butt log 20, 22, 24 and 26 feet long from which two grade 1 logs can be cut. This will increase the volume of high-grade lumber but the increase in high-grade lumber will be less than the increase in low-grade lumber. This is because the knotty core in a 16-foot butt log is shaped like an inverted cone with a 3- to 4- inch base at the top of the log. The second 16-foot log has a knotty core shaped like an inverted frustum of a cone beginning at the top of the butt log and expanding to a diameter of 12 to 14 inches at the top of the second log (Holsoe 1947). A second log of any length must contain a smaller proportion of clear wood than the butt 16-foot log.

It is costly and difficult to prune and apply other cultural treatments to the second log because it is higher from the ground and normally has more and larger branches than the butt log (Krajicek 1959; Brinkman 1955). Therefore, the largest percentage of top-grade lumber and veneer will be most easily grown in the shortest time by concentrating cultural and genetic practices on the 16-foot but log.

STRAIGHT AND VERTICAL STEMS

Straight and vertical stems are more efficiently processed. Lean and crook increase the amount of gelatinous fiber and increase the variability in wood structure, specific gravity, and ring width. All of these cause problems in machining, drying, and finishing (Boyce and Kaeiser 1964); Davis 1962). Buckling and splitting of veneers, for example, are often caused by variations in specific gravity and the presence of gelatinous fibers. For machining, uniformity in wood properties is usually more important than specific gravity (Davis 1962). The presence of large numbers of gelatinous fibers in leaning and crooked stems creates problems in surfacing, sanding and drying. In addition to causing processing problems, crooked and leaning trees are more difficult and expensive to harvest, transport, and saw or slice than straight, vertical trees.

The production of a straight, vertical butt log begins with fast initial growth of seedling sprouts and seedlings (Bey 1964). After harvesting a natural stand, all advanced growth should be cut near the ground to give the seedling sprouts and seedlings the best possible opportunity for fast height growth (Roach 1965). If the first stand of sprouts does not contain a sufficient number of straight, vertical stems, it should be cut again near the ground. It is better to add a year or two to the rotation at this age than to invest in stems that cannot possibly grow into straight logs.

Hardwood plantations can have fast-growing trees with vertical, straight stems if only the most productive soil is used; the soil is prepared as for a corn crop; and large vigorous seedlings are planted in deep pits. Pits can be drilled to 2 feet deep with power augers. Root collars should be placed several inches below the ground, and the original

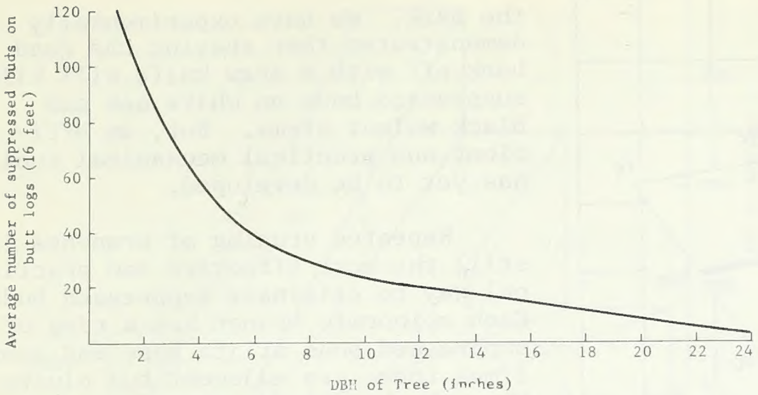

Figure 2 -- As oak trees grow in diameter, the number of suppressed buds decrease. This diagram is based on dissections of white oak, scarlet oak, black oak, and northern red oak trees. There were no important differences among species.

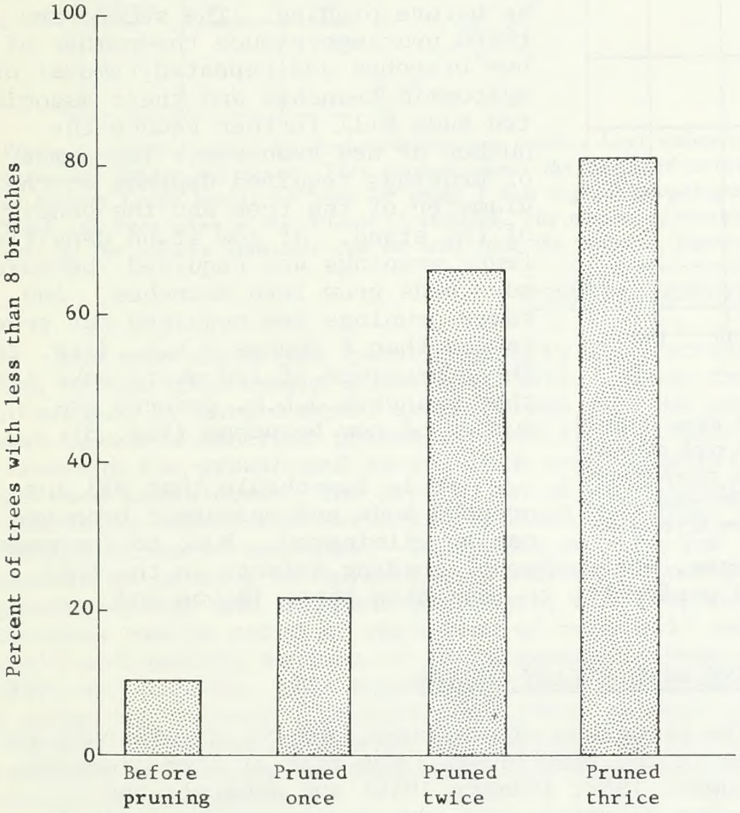

Figure 3 -- Repeated pruning at 2-year intervals can increase the proportion of hardwood trees with less than eight new branches on the butt log. These white oaks were about 5 inches d.b.h. when first pruned.

stems cut so the seedlings sprout near the ground. Only one sprout should be permitted to develop. Weeds should be completely eliminated and fertilizers added to nutrient-deficient soils. Weed and grass competition must be eliminated because it causes slow growth, forked and crooked stems, and frequent failure in hardwood plantations.

SMALL KNOTTY CORES

Knots are the most common defect limiting the size of clear cuttings in factory lumber, and the usefulness of hardwood veneers. Knots, regardless of size, character, and condition, are not admitted in clear cuttings or in first-grade veneers (Lockhard et al. 1950; Henley et al. 1963). Although we have not learned to grow hardwoods without buds and branches, we can confine them to a small core in the butt log.

Knots outside the central core of butt logs are rarely caused by crown branches. The crown branches on the lower 17 feet of most hardwoods normally die and fall off at an early age. But new branches develop from suppressed buds that originate from apical meristems. These buds are suppressed by chemicals formed in the crown and may be released to expand into branches by environmental changes such as thinning and pruning (Brinkman 1955; Krajicek 1959). Each year suppressed buds grow an amount equal to the radial growth of the stem and are thus maintained just outside the cambium. In young trees suppressed buds form small branches that persist for varying lengths of time but rarely for more than 15 to 20 years. As trees grow in diameter the number of suppressed buds in the butt log decreases (fig. 2). The buds die earlier and epicormic branches are smaller on dominant trees in dense stands than in thin stands (Ward 1964). It is often suggested that stands be kept dense to kill these buds and branches. But this practice limits diameter growth.

Since practically all epicormic branches form from suppressed buds, epicormic branching can be prevented by killing these buds. As soon as the lower one-third of the tree is tall enough to form the core of a butt log (Holsoe 1947), buds and branches on this section should be killed (Boyce 1962).

Certain oils and other chemicals kill suppressed buds but practical methods for controlling the concentration and making efficient applications have not been developed (Boyce and Neebe 1963).

Mechanical removal of suppressed buds is possible because the meristem projects into

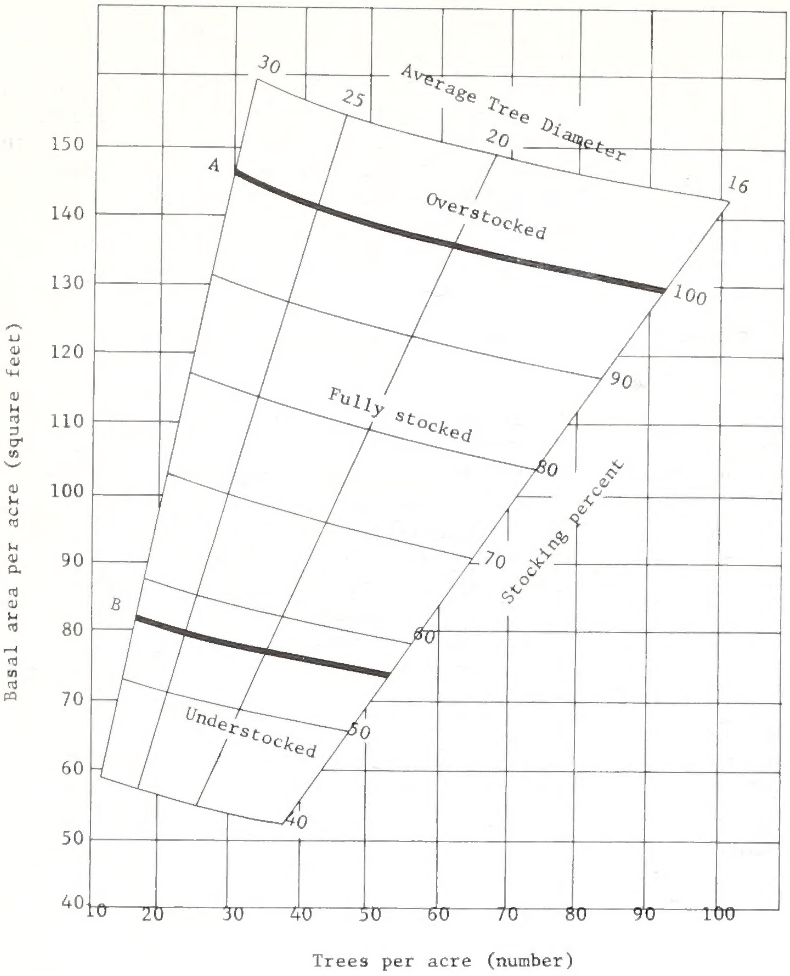

Figure 4 -- An extension of Gingrich's stocking guide for trees 16 to 30 inches d.b.h. Below the B-line crowns are independent of each other and diameter growth is maximum. Between the B- and A-lines crown growing space is fully used and diameter growth decreases with increased stocking. Above the A-line mortality is high and yield per acre is reduced.

the bark. We have experimentally demonstrated that shaving the dead bark off with a draw knife will kill suppressed buds on white oak and black walnut stems. But, an efficient and practical mechanical tool has yet to be developed.

Repeated pruning of branches is still the most effective and practical way to eliminate suppressed buds. Each epicormic branch has a ring of suppressed buds at its base and sometimes there are adjacent bud clusters. When the branch is pruned, the adjacent suppressed buds can be removed by scraping the saw blade over this part of the tree stem. The first pruning releases additional buds and sometimes results in as many branches as before pruning. The second and third prunings reduce the number of new branches and repeated removal of epicormic branches and their associated buds will further reduce the number of new branches. The number of prunings required depends on the diameter of the tree and the density of the stand. At low stand densities fewer prunings are required because more buds grow into branches. And, fewer prunings are required for trees larger than 8 inches d.b.h. (fig. 2). Three prunings of 120 white oaks less than 5 inches d.b.h. reduced the number of new branches (fig. 3).

It is improbable that all suppressed buds and epicormic branches can be eliminated. But, to increase the proportion of top-grade lumber and veneer, the number of grading defects on the butt log must be reduced to less than eight and preferably to less than three (Boyce and Schroeder 1963).

CYLINDRICAL STEMS WITH STEADY GROWTH

The shape and diameter of the stem, the structure of the wood, and the growth rate are all related to the physiological activities in the tree crown. The rate of stem diameter growth is related to crown expansion (Kozlowski 1962; Thimann 1958; and others); the stem diameter is directly related to the crown diameter, and asymmetric crowns result in asymmetric annual rings (Sorensen and Wilson 1964). Therefore, steady growth of approximately cylindrical logs requires trees with symmetrical crowns centered and balanced over vertical, straight stems and provided with growing space continually increasing at the rate required to produce the desired ring widths.

This is possible. Krajicek, Brinkman, and Gingrich (1961) found a very high correlation between the d.b.h. and crown diameter of open-grown hardwoods. This relation was used to develop a simple stocking guide for even-aged hardwood stands and plantations (Gingrich 1965). An extension of this guide is shown in figure 4 for trees 16 to 30 inches d.b.h. At the B-level of stocking the crowns begin to compete for space. As the stocking continues to increase the annual rings begin to narrow and crowns become asymmetric as spacing becomes uneven. The higher the percent stocking above the B-line, the slower the diameter growth and the longer the rotation. To grow the maximum volume on the shortest rotation the stocking percent should be kept near the B-line (Roach 1965).

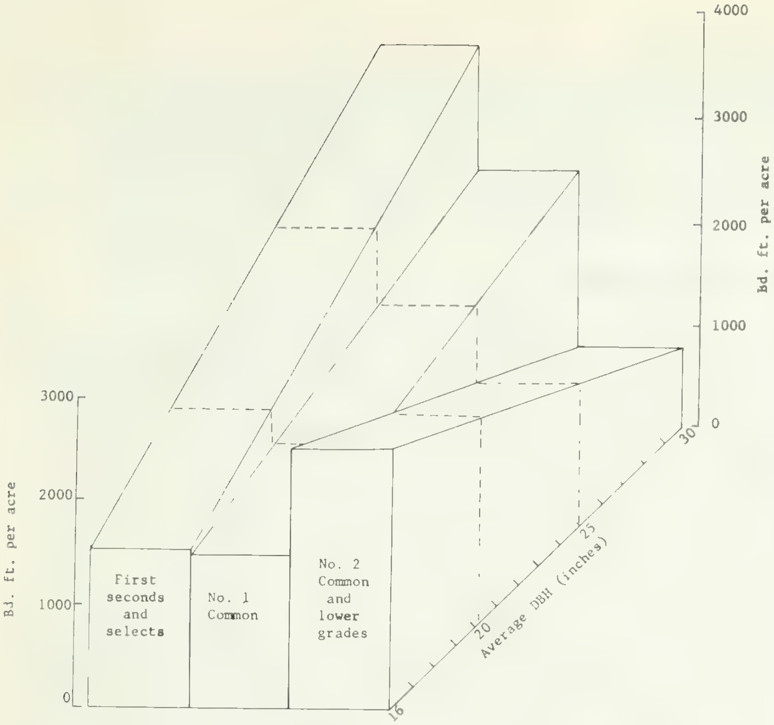

Figure 5 -- Open-grown, 1-log hardwood trees can produce large volumes of first-grade lumber and veneer. This diagram shows the expected recovery of Factory Grade lumber per acre for grade 1 butt logs from open-grown black oak trees when at the B-level of stocking. The number of trees per acre of the various diameters can be read from the chart in figure 4.

But, to grow the largest log of top-grade wood in the shortest time the stocking percent must be low enough for each crown to be independent of every other crown. This occurs below the B-line. This may reduce total yield per acre but, in conjunction with the other concepts described here, it produces the largest proportion of recoverable FAS and Select grades of lumber and veneer. During most of the rotation stands should be kept at 40- to 50-percent stocking. Near the time for harvesting the stocking may be permitted to approach or exceed the B-level. Figure 5 shows the expected recovery of Factory Grade lumber per acre from grade 1 butt logs of open-grown black oak at the B-level of stocking. Total yield is 5,600 to 6,800 board feet per acre but, most important, the proportion of high-grade lumber is from 28 to 54 percent. In trees larger than 16 inches d.b.h. the volumes of FAS and Select grades of lumber increase and grades below No. 1 Common decrease. Similar relationships occur for other eastern hardwoods.

GENETIC IMPROVEMENT

The most important genetic quality for increased utilization of hardwoods is adaptation to the environment (Limstrom 1965). Since the rate of physiological processes is influenced by environment, useful trees must be adjusted to their surroundings. Trees must have the inherent potential both to efficiently use the energy and materials of the environment for growth and to tolerate environmental extremes without serious losses in growth and wood usefulness. The protection of investments in intensive cultivation requires trees inherently capable of surviving unusual droughts, ice and wind storms, late frosts, and similar climatic extremes. Intensive culture for top-grade wood requires trees inherently capable of growing in nurseries, recovering from planting damages, efficiently using large growing spaces and abundant nutrients, and responding favorably to other cultural practices. Examples can be cited of varieties of many wild and cultivated plants that are superior in yield and quality because of their generally more efficient physiological processes (Allard 1960; and others). The major problem of the tree geneticist is to find strains to fit a given environment. In fact, all other genetic modifications must be made within the limitations of environmental adaptation. We are now devoting a large part of our genetics research to finding and developing strains and clones of black walnut best fitted to various environments.

It also may be possible to breed and select stains and clones of most hardwoods with the inherent potential for forming straight, vertical stems. This feature is inherited in the genus Populus and our observations of oak, yellow-poplar, and walnut suggest that it may also be inherited in this species. These qualities are so important for increased utilization that we can devote much genetics research toward this goal. We do not have these inherently straight strains and clones now but we do have geneticists working on the problem.

Selection and breeding programs also should aim to develop races of hardwoods that inherently form four or less knots outside a small core of the butt log when 16 inches d.b.h. (Boyce and Schroeder 1963). These are superior phenotypes that should be evaluated for their ability to transmit genes for few epicormic branches. Those with proven ability can then be used in breeding and selection programs.

Since suppressed buds are a part of the inherently controlled developmental process of trees, it may be possible to find genotypes that do not retain or form suppressed buds. For millions of years oaks and other hardwood seedlings that retained suppressed buds had the best chances for sprouting and surviving after fire, browsing, freezing, and other injuries. This selective pressure is reduced in nurseries and plantations and these are the best places to look for trees without suppressed buds. But, to date, we have not found an oak, yellow-poplar, or walnut that does not form and retain suppressed buds. Our search continues.

ONE-LOG SILVICULTURE

Intensive culture of hardwoods for maximum utilization implies the growth of one-log trees with straight, vertical stems made up of small knotty cores encased in thick cylinders of uniform wood. The method is to plant inherently superior hardwoods on soils with the best physical properties; eliminate weeds and brush; fertilize nutrient-deficient soils; protect trees from diseases, insects, and fire; irrigate when needed; repeatedly prune the butt log; and maintain stocking at 50 percent or less. Retired but fertile farmland is ideal for this system. Soybeans and other crops can be grown for several years between the widely spaced rows of trees. The Central States Forest Experiment Station is currently developing this system for the production of large volumes of high-quality walnut.

I have presented a group of model concepts. Economic considerations rarely permit investment in this sort of biological perfection; practices must be fitted to economic and physical limitations. However, a cultural system based on these concepts but subject to other limitations can be devised now to improve hardwoods for increased utilization. Later, when better strains and clones are developed, they can be incorporated into the system.

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Problems and Progress in Hardwood Regeneration

R. L. McELWEE and E. M. JONES[1]

New technological procedures and increased production requirements in the past ten years have gained for our hardwood species a significant place in the total wood economy of the South, particularly for pulping. Pulpwood production of hardwoods has increased some 250% in the past ten years, causing concern for the continuing availability of both the soft and dense hardwood species.

Pulpwood drain prior to 1960 mainly comprised soft hardwoods, principally the gums, but present needs lean more heavily on production of dense hardwoods, primarily oaks. Needs for hardwood logs of sawtimber and veneer size continue at levels approximately the same as in the past ten years. When these needs are added to the future requirements for pulpwood, one does not need to be a prophet of gloom to foresee a possible shortage of hardwoods in certain species, sizes, and grades. Although shortages may not occur everywhere, or simultaneously, they will surely materialize in localized areas. Indeed, shortages are already felt in some localities.

Faced with a scarcity of hardwoods, those responsible for wood production have revamped policy and are earnestly considering what it takes to manage hardwood stands on a sustained yield basis. This represents a reversal from ten years ago when major concern focused on elimination, not propagation, of hardwoods. Understandably, knowledge based on critical study of hardwood management and silvicultural practices is still very meager. No phase of silviculture from seed collection and regeneration to harvesting techniques has as yet been sufficiently explored to allow development of adequate silvicultural prescriptions. Industrial, public, and private organizations are now scrambling to plug some of the widest gaps in the knowledge of hardwood culture. In sizing up where those gaps occur, regeneration looms as the first and surely a vital phase of hardwood management. To grow usable hardwoods for the future requires a reasonable measure of control over the amount and composition of regeneration. We have been asked to explore regeneration in this paper, and this is what we shall now attempt to cover, emphasizing those areas which are most important and briefly describing where we stand with respect to adequate solutions to them.

HOW BIG IS THE PROBLEM OF REGENERATION?

Some 45 million acres of forest land in the southeast have been classified as primarily hardwood sites by Putnam, Furnival, and McKnight (1960). This area excludes the Appalachian Hardwoods and those of lesser mountain chains to the west, but includes the hardwood areas of all major and minor drainages in the Atlantic and Gulf Coastal Plains, the Mississippi Delta, and lower Piedmont. A major percentage of this vast area is now understocked or consists of stands with a high proportion of unmerchantable species and cull trees. This present sad state is the result principally of past wanton high-grading practices, failure to prepare suitable seed beds, lack of an adequate seed source, grazing, and frequent recurrence of fire. The establishment of vigorous stands of the better species on these sites, i. e., regeneration of usable species and species complexes, poses perhaps the most challenging task in our efforts to assure adequate amounts of hardwood timber for all future needs.

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[1] Director and Associate Director; respectively, Hardwood Research Program, School of Forestry, North Carolina State University, Raleigh, N. C.

IS SITE IDENTIFICATION NECESSARY?

When hardwood regeneration is planned, a problem always arising is how to define and identify those sites capable of supporting satisfactory growth as distinct from those assumed to be better suited for pine. In wetter areas of the Coastal Plain and especially along stream bottoms in both the Coastal Plain and Piedmont, areas often are summarily classified as hardwood sites simply because of their current lack of pine stands or pine regeneration, regardless of the quality of existing hardwood stands. This classification, however, is too coarse for efficient allocation of soil resources. Normally a transition area exists between the pine and hardwood site. Soils and site differences between the alluvial bottom and the terrace or Piedmont hillside are often subtle, and our knowledge is not sufficiently advanced to select the most productive species to regenerate and the kinds of soils and sites that should be "off-limits" to them.

Site quality can be measured by (a) the occurrence and response of vegetation, or (b) some attribute of the environment. The vegetational response method is exemplified by the frequently flooded bottomland sites on which tupelo gum (Nyssa biflora) is found to make its best growth as shown experimentally by Klawitter (1964) and others, or the moist well-drained hardwood coves and bottoms in which yellow-poplar is found to reach dominance as reported by Smalley (1964).

Species-site plantings provide a direct method of site assessment but have the handicap of time lapse before definitive results can be gleaned. In its simplest form, adjacent rows are planted across contours. Initially, height-growth and later, volume and quality can be compared among species or species combinations to see if soil, topography, aspect, or watertable appear to influence growth differentially, and whether any useful order in differential response can be detected.

Development of site indices for hardwood species has been attempted in several ways, all with the common objective of formulating rapid but reliable methods of field determination of hardwood site potential. Broadfoot and Krinard (1959) developed three methods for site index determination for sweetgum in the Mississippi Delta. In one, site index is shown to vary inversely with the clay content of the soil at a depth of 36-48 inches and directly with amount of exchangeable potassium in the same zone up to 550 lbs/acre, the limit of their study. In another method, site index is shown to be higher on medium textured soils than on those of fine or coarse texture. Good internal drainage and absence of hardpan further enhance the site potential within each soil texture class. In a third method, site indices for sweetgum are shown to be related to soil series and phase within the Delta; obviously this method requires a type map for series and phase identification. Similarly, Phillips and Markley (1963) in the New Jersey Coastal Plain have developed site indices based on soil series, which are further subdivided by subsoil texture and drainage class.

In yellow-poplar, a study by Smalley (1964) shows that height growth increases with available water and soil depth. Both survival and growth of yellow-poplar were shown by Schomaker (1957) to decrease with elevations up the slope. At comparable elevations above the bottom, height and survival were better on north than on south-facing slopes, as Einspahr and McComb (1951) found for oaks in Iowa. Also for yellow-poplar, McAlpine (1960) found flooding during the growing season extremely deleterious in Georgia. The same author (McAlpine 1961) with in vitro tests of seedlings found flooding during the dormant season not harmful, but after three days flooding during the growing season mortality was high. Hocker (1953) found yellow-poplar to be sensitive to depth of the A-horizon on soils derived from acid crystalline rocks in the lower Piedmont. His equation was:

$$SI = 74.88 + 0.730 \text{ (Depth of A-horizon in inches)}.$$

Applequist's (1959) studies for tupelo show that site conditions characterized by poor drainage and long periods of wetness were conducive to best tupelo growth. Similar trends were indicated in the work of Klawitter (1964).

For the red oaks and cottonwood, Broadfoot (1960, 1961, 1963, 1964) has determined best growth in the Mississippi Delta to be on sites which are medium textures and inherently moist with good internal drainage. Broadfoot's papers and that of Beaufait (1956) include tables giving site indices for water, willow, and cherrybark oak on both Delta and upland sites. Examination of the environmental factors found to be limiting for the oak species studied points to the complexity of factors influencing growth. For instance, best water oak sites in the Delta were found to be those moist well-drained sites having little exchangeable sodium per acre while willow oak growth was enhanced by the availability of exchangeable potassium up to 300 lbs/acre, after which growth was reduced. It would seem that several factors including soil depth and texture, drainage, exchangeable cations, and topography all influence growth of hardwoods, but the relative importance of each and their interactions in general or on specific species are as yet unknown.

Few attempts have been made in the Southern hardwoods to relate site indices for several species growing together on common sites such as has been done in the Northern hardwoods by Curtis and Post (1962) or Doolittle (1958) in the Southern Appalachians. Nelson and Beaufait (1956) reported on surveys relating comparative site indices of eight hardwoods and loblolly pine in the Georgia Piedmont. Results from over 130 plots established show none of the hardwoods investigated to have as high site index as loblolly pine below site index 90 for loblolly. Above loblolly site 90, both sweetgum and yellow-poplar have a higher site potential than loblolly. Only on the poorer sites was the index for any of the oaks superior to sweetgum and poplar, but all are inferior to pine on these lower sites. Site index per se does not tell the whole story since it does not necessarily reflect stand density. Miller (1954) and Timko (1962) showed volume differentials of from 2 to 4 times greater for pines over mixed hardwoods in the lower Piedmont.

Delimitation of hardwood sites, and the optimum species to plant or sow on given sites pose one of the major hurdles which must be overcome in order to efficiently produce hardwoods in the South. Site identification, site index, and yield information are being sought by several groups, public and private. For instance, we in our Cooperative Program have initiated a study to determine both site indices and yields for sweetgum in the many soils on which it grows in the Coastal Plain and Piedmont. Information on individual tree growth, stand structure, and physiographic soils information is being collected on some 300 plots for analysis.

SEEDING HABITS

For satisfactory progress in both natural and artificial regeneration, it is essential that periodicity of seed production, phenology of flowering, time of seed ripening, methods of dissemination, germination, etc., be unequivocally understood. Detailed information is available for some species, but only partly for others. The Woody Plant Seed Manual (1948) contains much valuable data on seed yields, time of seeding, collection, extraction and storage methods, and phenological information for many species, but about twenty years have elapsed since the data were compiled. The badly-needed updating work is now underway at the Eastern Tree Seed Laboratory in Macon (Jones, 1962). The Manual information has been recently strengthened on seeding habits by such work as that of Boyce and Kaeiser (1961) and Taft (1962) for yellow-poplar, Minckler and McDermott (1960) and Tryon and Carvell (1962) for oaks, and by Fenton (1964) and Schmitt (1964) for sweetgum. Seeding habits also are covered in a general way in the silvical characteristics of individual species published by various U. S. Forest Service Experiment Stations. Some phenological observations and factors affecting seed yields are being obtained each year to bolster our knowledge of reproductive behavior in hardwoods. For example, in our current program we are making such observations on sweetgum, certain of the red oaks, swamp black gum and tupelo. To compile a detailed list on seeding habit and related facets of seed production at this time is beyond the scope of this paper, but we do want to stress here the great importance of such information to both silvicultural and genetic practices which are being developed for hardwoods.

SITE PREPARATION

For successful establishment of hardwoods, naturally or artificially, some type of site preparation appears necessary. For cottonwood it is clearly a must, and for other species some degree of preparation is indicated. As yet, except for cottonwood, no factual data are available on net value of increase in yield attributable to different kinds or degrees of site preparation; however, we feel that sweetgum, tupelo, swamp black gum, ash, and others require full sunlight for best germination, establishment and growth. In seeding we know the soil must be exposed. On many sites reduction of competition from undesirable species must somehow be achieved, preferably at the time of initial establishment.

Site preparation requirements for hardwoods can be somewhat different from that for pine. In swamps, water or soil moisture may restrict the period and kind of mechanical equipment used on an orderly basis. Compaction and puddling may prove to be important. Fire at the time of stand renewal is beneficial, but its use is restricted to the drier sites and reasonably continuous fuels. Chemical methods are not sufficiently selective to use beyond an initial application, i.e., they cannot be used for subsequent release as in pines, except perhaps Fenuron (Dybar) where yellow-poplar is to be favored.

Currently, site preparation studies are underway testing the biologic and economic feasibility of site preparation by chemical and mechanical means. With luck, in a few years we will know the feasibility of these techniques.

STAND ESTABLISHMENT

Hardwood regeneration differs from pine in that for some species cuttings can be used (i.e. cottonwood, willow, sycamore), and in natural regeneration coppice is often feasible. In planting, seed source obviously is as important to hardwoods as to conifers, though it may involve greater complicating factors such as root suckering, layering, etc. which reduce degree of independence. The task of seed collection itself can be formidable unless collection is made behind logging operations, and even then it can be laborious and costly.

Seed cleaning, processing, and presowing treatments are reasonably well established, although these are continually being modified as new techniques are firmed up. The Woody Plant Seed Manual (1948) contains still the most comprehensive coverage of recommendations for seed collection, storage, and pretreatment, but much information in it has been superseded by later investigations. Many nurserymen have devised their own collection and seed handling techniques, but few of these prescriptions find their way into print. Storage techniques for most Southern hardwoods can be found in the recommendations of Jones (1962).

Nursery practices, i.e., sowing methods and rates, pre- and post-emergence treatments, seedbed maintenance, and seedling lifting, grading, and packaging comprise another area for which nurserymen have devised their own techniques. The lack of uniformity in methods is frightening. For instance, several nurseries sow sweetgum at a density to yield 60 seedlings per square foot (Coleman, 1962); Webb (1964) however, recommends seedling densities of 15-25 per square foot. Similar recommendations of 25 per square foot for sycamore seedlings have been made by Vande Linde (1960). At N. C. State our target is about 25 per square foot. Sowing densities to achieve desirable seedling sizes are being determined. Preliminary information for seedling densities for several oaks is available from the studies of Shipman (1962), and for yellow-poplar by Shipman (1962), Lovin (1959), and others.

PLANTING

Lower seedbed densities are necessary to produce husky, high quality seedlings which for several hardwood species have definitely shown better survival and growth performance when outplanted. Ike (1962a) found seedling height of sycamore correlated to root collar diameter and this in turn significantly correlated to first year height growth. Mean height growth the first year in the field increased from 2.59 feet for seedlings less than .30 inch root collar diameter to 5.90 feet for seedlings greater than .50 inch at the root collar. Significant differences were also apparent in survival, although only 5% differences separated the larger from the smaller groups. Similar trends are becoming apparent in sweetgum and tupelo in studies we have installed (Terzi, 1965) and in yellow-poplar (Lovin, 1959).

Planting techniques for hardwoods are not necessarily different than for pines, except where cuttings can be used. Some species respond to pre-planting treatments including top pruning, root pruning, or both. Talli (1962) showed top pruning of yellow-poplar to be feasible so far as form and growth are concerned. Talli also showed that after five years in the field, there was no difference in bar-planted growth or stem form of yellow-poplar as against center hole mattock planted seedlings. Pruning recommendations by species along with other planting information for several of the Southern hardwoods have been summarized by Bonner (1964).

At this juncture we can say little about spacing. Trials have been installed utilizing spacings from the very close to wide. Spacings are expected to show differences by species, site, and final product desired. Wider spacings could be used if only pulpwood is desired, but for sawtimber rotations closer spacings with more opportunity to select for final crop trees of high quality seem preferable. Hand planting has been the method most often used but there is no reason why on firm uplands and bottomland terraces machine planting can't work, especially if the equipment is modified to handle the generally greater root mass of most hardwoods.

The satisfactory methods worked out for planting cottonwood cuttings could possibly be devised for other species as well. Successful rooting procedures have been found for yellow-poplar (McAlpine, 1964) and for sweetgum (Brown and McAlpine, 1964). Although McAlpine (1963) found seedling sycamores to survive and grow better than rooted cuttings, and feasible methods for rooting sweetgum and yellow-poplar on a commercial basis are not yet available, the possibilities for developing successful methods have not been exhausted. Maisenhelder (1954) contends that for cottonwood, willow, and possibly sycamore and other easily-rooted species, establishment for cuttings should be cheaper than by using seedlings.

Improving hardwood establishment through use of fertilizers holds more promise than with pines. Most hardwoods are more sensitive to increased fertility levels; and their initial height growth rates are greater, giving greater assurance of successful competition against surrounding weeds. This seedling reaction has been successfully demonstrated for yellow-poplar and sycamore in the Georgia Piedmont (Ike, 1962b) and for black locust in Maryland (McQuilkin, 1946). At the end of the fourth growing season after outplanting, yellow-poplar fertilized with diammonium phosphate on a well-drained small streambottom exceeded height of controls in every level of fertilizer tested. Heights in plots fertilized with 500 pounds per acre exceeded height in control plots by 100 percent, the average being 8.38 feet and 4.13 feet, respectively. In plots fertilized with 1000 pounds per acre, fourth year average height was 10.21 feet with no difference in survival among treatments. In similar tests, sycamore seedlings fertilized at the rate of 1100 pounds of 10-5-5 per acre had a mean height of 6 feet at the end of one year in the field as compared to 3.5 feet for controls (Ike, 1962c). A similar response was noted in sycamore by McAlpine (1963) using 8-8-8 at the rate of 4 ounces per seedling.

Although not constituting a fertilizer treatment, burning of heavy accumulations of logging slash was found to change the concentration of minerals (P, K, Ca, etc.) in the surface soil and to result in a spectacular increase in the growth of yellow-poplar which attained a height of 23 feet in the ash as against 15 feet outside the burn nine years after planting (Terzi, 1965).

SEEDING

Direct seeding of hardwoods offers an alternate approach to artificial regeneration just as it does for pines. Before such techniques can be widely used, however, satisfactory methods of discouraging predators must be devised. Results of direct seeded oaks in the Piedmont and mountains of North Carolina by Sluder et. al. (1961) show this method to be effective if acorns are seeded to a depth of one inch on mineral soil. Protection with screens was found to be unnecessary and actually harmful in some instances. An Arasan 75-Endrin 50-W mixture on acorns was shown to be ineffective against predators, treated acorns being readily eaten by both squirrels and mice when other foods were in short supply (Klawitter et. al. 1963). Development of an effective repellent would aid materially in oak regeneration by allowing wider use of direct seeding. With yellow-poplar, protection from predators also appears to be necessary for successful establishment (Sluder and Rodenbach, 1964).

In seeding hardwoods, exposure of mineral soil, planting of seed at tolerable depths below the soil surface, and reduction of seed loss to birds and rodents are major problems that must be solved. They appear at this stage generally more critical than with pines. Techniques developed for pine have resulted in wide acceptance of direct seeding at reduced costs. Similar techniques, if successfully developed, will put hardwood regeneration in a very favorable light.

NATURAL REGENERATION

Natural regeneration in many instances has been achieved without intent or design, and most of the hardwood stands existing today result from operations where accident has been the silviculturist. Under these circumstances, directed natural regeneration would seem to deserve serious consideration for stand establishment. Most of our hardwoods seed prolifically either annually or periodically. With adequate seedbed preparation and complete protection against fire after a seed catch, satisfactory stands should frequently result through natural regeneration. We can already speculate for individual species the probable value of clearcutting in strips, or with seed trees, or use of shelterwood where protection from insolation seems important in the initial seedling stages, but critical studies of harvest cutting methods to secure regeneration are still needed. Not only seed matured at the time of cutting but also that stored in the forest floor must be considered. There is mounting evidence that seed of tupelo, white ash, hackberry, yellow-poplar, and other hardwood species remain viable for a year or more in the forest floor. Following removal of the overstory such seed can produce an abundant stand of natural regeneration.

Most of the existing oak stands of the Eastern United States are believed to be the result of coppice regeneration (Roth and Sleeth, 1939). Our observations lead us to believe that several other species, particularly sweetgum, frequently becomes established through coppice regeneration where harvest cuts are followed by extremely hot burns or where overstories of pine are wiped out by fire. Coppice from root sprouts develop into satisfactory stems, but sprouts originating high on the stump are likely to be more vulnerable to entrance of decay from the deteriorating parent stump (Roth and Sleeth, 1939). Species vary as to vulnerability. Tupelo appears surprisingly immune to basal rot despite the high stumps that are invariably left. Johnson (1964) believes sweetgum sprouts of low origin may be superior to seedlings because of their more rapid initial height growth.

ANIMAL LOSSES

Hardwood regeneration, once established, is perhaps more vulnerable than pine to losses or injury from deer, rabbits, cotton rats, mice, etc., as well as from domestic livestock. With livestock the answer is complete exclusion of grazing, but with wild animals and rodents no satisfactory control programs have yet been devised. Fencing against deer is too costly, and against the smaller marauders clearly impossible on a meaningful scale. In our own experience, we have observed deer to have cropped back virtually every seedling on a three-thousand acre tract annually for five years. Rabbits, mice, and other rodents locally are capable of inflicting severe losses.

Each animal apparently shows enough preference so that seedlings of certain tree species will be bypassed if more palatable specimens are present. Results with repellents have been too erratic and costly to provide a satisfactory solution to date. It would seem that relief from losses to game and rodents should be sought through other approaches than reliance on repellents. Deer herd size is subject to some control by regulating hunting; however, this approach has not yet shown sufficient promise of success. Poisons have been tried but these too often meet with failure. In hardwood establishment, development of control measures to prevent undue losses to wildlife presents a challenge which must be met to insure consistent success in forest renewal with desired species.

SUMMARY

Increased demands for Southern hardwoods by all segments of the wood-using industry, but particularly the pulpwood industry, have suddenly emphasized the very genuine need to begin developing the silvicultural and management techniques necessary to provide a continuing supply of both soft and firm-textured hardwoods. This interest represents a reversal of the pulp industry policy of only a decade ago, when large expenditures were made to kill hardwoods and convert all sites to pine.

Although suitable practices for hardwood production have been under study and development for a good many years, many gaps still exist in the information for specific areas and regions, and for many desirable species. To insure efficient production of wood in the quantities called for, these voids in our knowledge must be plugged. Additional information needs range all the way from species- site relationships through techniques of regeneration to stand management and harvesting relationships.

This paper outlines the major hardwood regeneration problems by both natural and artificial methods, describes the present state of knowledge on various aspects of regeneration, and considers in a general way the problems yet to be solved to provide reasonable assurance that hardwood supplies will fulfill future needs.

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Vegetative Propagation Methods for Hardwoods

R. G. McALPINE[1]

Man has been propagating plants by vegetative means for many centuries. Grafting, for instance, was a well-known art among the ancient Greeks and Romans, and the Chinese have been successfully air-layering plants for well over 2000 years. More recently, horticulturists and pomologists have been propagating fruit, nut, and shade trees on a production scale. Some of these species are of primary interest to foresters.

Beginning about 30 years ago, foresters began selecting, breeding, and propagating trees that evidenced superior traits in an effort to increase volume and quality production. These first efforts were confined largely to conifers. Only recently have hardwoods been given serious consideration. Today, hundreds of acres of seed orchards attest to the success of the attempts to upgrade quality of conifers. Many organizations are now beginning

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tree improvement programs aimed exclusively at the selection and breeding of hardwoods.

Methods of vegetative propagation fall into three general categories: grafting, layering, and rooting of cuttings. The use of any, or all, of these may well depend upon the objectives of propagation, the particular species involved, and the age of the trees to be propagated. The objective may be to create genetically identical lines or clones for use in environmental studies where control of genetic variation is desirable, or to preserve a particular clone, or to bring trees into a central breeding area for ease and convenience of working. It may be to bring together a number of superior clones in order that natural pollination can take place among these individuals. Sometimes overlooked in tree improvement programs is the use of vegetative propagation as a simple means of providing planting stock for artificial regeneration.

Hardwoods vary in their ability to root, graft, or layer. This variation exists among trees of the same species as well as among the various species. For instance, Populus species, in general, root very easily from stem cuttings, but aspen is rooted with difficulty except from root cuttings or suckers. Oaks have been considered difficult to root or graft, yet one or two species have rooted fairly well from young stem cuttings.

The problem of aging is an ever-present factor in asexual reproduction. Sax (1962), in his review of some aspects of aging, states that probably one of the most universal and consistent characteristics of juvenile trees is the relative ease in rooting cuttings. Older trees root with difficulty, if at all. Many studies have shown that with most species of forest trees rooting drops off sharply at ages much exceeding 2 to 5 years. The success of grafting, on the other hand, is more closely associated with vigor of the ortet than with its age. It is quite possible to graft relatively old trees with some facility. This is important, for a tree must attain some degree of maturity before it exhibits those characteristics which are important in a selection program. One other important trait associated with grafting is the shortening of the period necessary for flowering and fruiting. Horticulturists have recognized this characteristic for some time, and they often resort to grafting scions on dwarfing root stocks not only to decrease the age required for fruiting but to keep the trees small and workable.

Tree improvement work now underway at a number of locations in the south includes several vegetative propagation trials. The Tennessee Valley Authority, with a long history of propagating both forest and nut trees, is presently engaged in a seed orchard program which includes several species of the more important hardwoods. Their program depends mainly on grafting and budding, although they are doing some experimental rooting. Species receiving primary attention at this time are yellow-poplar, black walnut, black cherry, and white, chestnut, and northern red oaks.

GRAFTING

Several grafting and budding techniques are used by the T.V.A. at the Clinton Nursery. Some species are best propagated by using a particular technique, others may be grafted or budded in a number of ways and at different times of the year. Bench grafts are preferable, not because of better success, but because grafting can be done during the dormant season when the work load is relatively light. If a species lends itself well to this method, dormant scions are grafted to dormant rootstocks using whip, whip-tongue, or various other grafts and stored, bound, and waxed, in moist spaghum moss in a cool place for callusing. After about 30 days the grafts are outplanted.

Yellow-poplar may be field grafted or budded on lined-out stock but usually bench grafting is preferred. Field grafting is usually done in late winter or early spring, and budding is done in late summer. Grafts are made as low as possible on the stock using a modified cleft graft with complete waxing of the union and scion. Chip budding is used primarily for simplicity, although other budding methods work very well.

Churchwell (1965), at the Pinson Nursery, Tennessee Division of Forestry, grafted dormant yellow-poplar scions to both dormant and growing rootstocks. A side graft was used to join the scion to the rather large 3- and 4-year-old stock trees. The scion and union were covered with a polyethylene bag and shaded by a kraft bag. Only 5 percent of the grafts on dormant rootstocks lived, whereas 85 percent of the grafts were successful on stocks which had begun to grow prior to grafting.

Churchwell pruned the stock trees rather heavily after it was apparent that grafts had taken. This stimulated the scions to grow so rapidly that many were damaged by high winds. His recommendations are: (1) Prune gradually in order to prevent excessive growth of the scion, and (2) Keep grafts as low as possible on the stock.

David Funk (1962), near Athens, Ohio, tried bud grafting young stock at different times of the year, in the open and in the lathe house, and with and without cutting back the tops. He found a general trend for "takes" to be rather low in June, to increase toward fall, and by September to be 100 percent successful. His recommendations are:

(1) Schedule budding between 3 and 6 weeks after height growth ends in the woods.
(2) If stock plants happen to have basal sprouts (either because of damage or deliberate cutting back), graft buds at the base of these new sprouts.
(3) Cut the tops off stock trees just above the bud about 10 days after budding.

He found little difference between trees budded in the open and in the lathe house.

The University of Tennessee has 5 yellow-poplar seed orchards, the oldest of which is 5 years. According to Dr. Eyvind Thor, [2] some of the clones began flowering within 3 years after grafting. Side grafts on lateral branches were used to establish these orchards. Dr. Thor says that he usually makes 2 grafts on each 2- or 3-year-old rootstock. All grafting is done outdoors and the union and scion covered with a liquid plastic wound dressing. Plastic and kraft bags used earlier were discarded as being unnecessary.

Budding by the T method in August and September has given fair results, but vigorous shoot growth presumably due to nursery fertility often leads to damage from early fall frosts.

Weyerhaeuser, in eastern North Carolina, has begun a clonal seed orchard program using dormant scion material grafted by the cleft or side method to potted wildings of yellow-poplar. All work is performed in a polyethylene-covered hot house where temperatures are kept above freezing. Mr. Peevy [3] obtains wildings, approximately 2 years of age, and pots them in 14-inch fruit baskets. Scions are taken from selected trees and grafted the next day to stock which is just breaking dormancy. Grafts are outplanted in the seed orchard after danger of frost is over. Mr. Peevy tells me that he locates grafts for good diameter match of scion and stock rather than specifically high or low on the root stock.

The Southeastern Forest Experiment Station, at Bent Creek near Asheville, North Carolina, has begun an improvement program for mountain hardwoods. Yellow-poplar selections are being grafted or budded to potted nursery stock in the greenhouse. Dormant scions are shot from the crowns of trees selected for their apparent ability to sprout heavily or remain relatively free of epicormics. Grafting is done on forced rootstock and successful grafts will be outplanted in spring along with single parent progeny from the same parents.

Black cherry, like yellow-poplar, can be easily propagated by grafting or budding. Horticulturists have been propagating species of Prunus for years, and techniques are well established. Hatmaker, [3] at Clinton Nursery, T.V.A., prefers to bench graft cherry during the winter slack period, but he has also field grafted it during early spring, handling it very much like yellow-poplar. Slunder [3] at Bent Creek, is doing similar propagation work with some success.

Black Walnut is field grafted at the Clinton Nursery using a modified cleft graft on decapitated stock. This species does not lend itself well to bench grafting. One of the problems recognized by people who graft black walnut is lengthy bleeding of the decapitated stock once dormancy is broken. Hatmaker recommends waiting until bleeding stops before attempting to graft. Budding done in late July or August is not affected by bleeding if pruning is delayed until the following spring. It is preferable to delay pruning so buds remain dormant over winter to prevent injury from early frosts.

Weber (1961), speaking at the annual meeting of the Northern Nut Growers Association, gave 28 specific recommendations for the vegetative propagation of several nut trees including black walnut. Among these, he recommended grafting black walnut on black walnut

[2] Personal communication.

[3] Personal communication.

understock, not grafting on bleeding stock, use of understock less than 2 inches in diameter use of splice graft where stock and scion are same diameter, use of modified cleft graft where scion is smaller than stock and stock is not over 1 inch in diameter, and the use of either the cleft graft or the bark graft when the stock is more than 1 inch in diameter.

Oaks as a group are hard to handle. Wright (1953), at the Second Southern Conference on Forest Tree Improvement, was prompted to say that oaks are nearly impossible to root and are difficult to graft. Today, some oaks are being grafted and budded. Hatmaker, of T.V.A. using a modified cleft graft, has field grafted white, chestnut, and northern red oaks. White oak has been grafted on sawtooth oak with fair success. Northern red oak has been budded in the field using both chip and patch budding. Patch budding appears to be more likely to succeed at this time. Bleeding is a problem in oaks as in walnut and grafting should be delayed in decapitated stocks until bleeding ceases.

Weyerhaeuser presently has about 8 acres of seed orchards in eastern North Carolina. About 800 ramets from 25 selections of sweetgum have been outplanted thus far. Of particular interest is the fact that Mr. Peevy was not able to graft sweetgum during the dormant season, but was successful in field grafting in late June and throughout the month of July. All were side grafts without pruning of the stock. Pruning was begun after the scion began to grow. Sweetgum proved to be a persistent sprouter and pruning became a continuous job throughout the first season. Takes for both sweetgum and yellow-poplar ranged from 65 to 70 percent at the Weyerhaeuser Orchard.

At Stoneville, Mississippi, the Southern Forest Experiment Station is conducting research in vegetative propagation of sweetgum and other hardwoods. Bottle grafting of scions having flower buds is being used as a technique in controlled pollination. More about this technique is given in Dr. Webb's article on improvement of sweetgum.

Red maple grafting at Weyerhaeuser has been disappointing. So far, all grafting has been done on 1-year-old wildings which have been dug and lined out in the orchard. Successful grafts, thus far, have numbered less than 10 percent. Mr. Peevy is planning to change from dormant season grafting to summer grafting in an attempt to increase the number of successful grafts.

Most, if not all, of the important hardwoods have been propagated vegetatively by one or more methods of grafting or budding. Included are the maples, oaks, ash, elms, persimmon holly, honey locust, cherry, dogwood, chestnut, walnut, hickory, pecan, yellow-poplar, sweetgum, and even poplar and willow, normally considered so easy to root that grafting is unnecessary.

There are some problems and inadequacies in the grafting method which limit its use or make it less desirable than other methods. For instance, own-rooted trees are not obtained by either grafting or budding. In propagation for disease resistance, in many cases, the clonal root system is desired. This is true also of remets propagated primarily for studies of environmental effects. The problem of incompatability of scion and rootstock is often evident only after 5 or 6 years of apparently good growth.

LAYERING

Layering involves the rooting of plant parts while they are still attached to the ortet Often this can be accomplished by simply bending down the main stem or branch, wounding by girdling, scraping or strangling, and covering the wounded part with soil or organic matter. After rooting, the terminal part is removed from the parent and outplanted. Foresters are generally working with trees much too large to bend over and they find it convenient to take the rooting media into the crown of the tree. This is commonly called air-layering. The part to be rooted is wounded in some manner, a rooting hormone is brushed on the wound surface or dusted on a handful of moist spaghnum moss which is then pressed around the wound, and the whole covered with plastic film. Often, aluminum foil is wrapped around the layer to help prevent build-up of heat, and some splinting arrangement is made to keep the wind from breaking the layer.

Bonner (1963) has done some of the most recent work in air-layering. He treated green ash, sweetgum, cherrybark oak, nuttall oak, and yellow-poplar during April, June, and August Yellow-poplars were 4 years old and the others ranged from 5 to 20 years of age. Air-layering succeeded in April and June on green ash, sweetgum, and cherrybark oak. Green ash also rooted in August. Two out of 50 layers on nuttall oak rooted in late summer. Yellow-poplar did not root.

Air-layering is very limited in its use. Layering in the crowns of large hardwoods, most with very brittle branches, is very hazardous. On younger trees or grafts, however, the method may provide a convenient way of producing own-rooted stock of species which are difficult to root by cuttage.

ROOTING OF CUTTINGS

Rooting or cuttage, as it is often called, is the simplest and least expensive method of vegetative propagation. It is probably the only method by which clones of forest trees may be mass produced economically. The technique involves planting a short stem or root section in a suitable medium, such as sand, vermiculite, perlite, or soil and waiting for a few weeks for roots to form.

The natural rooting ability depends primarily on species and age. As mentioned earlier, species such as Populus root fairly easily, whereas species such as the oaks root with difficulty. The age of the tree from which the cuttings are taken has a very definite effect on rooting. As a rule seedling or sprout material roots much easier than branch or stem material from trees more than 2 or 3 years old.

Rooting may also depend on factors which can be controlled. The part of the tree made into cuttings, for instance, may be very important, as is the time of year cuttings are taken. Of equal importance is the rooting media, rooting hormones used, the rooting environment, and techniques used in handling the cuttings.

Cottonwood and sycamore are species which root so easily that unrooted cuttings may be planted directly in the field. Rather large acreages in the Mississippi Delta are devoted to the propagation of cottonwood cuttings for planting, and each year several thousand acres in the South are planted to cottonwood. Sycamore cuttings have been planted experimentally, and early growth compares favorably with that of medium grades of seedlings. Survival of cuttings, usually around 60 percent in field plantings, is less than seedlings which with reasonable care should exceed 90 percent.

Other species are not rooted as easily. The use of mist systems, however, allows rooting of greenwood cuttings during the growing season and has materially increased rooting in some cases. Yellow-poplar, previously considered very difficult to root, was rooted easily by Enright (1957) in a greenhouse mist bed. Cuttings from the lower crowns of trees 30 years old and older were treated by dipping in aqueous solutions of indolebutyric acid (IBA) at 3 concentrations and were planted in a sand media under intermittent mist. Cuttings taken during August and dipped in a 2 percent solution of IBA rooted best (78 percent). Enright does not mention survival or growth after transplanting.

We attempted for several years at Athens to determine the relation of age to rooting by taking cuttings from trees of 5 age classes and using a modification of Enright's method. Our beds were constructed outdoors and the media used was fine sand mixed half-and-half with peat moss. Cuttings were collected in April, May, June, and July of 1959 from yellow-poplar trees ranging in age from 1 to over 60 years. The best rooting obtained was 36 percent for the 1- to 5-year class in April. In May, 13 percent of the cuttings, from the 5- to 20-year class, and 5 percent, from the 20- to 40-year class, rooted. One cutting taken in May from 40- to 60-year-old trees rooted, and none rooted from trees older than 60 years.

In 1960 the rooting bed was elevated above ground for better drainage; three kinds of media were used. Cuttings were collected in late May from the same age classes, and in most cases the same trees, as in 1959. These were treated as before by dipping in IBA and planted in fine, medium, or coarse sand. Cuttings were examined periodically, and those that rooted were lifted and potted for use in another study. The type of media used had a very definite effect on rooting percent. In fine sand, 36 percent rooted; in coarse sand, 17 percent; and in medium textured sand, only 8.0 percent rooted. In this trial 19 cuttings from trees over 60 years of age rooted.

It became apparent from this study that age influences not only rooting ability but also the subsequent survival of transplanted cuttings. After one year, 19 transplants of the 1- to 5-year class were living and in good condition, whereas only one survived from the 5- to 10-year class and only a single propagule from the 20-year-old trees was living but in poor condition. All others died.

More recently, using soft tissue cuttings from stump sprouts, we have been able to root from 60 to 100 percent of almost all clones tested, McAlpine (1964). The yellow-poplar ramets propagated from this lush juvenile material have survived and have grown exceedingly well, although taken from stumps as old as 165 years and transplanted in mid-summer. The media used was composed of one-half fine sand and one-half well decomposed sawdust. All cuttings were dipped in a powder containing 0.8 percent indolebutyric acid and mist was applied intermittently during daylight hours. The ramets were planted during the winter following rooting in a clonal orchard where in the succeeding 2 years they have grown sufficiently large to be cut back and allowed to sprout. Cuttings obtained from these stumps will be used to multiply selected clones to furnish material for use in environmental studies.

We anticipate some reluctance in cutting selected yellow-poplar trees in order to obtain sprouts for rooting. To eliminate this problem, we suggest either partial girdling to stimulate sprouting, or the grafting of branch material, and then cutting back the scion to obtain sprouts that will root. We have used the latter method at Athens and have obtained 20 percent rooting. Once we have rooted cuttings the problem of future multiplications of clonal material is solved.

Sweetgum behaves very much like aspen. It sprouts and suckers prolifically but can be rooted only sparingly from cuttings. Usually, any species which suckers can be propagated vegetatively from root cuttings (Adriance and Brison, 1955). At Athens we were successful in rooting only a few sprout cuttings, so we tried root cuttings. Roots from several 3-year-old and three 20-year-old trees were dug in mid-July, cut into 4-inch sections, and planted in serial order in a medium of fine sand and peat moss (Brown and McAlpine, 1964). By October from 20 to 94 percent of the root sections had budded and produced new roots. Cuttings from younger trees budded earlier and shoots grew faster than cuttings from the 20-year-old trees. Kinetin applied as an aid to budding was ineffective.

Other tree species which may be propagated from root cuttings include mimosa, black locust (Swingle, 1937) honey locust (Stoutemeyer, et al, 1944), and elm (Doran, 1949; Schreiber, 1963).

Oaks still remain difficult to propagate. Thimann and Delisle (1939) rooted 82 percent of the cuttings taken from basal parts of 4-year-old northern red oaks after treatment with indoleacetic acid. Recently Farmer (1965) reported rooting of as high as 78 percent of cuttings taken from 1- to 4-month-old cherrybark oak and treated with indolebutyric acid. Our trials at Athens to root soft tissue sprout material from white oak stumps failed. The prospect of rooting cuttings taken from the crowns of mature trees is not promising at this time.

Red maple is a species which has received considerable attention from propagators. Snow (1941), rooted stump sprouts of red maple in an outside rooting bed after treatment with indolebutyric acid. Best results were obtained by soaking cuttings for 6 hours in an aqueous solution of IBA at a concentration of 200 mg. per l. Among the 24 clones tested, rooting varied from 17.5 to 97.5 percent, indicating the possibility of clonal differences in rooting ability. In later work, Snow (1942) found that the rooting ability of different clones of red maple was apparently correlated in some way with the sex of the tree. Average rooting for male trees was 52 percent and for female trees 33 percent. In a later study, Edgerton (1944) used the same clones and the same treatments used by Snow and found that the rooting of cuttings was more closely associated with seeding habits of red maples than with sex. He also found that cuttings from the lower portion of the crowns rooted an average of 49 percent, whereas cuttings taken from upper-crown positions rooted only 27 percent.

At Athens we have found that 1-year-old greenwood cuttings from stump sprouts will root at better than 90 percent within 2 or 3 weeks. All rooting is done in an outdoor mist bed in a media of sand and sawdust at a 1 to 1 ratio. The basal portion of each cutting is dipped in Hormodin No. 3 (0.8 percent indolebutyric acid in talc). The very small sprout tips and the large basal portions are discarded.

In summation it is well to repeat that the method of propagation which is chosen depends (1) upon the objectives of propagation, (2) the species we wish to propagate and

(3) the age of the trees to be propagated.

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Breeding for Disease and Insect Resistance in Hardwoods

E. RICHARD TOOLE [1]

Pest resistance often is the major consideration in tree breeding and always must be taken into account.

Although little breeding for pest resistance in southern hardwoods has been undertaken, the need for it has been recognized. It should receive increased attention because of: (1) the disadvantages of pesticides; (2) the probable increase in pests with increase in hardwood planting; and (3) the ease of vegetatively propagating some species.

I will discuss resistance and breeding methods as they relate to southern hardwoods.

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HOW RESISTANCE IS TESTED

By resistance, we generally do not mean immunity but only a greater ability than normal to withstand some pest.

Disease resistance is governed by morphological or physiological variation of the host. Thus, such morphological variations as a slightly thickened epidermis, cork formation, or lignin or cutin development may prevent the germ tube of a fungus spore from entering the host plant. Physiological variation may prevent the development of the disease. For example, attack is prevented when the cell sap of a host is so concentrated or so acid that a fungus cannot thrive or live, or when substances toxic to the fungus are present in the cell protoplasm, or when growth substances essential to the fungus are lacking.

Resistance to insects usually is complex and varies with each insect and host. Segaard (1964) lists three mechanisms: (1) preference or nonpreference of the insect for the host; (2) antibiosis, the detrimental effects of the plant on the biology of the insect; and (3) tolerance, the ability of the plant to withstand an insect population that might damage a more susceptible host.

In breeding for pest resistance, the first step often is to select resistant individuals out of a host population that is heavily attacked by the pest. As Schreiner (1960) points out, however, the search should not be limited to populations that have been exposed since resistant genes often occur in nonexposed populations.

Following selection, controlled cross-pollination between resistant clones of the same or different species often leads to further improvement. To reveal the pattern of inheritance of resistance, Venkatesh (1963) proposed five methods of controlled breeding: 1) Self-pollination of resistant trees found in an infected stand. 2) Cross-pollination between pairs of resistant trees. 3) Self-pollination of diseased trees. 4) Cross-pollination between pairs of diseased trees. 5) Cross-pollination between diseased and healthy trees.

When the host is highly susceptible, induced mutation may confer resistance. Methods of inducing mutation include X-rays, radio waves, neutrons, a-particles, b-particles, chemical agents, and temperature shocks.

After the apparently resistant host has been found, either through selection, hybirdization, or induced mutation, it must be subjected to clonal tests that take into account the three-way relationship between host, parasite, and environment.

A detailed knowledge of the life history of the fungus or the biology and feed habits of the insect is basic in any resistance studies, for it enables the worker to distinguish true genetic resistance, and to separate types of resistance.

Populations of the pest must be maintained. As Painter (1951) says, "The most useful insect population is one which gives the maximum difference between resistant and susceptible types." When natural populations are not satisfactory for testing for resistance, the experimenter resorts to inoculations or caged populations. The validity of such controlled tests must be checked repeatedly under field conditions. Massive inoculations with pathogens, or cage tests with insects, may be so severe that they assess immunity rather than relative resistance.

In any test, a susceptible, well-known variety is useful as a standard of comparison.

In discussing tests for disease resistance, Schreiner (1963) stresses the need for considering (1) the establishment and progress of parasitism; (2) the nature of host resistance; (3) the biology and genetic variability of the pathogen; and (4) the effect of internal and external environmental factors on host-resistance, on pathogenicity and virulence of the pathogen, and on the host-pathogen relationship.

Artificial inoculations may be confounded by variations in the time of inoculation and the assessment of results, the procedure, and the age of the host.

DISEASES

I will review breeding possibilities in southern hardwoods under the four major types of diseases: wood rots, leaf diseases, cankers, and diebacks and wilts.

Wood rots. --Heart rots cause more volume loss in southern hardwoods than all other diseases combined. Tree species of first importance include eastern cottonwood (Populus deltoides Bartr.), sweetgum (Liquidambar styraciflua L.), and the oaks (Quercus spp.). The fact that several dozen fungi are involved will make the development of resistant clones particularly difficult. Furthermore, direct tests of resistance must be delayed until selections have become old enough to form heartwood. Although no active research is under way as yet, the possibilities are indicated by a recent study in which heartwood of cherrybark oak (Quercus falcata var. pagodaefolia Ell.) growing on good sites was more resistant to decay by Pleurotus ostreatus (Jacq.) Fr. than heartwood of trees growing on poor sites (Toole, 1963). An example from the Northeast is resistance to wood decays in Robinia pseudoacacia L.: the clone called shipmast locust is highly resistant to four rot fungi that badly damage other clones (Hirt, 1938; Toole, 1938).

Leaf diseases.--Heavy infections of Melampsora rust on cottonwood, leaf blister on oak, anthracnose on sycamore and oak, and other leaf fungi occur periodically in the South. The possibilities of breeding for resistance to these leaf diseases appear excellent. At Stoneville a start has been made on Melampsora rust. This disease has long been a serious pest of various Populus species throughout the world, and several workers outside the South have developed resistant clones (Chiba, 1964; Schreiner, 1963) that are widely cultivated in both the United States and Europe.

In recent studies on resistance to the leaf rust caused by M. laricipopulina Klebahn in Japan, Chiba (1964) found marked differences in susceptibility among sections of Populus as well as clonal differences within sections. Clones of poplar resistant to the Septoria and Marssonia leaf diseases have been selected in Italy (Castellani, 1964).

Cankers.--Most of the common canker fungi in southern hardwoods are associated with trees of low vigor growing in mixed stands. As planting expands the acreage of pure stands, canker fungi are likely to increase in importance. Cytospora canker on cottonwood has on occasion reached epiphytotic proportions in plantations in the Mississippi Delta. No breeding for resistance to cankers is being done in the South, but in other parts of the world Populus clones resistant to a number of canker diseases have been selected and propagated in the last 40 years(Donaubauer, 1964; Muhle, 1963; Persson, 1955, 1962; Schreiner 1949, 1963).

The canker or bark disease called chestnut blight has practically exterminated the American chestnut. Selection for resistance has not been successful, although sprouts have shown juvenile resistance. The failure of selection is probably due to the fact that blight resistance is not inherited as a dominant characteristic (Clapper and Gravatt, 1943). During the first 10 years after the blight struck, it was found that the oriental species were resistant. Several thousand hybrids have been produced with varieties and strains of Chinese and Japanese chestnuts, Chinese chinkapin, American chestnut, and native chinkapins. Some of the first-generation hybrids of Chinese and American chestnut show promise of resistance when grown on suitable sites. The most promising hybrid is an American x Chinese backcrossed with the American parent (Diller and Clapper, 1965).

Diebacks and wilts.--A number of diebacks and wilts occur in southern forests. At present none need prime consideration, but breeding for resistance to several hardwood wilt diseases is possible.

An example is the wilt of the mimosa tree. This disease was already widespread in the southeastern United States in 1939, when selection for resistance was started. Fifty seemingly resistant trees--scattered from Maryland to Louisiana--were located, and their seedlings were inoculated with the wilt fungus. Twenty of the seedling trees survived 8 years or longer, and two clones have been distributed commercially (Toole and Hepting, 1949).

Another example is the work with elm trees. American elms are threatened by both the

Dutch elm disease and the virus-caused phloem necrosis. Resistance to the Dutch elm disease in the uniformly susceptible tetraploid *Ulmus americana* L. seems to be governed by many minor genes, and selection has not been useful. Thus, 32,000 seedlings from seed collected from 309 elms were all susceptible: it seems unlikely that resistant strains occur in nature (Ouellet, 1964).

Arisumi and Higgins (1961) have demonstrated resistance in a clone of *U. hollandica* X (*U. carpinifolia* X *U. pumila*). Subtropical elms show resistance (Smalley and Riker, 1962) and can be crossed with the generally susceptible American elm. However, lack of cold-hardiness increases susceptibility to Nectria canker (Heybroek, 1957).

In Canada, tests were made of 146,000 American elm seedlings from seed treated with X-rays or thermal-neutrons. Four seedlings were considered promising--two from seed treated with X-rays and two from seed treated with thermal-neutrons. One of the former has remained free of symptoms after seven consecutive years of inoculation. The others showed only light symptoms in 2 of the 7 years (Ouellet, 1964).

With the virus disease of elm, phloem necrosis, selections for resistance were made among open-pollinated stock collected from an area where the disease had occurred for over 50 years (Swingle, 1942).

INSECTS

The wood borers and defoliators are the most damaging southern hardwood insects, and hence are of chief concern in the search for insect-resistant trees.

Wood borers.--Trunk-boring and bark-scarring insects attack living hardwoods and cause defects in the wood which seriously degrade and lower values for lumber and veneer. Average loss may be over $20 per thousand board feet for oak lumber. The selection of resistant strains should be encouraged. Although no research is under way, local observation by entomologists at Stoneville has discovered individual trees possibly resistant to the carpenterworm, one of the most important borers. Black locust is the only example of successful selection for resistance to borers--resistant clones have been developed (Hall, 1937 and Heybroek, 1957).

Defoliators.--Outbreaks of hardwood defoliators occur frequently. An example is the forest tent caterpillar, which seriously reduces growth in southern gum forests, destroys flowers so that no seed develops, and may kill trees and cause stand deterioration. One undamaged sweetgum was observed by Stoneville entomologists in an area where all others had been defoliated. It is likely that such a tree is resistant. There are no records of active research on breeding for resistance to defoliators, but possible resistance to leaf-feeding insects in poplar has been reported by Riker (1954) and Schreiner (1949).

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Application of Nelder's Designs in Tree Improvement Research[1][2]

GENE NAMKOONG[3]

Silviculture can be roughly described as the art and science of controlling the competitive use of the resources of the site. Thus, in one sense, site preparation and weed eradication constitute the control of interspecific competition for young trees,

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while initial spacing and subsequent thinning regulate intraspecific competition. Spacing is therefore a major environmental variable, and probably the one under most direct silvicultural control. The effects of spacing (or stand density) vary with soil and other physical factors of the environment and also with species (DeWit, 1960; Donald, 1963). It is reasonable, too, to expect that genotypes within species will vary in their responses to density, and therefore that genotypic selection may be affected by the spacing of the test environment. Present practices of testing under single spacing regimes are satisfactory only if there exists little or no genetic variance in response to a reasonable range of densities. In evaluating family performance, therefore, breeders must regard competition as an integral part of the environmental complex.

Evidence for genetic variation in density response exists, but is limited and indirect. For instance, Toda (1956) has reported genetic variation in crown diameter of Cryptomeria. Also, since density response and growth rate are interdependent variables, and genetic variance in the latter exists, genetic variance in the former must also be expected. If that variance is assumed to exist, then it is critically important that density response be measured as carefully as growth rate, especially when breeding in speceis for which the silviculture is rapidly developing.

GROWTH RESPONSE

In measurements of growth and competition effects, time or some other factor usually is the independent variable and vegetative growth the dependent variable. Several equations are reviewed by Nelder (1961), Turnbull (1963), and by Van Slyke (1964a), but the general function of Richards' (1959) is apparently flexible enough to encompass any form of vegetative growth likely to be encountered in forest genetics experiments. The equation is:

$$w^{(1-m)} = W^{(1-m)}(1 + be^{-kx})$$

where w = momentary plant or average plant yield (i.e., weight or volume),
W = the ultimate or asymptotic limit of yield, per plant,
k = growth rate constant,
m = constant determining inflexion of the growth curve,
$b = \left[\frac{w_0}{W}\right]^{(1-m)}$, and w at $x = 0$ is w_0,
x = the time or environmental variable.

If x is allowed to be time, and if the relation of $W = \frac{\text{total yield per unit area}}{\text{number of trees per unit area}} = \frac{Y}{\rho}$, is used where ρ = plant density or number of plants per unit area [as in Shinozaki and Kira (1956)], then Bleasdale and Nelder (1960) derive the equation:

$$\frac{1}{w^{\theta}} = \rho^{\theta} A + B \qquad A = y^{(1-m)}(1-e^{-kx})$$

$$\text{where } \theta = m - 1 \qquad B = w_0^{(1-m)}\, e^{-kx}$$

They also suggest using $w^{-\theta} = \rho^{\emptyset} \beta + \alpha$ where the constants θ and $\emptyset$ differ.

A less general form of the Richards' equation takes $m = 2$ and it becomes:

$$w = \frac{W}{1 + be^{-kx}} .$$

This is the so-called logistic, or auto-catalytic, or Pearl-Reed function. Using this equation and $W = Y/\rho$ as before, Shinozaki and Kira (1958) derive $w^{-1} = \rho A + B$, when $A = \frac{1-e^{-kx}}{Y}$,

$$\text{and} \quad B = \frac{e^{-kx}}{w_0} ,$$

for the linear equation for density response. The same form has been independently derived by Holliday (1960), among others. Thus, for several possible forms of the density response, the parameters can be estimated for any given time and their development traced over a time interval. Ways of estimating growth curve parameters have been investigated by Stevens (1951), Patterson (1956), Nair (1954), Nelder (1961), Day (1963) and Turnbull (1963), among others, and the reader is referred to them for discussion of estimation techniques.

The response of other traits such as branching pattern will have different forms which must also be estimated, but at possible different levels of density for efficient estimation.

EXPERIMENTAL CONSIDERATIONS

To study the relations between density and parameters of growth, branching, and other traits, it is necessary to sample an adequately wide range of densities in any single field experiment. To efficiently span a given range in densities, it would be best to adjust the sampling points of density to minimize errors in estimating the time-dependent functions, such as the A and B of Shinozaki and Kira's growth equation. If the exact form of the equation is known, maximally efficient estimators can be derived. Nelder (1962) suggests that graphical methods are sufficient when his four-parameter density equation is assumed. With the equation of Shinozaki and Kira (1958), simple linear regression techniques suffice. As conceived by Nelder, the problem is further complicated by effects due to the shape of the area available for individual plant growth. Thus, simple considerations for spacing alone are insufficient, at least for seed (Fawcett, 1964) and vegetable crops (Nelder, 1962).

If a test is to be made at high and low densities in rectangular spacings, many more trees are required at the high densities to occupy the same area as at the low densities. The result is differential precision of estimate and a great waste in trees. Alternatively, keeping equal numbers of trees per density level confounds density with size of plot and introduces error heterogeneity. With either spacing or number held constant the most serious of all defects probably is the separation of density levels into separate blocks and the inclusion of block variation in errors of estimate for the density response. Unless many density levels are sampled, the error thus introduced may be overwhelming. Also, since it is often desirable to use multiple-tree plots to minimize whthin-plot error (Conkle,1963) and avoid intergenotypic competition, the rectangular designs become excessively large. Single-tree plots, however, are economical of space and often also of trees, and should be seriously considered for density tests. The land areas (exclusive of borders) required for single-tree and three-tree plots are given in Table 1.

In order to sample a range of spacings independently of the shape of the individual plant's growing space, Nelder developed a set of systematic planting designs that deserve the close attention of foresters in silvicultural research and tree breeding. These designs are well described by Nelder (1962) and have been excellently reviewed by Van Slyke (1964) for their application to forest trees. The Continental Can Company, which is participating in the N. C. State University Hardwood Research Program, has installed two studies with Nelder's designs. International Paper Company, at its Southlands Experiment Forest, has put in studies with slash pine and Freeman (1962) reports the establishment of these designs with cocoa.

Table 1. Areas required for plots in rectangular designs without border trees. Values are sums of areas required for one replication of one family.

Number of densities sampled	Single-tree plots	Three-tree plots
	Density span = 20 — 2,020 trees per acre	
	Acre	Acre
3	.0515	.152
4	.0527	.158
5	.0541	.162
6	.0565	.170
7	.0571	.171
8	.0587	.176
9	.0604	.181
10	.0622	.187
11	.0639	.192
12	.0657	.197
13	.0676	.203
	Density span = 50 — 1,250 trees per acre	
3	.0223	.067
4	.0242	.073
5	0263	.079
6	.0284	.085
7	.0307	.092
8	.0330	.099
9	.0354	.106
10	.0378	.113
11	.0402	.121
12	.0420	.126
13	.0452	.136

Briefly, Nelder suggested five designs, four based on polar coordinates and one on a rectangular logarithmic grid. All may be made suitable to silvicultural experiments, but only two can be adapted for small family or genotypic plots of interest to tree breeders. Of these two, design la varies plant spacing while the other varies shape of the growing space.

The components of design la are angles of arc turned by successive spokes of an imaginary wheel which intersect successive rims or circumferences at specified radial distances. The intersections of spokes and radial distances are the planting point locations. A circular block of 100 trees could be laid out on 10 spokes at successive angles of 36°, with 10 trees planted along each spoke. By specifying that the shape of the growing space available for each plant is to be the same throughout the whole circular plot, and that plants at different spokes but at the same radius shall have equal spacing, Nelder derives the relations:

$$r_n = r_o \alpha^n, \text{ and} \qquad (1)$$

$$\theta = \text{constant}$$

where r_n is the radial distance of the nth plant in the spoke, radial distance of the nth circumference,

r_o is the radial distance of the starting plant in each spoke,

α is the constant determining the rate of change in growing space, and

θ is the angle between adjacent spokes.

The other three circular designs alternatively specify that:

lb) Growing space is constant, shape changes with radius;
lc) Space changes on a rectangular grid, shape changes with spoke;
ld) Space changes with spoke, shape changes on a rectangular grid.

The fifth design (2) is on a rectangular grid on which spacing and shape are varied by making each axis logarithmic. Designs lc, ld, and 2 can be used to estimate both spacing and shape parameters but require many plants and large plots. Therefore, they are most suitable for studies in which genetic and environmental effects can be confounded (as is mostly done in silvicultural work) or in which few genetic entries are used. Design lb is useful for studying the effects of growing space shape -- a factor that may be of critical importance when trees are to be planted and harvested in rows. However, if interest lies primarily in spacing and restrictions are placed on plant numbers and plot size, only design la is suitable. Further discussion will be limited to it.

For laying out the planting areas, Nelder suggests marking two planting wires at the appropriate intervals for within-spoke spacing and attaching these to a center post. The first planting point of each wire corresponds to the inner border row, the second point marks the first and most densely crowded experimental planting location, the third marks the next most dense. If the two wires are joined by a length of wire equal to [$2(r_{\text{outer border}})$ sine $(\theta/2)$] at their outer ends and the three wires pulled taut, the angles between the spokes will be θ and the planting points along the spokes easily marked. By leap-frogging one wire over the other, the successive spokes of the circular plot can be turned and the planting spots marked. A segment of a plot is shown in Fig. 1. It may be easier, however, to make the layout with a transit, since tree plots are quite large.

SPECIFYING DESIGN PARAMETERS

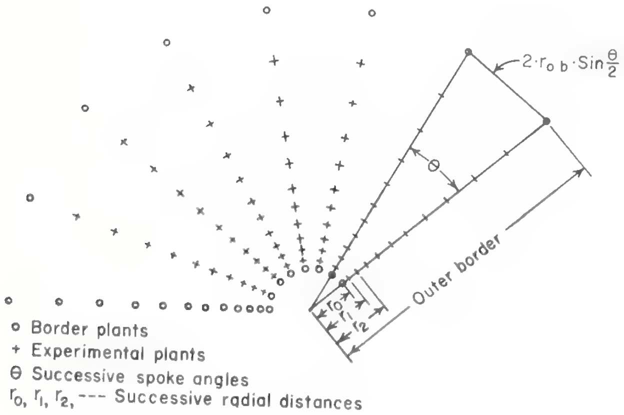

Figure 1 -- Segment of a variable-density plot.

The design parameters are easily computed if the growing space of the most and least crowded experimental plants and the number of plants per "spoke-plot" (N) can be specified. If the plot shape is also specified by the desired ratio (β) of within-spoke spacing to between-spoke spacing α, θ, and r_o can be found by using the equations:

$$\log \alpha = (\mathrm{Log}\ A_n - \mathrm{Log}\ A_1) / (2N - 2), \tag{2}$$

$$2 \tan(\theta/2) = (\alpha - \alpha^{-1}), \tag{3}$$

$$r_o = \sqrt{4A / [\tan(\theta/2) \cdot f(\alpha)]}, \tag{4}$$

where $f(\alpha) = \alpha^2 [(1 + \alpha)^2 - (1 + \alpha^{-1})^2]$,

where A is the area of the n^{th} or first plot and all other symbols are as given by Nelder. It is simple then to compute r_1, r_2, etc. by formula (1). Formulae 3 and 4 differ from Nelder's and are discussed in Appendix A.

If lengths of spoke-plots are uniform, planting genotypes or families one to a spoke, or in three adjacent spokes, will achieve freedom from intergenotypic competition. The larger angles become awkward to handle physically and stretch the concepts of linear intraspecific competition. If the number of spokes is less than that required for a full circle, guard spokes of the sector borders are required. Since the minimum number of spokes per center is 3, any number between 3 and 360/θ can be used, and successive centers can be located for as many sets of plots as desired. Some possible arrangements are shown in Figure 2. I would suggest that border spokes be maintained to enclose the test spokes and that they be made up of "controls" so that soil trends within plots may be adjusted for. Also, the numbers of spokes per center may be varied in order to "turn" the plot sequence in any desired direction. A great deal of freedom is thus obtained in replication shape and arrangement of genotypes, and one may construct randomized block or any partially balanced incomplete block design.

It may be specifically desired to test the response of genotypes to particular competitors or to isolate genotypes from other specific competitors. In such cases, the use of the same or different "center-hubs" is indicated. For instance, in studies involving families of different provenances in which interprovenance competition is undesirable, separate provenance circles or sectors could be established and the spokes within each could be allocated to the genotypes within each provenance.

In general, two conflicting restrictions are imposed by the nature of tree breeding, particularly in hardwoods. These are lack of knowledge of the size and form of genetic variability in density response and the desirability of distributing the usually small numbers of seeds among several environments. The first factor forces the experimenter to span a wide range in density levels and the latter restricts the number of levels he may sample in any one plot. If he wishes to estimate early density responses, close spacings are required; as many as 2,000 trees per acre may be needed for species with slow early growth. In order to sample among the light or late density responses such as occur at the

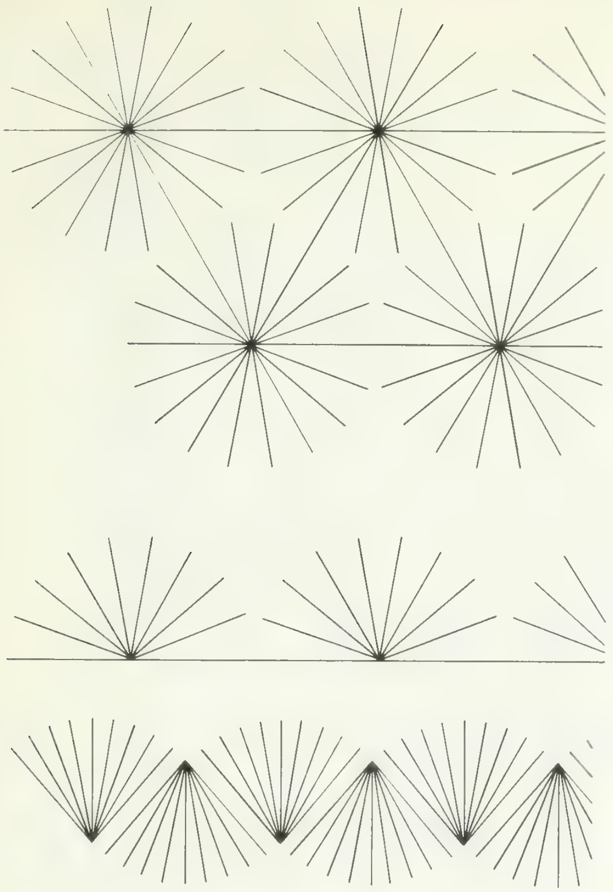

Figure 2 -- Alternative spoke arrangements.

lower limit of competition with mature trees, as few as 20 trees per acre may be required. In fast-growing, short-lived species, the span may be cut to approximately 50-1,250 trees per acre or less. Much smaller intervals will often be desired, but these two are chosen as examples to illustrate the difficulties encountered at the extreme levels of testing.

For these spans, a minimum of four and a maximum of 13 trees would normally be available for each plot for each family. The minimum of four is required for precision in estimation and a miximum of 12 or 13 per replication will rarely be exceeded. Several optional planting regimes may be followed. These are given in Table 2, according to span of densities (either 2,000 or 1,200), and for roughly square and roughly rectangular growing-space shapes. For each plot size of 4 through 13 plus two border trees, the table shows planting point distance from the center hub and the density represented by the space available. The area, number of spokes, angle θ, and α are given for each plot size. The departure of the plants from the center of the space is given as β, a percentage of the growing space length. If there are more test families than spokes, more centers are required and analysis for incomplete blocks may be followed. The two shapes chosen in Table 2 include one in which within-spoke spacing equals that between spokes at any planting spot which would be suitable if intergenotypic competition were desired or if border rows were used. The other shape has within-spoke spacing at half that of between-spokes. This forces the earliest competition to be within genotypic families and delays intergenotypic competition. It also forces the rhomboid shape of the growing space into greater deviation from circular than for the first case.

In no case does the plant occur at the center of the space available to it, but since the angle between successive spokes is constant, the only dimension of concern is the non-central location of the plant between its two neighbors on the same spoke. Nelder suggests that a departure of less than 5% from the intraspoke distance of the theoretical growing space may be acceptable for vegetable crops. Small deviations require slow increases in spacing. For a maximum non-centrality of 5%, α must be less than 1.1. Otherwise, there will be bias if intergenotypic differences occur in response to shape variations. Because trees have more time to make appropriate growth adjustments, non-centrality and non-regularity of the growing space perimeter probably affect them less than annual crops. It would be reasonable at least to assume that such effects would rapidly diminish with age and that in testing for many traits considerable latitude can be afforded at the wider spacings.

ALTERNATIVE RADIAL SEQUENCES

Nelder's designs allow spacings to vary systematically but keep the plots in reasonable proximity. They require relatively few guard plants and are economical of experimental plants or area. However, several difficulties exist in the direct application of design la to forest genetics. Primary among these is the excessive sampling of low densities, with consequent waste of land area. For example, when a plot size of six spans the 50-1,250 interval, all but one tree are at the lower half of the density range. One alternative is to establish two series of tests, one for the upper, and one for the lower densities. This course will introduce plot errors into the response curve and may only lightly sample the middle range of densities, which is likely to be of greatest practical importance.

Another alternative is to relax the requirement for constant shape of growing space and to allow variation in shape to be confounded with density. Nelder suggests that one of his

Table 2. Planting Points for Nelder's Design 1a.

Density Span 20 - 2020

Growing Space Shape 1 : 1

Plot Size 4	$\theta = 45.92^\circ$	$\alpha = 2.1580$		β(max.) = 18%		No. of experimental spokes = 6					Area per plot = .147 acres					
	Plant. Pts.	2.36	5.09	11.00	23.74	51.24	110.58									
	Density		2020	434	93	20										
Plot Size 5	$\theta = 33.89^\circ$	$\alpha = 1.7800$		β(max.) = 14%		No. of experimental spokes = 9					Area per plot = .137 acres					
	Plant. Pts.	4.10	7.31	13.02	23.18	41.28	73.49	130.86								
	Density		2020	637	201	63	20									
Plot Size 6	$\theta = 26.88^\circ$	$\alpha = 1.5864$		β(max.) = 11%		No. of experimental spokes = 11					Area per plot = .149 acres					
	Plant. Pts.	5.96	9.46	15.00	23.81	37.77	59.92	95.07	150.83							
	Density		2020	803	319	127	50	20								
Plot Size 7	$\theta = 22.29^\circ$	$\alpha = 1.4690$		β(max.) = 10%		No. of experimental spokes = 15					Area per plot = .140 acres					
	Plant. Pts.	7.87	11.56	16.99	24.96	36.67	53.86	79.13	116.24	170.77						
	Density		2020	936	433	201	93	43	20							
Plot Size 8	$\theta = 19.05^\circ$	$\alpha = 1.3904$		β(max.) = 8%		No. of experimental spokes = 17					Area per plot = .154 acres					
	Plant. Pts.	9.81	13.64	18.97	26.38	36.69	51.02	70.94	98.65	137.17	190.73					
	Density		2020	1045	540	279	145	75	39	20						
Plot Size 9	$\theta = 16.63^\circ$	$\alpha = 1.3343$		β(max.) = 7%		No. of experimental spokes = 20					Area per plot = .160 acres					
	Plant. Pts.	11.77	15.71	20.96	27.97	37.33	49.81	66.47	88.69	118.35	157.92	210.73				
	Density		2020	1135	637	358	201	113	63	36	20					
Plot Size 10	$\theta = 14.76^\circ$	$\alpha = 1.2922$		β(max.) = 6%		No. of experimental spokes = 23					Area per plot = .167 acres					
	Plant. Pts.	13.74	17.76	22.96	29.67	38.34	49.55	64.03	82.74	106.93	138.18	178.57	230.76			
	Density		2020	1210	724	434	260	156	93	56	33	20				
Plot Size 11	$\theta = 13.27$	$\alpha = 1.2595$		β(max.) = 6%		No. of experimental spokes = 26					Area per plot = .174 acres					
	Plant. Pts.	15.73	19.81	24.95	31.43	39.59	49.87	62.81	79.11	99.65	125.51	158.09	199.13	250.81		
	Density		2020	1273	803	506	319	201	127	80	50	32	20			
Plot Size 12	$\theta = 12.06^\circ$	$\alpha = 1.2334$		β(max.) = 5%		No. of experimental spokes = 28					Area per plot = .189 acres					
	Plant. Pts.	17.71	21.85	26.95	33.24	41.00	50.57	62.38	76.94	94.90	117.05	144.37	178.07	219.63	270.89	
	Density		2020	1328	872	573	377	248	163	107	70	46	30	20		
Plot Size 13	$\theta = 11.05^\circ$	$\alpha = 1.2120$		β(max.) = 5%		No. of experimental spokes = 31					Area per plot = .197 acres					
	Plant. Pts.	19.71	23.89	28.95	35.09	42.53	51.55	62.48	75.73	91.79	111.25	134.84	163.43	198.09	240.09	291.00
	Density		2020	1375	936	637	434	295	201	137	93	63	43	29	20	

Table 2 (continued).

Density Span 20 - 2020

Growing Space Shape 1 : 2

Plot Size 4	$\theta = 80.54^{\circ}$	$\alpha = 2.1580$		β(max.) = 18%		No. of experimental spokes = 3				Area per plot = .147 acres						
	Plant. Pts.	1.67	3.60	7.78	16.79	36.23	78.19									
	Density		2020	434	93	20										
Plot Size 5	$\theta = 62.71^{\circ}$	$\alpha = 1.7804$		β(max.) = 14%		No. of experimental spokes = 4				Area per plot = .154 acres						
	Plant. Pts.	2.90	5.17	9.20	16.39	29.18	51.97	92.53								
	Density		2020	637	201	63	20									
Plot Size 6	$\theta = 51.10^{\circ}$	$\alpha = 1.5864$		β(max.) = 11%		No. of experimental spokes = 6				Area per plot = .137 acres						
	Plant. Pts.	4.21	6.68	10.61	16.83	26.71	42.37	67.22	106.65							
	Density		2020	803	319	127	50	20								
Plot Size 7	$\theta = 43.02^{\circ}$	$\alpha = 1.4690$		β(max.) = 9%		No. of experimental spokes = 7				Area per plot = .150 acres						
	Plant. Pts.	5.56	8.17	12.01	17.65	25.92	38.09	55.95	82.20	120.75						
	Density		2020	936	434	201	93	43	20							
Plot Size 8	$\theta = 37.10^{\circ}$	$\alpha = 1.3904$		β(max.) = 8%		No. of experimental spokes = 8				Area per plot = .164 acres						
	Plant. Pts.	6.94	9.65	13.42	18.66	25.94	36.07	50.16	69.75	96.99	134.86					
	Density		2020	1045	540	279	145	75	39	20						
Plot Size 9	$\theta = 32.60^{\circ}$	$\alpha = 1.3343$		β(max.) = 7%		No. of experimental spokes = 10				Area per plot = .160 acres						
	Plant. Pts.	8.32	11.11	14.82	19.78	26.39	35.22	47.00	62.71	83.69	111.67	149.00				
	Density		2020	1135	637	358	201	113	63	36	20					
Plot Size 10	$\theta = 29.06^{\circ}$	$\alpha = 1.2922$		β(max.) = 6%		No. of experimental spokes = 11				Area per plot = .175 acres						
	Plant. Pts.	9.72	12.56	16.23	20.98	27.11	35.03	45.27	58.51	75.61	97.71	126.26	163.17			
	Density		2020	1210	724	434	260	156	93	56	33	20				
Plot Size 11	$\theta = 26.21^{\circ}$	$\alpha = 1.2595$		β(max.) = 6%		No. of experimental spokes = 12				Area per plot = .189 acres						
	Plant. Pts.	11.12	14.01	7.64	22.22	27.99	35.26	44.41	55.94	70.46	88.75	111.79	140.80	177.35		
	Density		2020	1273	803	506	319	201	127	80	50	32	20			
Plot Size 12	$\theta = 23.86^{\circ}$	$\alpha = 1.2334$		β(max.) = 5%		No. of experimental spokes = 14				Area per plot = .189 acres						
	Plant. Pts.	12.52	15.45	19.06	23.50	28.99	35.76	44.11	54.40	67.10	82.76	102.08	125.91	155.30	191.55	
	Density		2020	1328	873	574	377	248	163	107	70	46	30	20		
Plot Size 13	$\theta = 21.90^{\circ}$	$\alpha = 1.2120$		β(max.) = 5%		No. of experimental spokes = 15				Area per plot = .204 acres						
	Plant. Pts.	13.93	16.89	20.47	24.81	30.07	36.45	44.18	53.55	64.90	78.67	95.35	115.56	140.07	169.77	205.76
	Density		2020	1375	936	637	434	295	201	137	93	63	43	29	20	

Table 2 (continued).

Density Span 50 - 1250

Growing Space Shape 1 : 1

Plot Size 4	θ = 31.42°	α = 1.7099		β(max.) = 13%		No. of experimental spokes = 10				Area per plot = .054 acres						
	Plant. Pts.	5.92	10.12	17.31	29.61	50.63	86.58									
	Density		1250	427	147	50										
Plot Size 5	θ = 23.35°	α = 1.4953		β(max.) = 10%		No. of experimental spokes = 14				Area per plot = .056 acres						
	Plant. Pts.	9.36	13.99	20.93	31.30	46.80	69.99	104.66								
	Density		1250	559	250	112	50									
Plot Size 6	θ = 19.59°	α = 1.3797		β(max.) = 8%		No. of experimental spokes = 17				Area per plot = .064 acres						
	Plant Pts.	12.89	17.79	24.55	33.87	46 74	64.48	88.97	122.76							
	Density		1250	657	345	181	95	50								
Plot Size 7	θ = 15.45°	α = 1.3076		β(max.) = 7%		No. of experimental spokes = 22				Area per plot = .065 acres						
	Plant. Pts.	16.48	21.55	28.18	36.85	48.19	63.01	82.40	107.75	140.90						
	Density		1250	731	427	250	146	85	50							
Plot Size 8	θ = 13.23°	α = 1.2584		β(max.) = 6%		No. of experimental spokes = 26				Area per plot = .070 acres						
	Plant. Pts.	20.08	25.28	31.81	40.04	50.39	63.42	79.81	100.44	126.41	159.09					
	Density		1250	789	498	315	199	125	79	50						
Plot Size 9	θ = 11.56°	α = 1.2228		β(max.) = 5%		No. of experimental spokes = 30				Area per plot = .076 acres						
	Plant. Pts.	23.71	28.99	35.46	43.36	53.02	64.84	79.29	96.96	118.57	144.99	177.30				
	Density		1250	836	559	374	250	167	112	75	50					
Plot Size 10	θ = 10.27°	α = 1.1958		β(max.) = 4%		No. of experimental spokes = 34				Area per plot = .081 acres						
	Plant. Pts.	27.34	32.70	39.10	46.76	55.92	66.87	79.97	95.62	114.35	136.74	163.52	195.54			
	Density		1250	874	611	427	299	209	146	102	71	50				
Plot Size 11	θ = 9.24°	α = 1.1746		β(max.) = 4%		No. of experimental spokes = 37				Area per plot = .089 acres						
	Plant. Pts.	30.99	36.40	42.75	50.22	58.99	69.29	81.39	95.61	112.30	131.92	154.95	182.01	213.79		
	Density		1250	906	657	476	345	250	181	131	95	69	50			
Plot Size 12	θ = 8.39°	α = 1.1575		β(max.) = 4%		No. of experimental spokes = 41				Area per plot = .095 acres						
	Plant. Pts.	34.63	40.09	46.41	53.72	62.19	71.98	83.33	96.46	111.65	129.25	149.61	173.19	200.47	232.06	
	Density		1250	933	696	520	388	289	216	161	120	90	67	50		
Plot Size 13	θ = 7.69°	α = 1.1435		β(max.) = 3%		No. of experimental spokes = 45				Area per plot = .100 acres						
	Plant. Pts.	38.28	43.78	50.06	57.25	65.47	74.87	85.61	97.90	111.95	128.02	146.40	167.41	191.44	218.92	250.34
	Density		1250	956	731	559	428	327	250	191	146	112	85	65	50	

Table 2 (continued).

Density Span 50 - 1250

Growing Space Shape 1 : 2

Plot Size 4	θ = 58.72°	α = 1.7099		β(max.) = 13%		No. of experimental spokes = 5				Area per plot = .054 acres						
	Plant. Pts.	4.18	7.16	12.24	20.93	35.80	61.22									
	Density		1250	427	146	50										
Plot Size 5	θ = 44.91°	α = 1.4953		β(max.) = 10%		No. of experimental spokes = 7				Area per plot = .056 acres						
	Plant. Pts.	6.61	9.89	14.80	22.13	33.09	49.49	74.00								
	Density		1250	549	250	112	50									
Plot Size 6	θ = 36.26°	α = 1.3797		β(max.) = 8%		No. of experimental spokes = 8				Area per plot = .070 acres						
	Plant. Pts.	9.12	12.58	17.36	23.95	33.05	45.60	62.91	86.80							
	Density		1250	657	345	181	95	50								
Plot Size 7	θ = 30.37°	α = 1.3076		β(max.) = 7%		No. of experimental spokes = 10				Area per plot = .072 acres						
	Plant. Pts.	11.65	15.23	19.92	26.05	34.07	44.55	58.26	76.19	99.63						
	Density		1250	731	427	250	146	85	50							
Plot Size 8	θ = 26.11°	α = 1.2584		β(max.) = 6%		No. of experimental spokes = 12				Area per plot = .076 acres						
	Plant. Pts.	14.20	17.87	22.49	28 31	35.63	44.84	56.43	71.02	89.38	112.44					
	Density		1250	789	498	315	199	125	79	50						
Plot Size 9	θ = 22.89	α = 1.2228		β(max.) = 5%		No. of experimental spokes = 14				Area per plot = .081 acres						
	Plant. Pts.	16.76	20.50	25.07	30.66	37.49	45.85	56.06	68.56	83.84	102.52	125.37				
	Density		1250	836	559	374	250	167	112	75	50					
Plot Size 10	θ = 20.38°	α = 1.1958		β(max.) = 4%		No. of experimental spokes = 16				Area per plot = .086 acres						
	Plant. Pts.	19 33	23.12	27.65	33.06	39.54	47.28	56.54	67.62	80.86	96.69	115.62	138.27			
	Density		1250	874	611	427	299	209	147	102	71	50				
Plot Size 11	θ = 18.36°	α = 1.1746		β(max.) = 4%		No. of experimental spokes = 18				Area per plot = .092 acres						
	Plant. Pts.	21.91	25.74	30.23	35.51	41.71	49.00	57.55	67.60	79.41	93.28	109.57	128.70	151 17		
	Density		1250	906	657	476	345	250	181	131	95	69	50			
Plot Size 12	θ = 16.70°	α = 1.1575		β(max.) = 4%		No. of experimental spokes = 20				Area per plot = .097 acres						
	Plant. Pts.	24.49	28.35	32.81	37.98	43.97	50.90	58.92	68.20	78.95	91.39	105.79	122.46	141.75	164.09	
	Density		1250	933	696	520	388	289	216	161	120	90	67	50		
Plot Size 13	θ = 15.32°	α = 1.1435		β(max.) = 3%		No. of experimental spokes = 22				Area per plot = .103 acres						
	Plant. Pts.	27.07	30.96	35.40	40.48	46.29	52.94	60.53	69.22	79.16	90.52	103.52	118.38	135.37	154.80	177.01
	Density		1250	956	731	559	427	327	250	191	146	112	85	65	50	

Table 3. Planting Plans for Constant Density Increments.

Density Span 20 - 2020

Plot Size 10 $\theta = 24^{\circ}$ Growing Space Shape 1:4 through 1:4.3 up to 1:1 No. of exp. spokes = 15 Plot area = .137

Plant. Pts.	19.79	22.09	24.39	26.92	29.63	32.85	36.71	42.18	52.19	78.59	104.44	168.50
Length/Width		.25	.23	.23	.24	.25	.30	.43	.82	.78	1.01	
β		0%	2%	2%	4%	5%	9%	15%	23%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{\circ}$ Growing Space Shape 1:4 through 1:4.8 up to 1:1.2 No. of exp. spokes = 12 Plot area = .135

Plant. Pts.	15.35	17.63	19.91	22.33	24.93	27.92	31.53	36.54	45.68	69.49	92.60	149.87
Length/Width		.24	.22	.21	.21	.22	.26	.36	.67	.63	.81	
β		0%	1%	2%	3%	5%	8%	15%	22%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 26^{\circ}$ Growing Space Shape 1:2 through 1:3.2 up to 1:1 No. of exp. spokes = 12 Plot area = .156

Plant. Pts.	11.17	14.41	17.65	20.60	23.94	27.37	31.73	37.32	47.75	73.85	99.02	161.03
Length/Width		.49	.38	.33	.31	.31	.34	.46	.83	.75	.95	
β		0%	2%	3%	1%	6%	6%	15%	21%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{\circ}$ Growing Space Shape 1:2 through 1:3.6 up to 1:1.2 No. of exp. spokes = 12 Plot area = .134

Plant. Pts.	9.24	12.47	15.69	18.48	21.73	24.92	29.09	34.29	44.10	68.36	91.81	149.38
Length/Width		.48	.36	.30	.28	.28	.30	.41	.72	.65	.82	
β		0%	4%	4%	0%	7%	6%	15%	21%	0%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 24^{\circ}$ Growing Space Shape 1:1 through 1:2.7 up to 1:1 No. of exp. spokes = 15 Plot area = .124

Plant. Pts.	5.60	10.19	14.77	17.76	21.98	25.22	30.35	35.71	46.95	72.97	98.72	160.55
Length/Width		.97	.55	.44	.37	.36	.37	.50	.86	.77	.96	
β		0%	10%	9%	7%	11%	1%	18%	20%	1%	21%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Plot Size 10 $\theta = 30^{\circ}$ Growing Space Shape 1:1 through 1:3.1 up to 1:1.2 No. of exp. spokes = 12 Plot area = .133

Plant. Pts.	4.25	8.81	13.38	16.09	20.21	23.10	28.05	32.91	43.54	67.58	91.65	148.92
Length/Width		.97	.50	.40	.32	.32	.33	.44	.74	.66	.83	
β		0%	13%	11%	9%	13%	5%	19%	19%	1%	20%	
Density		2020	1734	1449	1163	877	591	306	100	50	20	

Density Span 50 - 1250

Plot Size 7 $\theta = 18^{\circ}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 20 Plot area = .055

Plant. Pts.	34.57	37.51	40.44	44.20	48.50	54.80	65.47	94.11	123.76
Length/Width		.25	.26	.29	.34	.49	.95	.98	
β		0%	6%	3%	9%	13%	23%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 7 $\theta = 20^{\circ}$ Growing Space Shape 1:2 through 1:2.3 up to 1:1 No. of exp. spokes = 18 Plot area = .052

Plant. Pts.	19.71	23.85	28.00	32.56	37.80	44.75	56.35	85.44	114.24
Length/Width		.49	.44	.43	.46	.59	1.02	.96	
β		0%	2%	3%	9%	13%	21%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 7 $\theta = 22^{\circ}$ Growing Space Shape 1:1 through 1:1.9 up to 1:1 No. of exp. spokes = 15 Plot area = .056

Plant. Pts.	9.48	15.32	21.17	25.94	32.23	39.01	51.36	79.53	107.72
Length/Width		.98	.64	.55	.53	.63	1.01	.91	
β		0%	5%	7%	2%	15%	20%	1%	
Density		1250	1010	770	530	290	100	50	

Plot Size 10 $\theta = 16^{\circ}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 21 Plot area = .070

Plant. Pts.	39.28	42.21	45.15	48.44	51.88	55.89	60.39	66.10	73.70	86.75	108.55	142.33
Length/Width		.25	.25	.25	.26	.27	.30	.36	.50	.71	.91	
β		0%	3%	1%	4%	3%	6%	7%	13%	13%	11%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 10 $\theta = 16^{\circ}$ Growing Space Shape 1:2 through 1:2.6 up to 1:1 No. of exp. spokes = 21 Plot area = .067

Plant. Pts.	25.69	29.85	34.00	38.14	42.54	47.23	52.60	58.96	67.49	81.47	104.51	139.19
Length/Width		.50	.43	.40	.38	.38	.40	.45	.59	.81	.98	
β		0%	0%	2%	2%	3%	4%	7%	12%	12%	10%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 10 $\theta = 18^{\circ}$ Growing Space Shape 1:1 through 1:2.4 up to 1:1 No. of exp. spokes = 20 Plot area = .060

Plant. Pts.	12.88	18.75	24.62	29.06	34.50	39.08	45.22	51.26	60.33	73.66	96.50	129.24
Length/Width		.99	.66	.54	.46	.43	.42	.47	.59	.78	.91	
β		0%	7%	5%	4%	7%	4%	10%	10%	13%	9%	
Density		1250	1100	950	800	650	500	350	200	100	50	

Plot Size 6 $\theta = 20^{\circ}$ Growing Space Shape 1:4 up to 1:1 No. of exp. spokes = 18 Plot area = .047

Plant. Pts.	30.81	33.74	36.67	40.77	45.93	55.76	85.26	113.87
Length/Width		.25	.28	.33	.47	1.01	.98	
β		0%	8%	6%	16%	25%	1%	
Density		1250	950	650	350	103.5	50	

Plot Size 6 $\theta = 28^{\circ}$ Growing Space Shape 1:2 through 1:2.4 up to 1:1 No. of exp. spokes = 11 Plot area = .056

Plant. Pts.	12.88	16.99	21.11	25.66	31.46	41.06	69.61	92.34
Length/Width		.50	.42	.42	.51	.96	.76	
β		0%	2%	6%	12%	25%	6%	
Density		1250	950	650	350	103.5	50	

Plot Size 6 $\theta = 30^{\circ}$ Growing Space Shape 1:1 through 1:2 up to 1:1.1 No. of exp. spokes = 12 Plot area = .047

Plant. Pts.	5.40	11.21	17.01	21.47	28.34	37.53	65.10	88.33
Length/Width		1.00	.58	.51	.55	.95	.75	
β		0%	7%	11%	7%	25%	4%	
Density		1250	950	650	350	105.0	50	

density-response parameters (B) does vary with space shape in vegetable crops. For forest trees, there is meagre evidence on this aspect of growth. One may guess that the effect of non-isometric spacing, if any, would occur most predominantly with young plants, on traits sensitive to crown form, and at extremes of rectangularity. Therefore, it is reasonable to allow some freedom in this restriction in order for the other variables to be adequately studied. It remains highly desirable to test the effects of rectangularity with trees, as for instance with Nelder's design 1b. Also, some freedom as regards non-centrality may be allowable for trees. It is for the individual experimenter to decide what liberties to take.

To provide guides for constructing plots with variable spacing, it was assumed that a planting system with equal intervals of density is usually easiest and most economical to establish. Therefore, two series of possible planting layouts were computed, one to span the range in densities from 20 to 2,020; and the other to go from 50 to 1,250. Each series was tested in intervals of two degrees from 2° to 40° for the angle between spokes and for plot sizes (exclusive of borders) of 4 to 13. At these density intervals and plot sizes, the ratios of within-spoke to between-spoke spacing generally decreased then increased with the distance from the hub. Therefore, a series of ratios for the innermost experimental tree was established for each plot size and angle series. The analytical steps are given in Appendix B. It became necessary to depart from perfect regularity of density intervals in order to keep the non-central location of the plant within the growing space within reasonable bounds. If only the plants at the widest spacings are allowed to depart very much from centrality and these only to a maximum of 25 percent, then an extra plant or two at the wider spacings will provide sufficient control. Methods for using these extra plants were examined and a computer program was written to give the planting points for the most acceptable designs, examples of which are given in Table 3. In this table, the shape index is taken as the ratio of within-spoke to between-spoke spacing, and is allowed to vary in three ways:

1:4 up to 1:1,
1:2 up to 1:1,
and 1:1 through 1:2, up to 1:1.

Non-centrality is allowed to vary up to 25% at the wider spacings. Within these limits, other plot sizes and angles can be successfully used. These are listed in Table 4. One may wish to establish some other function for the sequence of densities. This may easily be done by formulating the function of radial distance sequences, solving for the initial radius, and sequentially solving for the remaining distances.

Table 4. Plot Sizes and Angles with Acceptable Growing Space Shape and Centrality.

Plot Shape	1:5 up to 1:1	Plot Shape	1:3 up to 1:1	Plot Shape	1:2 up to 1:1
Density Span = 20 - 2020					
N = 10	$\theta \geq 24^{\circ}$	N = 10	$\theta \geq 26^{\circ}$	N = 8	$\theta \geq 38^{\circ}$
N = 11	$\theta \geq 24^{\circ}$	N = 11	$\theta \geq 24^{\circ}$	N = 10	$\theta \geq 26^{\circ}$
N = 12	$\theta \geq 24^{\circ}$	N = 12	$\theta \geq 24^{\circ}$	N = 11	$\theta \geq 26^{\circ}$
N = 13	$\theta \geq 22^{\circ}$	N = 13	$\theta \geq 24^{\circ}$	N = 12	$\theta \geq 26^{\circ}$
				N = 13	$\theta \geq 26^{\circ}$
Density Span = 50 - 1250					
Plot Shape	1:5 up to 1:1	Plot Shape	1:3 up to 1:1	Plot Shape	1:2 up to 1:1
N = 5	$\theta \geq 26^{\circ}$	N = 5	$\theta \geq 28^{\circ}$	N = 5	$\theta \geq 38^{\circ}$
N = 6	$\theta \geq 20^{\circ}$	N = 6	$\theta \geq 28^{\circ}$	N = 6	$\theta \geq 30^{\circ}$
N = 7	$\theta \geq 18^{\circ}$	N = 7	$\theta \geq 20^{\circ}$	N = 7	$\theta \geq 20^{\circ}$
N = 8	$\theta \geq 18^{\circ}$	N = 8	$\theta \geq 18^{\circ}$	N = 8	$\theta \geq 20^{\circ}$
N = 9	$\theta \geq 16^{\circ}$	N = 9	$\theta \geq 18^{\circ}$	N = 9	$\theta \geq 20^{\circ}$
N = 10	$\theta \geq 16^{\circ}$	N = 10	$\theta \geq 16^{\circ}$	N = 10	$\theta \geq 18^{\circ}$
N = 11	$\theta \geq 14^{\circ}$	N = 11	$\theta \geq 16^{\circ}$	N = 11	$\theta \geq 16^{\circ}$
N = 12	$\theta \geq 14^{\circ}$	N = 12	$\theta \geq 14^{\circ}$	N = 12	$\theta \geq 16^{\circ}$

DISCUSSION AND CONCLUSIONS

Anyone desirous of examining density-time responses may choose among several possible plot designs, arrange his plot sequences and border plots to fit his planting area, and analyze his results on a single-plant basis or on parameters of plot-response variables. Non-linear responses to density would suggest that Bleasdale and Nelder's equation is more appropriate than the logistic growth relations. In any case, estimates of the rate constant can be obtained over a series of years and environments.

The desirability of including density as an important variable of the cultural environment seems clear, especially for species with non-standardized spacings.

The circular plots developed by Nelder make it possible to avoid the difficulties of the rectangular plots and still study density response over a wide range. For instance, densities of 50 to 1,250 can be samples with six-tree plots occupying only .064 (for 1:1 spacing) or .070 (for 1:2 spacing) acres per plot including border trees. Rectangular three-tree plots sampling six densities would require .085 acres per family even without border rows.

The alternative sequences developed in this paper allow limited variability to exist for various shape parameters but improve the sampling of densities and are even more economical of space than Nelder's designs. A six-tree plot constructed as for the above designs requires only .047 acre including all borders.

Circular plots have the serious disadvantage of not being amenable to easy mechanical planting, cultivation, and maintenance. If the differences in size of plots or areas are of no concern, intergenotypic competition is desired or can be ignored, and single-tree plots are otherwise acceptable, the traditional rectangular planting is more efficient. In many cases when density responses are desired, however, circular plots will be found to be the most economical design.

APPENDIX A

Nelder (1962) uses the relations:

$$r_n = r_o \alpha^n$$

and $r_{n + 1/2} = r_o \alpha^{n + 1/2}$,

for his developments. Instead, assume that

$$r_{n + 1/2} = 1/2(r_n + r_{n + 1}). \quad \text{Then,}$$

$$r_{n + 1/2} = r_o \alpha^n (1 + \alpha)/2.$$

Also, if we assume that the growing space border approaches a straight line more closely than a curve, the length of the border between adjacent plants of the same spoke is 2 [tan (θ/2)]. The following equations for Nelder's design 1a would then be appropriate:

$$A_n = \tan(\theta/2) \left[r^2_{n + 1/2} - r^2_{n - 1/2} \right]$$

$$= \tan(\theta/2) \left[\frac{r^2_n}{4} \cdot f(\alpha) \right],$$

where $f(\alpha) = (1 + \alpha)^2 - (1 + \alpha^{-1})^2$,

$$= 2 \tan(\theta/2) \,/\, (\alpha - \alpha^{-1}),$$

$$A_1 = 1/4 \tan(\theta/2) \left[r^2_o \alpha^2 \cdot f(\alpha) \right],$$

$$A_N = 1/4 \tan(\theta/2) \left[r^2_o \alpha^{2N} \cdot f(\alpha) \right],$$

$$(2N - 2) \log \alpha = \log A_N - \log A_1,$$

$$r_o = \sqrt{4A_1 \,/\, \left[\tan(\theta/2)(\alpha^2 \cdot f(\alpha) \right]}$$

APPENDIX B

Using the relationships

$$\text{Area}_n = \tan(\theta/2)\alpha \, (r^2_{n + 1/2} - r^2_{n - 1/2})$$

and Density = 43560 / Area,

and specifying any form for the distribution of densities, one may sequentially solve for the location of the growing spaces.

Since interplant spacing between spokes is $2r \cdot \sin(\theta/2)$, the shape of the space may be taken as

$$(r_{n+1/2} - r_{n-1/2}) : (r_{n+1/2} + r_{n-1/2}) \sin(\theta/2).$$

Therefore: $r^2_{n-1/2} = \dfrac{r^2_{n+1/2} - r^2_{n-1/2}}{f(\theta)}$, where $f(\theta) = \left(\dfrac{1 + k \sin(\theta/2)}{1 - k \sin(\theta/2)}\right) - 1$,

and k = the shape fraction. Then, for any given angle (θ), sequence of densities and therefore a sequence of $(r^2_{n+1/2} - r^2_{n-1/2})$, and initial or final shape fraction, the remaining borders to the growing spaces may be calculated. In order to place the maximum non-centrality at the wide spacings and to minimize it at the close spacings, the initial planting point was located at the center of its growing space. Other methods for locating the planting points are being investigated. The remaining planting points are those located according to:

$$r_n = 2r_{n-1/2} - r_{n-1}.$$

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Improvement of Yellow Poplar

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The process of compiling information about a species on which you have been working for the past six years can be very educational. Although a person constantly tries to keep up his reference file and attempts to stay in contact with other workers in the field, it is difficult to maintain a complete picture of what is becoming known.

There is considerable knowledge about some aspects of the silviculture of yellow-poplar (Liriodendron tulipifera). In recent times, methods have been developed so that the species can be propagated successfully, but knowledge related to the genetics of yellow-poplar is severely lacking. This should not be discouraging because even less is known about most other hardwoods, with the exception of Populus.

In many respects the present state of our knowledge and research effort with yellow-poplar may be compared with that of loblolly pine ten years ago. During the past decade an ever-increasing number of research projects have contributed to our knowledge about loblolly pine. It remains to be seen if similar progress will be made over the next ten years with yellow-poplar. Undoubtedly, the support for yellow-poplar breeding projects will be less than that for the southern pines. However, many accomplishments of the pine breeders, related to principles and development of methodology, will be of great value to those of us interested in hardwoods in general and yellow-poplar in particular.

Tree improvement must be an integral part of silviculture but it is sometimes difficult to determine just what segment of this discipline tree improvement covers. Since regeneration and vegetative propagation have already been discussed for hardwoods in general I will only touch upon propagation as it concerns the development of seed orchards. Other phases of the biology of yellow-poplar of interest to the breeder are flowering and seed production, variation in natural stands, seed source tests, hybridization, and the heritability of important characteristics with the ultimate objective being the gains that can be achieved.

General information on the silvical characteristics, growth and management of yellow-poplar has been summarized by McCarthy (1933) and Renshaw and Doolittle (1958). Characteristics and variation of wood properties have been discussed by Luxford and Wood (1944), Barefoot (1958), Thorbjornsen (1961) and Taylor (1963, 1964).

FLOWERING AND POLLINATION

Yellow-poplar trees may start flowering as early as 15 years of age, but these small trees have few flowers. As is true for other forest tree species, there is a relatively good relationship between dbh and flower production. By grafting material from the top of the crown of older trees to seedling understocks, we would expect early flowering. This seems to be the case in a yellow-poplar seed orchard near Knoxville, Teneseee, in which a few flowers have been produced two years after grafting.

Flowering may occur from late March to June, depending on geographic location and weather conditions. There is much variation in time of flowering among individual trees within a stand. Fortunately for the tree breeder, all the flowers on a single tree are not receptive at the same time and the flowering period for individual trees may vary from two to six weeks, thus affording the breeder an opportunity to make his crosses. Techniques for controlled pollinations have been developed by Carpenter and Guard (1950), Wright (1953) and Taft (1962).

The large, showy yellow-poplar flowers are bi-sexual. Nectaries are located on orange spots near the base of the petals. Insects - especially honey bees - get pollen on their bodies when collecting nectar and brush against the stigmas. Apparently, insects often move from flower to flower within the same tree; such a pattern could produce a considerable amount of self-pollination.

The low viability of yellow-poplar seed may be partially due to lack of fertilization which again is the result of ineffective pollination. Self-incompatibility is rather common in yellow-poplar. Boyce and Kaeiser (1961) obtained less than 2 filled seeds per

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100 samaras for all their controlled self-pollinations. Taft's[2/] selfings resulted in a seed set varying from zero to nine percent filled seed, and Thor (unpublished) obtained from zero to one percent germination from controlled self-pollinations. Similar effects of selfing in yellow-poplar have been reported by Carpenter and Guard (1950) and Guard (1943).

In addition to self-incompatibilities, there is also good evidence that certain trees may also be cross-incompatible. Kaeiser and Boyce (1962) found that widely separated trees usually had better seed set than those in the same stand. It is to be expected that trees of the same stand may be closely related and thus be less compatible than the wider crosses.

Controlled cross-pollinations usually result in higher percentages of filled seed than open or self-pollinations (Carpenter and Guard 1950; Boyce and Kaeiser 1961). Taft obtained twice as many filled samaras from controlled crosses as from open-pollinated flowers. In another study (Thor, unpubl.) open-pollinated seed germinated at a rate of from one to six percent while controlled out-crossing of the same trees resulted in germination percentages ranging from 6 to 36 percent.

SEED PRODUCTION

The yellow-poplar fruit is an erect conelike aggregate of samaras. The samaras ripen in the early fall and may contain two, one or no seed. The basal-most samaras are sterile (Boyce and Kaeiser 1961). Wean and Guard (1940) report that the middle portion of the "cone" has the highest proportion of filled seed, averaging about 20 percent. Size of cone and position in crown have little or no effect on seed viability (Perry and Coover 1933).

Guard and Wean (1941) found that trees with a dbh above 15 inches had a larger percentage of filled seed than those smaller than 15 inches. Also, a straight line relationship has been established between dbh and the number of viable seeds produced per tree (Carvell and Korstian 1955). In spite of the rather low percentage of viable seed, yellow-poplar usually produces such an abundance of seed that adequate reproduction often is obtained if seed bed conditions are suitable. More than a quarter of a million seeds per acre may be produced from a few seed trees (Carvell and Korstian 1955; Engle 1960).

Individual tree variation in seed viability is large. Limstrom (1959) used tree percents (the ratio of seedlings produced to the number of seed sown) and found wide variations in tree percents among mother trees within each source as well as among sources. Individual tree superiority in seed viability was consistent over a 3-year period. Sluder (1964) and Thor (1965) found that with the same sowing intensity seed-bed density varied strongly by mother trees.

HYBRIDIZATION

Inter-specific hybridization does not offer too great a promise in the genus Liriodendron. In addition to our native yellow-poplar, only one other species is known - the Chinese yellow-poplar (L. chinense). The Chinese tree is a small, relatively unimportant forest tree of Central China. Frost has killed back this species in several arboreta in the Northeast, but there is evidence that it may grow successfully in the South. The chromosome number (2N) is 38 for both the Chinese (Li 1954) and American (Whitaker 1933) yellow-poplar.

The outlook for improvement through intra-specific hybridization within the native yellow-poplar is much brighter. Carpenter and Guard (1950) noted that the seedlings produced as a result of cross-pollination tended to be more vigorous than those resulting from open-pollination. If reduction in vigor goes with inbreeding, we should expect improvement to be obtained in an orchard composed of numerous clones representing many different stands, assuming cross-pollination among trees can be secured.

There is no knowledge available on the result of crosses between trees from different physiographic regions. One breeding orchard has been established in Tennessee to produce intra-specific hybrids from crosses among trees from the same stand, among trees from different stands within the same region, and among trees from different physiographic regions.

VARIATION

Several studies of natural variation in yellow-poplar have been concerned with wood properties such as specific gravity and fiber length. Thorbjornsen (1961) found large among-tree variance components for specific gravity in Tennessee; however, individual trees did

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[2/] Undated references to Taft indicate personal communications with K. A. Taft, TVA, Norris, Tennessee.

not show as much variation in fiber length. These observations have been supported by Taylor (1964) in North Carolina. Both workers found some differences among stands of geographic areas. A rather large study of variation, including wood properties as well as various morphological properties, has been established by Kellison [3] in North Carolina. The Southeastern Forest Experiment Station is planning a large study of wood characteristics; trees will be sampled in Virginia, North Carolina, and Georgia to determine among-tree variation, geographic variation, variation associated with site differences, and changes associated with stand thinning.

When one works with a valuable forest tree which covers a large geographic range, the question of seed source must be considered. Unfortunately, often seed-source testing is not started before artificial reforestation has become an accepted practice and large areas reforested with poorly adapted sources have shown the need for such information. This question of provenance in yellow-poplar is a pressing one both in this country and in Europe (Querengasser 1961).

Some of the earliest seed source studies of yellow-poplar were established in 1952 (Limstrom 1955, Lotti 1955). Early results from these tests indicate that seed source has a strong effect on height growth. Sluder (1960) reported large differences in survival and height growth among 16 sources after one growing season. However, after 10 years growth Sluder [4] found no significant differences in height among the sources. Limstrom and Finn (1956) found significant differences among six different sources in height of 1-year-old seedlings.

Funk (1958) studied the relationship between seed source and frost damage and found that the extent of dieback was generally related to latitude of the seed source. Trees grown from seed of the southernmost sources were much more severely damaged than those from the more northern sources. Differences in photoperiodic response have been investigated in growth chambers by Vaartaja (1964). The northernmost source (Michigan) grew best under very long days (3-hr. dark periods), while the southernmost source (Georgia) grew best under long days (6-hr. dark periods). Under short day conditions, the Georgia source grew almost twice as much in height as the Michigan source, while the Indiana source was intermediate. There were indications that the variation was gradual and continuous.

Data on two additional seed source tests have not yet been published, but early results have been analyzed. Four seed sources from northern Alabama and Mississippi and southern Tennessee did not show any significant differences after three years (Southern Forest Experiment Station). Five-year data from a series of seed source tests in Tennessee (University of Tennessee) indicated large differences in mean height among sources, but these differences were only significant at the 10 percent level due to large error terms.

It is, however, interesting to note that the source from West Tennessee had the best height growth in the West Tennessee plantation but did poorest in the Cumberland Mountains. The Cumberland Mountain source was the best source in the Dumberland Mountain plantation while it grew poorer than the same sources when tested in West Tennessee.

In future seed source tests, it should be recognized that yellow-poplar is extremely sensitive to relatively minor changes in site conditions. Even large mean differences in height growth will not prove to be statistically significant if care is not exercised in the selection of uniform test areas. While four replications usually give enough accuracy for testing sources of loblolly pine we must probably double this to obtain comparable accuracy in yellow-poplar seed source tests.

HERITABILITY

Heritability is a term used to express inheritance in a quantitative manner. It is the ratio of the genetic variability to the phenotypic variability. Heritability in the "broad sense" considers total genetic variability, while "narrow sense" heritability considers only the additive portion of the genetic variability. Due to the difficulties in propagating yellow-poplar vegetatively we are mainly interested in determining the "narrow sense" heritabilities for different characteristics.

[3] Undated references to Kellison indicate personal communications with R. C. Kellison, N. C. State University, Raleigh.

[4] E. R. Sluder, unpublished progress report, Southeastern Forest Expt. Station.

Many forest geneticists are busy determining narrow-sense heritabilities for a number of characteristics in various species of pine. The question may be asked as to how this work is useful in tree improvement and if such information should be obtained for yellow-poplar. Since knowledge of heritability is basic to determination of genetic gain and expected improvement, this information is essential to determine which characteristics to work with in a selection program, and to obtain reliable estimates of expected improvement for justification of the expense.

Unfortunately we do not now have any reliable estimates of expected gain for any characteristic of yellow-poplar. There is ample evidence (Limstrom and Finn 1956; Sluder 1964; Thor unpubl.) that one-year-old seedlings differ in size depending upon the mother tree. However, this may be caused by different amounts of self-fertilization (Carpenter and Guard 1950).

Taft is investigating the inheritance of various characteristics using a diallel test with a total of 78 cross-pollinations. He found indications that heights of seedlings are determined by dominance rather than additive gene action. Leaf shape, however, seems to be determined by additive genes, particularly the ratio of leaf length to leaf width.

In an open-pollinated progeny test in Tennessee, Thor (unpubl.) found large differences in heights among progenies after three growing seasons in the field. In the Cumberland Mountains the four best progenies were from the Cumberland Mountains; in West Tennessee the four best progenies were from West Tennessee. However, even within one provenance there were large differences - in both locations the best and poorest growth was made by progenies from local mother trees.

Sluder[5] has established a test to determine the heritability of epicormic sprouting in yellow-poplar. Five heavy-sprouting and five light-sprouting trees have been selected and an open-pollinated progeny test has been established. Also, Sluder is propagating his selections by grafting to determine "broad sense" heritability for epicormic sprouting. Kellison designed an open-pollinated progeny test involving 108 trees in North Carolina. Outplantings have been made in the Mountains, Piedmont and Coastal Plains.

Results from the heritability studies already established, and others which are still in the planning stage, should yield information which will be of great help in our breeding efforts with yellow-poplar. We should keep in mind that many plants were greatly improved long before we had any knowledge of quantitative genetics and heritabilities. There is no reason for delaying a program of selection and seed orchard establishment because of our present lack of knowledge of heritabilities.

SELECTION

Without knowledge of the inheritance of different characteristics, the breeder has an almost unlimited number of characteristics to choose from. Practical consideration, however, will usually limit his choice to those criteria which have strong economical implications. Secondly, since the amount of gain is based on variation present as well as the heritability, the characteristics chosen for selection should express large phenotypic variation.

Density of yellow-poplar wood is of great economic importance since it is related to most strength characteristics (Luxford and Wood 1953). Also, there is much phenotypic variation present among trees (Thorbjornsen 1961), and relatively little of this among-tree variation appears to be caused by site differences (Thor unpubl.). Other wood properties, like fiber length and extractives, do not show as much promise for selection because of their more limited variation and lesser economic importance.

Most people are not aware of the variation in straightness in yellow-poplar. Compared to most other hardwoods, this species has a good, straight bole; but when one starts looking for superior phenotypes, with straight boles, it is often difficult to find acceptable trees. Since straightness is of great economic importance and there is surprisingly much variation in this characteristic, it should be one of the most important selection criteria in a breeding program.

High-quality large logs of yellow-poplar command a high price on the veneer market. It is essential that these logs be clear. Selection of trees with small branches, good pruning, and a minimum of epicormic branching may lead to a larger percentage of premium logs.

[5] Personal communication with E. R. Sluder, Southeastern Forest Expt. Station.

Wahlenberg (1950) studied heavy and light sprouters before and after thinning. He found that the heavy sprouters had nearly twice as many sprouts before thinning and nearly three times as many after thinning, suggesting that the trees which are naturally poor in this respect tend to become progressively worse. Large branch diameters are associated with stem rot and poor pruning. The phenotypic variation present for branching characteristics is well illustrated in Limstrom's latest publication (Limstrom 1965).

Although the emphasis probably should be on quality improvement in a selection program for yellow-poplar we cannot affort to sacrifice rate of growth. Selection for growth rate in yellow-poplar phenotypes may be rather ineffective because of the extreme site sensitivity of the species. The best we can do is probably to limit our selections to the largest dominant members of a stand. When the environmental conditions are relatively uniform, the prospect for effective selection in growth rate may be more favorable. Funk (1964) reported that large seedlings selected in the nursery were growing twice as fast as small seedlings; the premium seedlings increased their original advantage during eight years in the field.

Occasionally yellow-poplar trees have an abnormal grain, such as blister grain, which may be of considerable economic value. Bailey (1948) grafted blister-grained yellow-poplar, but the trees did not show any sign of abnormal grain soon after grafting. The trees were examined again this year by Zarger [6] and Thor, but no evidence of abnormal grain was found. Obviously, selection and breeding for such characteristics should be delayed until we have more knowledge about their inheritance.

Most breeders of yellow-poplar will probably stress characteristics such as straightness, pruning, branching habit, and wood density. In some localities two or more organizations may be looking for trees with approximately the same characteristics. To provide for maximum utilization of the best selected phenotypes, the University of Tennessee in cooperation with the Kentucky-Tennessee Section, SAF, has prepared lists of selected trees. The list submitted with his paper should not be considered as a "shopping list" - rather it is a "trading list." If all the organization working with yellow-poplar let other people know what type of breeding material they have available, we could probably make faster progress in both basic work in forest genetics and applied tree breeding.

Agency	Tree #	State	County	Height	DBH	Prun.	Straightn.	Crown	Sp. gr.	Fiber L.
U. T.	1	Tenn.	Sevier	*	**	0	*	0	*	0
U. T.	2	Tenn.	Monroe	*	0	*	**	*	*	-
U. T.	4	Tenn.	Monroe	*	-	0	**	*	*	*
U. T.	6	Ky.	Bell	0	0	*	**	*	0	0
U. T.	7	Ky.	Bell	*	0	*	*	**	**	*
U. T.	10	Tenn.	Coke	0	0	*	**	*	*	0
U. T.	11	Tenn.	Sevier	0	0	*	*	*	*	*
U. T.	12	Tenn.	Sevier	*	0	*	**	*	-	0
U. T.	14	Tenn.	Sevier	*	0	*	**	**	-	0
U. T.	15	Tenn.	Lauderdale	0	-	*	**	*	*	-
U. T.	16	Tenn.	Lauderdale	0	*	*	**	**	-	0
U. T.	17	Tenn.	Lauderdale	0	*	0	*	0	*	0
U. T.	18	Tenn.	Sevier	0	*	*	**	*	*	0
U. T.	20	Tenn.	Obion	0	0	*	*	**	*	0
U. T.	21	Ala.	Lawrence	0	0	*	**	*	*	-
U. T.	23	Tenn.	Madison	0	0	0	*	*	*	*
U. T.	26	Tenn.	Obion	0	0	*	**	*	*	0
U. T.	31	Tenn.	Morgan	0	**	0	**	*	-	0
U. T.	32	Tenn.	Morgan	0	-	*	**	**	0	0
U. T.	34	Tenn.	Morgan	*	*	*	**	0	0	*
U. T.	35	Tenn.	Morgan	*	0	*	**	0	*	0
U. T.	39	Tenn.	Morgan	0	0	*	**	*	0	0
U. T.	40	Tenn.	Morgan	*	0	0	*	*	*	0
U. T.	41	Tenn.	Morgan	0	0	*	**	*	**	0
U. T.	81	Tenn.	Shelby	**	0	0	**	*	-	0

** Excellent
Better than average

0 Average
\- Poorer than average

Figure 1. List of yellow poplar superior phenotypes. Forest Tree Improvement Committee, SAF Kentucky - Tennessee Section, Revised 1965.

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[6] The author is indebted to T. G. Zarger, TVA, for his assistance.

SEED ORCHARDS

Basically there are two ways of establishing a yellow-poplar seed orchard - either with seedlings or by clones. Since the advantages of clonal and seedling orchards have been discussed at great length by able men from all over the world (Silvae Genetica Vol. 13. 1964), I shall not attempt to contribute any new arguments. In the South there are only five or six organizations, mostly in North Carolina and Tennessee, working on the establishment of yellow-poplar orchards. To my knowledge all these orchards were established by vegetative propagation, usually grafting.

Rooting of mature yellow-poplar cuttings is a rather difficult task (Huckenpahler 1955). Enright (1957) reported that he was able to root up to 78 percent of his cuttings, but repeated trails with similar techniques have been unsuccessful (McAlpine 1964; Thor unpubl.). McAlpine was, however, able to root cuttings taken from stump sprouts of 7-year-old trees.

Grafting of yellow-poplar is by no means easy, but satisfactory results may be obtained by careful work and correct timing. After five years of grafting yellow-poplar, we have found that in the Knoxville area best results are obtained by grafting in early April. The scion wood is collected in February and stored in the refrigerator until grafting time. The importance of the relative vegetative stages of stock and scion has been noted by Churchwell (1965). In the most successful series of grafting in Knoxville (April 1964) we obtained 59 percent "takes" on our grafts. Since we usually put on two grafts per tree the percent of successfully grafted trees was boosted to 67 percent. In that same year we established an informal test in two locations to determine the effect of bagging on grafting success. Since there was no difference in survival between bagged and unbagged grafts we have now discontinued the use of bags and thus reduced grafting costs considerably.

Bud-grafting of yellow-poplar in the fall has the advantage of extending the propagation season. Funk (1963) reported good early success with budding between 3 and 6 weeks after height growth ended in the woods. Sluder [7] had poor results with bud-grafting on potted plants. Thor (unpubl.) had good early success with bud-grafting on sturdy 2-year-old stock in the nursery. When the top of the stock plant was removed 2 weeks after budding, the bud usually broke dormancy; however, the tender new growth formed did not harden off and the majority of the bud-grafts were lost during the winter.

Taft makes a conservative estimate that 20 percent of open-pollinated seed is selfed under natural conditions. Since some trees appear to have high selfing fertility it may be possible to develop selfed lines of high-quality trees. However, most orchards should probably be based on maximum cross-pollination. In order to secure a high proportion of outcrossing and a high germination percent of the seed, we must work with a relatively large number of clones which are well spaced in the orchard. It may be advantageous to pair highly compatible clones, or even graft such clones on the same under-stock.

The first three to four years after establishment there will be very few flowers and the management of the orchard should be directed to obtain as strong growth as possible. At the University of Tennessee we have found that both irrigation and fertilization-especially with nitrogen-are essential for rapid development. Other management practices, such as protection, mowing, mulching are not different from those necessary for any seed orchard.

We do not know when abundant flowering starts in grafted yellow-poplars, but my estimate would be between five and ten years. Problems with regard to maintenance of proper insect populations will have to be solved before the orchards become fully functional.

SUMMARY

1. A considerable amount of information on flowering, pollination, and seed production in natural stands of yellow-poplar is available. Individual tree variation in seed viability is large. In addition to self-incompatibilities there is also good evidence of cross-incompatibility.

2. Inter-specific hybridization does not offer much promise, but the outlook for improvement through intra-specific hybridization is good.

3. Results from studies of natural populations and provenance tests support the view

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[7] E. R. Sluder, unpublished progress report, Southeastern Forest Expt. Station.

that much variation is present for such characteristics as early height growth, frost hardiness, stem form, branching habit, and wood specific gravity.

4. Very little substantial information is available on the heritability of various characteristics in yellow-poplar. However, several studies have been established, and data necessary for prediction of gains in some characteristics will be obtained in the not too distant future.

5. Based on our present knowledge, a selection breeding program - using characteristics such as wood specific gravity, stem straightness, pruning, and branching characteristics - shows considerable promise.

6. The establishment of clonal seed orchards appears to be one practical solution to the problem of obtaining good quality seed of yellow-poplar.

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Improvement of Sweetgum

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The economic necessity of efficient land utilization, the rapidly expanding use of hardwoods in a variety of products, and the near famine for hardwoods in certain areas require that forest management plans place more emphasis on growing these species. This situation has come about because hardwood properties differ from those of pine, and technologists are constantly developing new ways to use these properties. If hardwoods are to be included in management plans, the species used should have not only high value and extensive utility, but also wide site adaptability. Sweetgum is such a species.

For some time industry has been aware of the high value of sweetgum. However, accompanying increased awareness of value has come awareness of problems in regenerating and growing the species. Tree improvement, through selection, breeding, and use of the proper seed sources, can alleviate some of the difficulties. Today, I want to mention some of the most pressing problems in growing quality sweetgum, and to suggest ways that the tree breeder can effectively use sweetgum's particular combination of characteristics. Then I will briefly review tree improvement activity currently being carried out on the species.

TRAITS NEEDING IMPROVEMENT

Workers who are improving sweetgum should concentrate on those problem traits that impair its economical inclusion in forest management programs or restrict its use in certain wood products. These problem traits can be grouped according to their effects on growth efficiency and on wood quality. Improvement must include numerous traits simultaneously; if only one trait at a time is improved, other important characteristics may regress and actually provide less net economic gain.

The often inadequate supply of sweetgum, especially during wet weather, poses a serious

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problem in many localities. Merely favoring the existing sweetgum will partially alleviate this, but planting and seeding will have to augment natural regeneration. When we are producing improved seed for artificial regeneration we should strongly emphasize growth efficiency. Selection should favor fast-growing trees that will produce high volumes per acre.

Some of the pulp and paper industry programs want to move sweetgum from its typical wetland habitat to areas that are operable year-round under most weather conditions. These operable sites are probably the best pine sites, site index 90 or better. If this becomes necessary, improved growth efficiency will assume even greater importance for two reasons: (1) sweetgum is difficult to establish artificially on these sites; and (2) it does not produce as much volume, or revenue per acre, as loblolly pine (Ralston 1955; Beaufait 1957). Although it may be permissible to accept fewer dollars per acre in order to provide sweetgum for the mill, it might be possible to improve growth efficiency to a high enough level to provide a program that is economically efficient at all stages of production.

When we are considering wood quality, it is helpful to equate uniform wood with high quality wood because, regardless of the technology of the future, uniform wood will always be valuable. Wood uniformity is controlled by a number of external characteristics of the tree as well as internal anatomical properties. Clear, knot-free wood is obviously more nearly uniform than knotty wood; therefore, early self-pruning must be emphasized. A high value should be placed on trees that are straight, round, and vertical (i.e. not leaning) because they have a minimum of tension wood. Pin knots, caused by dormant trace buds and epicormic branches, and interlocked grain are irregularities often causing costly defects. Selection should favor straight grain and discriminate against trace buds and epicormic branches. All of these, with the possible exception of interlocked grain, affect the paper-maker as well as the plywood and lumber manufacturer.

Just how important specific gravity, fiber length, and other fiber properties of sweetgum will be to the paper-maker remains a moot question. There may be some merit in breeding for long fibers and high specific gravity (i.e. more pounds of cellulose per acre). But, the inclusion of these traits as major objectives will dilute the effort spent on improving the sure problem traits: volume per acre, self-pruning, and straightness. In fact, it is possible that parents with extremely high or low specific gravities should be rejected to further improve wood uniformity. Regardless of the direction individual tree improvement programs may take, these two traits should be measured and recorded on each selected parent tree.

Sweetgum is relatively free of major disease and insect enemies, but intensive management will probably uncover new problems. At present, susceptibility to pests is not important enough to warrant its inclusion as a major consideration in selection. If unhealthy trees are never selected as parents, this rejection will provide some measure of selection for disease and insect resistance.

CHARACTERISTICS AFFECTING TREE BREEDING

It is fortunate that sweetgum has characteristics that the geneticist can work with easily. It is a wind-pollinated, strongly self-sterile species; seed set following self-pollination is rare (Schmitt 1964). These two traits maintain genetically diverse and phenotypically variable populations, both of which are necessary for effective tree breeding. Even a cursory examination reveals wide variation within the species in growth rate, branching habit, self-pruning, straightness, epicormic branching, and adaptability to a variety of sites. There is also much diversity in the wood properties: specific gravity, fiber length, and interlocked grain (Webb 1964).

However, other aspects of the variability in sweetgum, while being assets in most instances, present some complications during the selection process. The selection systems currently used in the pines compare a candidate tree with its neighbors. This is a good procedure, especially when estimating the growth potential of a tree, but its application in sweetgum is complicated by the species' variable growth habit. Sweetgum grows under a variety of stand conditions ranging from pure, even-aged stands or patches to mixed, even- or uneven-aged stands. Also, its tendency to regenerate itself from root suckers, and thence its clonal habit in certain areas, further complicates the use of this procedure. Yet, the practice of comparing a candidate tree with its neighbors is such a valuable procedure that it may be desirable to restrict selection to pure, even-aged stands where there are enough comparison trees. Whether or not this is practical will depend on the organization and the locality where it is working.

Once selections have been made, controlled pollination for progeny testing should proceed with no more difficulty than has been encountered in the pines. The floral buds are larger than the vegetative buds and can be recognized as much as 2 or 3 months prior to budbreak. Sweetgum is a monoecious species, with male and female flowers originating from the same bud. The staminate heads stand erect in a raceme 2 to 3 inches long; the pistillate flowers, in a round head, hang at the base of the raceme. Unlike pine, the flowers must be emasculated before being bagged for control-pollination, but this is easily done.

Pollen can be collected with little difficulty for the current season's control-pollinations, but means for storing pollen from one year to the next have not yet been developed. There is wide tree-to-tree variation in the time of pollen flight and female flower receptivity; individual female flowers are receptive for relatively long periods--2 to 3 weeks, contrasted with 3 to 5 days in the pines. The long receptive period simplifies timing of pollination but necessitates leaving the bags on 3 to 4 weeks after pollinations have been made, to avoid subsequent contamination.

Collection and extraction of seed is a simple process permitting the use of methods similar to those used in pines. As Wilcox (1965) points out, it is possible to collect seed during a 6-week period prior to seed fall. This allows flexibility in timing seed collection.

Seed-set following controlled pollination is generally good, and it may be as high as 45 to 85 seed per head with 1, 2, or 3 heads per pollination bag (Schmitt 1964). Germination, with or without stratification, is often 80 percent or better.

Several methods have been developed for vegetatively propagating sweetgum. Root cuttings and greenwood cuttings originating from root suckers have been rooted successfully (Brown and McAlpine 1964; Farmer 1965). According to McElwee,[2] Orion Peevy, with Weyerhaeuser Company, used cleft and side grafts to vegetatively propagate selected sweetgum for use in a clonal seed orchard in North Carolina. These results mean that we can use vegetative propagation to fulfill various research needs as well as to develop clonal seed orchards. It is still questionable whether sweetgum can ever be vegetatively propagated economically on a large scale like cottonwood.

In another application of vegetative propagation, Wilcox and Farmer[3] are working to develop a method for combining bottle-grafting and control-pollination for use on sweetgum. Branches bearing flower buds are bottle-grafted the fall before control-pollinations are to be made. When the flowers develop on the graft, they are emasculated, bagged, and control-pollinated in the greenhouse. The next fall seed are collected from the graft. So far, Wilcox and Farmer have had only limited success, but if this method is perfected, it will facilitate pollination of certain problem trees, especially those that are very tall or are in localities flooded during the spring. It is more important, however, that with this method, workers can start making controlled crosses for progeny testing early in a tree improvement program instead of waiting several years to make pollinations in the seed orchards. Eventual success of the method will probably depend on the technique of the person making and caring for the grafts.

POTENTIAL BREEDING METHODS

In the absence of detailed genetic information, it is only possible to speculate about the breeding methods and their variation that should be used. Selection and crossing within the species are assumed to have the greatest potential in sweetgum for several reasons. Mutation breeding using ionizing radiation has produced only limited success in certain agronomic crops, and then only when directed at very specific problems. Its application to sweetgum is not recommended at this time. Hybridizing with the two other species of Liquidambar, found only in the Orient, has rather remote chances of improving our native species (this procedure should and will be explored by organizations responsible for basic research on the species). The most important justification for first selecting within sweetgum is the existence of wide variation within the species, and of a "breeding system" that is easy to manipulate.

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[2] Personal correspondence, 1965.

[3] Personal correspondence, 1965.

Its wind-pollinated, self-sterile habit, and the availability of methods for vegetative propagation suggest using the clonal seed orchard approach. The first clonal seed orchards in the species will probably resemble closely those in pines and include 30 to 50 clones. Yet, the self-sterility trait may allow the development of special orchards with small numbers of clones in combinations that have proven superior in progeny tests. A conceivable approach is the development of two-clone orchards composed of pairs of clones that have exceptionally high specific combining ability. This method is currently not applicable in the pines because self-fertility in the pines is much more frequent than in sweetgum. Adoption of any of these methods to sweetgum hinges on future studies of pollen-flight patterns and on the time of pollen flight and flower receptivity of the specific clones in question.

Seedling seed orchards appear to have greater potential for use in sweetgum than in most species of pines, primarily because budgetary and time considerations in some programs will allow only limited investments in hardwood tree improvement. In such programs, once selections have been made, seedling orchards can be established using open-pollinated seed. If, however, the organization is willing to expend the extra effort and money to make controlled crosses to produce the necessary seedlings, it should seriously consider clonal orchards as an alternative. In either case, consideration should be given to the relative length of time required for seedling and clonal orchards to produce abundant seed crops. Theoretically, seedling orchards composed of control-pollinated seedlings will produce more gain, but it will come at a later time. Seedling seed orchards in sweetgum will have many of the same complications of roguing and subsequent spacing as the proposed seedling orchards for pines.

Provenance research will necessarily be emphasized at an early stage in the sweetgum improvement process. We have no idea about the magnitude of gains to be achieved in this species from use of the proper geographic seed source, or about the losses to be suffered from use of the wrong seed source. The growth potential of trees growing on poor sites may be quite different from that of trees found on good sites close by. In attempting to develop sweetgum that will grow favorably on sites that are operable year-round, it is logical to consider trying trees from the drier, westernmost part of the range of sweetgum in northeast Texas and Oklahoma.

CURRENT ACTIVITY

In response to the growing awareness of the value of sweetgum, industrial concerns, forestry schools, and governmental agencies have started sweetgum tree improvement programs. Activity is almost south-wide, ranging from Mississippi to North Carolina.

Although the Cooperative Industry--N.C. State Hardwood Research Program is initially emphasizing silviculture, its activities also include an increasing number of genetic studies. One of its cooperators, the North Carolina Division of Weyerhaeuser, has already made 37 field selections of sweetgum, and 20 or 25 of these have been accepted for use in the seed orchard. They are developing a clonal seed orchard and have about 800 successful grafts so far. The North Carolina State program is starting a provenance study including 28 seed sources from North Carolina to Texas. These will soon be planted in 14 different localities from North Carolina to Louisiana.

Sweetgum tree improvement activity by the U. S. Forest Service in the Delta region is centered in Mississippi; the applied breeding phase is conducted at Stoneville in close coordination with the basic genetic studies by the Institute of Forest Genetics at Gulfport. Of the several Delta hardwoods being studied, sweetgum has the second highest priority. Wind-pollinated progeny tests of some 50 selections have been initiated as well as quantitative genetic studies and seed source tests. Forest Service workers will soon plant, in cooperation with the State of Mississippi, a seed source study representing an intensive sampling of that State. Their activities also include development of methods for pollen collection, storage and germination, for controlled pollination, and for vegetative propagation.

At Auburn University work has started on the variation in the wood of sweetgum throughout Alabama. This will eventually be expanded to include a selection and breeding program.

In the territory of the Southeastern Forest Experiment Station, U.S. Forest Service, work has been underway for some time at Athens, Georgia. In addition to developing methods for rooting cuttings of sweetgum, investigations are being carried out on epicormic branching, and on methods for detecting epicormic tendencies of outstanding candidate trees. These investigations have laid a good foundation for the more intensive tree improvement work that will begin there at the end of this summer.

SUMMARY

Recent technological developments, increased demand, and the resultant short supply of desirable hardwoods have focused increased attention on hardwood management in the South. Fortunately, tree improvement is being included from the start. Because of its high economic value, wide adaptability, and broad utility, sweetgum is receiving a high priority. However, improvement of such problem traits as growth efficiency and wood uniformity will expand the utility and hence further increase the value of the species.

Sweetgum has characteristics that facilitate tree improvement; it is wind-pollinated, monoecious, and self-sterile. Seedlings can be grown easily, and vegetative propagation methods are being developed. It is a variable species and can be assumed to respond well to selection and breeding. Clonal seed orchards composed of many, few, or even only two clones seem promising. Seedling seed orchards seem more feasible in sweetgum than in pine.

Sweetgum tree improvement has been initiated by several industrial and governmental organizations. Now it appears that, unlike pine, when seeding and planting sweetgum does start on a large scale, only the highest quality seed available will be used.

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Cottonwood Improvement in the Lower Mississippi Valley

ROBERT E. FARMER, JR. [1]

In river bottoms of the lower Mississippi Valley, cottonwood (*P. deltoides* Bartr.) is a pioneer species of major economic importance. Because of its extremely rapid growth on suitable sites, it has considerable potential for intensive management in plantations. Poplar culture in the South may eventually approach agronomy in levels of investment and return. Cottonwood also has the potential for spectacular failure under a wide range of conditions. With few forest species is it so important that the silviculturist apply all the techniques and knowledge available. To merit costly attention, the material must be genetically worthy. Thus development of genetically superior cottonwood is simply an essential aspect of intensifying its culture.

Cottonwood is used by the lumber, veneer, and paper industries; tree improvement goals must derive from the requirements of all three uses. Briefly, the products of cottonwood breeding should be inherently straight, cylindrical, rapid-growing trees with clear wood having high specific gravity and long fibers. Good form and rapid growth will be partly dependent upon inherent pest resistance.

The object of this paper is to review the status of cottonwood improvement research in the lower Mississippi Valley. Specifically, I will discuss silvical characteristics strongly related to development and use of improved stock, patterns of natural variation,

[1] Southern Hardwoods Laboratory, Stoneville, Mississippi, maintained by the Southern Forest Experiment Station in cooperation with the Mississippi Agricultural Experiment Station and the Southern Hardwood Forest Research Group.

and the nature of breeding systems currently in use. My comments will deal largely with research centered at the Southern Hardwoods Laboratory of the Southern Forest Experiment Station. Active cottonwood improvement programs are presently limited to those of this laboratory and the Texas Forest Service.

SILVICAL CHARACTERISTICS RELATED TO IMPROVEMENT

Cottonwood is a dioecious species with prolific annual seed crops. Flowerbuds are formed in early summer; flowering and wind pollination take place the following spring, and seed dispersal occurs between May and August in the lower Mississippi Valley. Seeds germinate and become established on moist soil immediately after dispersal. Unlike some other *Populus* species, cottonwood can be easily grown from seed in the nursery.

Controlled crosses essential to breeding can be made on bottle-grafted scions bearing female flowers. These grafts to juvenile stock may be made under greenhouse conditions in early fall or immediately prior to forced flowering in late winter. Fresh pollen is easily obtained in late winter by forcing male flowers. One or two catkins containing several hundred seeds apiece are subsequently matured on each graft in two to three months. In short, cottonwood's reproductive characteristics lend themselves to genetic improvement research.

Populus deltoides is easily propagated by stem cuttings. Twenty-inch-long unrooted cuttings of juvenile material are predominantly used as planting stock. Products of genetic improvement research will undoubtedly be clones vegetatively propagated on a commercial scale.

Intensive cultural practices including thorough site preparation and weed control are now recommended in establishing cottonwood plantations. Irrigation and pruning may become common. Breeding programs must incorporate tests of the relationship between cultural practice and expression of genetic potential.

Site relationships are currently of major interest to cottonwood growers and improvers. River-channel deepening and straightening are reducing occurrence of natural cottonwood on new riverfront sites, and hence necessitating planting or seeding on older land. In some cases planting is being attempted, for pressing economic reasons, on soils whose nutritional or textural characteristics are marginal for cottonwood. Success on such sites may require especially adapted stock.

NATURAL VARIATION

While silvical considerations affect the nature of cottonwood breeding, improvement is fundamentally dependent upon natural variation and inheritance of characters to be modified. The literature on natural variation in European and North American *Populus* species is extensive, and there are a few data on inheritance; but the cottonwood population in the lower Mississippi Valley has received little investigative attention. Consequently, the first job of the Southern Hardwoods Laboratory has been to obtain data directly applicable to breeding in this area. This is being done through (1) direct sampling in natural stands, (2) clonal tests of randomly selected trees, and (3) progeny tests. I shall summarize some initial results.

In natural stands at several locations in the Mississippi Delta, specific gravity of wood samples from individual trees ranged from .32 to .46, and 98 percent of this variation was due to differences between trees within stands. Wide variation in dates of flowering and seed dispersal followed the same pattern as wood density; within-stand variation was much greater than that between stands or between locations. Further, dates of phenological events for individual trees in different years were significantly correlated; this indicates, for example, that within a given group of trees flowering occurs in the same sequence year after year.

Through clonal tests of random selections on several sites, we can determine the degree to which clones (genotypes) vary, and can evaluate the relative effects of genetics and environment. Variation in juvenile growth rate of clones is, as one would expect, strongly influenced by environment, but our data indicate that it is sufficient to provide around a 9-percent increase in early height growth if one selects the best 10 percent of an average population on the basis of test results. Form of juvenile cottonwood varies widely and is under moderate genetic control. Some clones have numerous small branches and a Christmas-tree-like shape; others are rangy, loose-limbed trees. The typical form is candelabra-like.

Clonal variations in bark color and morphology, under strong genetic control, are also strikingly evident in juvenile populations.

Phenological variation in clonal tests is as broad as that observed in natural stands, and has considerable genetic basis. An inherently early foliating clone can be developed simply by taking cuttings from the first flushers in a natural stand.

The most spectacular clonal differences observed to date are in relative resistance to Melampsora rust, a leaf rust that infects trees during August and September and may cause early defoliation. We have found a few clones that are almost completely resistant to this pathogen, even during heavy general infestations. Inheritance data indicate that a 100-percent improvement in juvenile rust-resistance can be made in one generation through intensive selection.

While field sampling and clonal tests may delineate natural variation in a population and determine the degree of genetic control over this variation, only progeny tests tell how genetic control is passed from one generation to another. To date, in one-parent (open-pollinated) progeny tests we have observed significant familial differences in juvenile growth, wood properties, phenology, and disease resistance. In one such test a strong positive genetic correlation was found between growth rate and fiber length, indicating that selection for one of these characters will result in a concomitant increase in the other. Perhaps the most significant feature of these tests, however, is the great diversity found within half-sib families. While this is not especially unusual, it indicates a good possibility for improvement through individual-tree selection in these families. We are now designing two-parent (control-pollinated) progeny tests that will yield more refined inheritance information.

Data from juvenile tests and field sampling give at best a limited conception of the population, one that may change with later results. However, we feel that a general picture is emerging. First, the population in the lower Mississippi Valley appears to be very heterogeneous. Second, most of this variation is accounted for by tree-to-tree differences within stands. Third, some characters with especially wide variation (i.e. phenology and morphology) appear to be under strict and perhaps simple genetic control.

In view of these tentative conclusions some ecological considerations are, I think, important. The Mississippi River has been influential in at least two ways. First, it brings a continuous supply of new germ plasm into the population. A whole tree may be carried on the spring flood from Cairo to lodge and disperse pollen at Natchez. Second, annual floods of varying scope and duration coupled with cottonwood's seed dispersal characteristics have probably kept the genetic pot pretty well stirred. The end result may be a population of unusual and continuing genetic diversity with geographical differentiation (if such exists) occurring between river basins. A major racial study now under way at the University of Illinois should test this hypothesis.

BREEDING SYSTEMS

Since cottonwood is propagated by cuttings, improvement once expressed in a single genotype can be maintained indefinitely on a commercial scale. Thus early improvement gains may be rapidly secured by selecting the better genotypes from a natural population and directly propagating them. A simple improvement program consists of selecting the best juvenile phenotypes in a natural population, testing them as clones, then selecting the genetically best clones for commercial use. This procedure is currently being used by the Texas Forest Service and a few industries. Improvement of characters which vary widely and have strong genetic control may be great. The technique guarantees some gain if enough clones are properly tested and is certainly a logical initial step toward improvement; but it has important deficiencies as a major long-term improvement system. One fault is that improvement is necessarily limited to the best genotypes in a natural population. Furthermore, an inordinate amount of time may be needed to find these genotypes.

The Southern Hardwoods Laboratory's program is essentially an extension of the above system. It includes progeny evaluation as well as field selection and clonal tests. Initial selections are made in mature stands and are based on growth, form, apparent pest resistance, and wood properties. Potential select trees are judged in relation to neighboring dominant and co-dominant "check" trees.

Field selections are vegetatively propagated and stored in replicated clonal tests.

Open-pollinated seed has also been collected from female selections and used to establish nursery progeny tests. Juvenile selections are then made from these progeny plantings. Commonly, the better trees in the better families are selected after 2 years' growth. Selection for growth rate includes at least the top 1 percent of the population; selection for characters less affected by environment may be more intensive.

These juvenile selections are then subjected to two clonal tests. The first is preliminary. It includes 100 clones and is run for 1 to 2 years on two alluvial sites representing extremes for cottonwood--Sharkey clay and Commerce silt loam. Approximately 60 percent of these clones are rogued. Clone-site interactions may be of major importance in selection for early growth. Some clones that perform well on the good site fall in the lower half of the test population on the poor one; others that are among the top 25 percent on Sharkey clay sometimes are relatively poor performers on Commerce loam.

Selected clones are placed in long-term tests that are more extensively replicated than preliminary tests. At least two sites are used, and clonal plots are large enough to allow two thinnings. A group of randomly selected clones is used as a control. The best clones in the long-term tests will be some of the program's final products.

The system still only sifts out the best genotypes in the natural population. Further manipulation will be required to produce uniquely superior stock comparable to products of crop breeding. The exact nature of this manipulation is unknown at present, but a modified form of "recurrent selection" is likely to be used. In such a system, parents evaluated in clonal and progeny tests are intercrossed to produce progeny from which individuals with favorable attributes of both parents are selected. Recurrent cycles of selection and intercrossing gradually accumulate favorable genes as undesirable individuals are eliminated. At any stage of the process, progeny from proven desirable crosses may be either mass-produced as improved seedling stock or selected, tested, and used commercially as clones.

SUMMARY

Cottonwood improvement in the lower Mississippi Valley, now in its initial stage, is an essential part of research leading to intensification of poplar culture in the region. The new trees should have superior genetic potential for growth, form, wood properties, and pest resistance. The nature of our current genetic improvement programs is strongly influenced by cottonwood's silvical characteristics, some of which are distinctly advantageous to effective breeding. Site relationships are of particular importance both in producing and utilizing genetically superior stock.

Natural variation of characters potentially important to improvement appears to be broad in the lower Mississippi Valley cottonwood population. Patterns of variation may be strongly influenced by rapid movement of germ plasm from more northern ecotypes into the population via river systems. Productive breeding systems utilizing this variation may range from simple mass selection and subsequent clonal testing to long-range programs of recurrent selection.

Improvement of Oaks

KINGSLEY A. TAFT, JR. [1]

This subject is by no means lucrative. A search of the literature and many personal letters failed to produce actual results of many oak improvement projects. This paper will have two primary aims; the first is to report current work being conducted on oaks and the second is to express some of my personal ideas on the selection and improvement of oaks.

Oak improvement started in Europe and Asia many years ago. It was believed that improvement could best be accomplished by crossing different species within the genus Quercus and selecting from among the hybrids. Therefore, until recently this has been the major breeding method employed for the improvement of oaks. However, within the last five years the trend has been toward the selection method so familiar to pine improvers.

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Ideally, one must determine whether racial or geographic differences exist within a species before individual selections can be made. One such study includes geographic sources of northern red oak (Quercus rubra L.) and is under the direction of the Ohio Agricultural Experiment Station and approved by the North Carolina-51 Committee. The study includes 31 origins and is planted in 12 localities in nine states. The cooperating agencies are the state experiment stations. Over-all nursery evaluation of this northern red oak study indicates, when all sources are included, that seed origin has a greater effect on seed weight and growth rate than female parent. However, exclusion of the most northerly origins reverses this conclusion. The implication is that individual tree selection will produce the greatest genetic gain and that racial differences within the areas from which selections will normally be made are relatively unimportant.

In addition, the effect of seed weight on seedling size was tested in the above study. Of the thirty-one origins only two were affected by seed weight. A similar study with chestnut oak (Q. montana Willd.) was established by the Tennessee Valley Authority. Three replicated lots of seed (20, 40, and 60 acorns per pound) failed to produce any difference in D^2H (diameter squared times height) in the seedlings produced. These two studies fail to confirm the common assumption that seed size affects seedling size.

A seed source study with southern red oak (Quercus falcata)under the direction of Clemson University and approved by the S-23 Committee will be started in the near future.

At North Carolina State University at Raleigh a Cooperative Industry Hardwood Research Program was started in 1963. Although initial efforts have dealt with site quality evaluation, and silvicultural and management explorations, genetic and variation studies will also be made. Currently an intensive research program is under way to study the variation in willow oak (Quercus phellos), water oak (Quercus nigra), and hybrids between the two. Preliminary results indicate no difference in specific gravity and fiber length when the two species are grown together. However, specific gravity does vary both within and between individual trees within a stand. This again points to individual tree selection as the best improvement method for these species.

Superior oaks are currently being selected by the states of Tennessee, Kentucky and North Carolina, and by the Tennessee Valley Authority. In the near future, the state of Georgia and the Hardwood Research Laboratory at Stoneville, Mississippi, will begin selection programs.

In addition to the above projects, there are several arboreta located throughout the area. The Michaux Quercetum at the Morris Arboretum in Philadelphia is one, and a replica of this is located at the Ohio Agricultural Experiment Station. Clemson University has an arboretum with over 250 exotic species including many oaks. TVA has a quercetum at Norris with 18 different species. An arboretum is to be established by Williams Furniture Company near Florence, South Carolina, and another is in the planning stages on the Land Between the Lakes in west Tennessee.

The Tennessee Valley Authority outplanted a small (four mother trees) open-pollinated chestnut progeny test this spring on University of the South land at Sewanee, Tennessee. Nursery evaluation of the material indicated a significant difference between families for diameter squared times height (D^2H). Future measurements will be made to see if this difference is maintained and also to obtain information on the optimum size for future progeny tests. In addition, exceptional northern red oak seedlings were selected from seedbeds this last spring and outplanted with other seedlings to see if the superiority is maintained. TVA is also investigating methods for stimulating early flowering in chestnut, northern red, and white oak, through the use of an early flowering rootstock, sawtooth oak (Quercus acutissima), and mature wood intergrafts. Results will not be available for several years.

Cross pollinations within species have been tried by the Central States Forest Experiment Station and the Southern Institute of Forest Genetics at Gulfport, Mississippi. One seed from 500 pollinations and 12 from 140 indicate the difficulty encountered in pollination work with oaks.

This is about all the information available on current oak improvement work. My apologies to any projects not mentioned.

The second subject to be covered is the selection and improvement of oaks. As you perhaps know, TVA is currently working with chestnut, northern red, and white oak, and therefore this discussion will deal with these species. Although we have only about 50 superior tree candidates of these species, many more have been looked at and rejected. To know what we look for and how we rank or grade various characteristics should be of interest to those of you who plan to start an oak improvement program in the near future. The best way to describe oak selection is to point out how it differs from pine selection, a subject you are all familiar with.

The greatest difference is the omission of "check" trees in oak selection. Basically, superior pine candidates are selected and compared with several surrounding "check" trees. The stand in which the tree is located is usually even aged and a pure or almost pure stand of that species. Most oak stands, on the other hand, are uneven aged with many different species. Here we have to deviate from the pine system with its check trees. We must be able to select and grade these superior oaks on the merits of each individual tree found on any site. We must be able to compare a good tree on a poor site with a good tree on a good site.

A second difference is one present today but one that could change considerably in the future. This is the different use of oaks as compared with pines. Current work with pines includes wood property studies because of the large use of these species for paper production. However, oaks are usually grown to sawlog size and used for veneer, flooring, furniture, etc. Wood properties are certainly important but not nearly as much so as in pines. Increased use of hardwoods for paper manufacture over the past few years is expected to continue and certainly wood properties should be included in oak and other hardwood improvement programs.

Now, let us take a hypothetical walk through a hardwood stand and look for superior oak candidates. We will eliminate all trees that are crooked, have epicormic branching, and are poorly pruned. We next approach apparently straight trees and look up the bole to be sure it is straight. If the tree is perfectly straight for at least two logs (32 feet), we look at the bark, noting ridges and pattern. If spiral grain is evident, the tree is eliminated. If the tree is perfectly straight for at least two logs, well pruned, and straight grained, we step back and look for defects in the first log (16 feet). These are usually branch-caused defects and will depend on the diameter of the tree. If the tree is still good at this point we grade it.

Let's look at each characteristic individually--

1) Straightness: Note that we consider only the first two logs, but let me add that this is the minimum standard. This length is based on a prediction of the size we will allow future oak plantations to attain. Once the butt log is large enough to grade as prime or veneer we have reached a plateau. Further value increase depends on growth rate. Therefore, since the highest value paid for oak timber is for veneer logs we should allow the plantation trees to at least attain this plateau. This means plantation crop trees should be at least 18-20 inches dbh before they are cut. In such a tree the second log will not grade better than number two and the third will probably not grade better than number three. Log studies have indicated that the monies received for lumber cut from a number three log will not cover the expenses of manufacturing such a log. In addition, if the remainder of a two-log tree is in crown, such a tree will attain a given diameter, say 20 inches dbh, in a shorter period of time than a three-log tree. These are the reasons that the first two logs are the most important part when oaks are being selected.

2) Spiral grain: This trait is present in almost all oak species. It has been shown to be a detrimental characteristic in cutting and finishing oak lumber and veneer. No one has proved that either the environment or genetics of a tree is the cause, but evidence and logic point toward genetic control of this trait. Spiral grain should automatically eliminate a potential superior tree no matter how good it is otherwise.

3) Defects: Presence of branch-caused defects indicates two things: first, that lumber quality will be poor and, second, that the tree did not prune itself well. This pruning ability must be qualified. Any tree 14 inches dbh and larger should be defect free for at least the first log. The smaller a tree is the more defects one allows. However, epicormic branches should not be tolerated. A 10-inch dbh tree without defects in the butt log indicates a good pruner. It can also be assumed that this tree will be free of defects at 20 inches dbh. However, you cannot assume that a 20-inch dbh defect-free tree was free of defects at 10 inches. Therefore, selection of small superior trees (down to about 7-8 inches dbh) seems surer than selection of larger trees. By selecting for lack of defect we are indirectly selecting for branch characteristics. Consequently, branch size and angle are not strong factors in our selection system.

4) Growth rate: In oaks, as in most hardwoods, extreme growth rates are not desirable.

Uniform rates are more important. Trees growing at the uniform rate of 2 inches in diameter every 5 to 10 years are desirable. Faster rates are acceptable, but slower rates should not be considered.

5) Form class: There is little we can say about this except that the higher the form the better.

6) Crown characteristics: In general, the crown should be well shaped, full, and healthy. The aim should be maximum growth on individual trees rather than trying to squeeze a few more small crowned trees on each acre.

7) Total height: This should be considered and measured, but because apical dominance is not prevalent in oaks it should not be a critical factor in selecting superior trees.

Ideally, selection criteria should be based on the results of genetic studies. Such results are not available in oaks. Therefore, we select trees on the basis of important economic characteristics but weigh these traits with genetic logic based on results of work with other species. If I had to rank the previously described characteristics in order of importance in oaks, my list would look about like this:

1) No spiral grain.
2) Perfectly straight for at least two logs.
3) Trees free of defects or with a minimum of defects in the butt log and no epicormic branching.
4) Uniform, relatively fast growth rate.
5) High form class.
6) Desirable wood properties.
7) Total height.
8) Desirable crown characteristics.

A close look at this list will show that we are not selecting for eight characteristics as the list implies. The first two are yes and no traits. We have simply restricted the population to trees that are straight for two logs and do not have spiral grain. The next step is to select fast-growing, defect-free trees from this restricted population. The last four--form class, wood properties, total height, and crown characteristics--are not heavily weighted. If a prospective tree can get by one and two and rates high in three and four, a poor showing in any one or all of the last four will not necessarily eliminate it. So really, the system is based on two major selection criteria, growth and defect, and four minor criteria.

Suppose we have made all our selections. The next step will be seed orchard establishment. Grafting has been covered in a previous paper and will not be discussed. But certainly the question must be asked, How large an orchard do you need. Let's assume that in 20 years the orchard will produce about 1,000 sound seed per tree. With this figure one acre of white oak seed orchard spaced at 30 feet by 30 feet would produce about 50,000 seeds. This acreage should be increased several times to overcome individual tree fluctuations of good seed years and thus insure seed each year. Therefore, an organization expecting to plant 500,000 oak per year might consider a 20-acre seed orchard adequate. This basic requirement should be available each year, but considerably more than is needed will be present in certain good seed years. Until successful storage methods are found, we can depend only on the current year's crop.

Another problem that must be faced is progeny testing. As previously mentioned, cross pollinations have been very unproductive. Where one makes 40 pollinations to insure getting 500 seeds in pines, one would have to make many, many times this number in oaks to obtain the same amount. We must conclude that until better success is possible, controlled pollinations for progeny testing will be impractical. This means that open-pollinated tests must be conducted to test oak seed orchards.

In conclusion, there are two points that I would like to make. It would be very helpful if oak pulpwood, sawlog, and veneer users would let us know what type of tree they want, particularly with reference to specific gravity, fiber length, and other wood properties. Second, the discussion on the selection of oaks includes my own ideas on the subject and is presented primarily to stimulate the thinking of current or future hardwood tree improvers. All inquiries and opportunities for discussion on oak selection are encouraged and welcome.

Research Programs with Species Other Than Yellow-Poplar, Sweetgum, Cottonwoods, and Oaks

KEITH W. DORMAN[1]

Several years ago the Committee on Southern Forest Tree Improvement directed a Subcommittee to prepare a survey of forest genetics research similar to those made in the Lake States and the Western states and Canada. The survey material finally has been pulled together and I hope will be published this year. Studies in forest genetics, forest tree improvement, and studies in closely related fields are included.

At this time it is my job to summarize briefly for you the work underway with hardwoods that was not covered in the papers on breeding oaks, poplar, sweetgum, and yellow-poplar.

I will not attempt to describe techniques used or give the amount of project work completed, but will give the agency, the tree species, and the subjects being investigated. Further information can be obtained from the survey report or from agencies concerned.

1. Auburn University, Department of Forestry. Hardwoods in general. Evaluation of promising exotics or replacements for currently grown species and establishment of exotics as a source of breeding material.
2. Clemson University, Department of Forestry. Ash species (Fraxinus spp.) and black tupelo (Nyssa sylvatica). Use of X-ray to correlate seed embryo conditions with viability.
3. Continental Can Company. American sycamore (Platanus occidentalis) and white ash (Fraxinus americana). Comparison of wood properties where age, site, and spacing are uniform; relationship between wood properties of certain sample trees and their ramets and their open-pollinated progenies; and relationship between wood properties, bole, and crown characteristics and pulp and paper properties.
4. Florida Forest Service. Various tropical forest species. Adaptation tests of species that will grow and produce forest products in south Florida.
5. Florida Forests Foundation. Several species of eucalyptus plus silk oak (Grevilla robusta). Adaptability of promising species to representative southwest Florida land types; relationship between applications of ground rock phosphate and species adaptability patterns; comparisons of various species and the importance of seed source; and, in eucalyptus, performance of progenies of Florida-selected plus trees; performance of Florida plus-tree progenies compared with Australian seed sources and the maternal parent; and comparison of several Australian seed sources.
6. Louisiana State University, School of Forestry and Wildlife Management. American sycamore (Platanus americana). Natural variation in botanical features and certain wood characteristics; relationship of such variation to existence of geographic races, clines, or to environmental influences.
7. North Carolina State University at Raleigh, School of Forestry. Hardwoods in general. Statistical methods applicable to quantitative genetics and to progeny testing of forest trees; inheritance patterns, variance components, and best breeding procedures; and, variation and inheritance of physiological and closely related traits. Water tupelo (Nyssa aquatica) and swamp tupelo (Nyssa sylvatica var. biflora). Variation within tree, among trees, and among stands in wood quality factors; isolation of wood quality factors important in final products; and inheritance patterns of wood quality factors. American sycamore (Platanus occidentalis) and white ash (Fraxinus americana). Development of vegetative propagation methods.
8. Tennessee Valley Authority, Division of Forestry Development. Chestnut (Castanea dentata), black walnut (Juglans nigra), black cherry (Prunus serotina), red maple (Acer rubrum), and birch (Betula verrucosa). Selection and development of trees of most rapid growth, highest quality, and greatest economic usefulness for growing in the Tennessee Valley. Development of vegetative and other methods of propagating and producing select plant material of hardwood tree species. Sugar maple (Acer saccharum). Determination of the geographic limits within which seed should be collected for production of forest planting stock used within the Tennessee Valley.
9. United States Forest Service, Southeastern Forest Experiment Station, Asheville, N.C. Black cherry (Prunus serotina). Inheritance of stem form, particularly crook and sweep.

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[1] U.S.D.A., Forest Service, Southeastern Forest Experiment Station

10. *Southeastern Forest Experiment Station, Athens, Georgia*. Hardwoods in general. Location, description, and cataloging of individual hardwood trees that exhibit characteristics useful in genetics and tree improvement programs. American sycamore (*Platanus occidentalis*). Variation in seedling size and optimum size or grade for use in underplanting.
11. *Southeastern Forest Experiment Station, Charleston, South Carolina*. Water tupelo (*Nyssa aquatica*) and swamp tupelo (*Nyssa sylvatica* var. *biflora*). Effects of saturated and flooded soil conditions on growth, anatomy, and morphology of seedlings from two locations, each in three ecotypes. For water tupelo: red river, black river, and nonalluvial swamp. For swamp tupelo: pond, black river, and nonalluvial swamp.
12. *Southern Forest Experiment Station, Gulfport, Mississippi*. Hardwoods in general. Application of theories of quantitative genetics to the special problems of breeding forest trees; relation of the concepts of character development and correlations to economically oriented selection and to the genetic variability structure of natural stands of forest trees; analysis, on the basis of present theories, of proposed methods for producing genetically improved seed.
13. *Southern Forest Experiment Station, Harrison, Arkansas*. Chinese chestnut (*Castanea mollissima*). Determination of blight resistance, survival, growth and adaptability to two of the better hardwood sites in the Arkansas Ozarks.
14. *Southern Forest Experiment Station, Marianna, Florida*. Hardwoods in general. Exploratory planting trials of available species, races, or hybrids.
15. *University of Georgia, Department of Botany*. Hardwoods in general. Growing of callus cultures of male gametophyte tissues *in vitro*; initiation of bud and root formation on such tissues to obtain haploid plants; and doubling the chromosome number *in vitro* in an attempt to produce a homozygous diploid; i. e., a true breeding strain which would have much utility in practical as well as basic utilization.
16. *University of Tennessee, Department of Forestry*. Chestnut (Castanea dentata). Development of trees with resistance to blight by selective breeding and irradiation of nuts. Chinese chestnut (*Castanea mollissima*) and black walnut (*Juglans nigra*) Testing of improved nut trees for their adaptability to Tennessee conditions.
17. *University of Virginia*. Chestnut (*Castanea dentata*). Testing of trees grown from irradiated seed for resistance to chestnut blight.

This completes the summary of work that was reported. If there is other information that should be included in our survey of genetics and tree improvement research, I will be very glad to have it.

Inheritance of Branching and Crown Characteristics in Slash Pine

RAY K. STRICKLAND and RAY E. GODDARD [1]

Although we seldom find a tree that is "ideal" for use in production of a given product, we try to keep the "ideal" in mind. It is usually a tree that is perfectly straight; has little taper throughout its length; grows at a rate at least 50 percent greater than its neighbors; and has a narrow, well-formed crown.

This study is concerned with the crown, the photosynthetic surface of the tree; specifically the slash pine tree. Slash pine crowns come in many shapes--long and narrow to short and broad--with short slim branches to long thick branches and with branch angles ranging from a ramicorm condition to 90 degrees. Occasionally the tree with a perfect crown is found, but one with a perfect crown, near perfect bole form, and outstanding growth rate is very rare. This latter type is in a class all its own, a jewel to the tree breeder.

Why is the "ideal" slash pine tree so rare? If the characteristics tree breeders seek in select trees had high natural selection values when in combination, our pine forests would be full of "ideal" trees. Branches which are short, small in diameter and have a flat angle are "ideal". These traits effect wood quality but are quantitative genetic traits with low to moderate heritability and our "ideal" is of doubtful survival value to the tree.

This study was made to learn correlations among branching and crown characteristics,

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their heritabilities, and their effects on total volume.

Materials and Methods:

The data used in this report was collected during the spring of 1964 on one of four parts of an intensive culture study [2]. The part measured was irrigated and contained four subplots; one was cultivated and fertilized, another cultivated alone, another fertilized alone, and the fourth neither cultivated nor fertilized (control). Treatment effects were not considered, but they do show up as replicate differences and line times replicate interactions.

Seedling lots used in this study were outplanted during the spring of 1961 and had grown four years from seed when measured. Included in the study were twelve seedling lots, nine half-sib (open-pollinated) progeny lines and three bulk check sources. The basic plot consisted of four seedlings from each lot; a total of 16 seedlings per lot were included in the study. Of the 192 seedlings planted, 188 survived. A 10 X 10 foot spacing was used.

The following tree measurements were taken on all 188 trees in the study:

1. Diameter breast high (inches and tenths).
2. Total height (feet and tenths).
3. Crown width/total-height ration (crown width taken at ½ total height)

The following branching characteristics were measured on every branch of the first whorl of the third growing season (from seed) on all 188 trees:

1. Branch length (inches).
2. Branch diameter (inches and hundredths taken at a point 1" from bole intercept).
3. Branch angle (to nearest 5 degrees).

A total of 793 branches were measured in this study. Records were kept in such a manner as to be directly read by a keypunch operator. Analyses were calculated, for the most part, using an I.B.M. 709 computer.

Results:

Regression analyses, correlations and analyses of variance were completed on these data.

A multiple (stepwise) regression analysis was calculated to discern the contribution of a number of crown characteristics to tree volume growth. The variables included in this analysis, the order in which they entered the stepwise regression, their regression coefficients and standard error of coefficients are shown in Table 1.

Table 1. Variables included in the stepwise regression analysis.

Variable	Characteristic	Coefficient	Std. Error of Coef.	Order Entering	Multiple Correlation Coef.
Y	Approx. Volume				
X-1	Cr. Width/height	-60.2435**	7.2693	3	0.510
X-2	Branch diameter	42.7538**	7.3192	1	0.322
X-3	Branch angle	0.5730**	0.0518	2	0.450
X-4	Branch length	0.6857**	0.1378	4	0.532

** Coefficient significant at the 1 per cent level.

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[2] Appreciation is extended to special problems student Robert W. Simons (currently at N.C. State College, Raleigh, N. C.) for assistance with the field data collection and to Dr. Frank G. Martin of the Statistics Department at the University of Florida, Gainesville, Florida for his assistance with the analyses.

The standard error of "volume" was reduced from 15.99 to 13.57 by the regression. Volume in this study is approximated by the formula, diameter breast high squared times tree height (dbh^2h). The constant 0.005454 and the taper factor for each tree were excluded from volume computations. The mean of "volume" was 31.17; therefore, the coefficient of variation was 51 percent based upon the standard deviation of "volume" and 44 percent after regression. The coefficient of determination (R^2) was 0.283 indicating that the independent variables explain 28.3 percent of the variation in approximated volume. All the regression coefficients were highly significant. The prediction equation from this analysis was:

$$Y = -17.730 - 60.244X_1 + 42.754X_2 + 0.573X_3 + 0.686X_4$$

The regression analysis was based on individual branch measurements. There was an average of 4.18 branches measured per tree on the 188 trees.

Six of the 10 simple correlation coefficients among the five variables used in the multiple regression were significant (Table 2).

Table 2. Simple correlation coefficients between the variables used in the stepwise regression.

Variable		$\frac{\text{Cr. Width}}{\text{Total Ht.}}$ X_1	Branch Diameter X_2	Branch Angle X_3	Branch Length X_4
Volume	Y	-0.201*	+0.322**	+0.080	+0.313**
Cr. width/height	X_1	- -	+0.127	-0.079	+0.140
Branch diameter	X_2		- -	-0.560**	+0.848**
Branch angle	X_3			- -	-0.554**
Branch length	X_4				- -

* Significant at the 5 per cent level.
** Significant at the 1 per cent level.

Branch angle was not directly correlated with "volume" but was the second variable entering in the stepwise regression. This is no doubt due to the fact that branch angle is moderately correlated negatively with both branch diameter and branch length which are themselves very closely correlated positively. Graphs of these relationships are shown in Figures 1 and 2. These correlations are in close agreement with the findings of Barber (1964).

Analyses of variance calculated for both approximated volumes and crown width/height ratios showed highly significant differences between lines plus check sources for approximated volume and significant differences between lines for the crown width/height ratio (Table 3). Intraclass correlations (even considering block X line interaction as a phenotypic component) were considerably higher than expected among half-sib progeny lines. Means for lines and check sources (Table 4) showed a particularly wide range of values for approximated volume and a considerable latitude of variation for the crown-height ratio. Also an element of common environment (not explained) contributed to the low variances within progeny lines.

Three branching characteristics (branch diameter, branch length, and branch angle) were analyzed to discern differences between lines and between trees within lines. The results of these analyses along with intraclass correlations and heritability estimates are shown in Table 5. Variation due to differences in individual branches was the residual error term. There were significant differences between lines for branch diameter and branch angle but no significant differences between lines for branch length. All three variables had highly significant differences between trees within lines when tested with the residual error term.

Discussion:

This study was designed to determine if our slash pine selection and breeding program is emphasizing characteristics of tree crown form that are readily attainable. Barber (1964)

Table 3. Analyses of variance and intraclass correlation for crown width/height ratios and approximated volumes.

Source of Variation	Degrees of Freedom	Mean Squares	Variance Components	Intraclass Correlation
Crown width/height				
Replicates	3	0.0267		
Lines	8	0.0128*	0.730 X 10^{-3}	0.312
Rep. X Lines	24	0.0045**	0.609 X 10^{-3}	
Trees/Lines	103	0.0010	0.100 X 10^{-2}	
Volume (d^2h)				
Replicates	3	1695.6		
Lines	11	1182.1**	64.48	0.266
Rep. X Lines	33	305.8	6.00	
Trees/Lines	140	171.6	171.64	

Table 4. Mean values of progeny lines and check lots.

Progeny line	Volume (d^2 Xh)	Crown width / height	Branch Dia. (ins.)	Branch Lgt. (ins.)	Branch Angle (deg.)	Diameter Breast high
1	29.7	39.2	0.552	25.6	61.7	1.68
2	32.8	41.3	0.574	27.5	56.8	1.73
3	45.2	40.6	0.565	26.9	56.4	1.99
4	42.2	41.9	0.581	27.9	55.9	1.92
5	31.6	47.4	0.625	29.9	51.8	1.78
6	29.2	44.6	0.544	27.4	53.8	1.63
7	32.5	40.1	0.572	26.8	54.4	1.76
8	12.1	44.3	0.476	24.2	55.3	1.12
9	27.1	45.5	0.567	29.2	56.8	1.58
10	24.4	42.1	0.537	25.5	56.4	1.54
11	31.8	45.1	0.576	29.6	52.5	1.70
12	18.9	43.9	0.573	27.0	51.7	1.37
$\bar{X}$	31.2	42.6	0.564	27.4	56.0	1.65

Check lots, other lots are half-sib progeny lines.

Table 5. Analyses of variance and variance components for branch diameter, branch length, and branch angle. (Based on individual branch measurements)

Source of Variation	Degrees of freedom	Mean squares	Variance Components	Intraclass Correlation	Heritability estimate
Branch Diameter					
Replicates	3	0.125			
Lines	11	0.066*	0.590 X 10^{-3}	0.0367	17.9%
Trees/Lines	139	0.024**	0.281 X 10^{-2}		
Branches/Trees	609	0.013	0.127 X 10^{-1}		
Branch Length					
Replicates	3	287.0			
Lines	11	179.1	1.16	0.0262	12.8%
Trees/Lines	139	76.9**	10.60		
Branches/Trees	609	32.4	32.38		
Branch Angle					
Replicates	3	48.33			
Lines	8	490.25*	11.44	0.0829	33.2%
Trees/Lines	104	213.13**	27.21		
Branches/Trees	446	99.28	99.28		

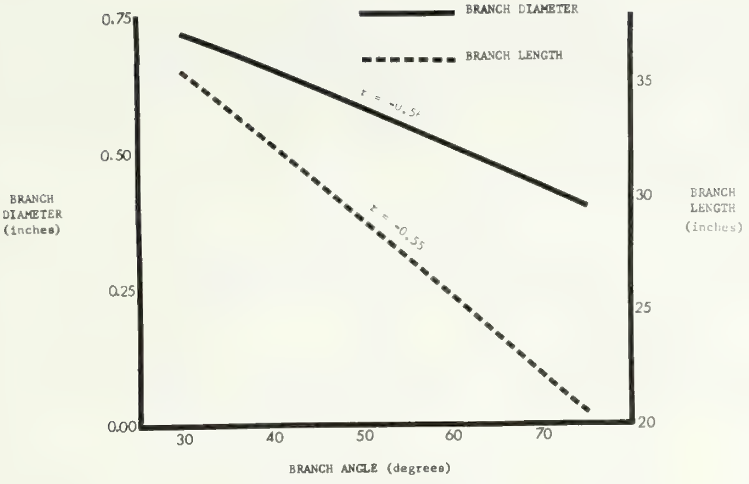

Figure 1 -- The regression of branch diameter on branch angle (Y = 0.9067 – 0.0062 X) and branch length on branch angle (Y = 45.4400 – 0.3262 X).

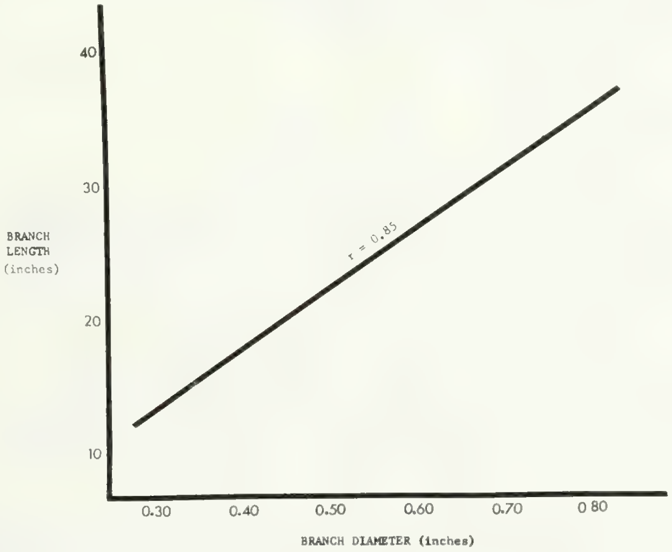

Figure 2 -- The regression of branch length on branch diameter (Y = 2.0927 + 44.8824 X).

reported negative correlations between some of the branching characteristics that are considered desirable in the selection of plus phenotypes. He found correlation coefficients of r= +0.95 for branch diameter X branch length, r= -0.43 for branch diameter X branch angle and r = -0.48 for branch length X branch angle. Our correlations (r = +0.85, r = -0.56 and r = -0.55 respectively) were in close agreement with Barber's. Since we are attempting to select slash pine trees with branches that are short, flat angled and of small relative diameter our job, in this respect, is simplified. These traits are favorably correlated. However, large branches tend to go along with large volume. The correlation coefficients for these characteristics were; branch length X volume, r = +0.31 and branch diameter X volume, r = +0.32 (both highly significant). The coefficients of determination were only about 10 percent and rigorous selection for volume carried on simultaneously with selection for branching characteristics may prevent losses in volume. Occasional select slash pine trees are found that have large volumes and branches that are short, thin and flat angled when compared to the dominant population. These individuals rate high on our selection index and if they are also straight, they are quite rare and extremely valuable.

The multiple (stepwise) regression analysis indicates that all of the dependent variables; crown width/total height ratio, branch diameter, branch angle, and branch length either add to or detract from "volume". The ratio of crown width to tree height was the only variable significantly correlated negatively with "volume". It also has a negative regression coefficient in the stepwise regression. Trousdell et al. (1963) concluded that the ratio of crown width to tree height was generally higher for loblolly pine progeny groups with short trees than for the tall groups. The close relationship between tree height and volume coupled with the above observation is an explanation of the negative relationship found. Branch angle, which is not directly correlated with "volume", contributes significantly in the stepwise regression. The reason for this is the close correlations between the three branching characteristics. Two of these, branch length and branch diameter were significantly correlated positively with "volume" However, only about 28 percent of "volume" variation is explained by the inclusion of all four independent variables in a multiple regression analysis with this trait.

Analyses of variance for the "volumes" and crown width/tree height ratios showed significant differences between lines for these traits and also much higher intraclass correlation coefficients than expected. The variance components from these data cannot be used to estimate "volume" and crown width/height ratio heritabilities because of an unusually wide range of mean values and relatively small components of phenotypic variance when compared to the additive component. The unexplained uniformity within lines plus a wide range of variation between lines makes such an estimate invalid. Using the formula for estimating heritability of half-sib lines (H = 4 X additive genetic variance/total variance) would give values greater than one.

Trees used in this study were among the early slash pine selections and were selected primarily on the basis of volume growth. Since several persons selected the trees it is probable that volume was sacrificed for form in some instances and form was sacrificed for volume in other instances. This is still the general case since it is very difficult to find all of the desirable characteristics of growth and form in one slash pine tree. It is probable that the branching traits themselves represent a random sample from the dominant slash pine population. Heritability estimates for the three branching characteristics were made on this assumption. The estimated variance components were obtained following the procedures outlined by Henderson (1953).

The heritability estimates found in this study were: branch diameter 18 percent, branch length 13 percent, and branch angle 33 percent. Comparisons of these findings with the results of other investigations are shown in Table 6.

Table 6. Comparison of heritability estimates on crown and branching characteristics of coniferous species by five investigators.

Investigator	Species	Trait	Heritability Broad Sense	 Narrow Sense
Barber (1964)	Pinus elliottii	Cr. width/ht.		0.16 & 0.19
Toda (1958)	Cryptomeria	Crown diameter	0.61	
		Branch angle	0.72	
Trousdell et al. (1963)	Pinus taeda	Cr. width/ht.		0.17 & 0.34
Ganzel (1965)	Pinus elliottii	Branch diameter	0.31 & 0.48	
		Cr. width/ht.	0.40 & 0.47	
This report	Pinus elliottii	Branch diameter		0.18
		Branch length		0.13
		Branch angle		0.33

The analyses of variance based upon the measurement of all the branches within the first major whorl of the third growing season showed that there is some consistency of measurements within trees. Branch diameter, branch length, and branch angle analyses showed highly significant differences between trees within lines for these traits. This was expected on the basis of half-sib lines and bulk check sources.

Repeatability of measurements on individual trees within lines can be calculated from these data. This was done and the repeatability results were: branch diameter, 18%; branch length, 25%; and branch angle, 22%. These estimates were obtained by dividing the variance component for trees within lines by the variance component for branches within trees. These repeatabilities indicate that there is considerable variation in the individual traits within a tree and that the measurement of a number of branches is required to obtain a reliable mean for an individual tree.

SUMMARY

Individual branches of the first major whorl of the third growing season (from seed) were measured on nine half-sib progeny lines and 3 bulk check sources. Measurements taken on the branches included branch diameter, branch length and branch angle; whole tree measurements included diameter breast high, total height and crown width at ½ height/total height ratio. Multiple regression analysis showed that all three branching characteristics and the crown-width ratio contributed significantly to the prediction of approximated volume ($\text{dbh}^2 \times \text{ht.}$). The four independent variables accounted for 28 percent of the variation in "volume" ($r = 0.53$). Correlations between the three branching characteristics showed negative relationships between branch angle and branch length ($r = -0.55$) and between branch angle and branch diameter ($r = -0.56$); branch diameter and branch length themselves were closely positively correlated ($r = +0.85$) (the greater the branch angle from the vertical, generally the shorter and thinner the branches). Branch length and branch diameter were both positively correlated with volume and have coefficients of determination of about 10 percent each. Breeding for decreased branch size may concurrently decrease volume unless

this selection pressure is coupled with rigorous selection for volume.

Heritability estimates for branch diameter, branch length and branch angle were 18, 13 and 33 percent respectively. Repeatability of measurements on individual trees for the above traits were 18, 25 and 22 percent respectively indicating that it is necessary to measure a number of branches for each trait in order to obtain reliable tree means.

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Inheritance of Stem and Branch Characters in Slash Pine and Relation to Gum Yield

CHARLES R. GANSEL [1]

The original tree improvement program at Olustee, Florida was confined to selection and breeding for increased gum yield. Recently the program has been modified to include combining gum yield with other desirable traits (Squillace, 1965). In accordance with the revised objective, the present study was designed to determine inheritance of number of crooks per foot, degree of crook, size of branches, and crown width ratio and to determine relationships of these traits with gum yield. Data for this study were obtained from three sources:

1. Progeny plantation 0-116.--This plantation was established from 1-year-old seedlings in June 1946, at Olustee. Parents of the trees had been selected for either high, average, or low gum yield ability. Both wind- and cross-pollinated progenies were included. The plot layout consisted of 7 blocks, each containing from 2 to 6 individuals per progeny, randomly positioned in each block. Spacing was 20 by 20 feet. Twenty-six of the progeny trees were selected for either high-or average-gum yielding ability and used as ortets in establishing clones for clonal plantation NS-112, described below. Likewise, 9 high yielders were selected and used as ortets for clones in clonal orchard G-24, also described below.

2. Clonal plantation NS-112.--This plantation was established at Olustee over the period 1957 to 1959. The plot layout consisted of a split block, split plot design with each of eight randomized treatments being replicated three times. The treatments were: irrigation, fertilization, cultivation, and combinations thereof. Spacing was 20 by 20 feet. There were 24 ramets of each of 24 clones and 12 ramets of each of 2 clones in this plantation.

3. Clonal plantation G-24.--This plantation was established in 1957-58 on the Osceola National Forest, several miles northeast of Lake City, as a seed orchard. It included 26 ramets of each of 6 clones and 22 ramets of each of 3 clones. It contained 13 blocks, with 2 ramets of each clone being located in each block. Spacing was 30 by 30 feet.

MEASUREMENTS

Crown and stem form measurements were made on all ortets and ramets in the spring of 1965. The following traits were measured: total height, number of crooks, degree of crook, size of branches, and crown width. Gum-yield data for plantation 0-116 were available from standard face chipping in 1964.

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[1] Research Forester, Southeastern Forest Experiment Station, U. S. Forest Service, Olustee, Florida.

The number of crooks were counted by the same individual on all plantations. The number of crooks were then divided by total height to obtain number of crooks per foot. This procedure minimized the effect of age and total height on the number of crooks. To have real meaning, the amount or degree of crook must also be considered along with the number of crooks. Goddard and Strickland (1964) used a "crook index," which was the product of the number of crooks in the first log times the deviation of the most severe crook from a straight line along the bole, to express this relationship. However, because of the large amount of time that would be required for obtaining such measurements, an ocular estimate of the degree of crook was used for this study. The trees were classified as straight, slightly crooked, crooked, and very crooked. These classifications were then arbitrarily assigned values ranging from one for straight to four for very crooked so they could be statistically evaluated.

Size of branches was also an ocular estimate, made by one person on all plantations. Branches were classified as small, medium, large, and extra large. These classifications were then arbitrarily assigned values ranging from one for small to four for extra large so they could be statistically evaluated. Crown widths were measured at the widest portion of the crown. Crown width ratios were obtained by dividing the crown width by total height. Fastigiate or upturned branches and forking or tendency to fork were also recorded in the ramets and ortets.

Table 1. Ortet data and clonal means for various traits studied.

Ortet (clone) number	Parentage	Ortet data					Clonal data			
		Gum yield (coded, x 1/10)	Crooks per foot	Index of degree of crook	Index of size of branches	Crown width ratio	Crooks per foot	Index of degree of crook	Index of size of branches	Crown width ratio
		Grams	Number				Number			
		0-116					NS-112			
8-8-1	1x2	488	.189	4	3	.321	.310	3.75	3.00	.700
4-2-7	1x2	626	.140	3	2	.442	.288	2.88	2.88	.671
2-5-6	1x2	749	.179	4	2	.339	.274	3.18	2.45	.740
6-9-6	1x2	852	.135	3	2	.365	.301	2.95	2.62	.583
3-3-5	1x7	745	.167	3	3	.389	.322	3.59	3.18	.728
2-1-4	1x7	1,123	.167	3	3	.407	.477	3.32	3.18	.620
1-3-7	1xW	539	.170	2	1	.340	.270	2.96	2.83	.706
1-6-4	2xW	378	.125	3	1	.268	.219	2.47	1.67	.591
7-5-4	2xW	609	.111	4	1	.278	.233	2.63	2.67	.666
4-7-5	2xW	628	.189	3	2	.358	.288	3.04	2.25	.673
3-8-3	2xW	852	.145	2	2	.327	.268	3.08	3.00	.658
1-1-4	3x2	314	.161	3	2	.357	.245	3.00	2.63	.695
7-7-1	3x6	460	.154	3	3	.423	.235	2.45	2.70	.638
7-4-3	3xW	466	.128	2	2	.340	.232	2.71	2.75	.644
2-3-4	4x1	678	.057	1	1	.358	.204	2.22	2.48	.623
6-4-7	4x1	749	.143	2	2	.306	.216	2.21	1.96	.530
6-9-7	4x1	975	.170	3	3	.340	.238	2.63	3.17	.619
3-8-7	4x1	1,092	.094	2	3	.396	.266	3.17	3.75	.727
4-3-2	4xW	619	.188	3	2	.354	.264	2.63	2.79	.590
6-2-3	4xW	851	.094	2	3	.340	.218	2.63	2.79	.581
2-9-1	6x3	276	.111	2	2	.378	.230	2.21	2.25	.644
7-9-5	8xW	609	.250	2	2	.375	.290	2.92	2.33	.722
3-9-6	10x7	684	.080	3	1	.340	.240	2.63	2.58	.660
2-7-3	10x7	693	.135	3	1	.346	.256	2.88	2.50	.667
4-7-3	10x7	796	.160	4	2	.380	.283	3.25	2.88	.715
4-10-5	25xW	356	.163	2	2	.395	.295	3.46	3.04	.732
		0-116					G-24			
1-7-5	1x2	685	.113	2	2	.340	.209	2.38	2.31	.445
2-6-2	1x2	785	.192	3	2	.346	.238	2.73	2.35	.471
8-9-2	2x1	604	.160	2	2	.340	.158	2.10	1.95	.400
3-8-7	4x1	1,092	.094	2	3	.396	.167	2.12	3.04	.471
4-3-4	4x1	1,186	.148	2	2	.370	.146	1.81	2.31	.423
7-1-7	4x1	1,348	.152	2	3	.413	.140	1.82	2.55	.447
8-9-3	4x2	820	.100	2	1	.280	.118	1.65	1.31	.315
8-10-3	4x2	833	.075	2	2	.283	.131	1.82	1.82	.394
8-7-3	4x2	1,128	.153	3	2	.305	.097	1.58	1.85	.345

STATISTICAL PROCEDURES

Analyses were computed for the traits shown in Table 1. Correlations were computed between identical traits in the ortets and clones, using clonal means for the latter. In addition, regressions were computed between gum yield of ortets and the four measures of crown and stem form, in both the ortets and clones. NS-112 and G-24 data were pooled in these analyses.

Analyses of variance were run on both NS-112 and G-24 data. One block of NS-112 was not used in this analysis because of missing trees, which reduced the number of ramets to 16 for each of the 24 clones. In G-24, 26 ramets of each of 6 clones were used in the analysis.

RESULTS AND CONCLUSIONS

Clone-ortet correlations were significant for all traits studied, with size of branches being highly significant. The following tabulation presents the pooled correlation coefficients (r) and regression coefficients (b).

Trait	r	b
Number of crooks per foot	0.424*	0.5415
Degree of crook	.396*	.2086
Size of branches	.635**	.4069
Crown width ratio	.435*	.5761

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*Significant at 5-percent level.
**Significant at 1-percent level.

The results suggest that all of these traits are inherited to a moderately strong degree.

Tendency toward fastigiate or upturned branching habit also seems to be inherited. Clones from ortets having fastigiate branches usually, but not always, had relatively large numbers of fastigiate ramets. Clones from fastigiate ortets had an average of 48 percent fastigiate ramets, while clones from non-fastigiate ortets had an average of only 4 percent fastigiate ramets.

Tendency to fork appeared to be more affected by environmental factors than did fastigiate branching. When the ortets were classified as having a tendency to fork, 34 percent of their ramets had a tendency to fork. When the ortets were classified as not having a tendency to fork, 17 percent of their ramets had a tendency to fork. There does not appear to be any correlation between fastigiate branching and tendency to fork. A more refined study is needed to determine heritability of fastigiate branching and forking.

Inheritance of the four major traits studied was also demonstrated by analysis of variance of clonal data (Table 2). Clonal effect was highly significant for the four traits studied in both NS-112 and G-24. Broad sense heritability estimates for the four traits follow:

Trait	NS-112	G-24
Number of crooks per foot	0.29	0.47
Degree of crook	.30	.38
Size of branches	.31	.48
Crown width ratio	.40	.47

Mergen (1955) previously examined sweep in progeny plantation O-116 of the present study. He found the progenies of parent trees with large sweep had a high percentage of undesirable trees. The number of undesirable trees in the progeny of one tree (parent tree No. 3), was highly significantly greater than in the progeny from the other trees.

Heritability of stem crook was demonstrated for loblolly pine by Goddard and Strickland (1964), who reported an intraclass correlation of 0.48 from progeny data.

Barber (1964) reported a narrow sense heritability of 0.16 to 0.19 for crown width in his study of slash pine. Squillace and Bengtson (1961) reported two estimates of narrow sense heritability for crown width, 12 percent and 24 to 48 percent, in slash pine.

Table 2. Analyses of variance and estimates of broad sense heritability (r_I) obtained from clonal data.

Source of variance	Degrees of freedom	Number of crooks per foot		Degree of crook		Size of branches		Crown width ratio	
		Mean squares	r_I	Mean squares	r_I	Mean squares	r_I	Mean squares	r_I
				NS-112					
Irrigation (I)	1	.2493*		25.010*		1.628		0.199	
Blocks (B)	1	.0370		.667		.211		.013	
Error 1 (IxB)	1	.0015		.011		1.966		.018	
Fertilization (F)	1	.0006		.010		2.190		.005	
Cultivation (Cu)	1	.0001		1.760		6.773**		.060*	
FxCu	1	.0154		.168		.066		.001	
IxF	1	.0006		.043		.586		.006	
IxCu	1	.0184		.668		.315		.001	
IxFxCu	1	.0023		.091		.752		.004	
Error 2	6	.0042		.561		.453		.006	
Clones (C1)	23	.0173**	0.29	2.450**	0.30	2.428**	0.31	.054**	0.40
C1xI	23	.0038		.282		.296		.003	
C1xF	23	.0025		.228		.304		.004	
C1xCu	23	.0021		.239		.377		.004	
C1xFxCu	23	.0021		.286		.310		.005	
C1xIxF	23	.0011		.389		.178		.005	
C1xIxCu	23	.0020		.275		.353		.005	
C1xIxFxCu	23	.0025		.413		.204		.009**	
Error 3	182	.0023		.318		.293		.004	
				G-24					
Clones (C1)	5	.0751**	0.47	5.299**	0.38	8.677**	0.48	.115**	0.47
Block (B)	12	.0043		.231		.728		.005	
C1xB (error)	60	.0040		.408		.433		.007	
Within plots	78	.0022		.217		.258		.003	

* Significant at the 5-percent level.
** Significant at the 1-percent level.

Some effects of cultural treatments were found. Trees in irrigated plots had an average of .27 crooks per foot and an index of degree of crook of 3.1, while those in non-irrigated plots averaged .22 and 2.6 respectively. Both differences were signficant at the 5-percent level. Trees in cultivated plots had an average size-of-branches index of 2.8 and a crown width ratio of .67, while those in non-cultivated plots average 2.6 and .65, respectively. Reasons for these effects are unknown.

Gum yield was not significantly related to any of the crown or stem characters studied.[2] Thus, high yielding ortets and their clones were found to have as good crown and stem form as low yielding ortets and their clones. This important finding suggests that high gum yield and good form can readily be combined in a selection and breeding program.

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[2] Crown width ratio studied here should not be confused with crown length ratio, which has previously been shown to be related to gum yield by Bengtson and Schopmeyer, 1959, and others.

SUMMARY

Ortet data were obtained from a 19-year-old progeny plantation (O-116), and ramet data were obtained from two clonal plantations, NS-112 and G-24. Stem and branch characters studied included numbers of crooks per foot, degree of crook, size of branches and crown width ratio. Ramet characteristics were significantly correlated with ortet characteristics for all traits studied. Gum yields of ortets were not significantly correlated to traits studied. Estimates of broad sense heritability, obtained from analysis of variance of clonal plantations NS-112 and G-24, respectively, were as follows: number of crooks per foot, 0.29 and 0.47; degree of crook, 0.30 and 0.38; size of branches, 0.31 and 0.48; crown width ratio 0.40 and 0.47.

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Selection in Slash Pine Brings Marked Improvement in Diameter and Height Growth Plus Rust Resistance

CHARLES D. WEBB and JOHN C. BARBER 1/

During the past 10 years, many thousands of dollars have been invested in tree improvement programs to provide high quality seed for artificial regeneration. Seed production areas have been established and are providing appreciable quantities of seed. Outstanding trees have been selected and grafted into clonal seed orchards; soon the orchards will be producing large quantities of seed. Undoubtedly, many of us are wondering just how much improvement the seed orchards and seed production areas will provide. Open- and control-pollinated progeny tests have been installed to determine both the genetic value of the selected parents and how much improvement will be achieved over what was planted in the past. We are all anxiously awaiting the results of these tests.

So far, the early results are very gratifying, and our data give more encouragement. Stated briefly, our results show that even mild selection provided substantial improvement relative to commercial check lots in height and diameter growth as well as in resistance to rust. Volume per acre was increased appreciably in a locality where severe rust years are common. The control-pollinated tests reaffirmed the wisdom of comparing outstanding trees with their neighbors in the stand.

EXPERIMENTAL MATERIAL

SELECTED PARENTS

The progenies grown in the three studies to be reported here originated from two groups of parent trees, both of unknown provenance. One group was selected from a slash pine plantation near Macon, Georgia, in Jones County, the other group of trees from plantations on the George Walton Experiment Forest in Dooly County, Georgia, near Cordele.

1/ U. S. Department of Agriculture, Forest Service: Southeastern Forest Experiment Station, Macon, Georgia; and Southern Forest Experiment Station, Gulfport, Mississippi, respectively. Work was conducted with financial assistance from the Georgia Forest Research Council; plantations were growing on land provided under cooperative agreement from Georgia Kraft Co.

The trees from the Jones County plantation were chosen at an age of 18 years to exhibit a variety of phenotypes rather than being "plus" trees. Selected trees encompassed a wide range of variation in such traits as height growth, crown width, crown density, and fusiform rust infection. Heights and diameters were measured on each selected tree and on 10 neighboring trees. Several of the selected trees might be considered fair when compared with today's standards, but as a whole, the group is merely average, not outstanding.

The parent trees from Dooly County, selected primarily for outstanding growth and good form, are generally better than those from Jones County. The plantations ranged from 14 to 18 years of age. Records made during the course of other silvicultural research were screened to pick out the largest individuals. This group was examined and the ones with poor form and evidence of rust infection were eliminated. However, rust infection in this area was very light, and, therefore, the selection differential for rust resistance was low.

For a point of comparison, several "commercial" lots of seed were obtained, and check seedlings were grown in the experimental nursery along with the progenies. Seedlings from commercial nurseries provided additional reference points. These check lots can be considered representative of the quality of seedlings being planted generally throughout the range of slash pine at the time these studies were established.

TEST PLANTATIONS

The first progeny test of the Jones and Dooly County trees was an open-pollinated trial planted in 1956--the H-38 plantation. Twenty-nine seedlots were planted, using 25-tree plots at a spacing of 10X10 feet in a randomized block design with three replications. The commercial checks were replicated twice in each block. This study was severely infected with fusiform rust; of the 2,325 seedlings originally planted, only 45 percent were considered potentially merchantable at 8 years of age. A tree was considered unmerchantable if it possessed a stem canker large enough to girdle the tree completely. Only potentially merchantable trees were included in this analysis.

While routine remeasurement of the H-38 plantation was underway, the area suffered a severe ice storm on December 31, 1963. In desperation, a salvage measurement was made within a month after the ice storm. Trees remaining erect after the ice were measured satisfactorily by means of a 30-foot measuring pole. Trees severely bent or uprooted were measured by bending the pole around the bend in the tree. Heights of trees with tops broken out were determined by adding the length of the broken top to the height from the ground to the break. Diameter breast height usually presented no problem. Granted, these measurements are not as precise as would ordinarily be desired, but we believe our measurements were within 1 foot of the true height.

In the absence of published volume tables for trees this small, the volume outside bark of an individual tree was calculated as that of a cone having a height equal to the height of the tree and a base equal to the basal area at breast height. This is suitable for comparative purposes at this age.

The younger 5-year-old tests included both open- and control-pollinated progenies from certain members of the two groups of parent trees. Two studies were planted; the larger, designated H-50, consisted of 25-tree plots planted in four replications of a randomized block design. In the smaller study, H-51, 5-tree plots were replicated five times in a randomized block design. Both were planted at a spacing of 10X10 feet. Rust infection in these two plantations was very light.

PROGENY PERFORMANCE

OPEN-POLLINATED PROGENIES - 8 YEARS OLD

Analyses of variance revealed that progeny differences were statistically significant for all the traits measured: height, d.b.h., tree volume, number of merchantable trees per plot, and total volume per plot (table 1). Even though these are not random progenies, heritability was calculated for individual tree volume; narrow-sense heritability within this particular plantation was 0.16 (table 2).

The relatively poor performance of the two commercial check lots is of vital interest. The commercial checks were generally the smallest of individual tree size; fourteen progenies were significantly larger at the 5 percent level than the best check lot (fig. 1). In terms

Table 1. Summary of F-tests of seedlots for plantation H-38.

Trait	F	Degrees of freedom	
		Seedlot	Error
Height	4.74**	28	55
D.b.h.	2.59**	28	55
Tree volume	2.05*	26	51
Number merchantable trees per plot	7.14**	28	56
Total volume per plot	8.19**	28	56

Table 2. Analysis of variance, expectations of mean squares, and calculation of narrow-sense heritability of tree volume in plantation H-38.

Source	df	MS	E(MS)	Estimate of variance components
Block	2	.791760	$\sigma_e^2 + 13.578\ \sigma_{rg}^2 + 316.229\ \sigma_r^2$	.002183
Progeny	26	.583765	$\sigma_e^2 + 12.225\ \sigma_{rg}^2 + 35.057\ \sigma_g^2$	.008407
Error	51	.284500	$\sigma_e^2 + 11.615\ {}_{rg}^2$	.007465
Within plot	870	.197792	σ_e^2	.197792
Total	949			

Computation of heritability, h^2:

$$h^2 \quad \frac{\sigma_A^2}{\sigma_w^2 + \sigma_{rg}^2 + \sigma_a^2} = \frac{.033628}{.172571 + .007465 + .033528} = 0.16$$

Where σ_A^2 = total additive genetic variance

σ_{rg}^2 = plot error

σ_w^2 = within plot environmental variance

if $\sigma_g^2 \quad 1/4 \quad \sigma_A^2$

$\sigma_w^2 \quad \sigma_e^2 - 3/4 \quad \sigma_A^2$

of number of merchantable trees per plot, which strongly reflects resistance to fusiform rust, the check lots were again well below average, but only four progenies were significantly better than the best check (fig. 2).

When tree size and number of merchantable trees per plot are combined and expressed as total volume per plot, a trend with great practical significance appears. Not only are the check lots well below average in production, but the best progeny has produced two times as much volume per unit area as the best check lot (fig. 3). Duncan's multiple range test showed that seven progenies produced significantly more volume, at the 5 percent level, than did the best check lot. These seven best progenies averaged 81 percent more volume per unit area than the best check lot.

When the progenies from Dooly County and Jones County were considered as separate groups, both groups showed substantial improvement over average of the commercial check lots (table 3). When 7 to 10 percent improvement

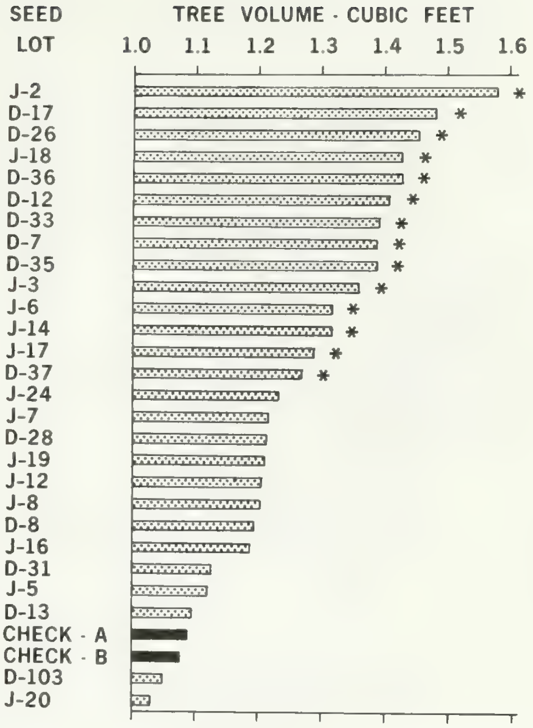

Figure 1 -- Volumes of individual trees varied widely among progenies, but the commercial checks produced consistently small trees (indicates progenies significantly larger at the 5 percent level than the best check lot).*

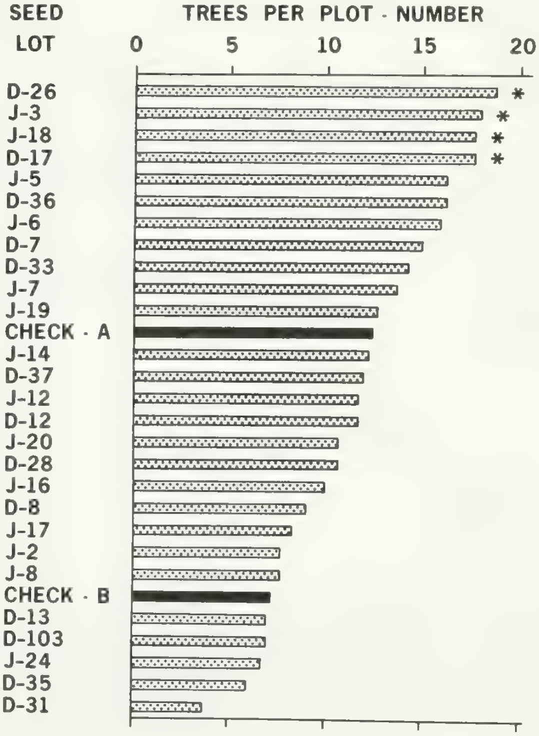

Figure 2 -- Progenies varied widely in number of potentially merchantable trees per plot, which is strongly associated with rust resistance (indicates progenies with significantly more trees, at the 5 percent level, than the best check lot).*

Table 3. Percent improvement of progeny groups over commercial check lots (plantation H-38)

Trait	Seed source Dooly County	 Jones County
Height	9.7	8.0
D.b.h.	[illegible]	7.1
Tree volume	23.9	17.1
Number potentially merchantable trees per plot	16.2	22.2
Total volume per plot	46.6	46.0

Table 4. Summary of F-tests.

PLANTATION H-50[1]

Source	df	F Height	 Percent free of rust
Seedlot	20	6.01**	5.44**
Block	3	7.78**	20.68**
Error	60		

PLANTATION H-51[2]

Source	df	Height	Percent free of rust
Seedlot	20	4.70**	--
Block	4	6.78	--
Error	79		

[1] Four replications, 25-tree plots
[2] Five replications, 5-tree plots

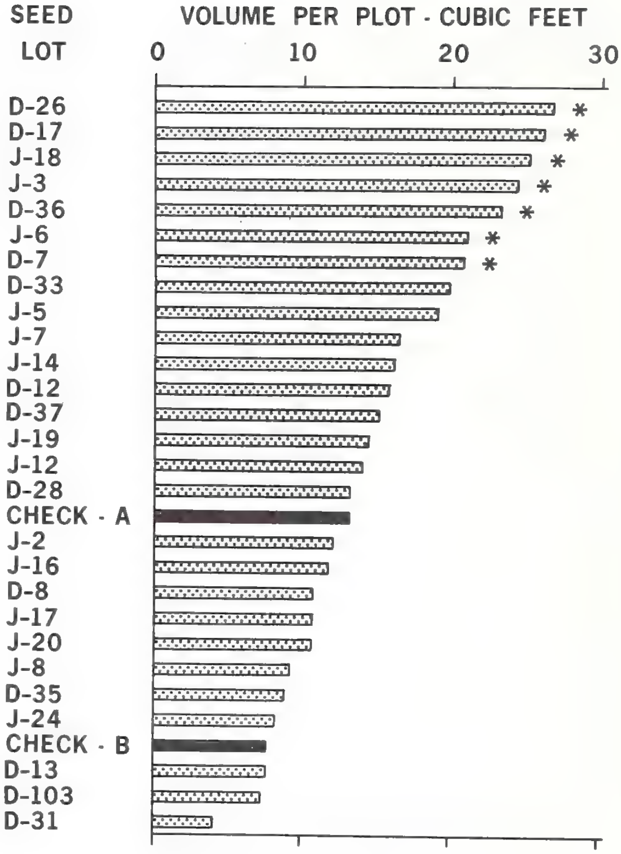

*Figure 3 -- Total volume per plot, an expression of both individual tree size and rust resistance, varied among progenies, but the commercial checks produced well below average volumes (*indicates progenies producing significantly more volume per plot, at the 5 percent level, than the best check lot).*

Table 5. Comparison of rust resistance and height growth of selected progenies (both open- and control-pollinated) with performance of commercial check lots (plantation H-50)

Seed source	Seed lots	Rust resistance Rust free trees	 Improvement over check lots	Height Height	 Improvement over check lots
	Number	-----Percent--------		Feet	Percent
Selected progenies	18	82.1	15.1	12.71	9.4
Commercial checks	3	71.3	--	11.62	--

in height and d.b.h. were combined, an improvement of 17 to 24 percent in tree volume resulted. Selection for volume was more stringent in Dooly County than in Jones County; hence, the greater improvement in tree volume. The two groups represent a 16 to 22 percent improvement in rust resistance. This culminated in a 46 percent improvement in volume per unit area. (It must be stressed that this plantation was severely infected with fusiform rust; at 8 years of age over half of the trees were considered unmerchantable primarily because of rust infection.)

Although group selection of maternal parents strongly affected volume growth of progeny, prediction for the influence of each individual parent tree was less accurate. Graphical plotting of the data showed nonsignificant correlations between height, d.b.h., and volume of the progeny and the superiority of the female parent relative to its 10 adjacent check trees. Dorman found the same to be true for height of young open-pollinated progenies of parent trees growing at Callaway Gardens near Pine Mountain, Georgia. Maybe this should be expected for open-pollinated progenies in view of the low heritability for tree volume ($h^2 = 0.16$).

CONTROL- AND OPEN-POLLINATED PROGENIES - 5 YEARS OLD

The younger tests (plantations H-50 and H-51), including both open- and control-pollinated progenies, cooroborate the trends in the older, open-pollinated test. Differences among progenies were highly significant for both height growth and disease resistance (table 4). Fusiform rust infection in these plantations was very light (only 20 percent) in comparison with the older, open-pollinated test.

At 5 years of age, the progenies, as compared to commercial checks, showed improvement comparable to that in the older test. When open- and control-pollinated progenies were grouped together, they were 15.1 percent more rust-resistant and 9.4 percent taller than the average of the three check lots (table 5, fig. 4). Unfortunately, these tests do not provide a good basis for evaluating the use of open-pollinated progeny performance to predict controlled cross performance. To do this, all parents used in the crosses should be represented by open-pollinated progenies in the same test.

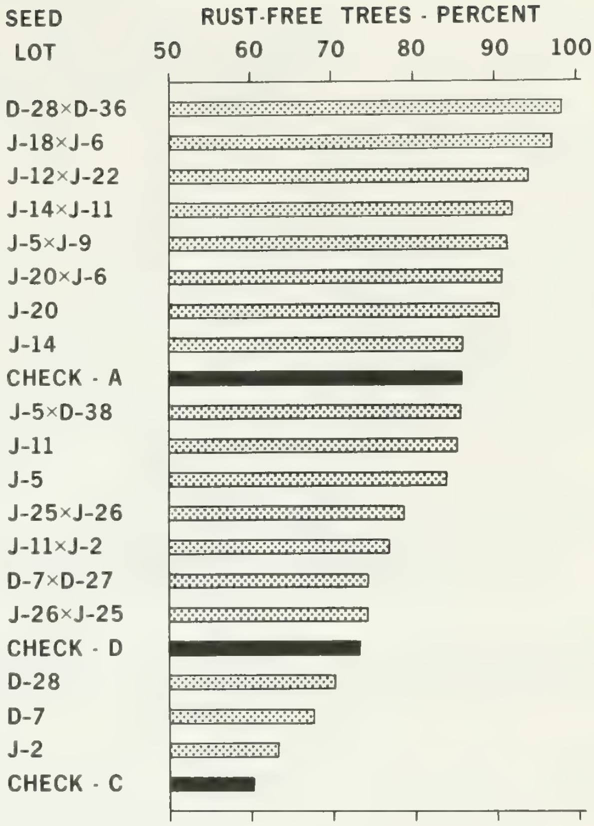

Figure 4 -- Open- and control-pollinated progenies and commercial checks varied significantly in percent of trees free of rust, but the checks contained fewer rust-free trees.

The offspring-parent regressions developed from these two plantations are of vital interest. Here the heights of single crosses among the Jones County trees were correlated with the mid-parent height superiority of their parents. The following examples illustrate the principle of "mid-parent height superiority:" two parents, one being 15 feet taller than its neighbors, the other being 5 feet taller, have a mid-parent height superiority of 10 feet. Two different parents, one being 10 feet taller, the other 2 feet taller, have a mid-parent height superiority of 6 feet. This expression of relative height is pertinent because most scoring systems compare a candidate tree with its neighbors in the stand.

These offspring-parent regressions were very strong in both plantations (figs. 5 and 6). Correlation coefficients were highly significant, and the slopes of the regression lines were very similar ($b = 0.26$ and 0.33). These regressions stand in strong contrast to the almost nonexistent relationship for open-pollinated progenies.

SUMMARY AND CONCLUSIONS

These data show that open-pollinated as well as control-pollinated progenies differed significantly in growth rate and resistance to fusiform rust. In terms of volume per unit area at 8 years of age, which combines individual tree size and rust resistance, progenies not only differed widely but also showed substantial improvement over commercial check lots. Only mild selection and the use of open-pollinated seed produced an improvement over commercial checks of 19 percent in individual tree volume, 19 percent more merchantable trees, and 46 percent more volume per unit area.

Offspring-parent regressions were very strong when 5-year heights of control-pollinated progenies were related to the average height superiority of both parents over their respective check trees. However, open-pollinated progenies in this study showed essentially no

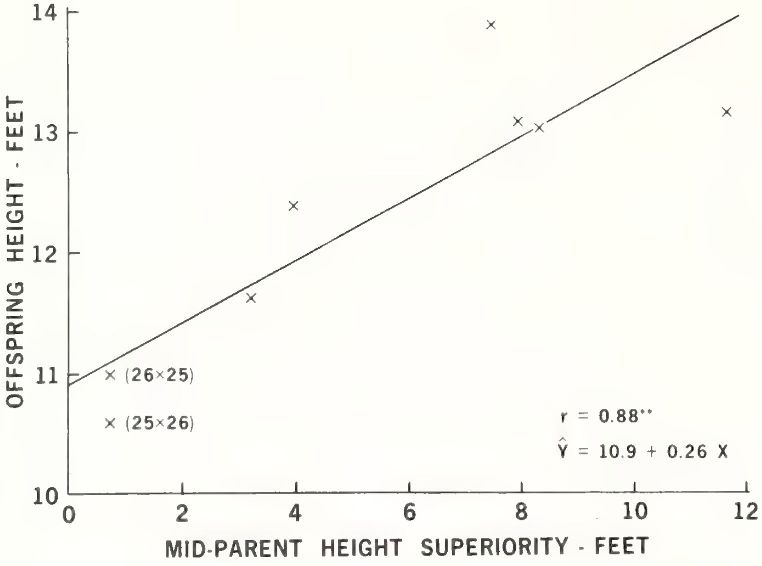

Figure 5 -- The offspring-parent regression for height in H-50 (25-tree plots, four replications). Note the reciprocal crosses among Jones 25 and Jones 26.

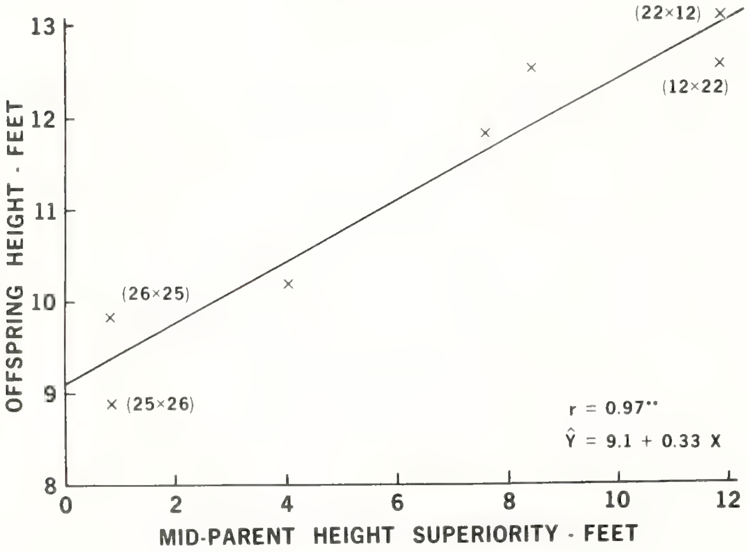

Figure 6 -- The offspring-parent regression for height in H-51 (5-tree plots, five replications). Note the reciprocal crosses involving Jones 25, Jones 26, Jones 12, and Jones 22.

relationship to the relative height and diameter superiority of their maternal parent. Yet, form and disease resistance are reflected well in open-pollinated tests. This may mean that the relative level of acceptance or rejection should be set higher in open-pollinated tests than in trials involving controlled crosses.

These early results substantiate several assumptions made in the initial phases of southern tree improvement activity. First, seedlings of variable and often low quality come from seed collected by the general public. This method of seed acquisition provides no control over the quality of the parent trees; usually the only criteria for collection are accessibility of the trees and abundance of cones. The performance of the checks in these studies suggests that such uncontrolled seed collection is accompanied by a high risk of susceptibility to disease and of generally smaller trees producing lower volumes per acre.

Second, selection for disease resistance and for size and quality of individual trees will provide substantial improvement of future generations. The data suggest that acceptable seed is provided through closely supervised collection of cones following logging operations. Seed production areas, in which only a mild selection intensity is possible, will give substantial, quick improvement over unimproved commercial seed. Furthermore, even greater advances should accompany seed from seed orchards, because they represent much higher selection differentials.

Third, the commonsense practice of comparing outstanding trees with their neighbors is a valid procedure for initially estimating the genetic worth of a candidate tree.

Combining Superior Growth and Timber Quality with High Gum Yield in Slash Pine[1]

A. E. SQUILLACE[2]

Until recently, the tree improvement work of the Naval Stores and Timber Production Laboratory at Olustee, Florida, was concentrated on the development of a high-gum-yielding strain of slash pine. Our success with this effort is well known. However, recent research results show that combining high gum yield with other desirable traits such as rapid growth, straight stems, and small branch size is feasible. In this report I shall give the basis for this statement and then briefly describe the development of seed-production areas and clonal orchards designed to capitalize on the research findings.

BASIS FOR COMBINING DESIRABLE TRAITS

In many plant breeding efforts, the task of attaining appreciable genetic gains for a number of traits in a single strain is difficult and time-consuming. Most breeders are aware of the problems frequently encountered, such as adverse genetic correlations, the reduction in genetic gains (when selecting from a limited population) as each new trait is added, the impracticability of screening all available trees, and the effects of unfavorable gene action. However, in our present effort to combine gum yield with other traits, these problems are not insurmountable, as indicated by the following recent research findings.

1. Gum-yielding ability in slash pine varies greatly among individual trees growing under comparable conditions. This is true even if the effect of stem diameter is discounted. The point is well illustrated in Figure 1, which is based upon microchip yields of 363 20-year-old trees growing in a plantation near Lake City, Florida. The sample includes all trees 2.6 inches d.b.h. and larger in nine systematically selected one-tenth-acre plots. Note that the distribution has a long tail toward the right, a feature also reported by Goddard and Peters (1965). The best 5 percent of the trees yielded an average of about 2.0 times as much as the average tree. The best 10 percent yielded 1.8 times as much as the average tree. The unusually high variation suggests that satisfactory selection differentials for gum yield can be attained, even within relatively small populations of trees selected for other desirable traits.

2. Heritability of gum yield is strong, with narrow sense estimates varying from 45 to 90 percent and broad sense estimates varying from 67 to 90 percent (Mergen, et al., 1955; Squillace and Bengtson, 1961; Squillace and Dorman, 1961; and Goddard and Peters, 1965). This feature assures relatively high genetic gains in gum yield even if selection differentials need to be reduced because of restricted population size.

3. Gum-yielding ability and growth rate seem to be genetically correlated to at least a moderate degree. This means that the two traits are probably affected by common genes (pleiotropy) and that, since the correlation is positive, a genetic improvement in one will cause simultaneous improvement in the other. Evidence for the relationship was obtained from two studies conducted with slash pine at Olustee.

In our 19-year-old progeny plantation, gum yield was found to be strongly correlated with d.b.h. A covariance analysis showed that, although some of this relation was due to environmental causes, a large part was due to genetic causes. The data suggest that if, through breeding for gum yield alone, we double gum-yielding ability, an increase of about 6 percent in stem diameter growth (or about 12 percent in volume growth) is attained simultaneously.

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[1] The seed-production area discussed in this report was installed in cooperation with the Osceola National Forest. In this effort special thanks are due to Forest Supervisor R.J. Riebold and District Ranger Wm. V. Cranston.

[2] Principal Plant Geneticist, Southeastern Forest Experiment Station, U. S. Forest Service, Olustee, Florida.

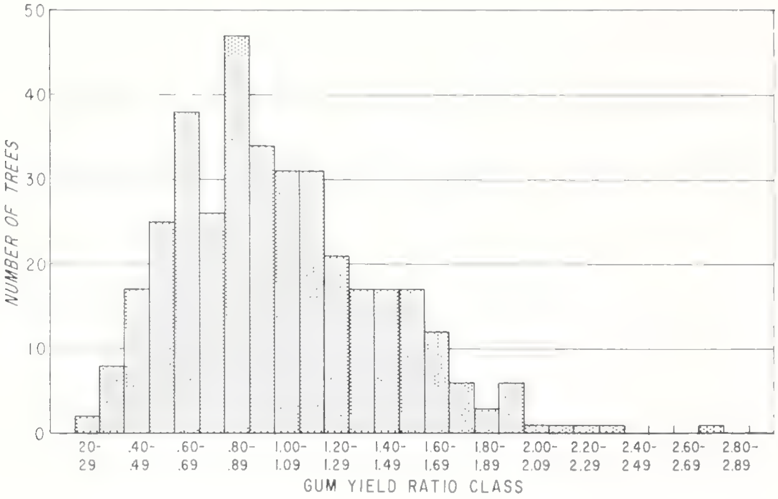

Figure 1 -- Frequency distribution of gum yield ratios (yield of tree/average yield of trees of same d.b.h.) of 20-year-old planted slash pines. Basis, 363 trees.

Table 1. Classification of 363 unselected slash pines in a 20-year-old plantation according to 1) stem straightness and gum yield and 2) branch thickness and gum yield.

Item	High yielders	Medium yielders	Low yielders
	- - - - - - - Percent - - - - - - - - -		
Stem Straightness			
Straight	3	5	3
Slightly crooked	84	83	86
Very crooked	13	12	11
Branch thickness			
Fine	10	11	15
Medium	75	69	61
Thick	15	20	24

In the other study, reported by Gansel, average heights of 7-year-old clones were found to be correlated with the gum-yielding ability of their ortets to a moderately strong degree (r = .41, significant at the 5 percent level). These results are in harmony with Sulgin's (1964) report that Pinus nigra var. caramanica trees with high resin yield have high rates of photosynthesis. This fortunate relationship will, of course, facilitate breeding work designed to combine gum yield and growth rate with other traits.

4. There seems to be little or no correlation between gum-yielding ability and stem straightness or branch thickness. This statement is made on the basis of two studies recently conducted at our Station.

In Gansel's report mentioned earlier, no correlation was found between stem straightness or branch size of 7-year-old clones and the gum-yielding ability of their 19-year-old ortets (Gansel, 1965). Likewise, data from the 20-year-old plantation discussed earlier showed very little correlation between gum yield and either stem straightness or branch size (Table 1). Thus, there seem to be no adverse relationships in respect to stem straightness or branch size to impede development of strains with good gum yield, growth, and form.

5. The frequency of trees that have combinations of all desired traits being considered is apparently relatively high. For example, in the 20-year-old plantation studied, two superior trees were found. One had 2-1/2 times "normal" yield, with a stem volume of 2-1/2 times "normal." The other had a yield superiority of 1-1/2 and a volume superiority of 2. Both were classified as "straight" and "finely-branched." Since only about 4,050 trees were evaluated in the plantation, the frequency of superior trees is very high and lends encouragement to our program.

SEED-PRODUCTION AREA

As an interim measure to obtain seed having modest superiority in gum yield, growth rate, and timber quality, we recently established a 10-acre seed-production area. It was installed on the Osceola National Forest, in the 20-year-old plantation mentioned earlier.

This seed-production area is unique in several respects. First, it was established in a plantation rather than in a natural stand, because selection is more efficient in a plantation than in a natural stand. Secondly, a young stand, 20 years old, was selected. A stand of this age permits evaluation of a greater number of trees than does an old stand, and yet is old enough to begin cone production upon release.

Table 2. Evaluation data for the original stand and selected seed trees in slash pine seed-production area.

Item		Original stand	Seed trees
Trees per acre	Number	404	22
Avg. microchip yield per tree	Grams	222	393
Avg. estimated standard-face, full-season, yield per tree	Grams	1360	2810
Avg. yield ratio[1/]	Ratio	1.01	1.41
Avg. d.b.h.	Inches	5.82	7.11
Avg. total height	Feet	45.3	50.4
Avg. stem volume per tree	Cu. ft.	3.8	6.4
Avg. stem volume per tree, excluding suppressed trees	Cu. ft.	4.4	6.4
Bole straightness:			
Straight	Percent	4	26
Slightly crooked	Percent	84	74
Very crooked	Percent	12	0
Branch thickness:			
Fine	Percent	13	18
Medium	Percent	68	80
Heavy	Percent	19	2
Trees with fusiform rust	Percent	3	0

[1/] Yield of tree/average yield of trees of same d.b.h., using estimated standard face yields.

The plantation is on a flatwoods site of about average site quality. The seed source was north Florida. Spacing was 8 by 8 feet, but subsequent mortality reduced the number of trees per acre to about 400. Systematically spaced sample plots were installed to obtain original stand data for comparison against selections.

We first made a preliminary screening, selecting trees for good growth, stem form, and branching habit, and for freedom from fusiform rust. Then these preliminary selections (about 200 per acre) were microchipped --four bi weekly, one-inch square chips were applied during June and July. A final marking was made, on the basis of gum yield in combination with the other desired traits, leaving about 22 seed trees per acre.

A comparison of data for the original stand and the final selections, or seed trees, is shown in Table 2. Significant features are the high increases in average gum yield, tree size, and proportions of good trees in respect to bole straightness and branch thickness.

It is of interest to estimate the genetic gains expected by using seed from the seed-production area. For gum yield, the gain should be considered as coming from two sources: (1) the superiority of seed trees over average trees of the same d.b.h. and (2) the gain in gum yield resulting from the expected increase in diameter growth.

Assuming a heritability of .50 for gum yield, and using relative yield data of Table 2, we estimated gain from the first source to be

$$\frac{.50\ (1.41-1.01)}{1.01} \times 100 = 20 \text{ percent.}$$

To estimate gain in gum yield from the second source, we first need to determine expected gain in d.b.h. growth. Assuming a heritability of .25 for d.b.h., the expected gain in d.b.h. is .25 (7.11 - 5.82) = 0.32 inch. Now, the estimated standard-face yield of the average tree, 5.8 inches d.b.h., is 1360 grams of gum, while a tree 0.32 inch larger in d.b.h. would yield 1510 grams. Thus, gain from this source is

$$\frac{1510 - 1360}{1360} \times 100 = 11 \text{ percent.}$$

Total expected gain in gum yield, then, is 20 + 11 = 31 percent.

The expected gain in growth rate is probably best estimated using volume increase data. If heritability of this trait is assumed to be 25 percent, expected gain is

$$\frac{.25\ (6.4 - 4.4)}{4.4} \times 100 = 11 \text{ percent.}$$

Genetic gains in stem straightness, branch size, and rust resistance are difficult to estimate because of the nature of these data. However, from our knowledge of the inheritance of stem straightness and branch size, appreciable gains can be expected for these traits. Little can be said of possible gain in rust resistance because of the low incidence of rust in the stand.

CLONAL SEED ORCHARDS

As mentioned earlier our long-term, concerted effort to develop a strain of slash pine having a combination of superior traits will be through the clonal seed orchard approach. Briefly, we are working within a framework of trees already selected for superiority in growth and timber quality, seeking out among them those individuals which are the highest gum yielders. The job entails cooperation with a number of organizations which in the past have made slash pine selections for growth and timber quality characteristics. Steps in the procedure are outlined briefly below.

1. Cooperators' superior trees will be evaluated for gum yielding ability by one of the following procedures, depending upon particular circumstances: (1) microchipping of clonal orchards (as done by Goddard and Peters, 1965); (2) microchipping of selections in the field; or (3) use of wind-pollinated seed in a nursery progeny test. The latter is a recently developed technique for evaluating gum-yielding ability of progenies grown at a very wide spacing, at 2 years in the nurserybed. It is expected that approximately 800 to 1,000 selections will be screened.

2. Selections showing promise under the preliminary screening will then be bred with three proven high-yielding clones at Olustee, using the selections as pollen parents.

3. Seed from the controlled pollinations will then be subjected to the same type of nursery progeny test for gum yield mentioned in step 1 above.

4. Selections whose control-pollinated progenies pass the short-term nursery test for gum yield will then be recommended for use in the establishment of clonal orchards. At the same time progenies of these selections will be outplanted for long-term testing of all traits.

5. At the end of the long-term tests (possibly about 10 years), recommendations for roguing of clonal orchards will be given.

Our goal in this clonal orchard program is a genetic gain of at least 50 percent in gum yield and this is reasonable according to data on variation discussed earlier. Just how much to expect in the way of gains in growth rate and timber quality is not possible to estimate until we get data on selection differentials. However, because of the intensity with which the original selections were made and the progeny testing, gains should be appreciable.

The feasibility of developing a special strain with an appreciable degree of resistance to fusiform rust, for use in high infection areas, will be considered. Screening for this purpose could be done in step 3 above, using artificial inoculation techniques. Although other desirable traits, such as improved gum composition and wood quality, are not strongly considered at present, we hope to keep the genetic base wide enough to permit screening for such traits in subsequent generations.

SUMMARY

Available data on the variation and inheritance of gum yield, growth rate, and timber quality traits and on the nature of correlations among them show that incorporation of high yield with superior growth and timber quality is feasible. A seed-production area and several clonal orchards are being established with this objective, in cooperation with several organizations. The seed-production area is an interim measure designed to provide modestly superior but immediately available seed. The clonal seed orchards will provide greater gains but will require more time.

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Pigment Inheritance in Slash Pine Seedlings

E. B. SNYDER, A. E. SQUILLACE, and J. M. HAMAKER [1]

In tree breeding, chlorophyll defectives and other pigment variants are useful for estimating the degree of natural selfing that may occur in seed orchards (Squillace and Kraus 1963). To be most valuable the aberrations must be subjected to genetic analysis--their variation and inheritance discerned. This paper reports studies of three groups of characters in wind- and controlled- pollinated progenies of slash pine (Pinus elliottii var. Engelm.): chlorosis in 2-1/2-month-old seedlings, cotyledon chlorophyll defectives, and hypocotyl anthocyanin variants. For the anthocyanin variants, we show how to derive combining ability values of wind-pollinated selections from different stands by calculating combining ability values for each stand.

SUSCEPTIBILITY TO CHLOROSIS

On April 10, 1964, self- and wind-pollinated seeds from 11 trees were sown in the nursery of the Harrison Experimental Forest in southern Mississippi. The design was a randomized block with 5 replicates and 22 seeds per plot. The nursery was not fertilized and by June 19 many of the seedlings were chlorotic. When nitrogen was applied the chlorotic symptoms disappeared. The self progenies were more chlorotic than their wind controls. The correlation between the two suggests an inbreeding depression. The selfs varied from 2 percent (parent 116) to 77 percent (parent 84) chlorotic seedlings (table 1).

In the self progeny of tree 84, all of the seedlings in two of the replications were chlorotic. A tree, all of whose self progeny were chlorotic, was noted several years ago by P. C. Wakeley (personal communication). These extreme cases were probably due to a general pologenic unbalance rather than to identifiable genes.

For the less extreme cases in table 1, we cannot distinguish between segregation and lack of penetrance. Monogenic chlorophyll mutants would be valuable in a physiological study of the metabolic nature of genetic blocks (Bell 1963).

Chlorosis is apparently unrelated to pigment characters expressing themselves shortly after germination and next discussed.

CHLOROPHYLL DEFICIENCIES OF THE COTYLEDON

Before discussing our data, it is necessary to review the color standards used in classifying the seedlings.

Table 1. Percentage of chlorotic plants in self- and wind-pollinated progenies after 2-1/2 months in an unfertilized nursery.

Parent identity	Self-pollinated progeny		Wind-pollinated progeny	
	Population size	Plants chlorotic	Population size	Plants chlorotic
	Number	Percent	Number	Percent
84	[1]152	77	91	32
6	89	62	86	26
87	55	49	86	15
2	110	38	86	19
[illegible]	94	36	75	16
45	46	15	86	13
85	166	13	76	4
11	244	11	74	12
161	508	8	79	10
23	37	3	89	3
116	340	2	85	5

[1] Variation below the nominal 110 seedlings was caused by poor germination of some self progeny; variation above 110 was due to extra rows of some entries.

The classification of Gustafsson (1940) has been widely used for many plants including Scots pine (Eiche 1955). A slight modification by Gustafsson, Walles, and von Wettstein is printed here, and should be of general use in forestry. Their scheme, which grades from white to light green, is characterized by four one-color classes: albina, xantha, yellow viridis, and viridis. In our

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Classification of the Chlorophyll Mutants of Higher Plants--Chlorophyll Mutants Characterized by a Quantitative or Qualitative Alteration of the Chloroplast Pigments of the Leaves [1]

Group I. Mutant plants of one color

1. Albina - white
2. Xantha - yellow
3a. Yellow viridis - yellow green[2]
3b. Viridis - light green

Group II. Mutant plants of two or more colors

4. Alboxantha - leaf tip white, base yellow
5. Xanthalba - leaf tip yellow, base white
6a. Alboviridis - leaf tip white, base green
6b. Xanthviridis - leaf tip yellow, base green
7a. Viridoalbina - leaf tip green, base white
7b. Viridoxantha - leaf tip green, base yellow
8. Tigrina - chlorophyll deficiency in the form of transverse stripes
9. Striata - chlorophyll deficiency in the form of longitudinal stripes
10. Maculata - spotted chlorophyll deficiency
11. Marginata - chlorophyll deficiency of the leaf margin or leaf center
12. Costata - chlorophyll deficiency of the leaf veins or intercoastal areas
13. Transformiens - the color of the first developed leaves is different from that of later leaves.

Group III. Mutant plants with color-changing leaves

14. Albescens - bleach to a white-white yellow color
15. Lutescens - bleach to a yellow, yellow green or light green color
16. Virescens - chlorophyll-deficient, but turns normal green later

Note that Code de Couleurs (1908) standards originally defined colors of Group I. However, readings by such an instrument as a "chlorophyllometer" has possibilities (Inada, K. 1963. Studies on a method for determining the deepness of green and color chlorophyll content of intact crop leaves and its practical applications. 1. Principle for estimating the deepness of green color and chlorophyll content of whole leaves. Proc. Crop Sci. Japan 32: 157-162).

[1] Gustafsson, A., Walles, B., and von Wettstein, D. 1962. (From Records of the Meeting of the Swedish Assoc. for Theoretical and Applied Mutation Res., Jan. 25-26, 1962 (mimeo.)) (In Swedish).

[2] Snyder-Squillace-Hamaker substitute is green *xantha*.

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research *green xantha* was substituted for *yellow viridis*. Eiche (1955) inserted an extra class, *xanthoviridis*. The *viridis* portion of his term referred to a particular hypocotyl color. Aside from finding *xanthoviridis* confusingly similar to the established two-color term, *xanthviridis*, we came upon no corresponding phenotype for slash pine.

Our classes are based on cotyledon color. In the following descriptions, however, other characteristics are also noted: Albina: white. In laboratory tests only one seedling with pure white cotyledons was seen. This seedling also had a white hypocotyl. In the field, seedlings tended toward yellow and usually had at least a spot of pink at the base of the hypocotyl. We applied *albina* to only the whitest seedlings with no hypocotyl color. These seedlings wilted and died in a couple of days' exposure to the sun.

Xantha: yellow. These seedlings had bright yellow cotyledons and vivid cherry-pink hypocotyls. They lived several weeks if weather was favorable.

Green xantha: greenish-yellow. Similar to xantha but greener, with less vivid hypocotyls, and higher survival potential.
Viridis: light green. Hypocotyls normal pink. Some of these seedlings died; some, having cotyledons which subsequently turned normal green, lived, i.e., they were virescens (see classification).

To determine the frequency and nature of such variants, we surveyed approximately 7,380,000 slash pine seedlings from south Mississippi seed in the U.S. Forest Service's Ashe Nursery with the following results:

Variants per million seedlings

	Albina (Albescens)	Xantha	Green xantha	Viridis
1963	0.0	17.2	37.9	41.7
1965	2.2	25.0	46.0	123.8

We speculate that the observed frequency of the albina class may have been more in 1965 than in 1963 because of the warmer, less cloudy conditions which existed. Under such conditions, some xanthas may have bleached to albescens. Indeed, later research may show that albescens is a preferable term to albina.

The difference between the two years in frequency of the viridis also suggests environmental influences. In both years the viridis frequency was largest even though some of the slight deviations from normal green are difficult to detect in outdoor illumination. If the rule for other plant species holds--that the viridis type mutant is the rarest--many of the viridis seen in the nursery must be non-genetic variants, i.e., non-mutants. Variability depending partially on environments is also suggested by data of Squillace and Kraus (1963), who for other nurseries and years reported the frequency of all mutants at 520 per million. Though the xantha frequencies are relatively constant, we will show later that they also are not good estimates of true occurrence.

Data on the frequency of carriers are available from two sources of wind-pollinated seed. In one, seeds were collected from 5 trees in each of 54 stands covering the natural range of slash pine, including south Florida (Squillace[2/]). Among 266 progenies which survived, we found that 38 (14 percent) contained one or more mutants. The carriers were in 28 of the 54 stands and were well distributed over the species range. The second source of information is from 446 trees in 8 counties of south Mississippi. Ninety-five (21 percent) of the progenies contained mutants. Thus over the entire sample there were 133 carriers among the 712 trees examined, i.e., 19 percent of them.

If the character is controlled by a single recessive gene, then self-pollinating a random group of trees would detect a high proportion of carriers. Indeed, Gustafsson (1962) has said, "We may safely presume that artificial selfing should reveal many more heterozygous trees (than wind-pollination), possibly the great majority of the trees examined." Contrary to this expectation, Pawsey (1964) failed to find mutant carriers more frequently in inbred Pinus radiata than in open-pollinated progenies. Bingham and Squillace (1955) and Barnes et al. (1962) found only 1 carrier among 28 Pinus monticola, and Fowler (1965) only 1 among 46 Pinus resinosa by selfing. Fowler (personal communication 1965) doubts that such failures apply to Scots pine, jack pine, white pine, and red pine. In no species did he find wind-pollinated progenies having mutants that were lacking in self progeny.

Forty-five slash pines whose progeny had never been examined were selfed, whereupon eight were identified as carriers in laboratory or nursery germination trials.

The deficiency of mutants after selfing may be explained by disturbed segregations. For a single red pine carrier, Fowler showed ratios deviating from the theoretical 3 normal: 1 mutant. Our data (table 2) from progenies of 29 trees, where mutants appeared either in selfs, crosses (including winds), or both, confirm Fowler (1964). We obtained segregations deviating from the 3:1 ratio (chi square, P = .05) in the self progenies of 19 of the 29 assumed carriers. Of these 19 there were 9 which produced 1 or more mutants. Six of these 9 had sufficiently large populations to show disturbed segregation with a high degree of confidence. Theoretically, only 11 seedlings are necessary to detect a mutant with 5 percent probability.

[2/] Squillace, Anthony E. Geographic variation in slash pine (Pinus elliottii Engelm.). April 1964. (Ph.D. thesis, University of Florida, 181 pp.).

The other 10 trees of the 19 had progenies which were non-segregating, i.e., produced zero mutants from selfing. Moreover, 2 of these trees, 84 and St 3-176, had 3 and 4 mutants, respectively, in their wind-pollinated progenies. The selfs of these two trees had large population sizes of 262 and 130 individuals, respectively. If a monogenic inheritance is assumed, it therefore appears that the disturbance in expected segregation can prevent phenotypic segregation entirely. Larger self populations may eliminate this difficulty for the majority of trees, but producing large self populations in slash pine is prohibitively expensive. Diluting self pollen to get norman ratios (Fowler 1964) should be tried to see if such dilution would make selfing more efficient.

In contrast to our failures with selfing, screening with wind-pollinated seed has been efficient. Only 1 of 22 xantha carriers would have been missed by using only wind progenies (table 2). Though self-pollination for detecting mutants is questionable, controlled pollinations, including selfing, are essential to further study.

It was of interest to see if crossing produced results similar to selfing and in addition, to see if trees were carrying the identical genes. Eighteen putative carriers were intercrossed in 52 combinations (table 3). Only one combination produced mutants in quantity: 32-42 X 32-58 had mutants in the ratio 6 normals: 1 mutant. These two trees may be related, as they are within a half mile of each other. More precision in classification and testing would have been desirable, but under the assumption of monogenic inheritance, our finding a quantity of mutants in only 1 combination among 18 carriers suggests that a number of genes are causing these types of chlorophyll deficiencies. Sprague and Schuler (1961) isolated 19 genes for yellow-green corn seedlings, but found 12 of them only once.

Twelve of our crosses produced a very small quantity of defectives (averaging 369:1). This quantity is too high to be reasonably attributed to current mutation in all 12 cases.

Table 2. Mutants in slash pine progenies from self- and cross-pollinations.

Parent identity and type pollination	Mutations	Normals: mutants	Fits 3:1 ratio (P + .05)	Parent identity and type pollination	Mutations	Normals: mutants	Fits 3:1 ratio (P ± .05)
[1] 2S	Vir	100:30	Yes	St 3-176S	Xan	130:0	No
2C	--	99:0	--	St 3-176C	Xan	2201:2	--
2C	Xan	98:1	--	St 3-176C	Xan-G	2201:3	--
6S	Vir	174:11	No	St 3-135S	Xan	35:15	Yes
6C	--	466:0	--	St 3-135C	Xan	1236:4	--
10S	Xan	7:1	Yes	St 3-135C	Xan-G	1236:1	--
10C	--	148:0	--	St 3-60S	Xan	5:3	Yes
17S	Vir	16:1	No	St 3-60C	Xan	1744:5	--
17C	--	425:0	--	St 3-36S	Xan-G	13:5	Yes
18S	--	0:9	No	St 3-36C	Xan-G	2030:1	--
18C	Xan	240:1	--	St 3-32S	--	10:0	No
23S	Vir	42:1	No	St 8-32C	Xan	1018:2	--
23C	--	118:0	--	32-58S	Xan	46:7	Yes
84S	--	262:0	No	32-58C	Xan	1704:34	--
84C	Xan-G	288:3	--	32-42S	Xan	85:4	No
86S	--	18:0	No	32-42S	Vir	85:5	--
86C	Vir	153:1	--	32-42C	Xan	2719:36	--
116S	Xan-G	437:1	No	32-9S	Xan-G	252:61	No
116C	Xan-G	215:4	--	32-9C	Xan-G	3578:10	--
136S	--	6:0	No	31D-S	Xan	146:67	No
136C	Vir	87:1	--	31D-C	Xan	721:76	--
145S	--	4:0	No	35A-S	Xan	9:2	Yes
145C	Vir	66:1	--	35A-C	Xan	864:95	--
160S	--	12:0	No	42E-S	Xan	27:0	No
160C	Vir	158:2	--	42E-C	Xan	360:4	--
163S	--	1:0	No	G27S	Xan	23:11	Yes
163C	Xan-G	190:1	--	G27C	Xan	1122:12	--
169S	--	3:0	No	G133S	Xan-G	6:2	Yes
169C	Xan-G	96:1	--	G133C	Xan-G	1952:23	--
169C	Xan	96:1	--	G157S	Xan-G	35:5	Yes
9-2S	Xan	19:1	No	G157C	Xan-G	1122:12	--
9-2C	Xan	88:4	--				
9-2C	Vir	88:3	--				

[1] S = Progeny from self-pollination, C = Progeny from cross-pollination, including wind-pollination.

Table 3 -- Normal:mutant ratios for controlled cross- and self-pollinations and from wind-pollinations.

Parent identity	Character[1]	Parent identity														
		3-176	3-162	3-135	3-60	3-36	3-32	32-58	32-42	32-9	31-24	11-6	10-135	8-7	Winds	Selfs
3-176	Xan		--	--	11:0	514:0	--	--	295:1	471:0	426:0		--	--	484:1	130:0
	Xan-G											449:0				
3-162	Xan	--		481:0	483:0	--	267:0	476:1	437:0	482:0	192:0	--	558:0	--	550:2	--
	Xan-G													346:1		
3-135	Xan		481:0		54:0	35:0	--	32:0	35:0		19:0	--	--	--	135:4	35:15
	Xan-G									445:1						
3-60	Xan[2] [3]	11:0	483:0	54:0		160:0	8:0	177:0	505:0	54:0	14:0	69:0	--	34:0	175:5	5:3
3-36	Xan-G	514:0	--	35:0	160. 0		496:0	193:0	--	15:0	14:0	77:0	--	416:0	110:1	13:5
3-32	Xan	--	267:0	--	8:0	496:0		66:0	66:0	3:0	16:0	--	--	--	96:2	10:0
32-58	Xan	--	476:1	32:0	177:0	193:0	66:0		189:30	217:0	10:0	--	--	--	344:3	46:7
32-42	Xan	295:1	437:0	35:0	505:0	--	66:0	189:30		185:0	493:0	--	--	--	514:5	85: 4
	Vir															5
32-9	Xan-G	471:0	482:0	445:1	54:0	15:0	3:0	217:0	185:0		144:0	488:1	--	--	1074:8	252:61
31-24	Xan	426:0	192:0	19:0	14:0	14:0	16:0	10:0	493:0	144:0		6:0	--	17:0	151:1	--
11-6	Xan-G	449:3	--	--	69:0	77:0	--	--	--	488:1	6:0		--	--	414:0	--
10-135	Xan	--	558:0	--	--	--	--	--	--	--	--	--		--	3	
	Xan-G														1005: 1	--
	Vir														1	
8-7	Xan-G	--	346:1	--	34:0	416:0	--	--	--	--	17:0	--	--		971:4	--
G-27[4]	Xan[4]	--	--	--	--	--	--	--	--	--	--	--	--		1122:12	23:11

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[1] Xan = Xantha; Xan-G = Greenish xantha; Vir = Viridis.

[2] Date are without regard to direction of cross; reciprocals are pooled.

[3] There were also no mutants of Xan-G or Vir.; i.e., the "zero" information is entered but once.

[4] Crosses of G-27 with other trees gave results as follows:

6A	42E	G-133	G-157
54:0	24:0	20:0	39:0

Possibly, multiple genes, epistasis, or unknown effects are involved. In the four cases where segregation in crosses can be compared to segregation in selfing, it appears to be no less disturbed in crosses than in selfs.

Segregation ratios can be modified. Fowler (1964) found that eliminating competitive selection at the zygotic or embryonic stage resulted in normal ratios. Eiche (1955) obtained more mutants in the greenhouse than in the nursery. We examined wind-pollinated progenies from 42 parents having mutants appearing in the laboratory, nursery, or both. There were 17 mutants per 1,000 in the laboratory in contrast to 3 per 1,000 in the nursery. For 79 percent of the parents, mutants appeared only in the laboratory. Because of the magnification of disturbance in segregation, the data indicate extreme loss of efficiency for nursery studies in comparison with laboratory studies. This disturbed segregation for cotyledon deficiencies is in contrast to the regular inheritance for hypocotyl color reported below.

HYPOCOTYL COLOR

While data for inheritance cotyledon of color were gathered under many environmental conditions, the methodology for hypocotyl color was standardized.

Seeds were given a 30-day, cold-moist stratification, exposed to 3 days of artificial light, and then germinated in the dark. After hypocotyl elongation, the hypocotyl colors were recorded as dark pink, medium pink, light pink, very light pink, or white. These five classes were compared to Munsell color standards (1960) and the colors converted to a numerical index. The change from dark pink to white involves an increase of value and a decrease in chroma of the hues 5.0R to 7.5Y. The hues were ignored on the expectation that color changes are due to different concentrations of a single substance, anthocyanin. However, joint action of the value and chroma was expressed as (10-value) X chroma. The resulting product is our color index. The color indices are graded according to human ability in distinguishing the colors

		Hue	Value	Chroma	Index
Dark pink	Almost red	5	7.0	8.0	24
Medium pink	Pink	10	7.0	6.0	18
Light pink	Lightest pink obvious	12.5	7.3	5.0	14
Very light pink	Trace seen only in detailed study	27.5	8.0	5.0	10
White	Separated from very light pink only by detailed study	27.5	8.0	4.0	8

A weighted mean index was calculated for each progeny from the frequencies of the several hypocotyl colors invariably found.

The wind-pollinated progenies of 605 parent trees each were examined. [3] Fifty to 100 seeds of each tree were sown. The distribution of parent trees, based on their progeny means, approached normality with a mean color index of 13.6 and a standard deviation of 1.8. Some skewness of distribution toward the lighter colors was observed. Most of the trees were from south Mississippi, but 159 were from the range-wide collection of Squillace (see footnote 3). Some of the skewness may be accounted for by geographic variation.

To examine the geographic pattern of variation, seeds were collected from trees at 48 locations over the range of slash pine--5 trees at 44 locations and 16 to 179 trees at each of four locations in south Mississippi. Mean hypocotyl color index for each location was determined and isogenes drawn. Results appear in figure 1.

Over most of the range, the indices averages 15. Along the north border, the index dropped to 14. There appeared to be an "invasion" of genes for low values northward from Cat Island, off the coast of Mississippi, with progressive indices of 12, 13, and 14. Finally, a horseshoe-like band of locations with indices of 14 penetrated northeast Florida from the Atlantic coast. Although the low values for the Cat Island trees may be a consequence of semi-isolation, no other characters or environmental conditions are known to be associated with this geographic pattern.

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[3] The writers thank Dr. Francois Mergen and students for examining a portion of these during their visit to the Institute in 1962.

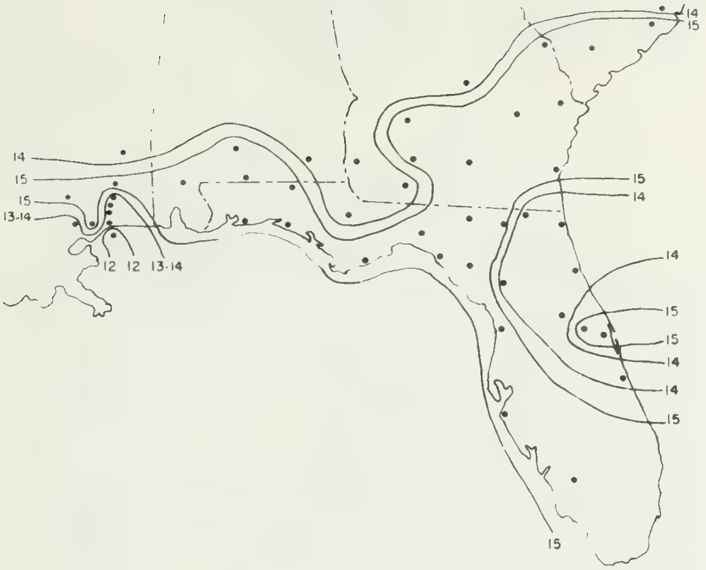

Figure 1 -- Isogenes for hypocotyl color. Indices are rounded. Larger numbers indicate pinker hypocotyls. The 48 dots generally represent 5-tree samples of stands.

In other trials of wind-pollinated progenies from 10 to 25 Mississippi parent trees, the intensity of pigmentation was not consistently associated with resistance to fusiform rust, ability to germinate without a light treatment, or seedcoat color. Trials with larger parental populations are continuing.

To determine inheritance of hypocotyl color, 14 trees whose progeny had previously exhibited a range of colors were intercrossed in 48 combinations (table 4). The observed phenotypes require no explanation, but the calculation of combining ability does. Combining ability is the value of a parent as derived from the mean value of its progeny. For a character limited to the juvenile stage, and when observation of the parents is limited to mature trees, there is no other efficient way to evaluate a parent. When there are no dominance effects and inheritance is polygenic, the observed average phenotype of the crossed progeny will be an average (mid-point) of the combining abilities of the two parents. Using this relation, the combining ability of each parent was calculated by simultaneously solving mid-point equations involving the parents.

The concept of combining ability is usually restricted to an individual parent. By enlarging the concept to include the pollen shower of a stand, an additional estimate of the value of a female parent can be made. That is, the stand is assumed to act as a single male parent having a value that is the average of the observed wind-pollinated progenies taken from the stand. Then the value for the female parent is: observed wind-pollinated progeny phenotypic mean = (female parent combining ability + stand combining ability) /2. In table 4, combining abilities from wind pollinations were calculated from stand values based on the progenies of 17 to 179 wind-pollinated trees.

Heritability estimates in table 5 indicate the precision of the combining-ability values

Table 4. Progeny hypocotyl color phenotypes observed following wind- and self-pollinations, and averaged over all controlled cross-pollinated progeny families of a parent; combining abilities.

Parent identity	Progeny phenotype observed								Combining ability determined from	
	Cross-pollination					Self-pollination			Wind-pollination	Controlled cross-pollination
	Wind			Controlled crosses						
	Trees	Reps.	Index	Number	Index	Trees	Reps.	Index	Index	Index
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
3-176	296	4	15.4	7	16.1	71	1	21.8	17.8	18.3
3-162	341	4	15.6	9	14.8	--	--	--	18.2	18.3
3-135	21	1	13.0	8	12.4	--	--	--	13.0	10.6
3-60	92	1	12.5	11	11.9	5	1	11.2	12.0	11.3
3-36	42	1	15.0	9	14.3	--	--	--	17.0	16.0
3-32	43	1	12.3	6	13.2	10	1	12.6	11.6	9.9
32-58	249	6	12.5	8	13.6	34	1	16.3	11.8	13.6
32-42	250	4	14.6	8	14.4	--	--	--	16.0	15.1
32-9	567	6	13.1	11	13.4	150	1	10.7	13.0	12.7
31-24	49	1	11.9	9	12.3	--	--	--	11.0	12.8
31-8	84	1	17.2	3	13.5	--	--	--	21.6	14.5
11-6	49	1	12.2	6	11.0	--	--	--	10.8	8.4
10-135	430	6	15.0	2	14.3	--	--	--	16.4	12.5
8-7	572	7	11.2	4	10.6	--	--	--	9.2	6.4

Table 5. Heritabilities of hypocotyl color index in slash pine.

Method	Number of families	Relation of family variance to additive variance	Heritability on family mean basis, h^2_f
Components of variance, full-sib	13	$\sigma^2_f = 0.3879\ \sigma^2 A$	.99
Components of variance, half-sib	27	$\sigma^2_f = 0.2500\ \sigma^2_A$	.90
Regression (b) of wind-pollinated half-sib families on (combining ability of female crosses + stand combining ability)/2.	5	--	.91

and illustrate that heritability can be calculated by applying the concept of a combining ability for a stand. Heritability is expressed only on a family-mean basis since selection will likely be for parents rather than for individual seedlings. The calculations are based on indices from 3 replications of 50-100 seedlings per entry. The full-sib coefficient 0.3879 differs from 0.5000 because some of the full sibs were related. The third method of table 5 indicates how the stand combining ability can be used to calculate heritability.

The indices of table 4 allow a comparison of wind- with controlled-pollination in obtaining parameters. First, if it is assumed that parents entering controlled crosses are a random sample of the stand, the average indices of their wind-pollinated progenies appear to approach quite well the indices of their crosses (column 4 vs. 6).

Secondly, combining abilities derived from wind pollinations agree satisfactorily with those derived from controlled cross pollination (column 10, vs. 11). It thus appears that where inheritance is polygenic with no dominance, combining abilities could be obtained more efficiently from enlarged but inexpensive tests with wind-pollinated seed than from slower and more expensive controlled pollinations. Such a possibility is discussed in the textbook of Williams (1964), and the general idea is accepted in ranking progeny means to indicate combining ability of polycrossed parents. However, calculating in a single test actual values for different unknown pollen sources (natural stands in our case) is a procedure not found in genetics literature by the authors.

Thirdly, observed values from self progeny should theoretically estimate exactly the value of the parent (column 9 vs. 11). Although there does appear to be a fair relation between results from crossing and selfing, the differences are too large to satisfy the theory. Some improvement might have occurred if larger self populations had been available, but small populations are characteristic of selfing. It is suspected that selfing produces subtle background changes in chlorophyll similar to inbreeding depression in growth. Change in background colors would lessen the reliability of anthocyanin readings.

The general correspondence between observed and predicted progeny mean values shown in figure 2 illustrates that the model of polygenic inheritance without dominance fits the data. In this figure the results from crossing among 14 parents (table 4) are shown. For example, tree 3-176 appears as the bottom parent in crosses 1, 2, 6, 9, 10 and 22. The progeny populations in 22 of the crosses were based on 2 to 4 replications of 50 to 100 seedlings each. The rest had only one replication and some, e.g., crosses 15 and 36, only 14 seedlings each. If the latter crosses had had more adequate populations, it is anticipated that they also would fit the model satisfactorily. Reciprocal crosses were made for combinations 1 and 38. The small differences between reciprocals are noteworthy. The figure indicates that the combining-ability concept may prove as applicable to forest trees as it has to other crops.

SUMMARY AND CONCLUSIONS

Three types of pigment inheritance were examined. First, in a nitrogen-deficient nursery there was inherent susceptibility to chlorosis of needles among 11 parent trees as judged by correlated performance of their wind- and self-pollinated progenies. Some of the self-progenies had two to three times as many chlorotic seedlings as their corresponding wind-pollinated progenies; one progeny had 77 percent chlorotic seedlings. This high susceptibility was attributed to an unbalanced polygenic system analogous to inbreeding depression.

Secondly, simple Mendelian inheritance--often with disturbed segretation--was found for cotyledon mutants classified *albina*, *xantha*, *green xantha*, and *viridis*. When 18 carriers were intercrossed a common gene was found in only two neighboring trees, thus indicating, if monogenic inheritance is assumed, that the same phenotypes are produced by several non-alleles. Annual changes in the frequencies of the *albina* and *viridis* classes in a total of 7,380,000 nursery seedlings were attributed to differences in weather conditions. The generally held hypothesis that self-pollination is the most efficient method for detecting carriers of mutant genes did not hold in 29 progenies where mutant types had shown up in self-pollinations, cross-pollinations, or both. The failure of more mutants to appear in

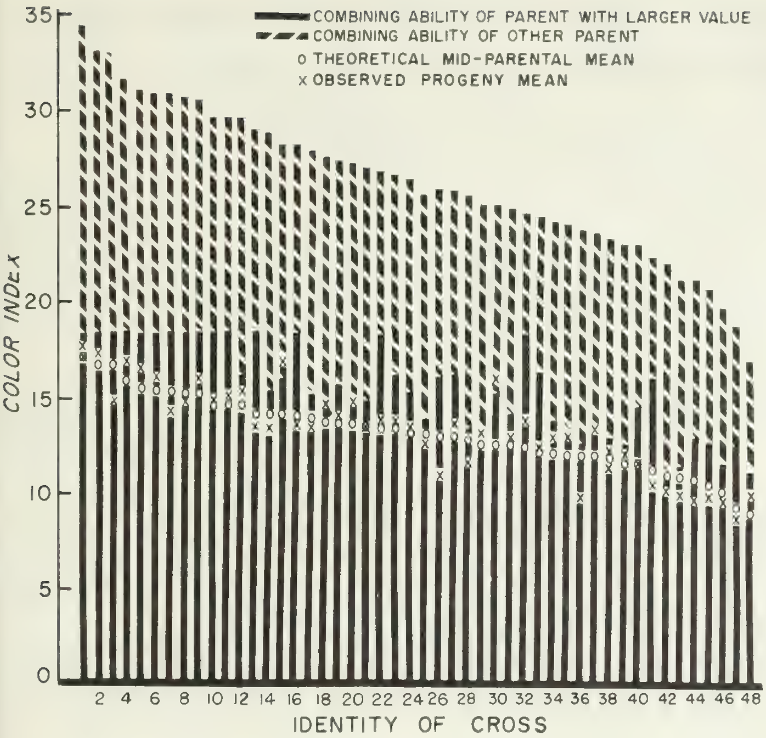

Figure 2 -- Observed mean values of hypocotyl color indices compared with theoretical means calculated from combining abilities.

the self than in the wind progenies was attributed to disturbed segregation, in some cases so severe that no mutants appeared in the small self populations. Disturbed segregation was as severe in crosses as it was in selfs. Part of the disturbance was due to mortality during nursery germination, since six times as many mutants per unit of material were detected in the laboratory.

Finally, inheritance of hypocotyl colors, which varied from white to dark pink, was additive polygenic with no dominance. A geographic pattern of variation was evident from isogenes drawn among 48 sampled stands over the southern United States. No association of this geographic variation was found with other characters or environmental factors. Limited sampling did not reveal any relationship between pigment intensity and resistance to fusiform rust, ability to germinate without a light treatment, or seedcoat color. A new method was derived for estimating heritabilities and combining abilities when the selections in a single experiment are from one or more stands. It entailed calculating combining abilities for each stand by averaging the wind-pollinated phenotypic values of the sampled trees per stand. With hypocotyl colors converted to a numerical index, $h^2_f = .90-.99$. Open-pollinated progenies may be more efficient than control pollinations for estimating combining abilities.

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Estimates of Components of Variance and Covariance in Root and Shoot Characteristics of Loblolly Pine After One Growing Season

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INTRODUCTION

Although a considerable amount of effort has been expended on delineating various types of root systems within and between tree species, there is practically no knowledge of the variation patterns in root development within a local population, or of the inheritance of such growth patterns. This information would be extremely valuable to the tree breeder. It would serve as a guide for improving such characteristics as ability to withstand transplanting shock, drought resistance, resistance to wind throw, as well as growth rate. Such information would also be very useful in tree improvement programs which might be aimed at providing genotypes for problem sites where specialized root systems would be advantageous.

Nearly all the attention of foresters has been focused on crown growth and resultant competition, and the patterns of tree to tree variation of root systems have been largely ignored. It seems logical that root development, efficiency, and competition might play a very large role in the performance of a tree. It is, therefore, essential to have some idea of the magnitudes of genetic and environmental variances for root characteristics.

The study reported here was designed to estimate genetic and environmental components of variance and covariance for several root and shoot characteristics of young loblolly pine from a single geographic source.

LITERATURE REVIEW

There is abundant evidence that various environmental factors affect the form and growth rate of tree roots. Lodgepole pine root form varies widely with soil conditions and between individuals in the same soil (Horton, 1958). Root and shoot growth of loblolly pine was significantly affected by scalping, shading, and mulching in Texas (Bilan, 1960). Redmond (1954) demonstrated the fact that birch roots made their optimum development in loam as compared to sand. while Meyer (1961) found relative root length (root length per square centimeter of leaf area) in beech decreased with increasing soil fertility. Several investigators have noted that the general growth pattern of roots within a species is inherently controlled, but just as for top development, environmental influence will modify this pattern (Lenhart, 1934; Ogievskij, 1958; Merritt, 1960).

Growth patterns generally differ between species, and in the case of shortleaf and loblolly pine, the quantitative differences were maintained under differing environmental conditions (Reed, 1939). Quercus species also evidenced form and growth differences which were modified by different soils, and Carpenter and Guard (1954) were able to recommend transplanting certain species on the basis of root branching.

Genetically, little is known about root development and morphology. As early as 1949, Righter and Duffield demonstrated differences between the root system of ponderosa pine and the ponderosa - apache pine hybrid (P. ponderosa x latifolia). This hybrid has a more vigorous root system with a well developed tap root while the ponderosa pine seedling has a less vigorous root system with a poorly defined tap root. Similar differences were found in Willow hybrids by Ortman (1958).

Selection of tree and shrub willow forms was expedited by root type (Ortman, 1961), and drouth resistance of Acer saccharum from west of the Appalachian mountains was attributed to the extensive, vigorous fibrous root system of that ecotype (Kriebel, 1961).

Racial variation in root form was noted by Snyder (1961) with longleaf pine (Pinus palustris) where the root systems of seedlings from the Southeast Georgia seed source were more fibrous than those from further west. The number of lateral roots was also greater for the Eastern form. Successful clonal selection for growth rate of hybrid poplar was based on bark thickness of roots of equal size (Anonymous, 1959) and Ruggeri (1963), also noted

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anatomical differences in the roots of certain hybrid poplars involving bark thickness. In a study of blue and green races of douglas fir, Hengst (1958) noted that the influence of race on most root characteristics was negative but tree class and soil difference were important.

From this information it might be postulated that there are differences in root form due to environmental influence, but superimposed on these differences various species and sub-species possess unique root types. Within a species there are racial differences which have arisen because of differences in environment. For example, there is some indication that pines growing on the deep peat lands in the Coastal Carolinas have a stilt-like root form rather than the typical tap root usually found in the species. When trees with tap roots are planted in the deep peat soils they will grow for several years and then fall over while native trees of the same species are wind-firm even through hurricanes.

More recently Ledig (1965), has reported differences in shoot-root ratios between progenies of one-year-old loblolly pine, and further concluded that shoot-root ratios are only suitable for comparison of material which is the same age and has been grown under similar conditions.

MATERIALS AND METHODS

Experimental Design

The seedlings used in this study were from control pollinated crosses made as a part of the overall International Paper - North Carolina State University Cooperative Heritability Study. The mating design used and objectives of the study were described by Cech et. al. (1962). For the control pollination phase, Design I developed by Comstock and Robinson (1948, 1952), was used. Using this mating design, one tree was arbitrarily designated as male and mated to four different females; the four crosses with each male is termed a male group. One male and four females were used because of considerations of statistical efficiency, but as often happens when making controlled pollinations on forest trees, some crosses failed to produce viable seed. Because of such failures, fewer than four crosses were frequently obtained for a male group. Although the necessity of using fewer than four females for each male group decreases the statistical efficiency, the three and even two female "male groups" can be used to make estimates of the genetic and environmental parameters desired with very little computational difficulty.

The root study reported here was initiated with 50 full-sib families from excess seed remaining after the planting of the main study. Because this was excess seed, it was possible to use only one male group with four females present; the remainder had either three or two females per male. Sixty stratified seed from each family were divided equally and sown on April 19, 1963, in six metal pots which were eight inches in diameter and approximately seven inches deep. The seeds of each cross were weighed to the nearest 0.001 gm. prior to stratification and sowing.

Soils used were obtained from two locations and were placed in the pots with as little disturbance of the soil profiles as possible. The soils were obtained from the east and west properties of the Southlands Experiment Forest. The U.S.D.A. soil texture classification of the west property, hereafter referred to as soil A, was sand. The east property soil, hereafter referred to as soil B, was classified as loamy sand. Although fairly detailed laboratory analyses showed soils A and B to be quite similar, the natural vegetation growing on the east and west properties is definitely different. The east property supports stands of loblolly and shortleaf pines and is typical of the Southeastern Piedmont, while the west property has extensive stands of longleaf pine and scrub oak. The specific locality from which soil A was obtained has been under cultivation and now supports a slash pine plantation. Soil B was obtained from an area, which as far as is known, was never under agricultural cultivation.

Where necessary, the seedlings were thinned on June 26, 1963, so that no more than five seedlings were growing in each pot. Seed of some crosses had poor germination or survival which resulted in fewer than five seedlings in each pot.

Measurements

Starting September 17, 1963, the seedlings were lifted from the pots and soil was carefully removed from the roots by a low-pressure stream of water. The group of seedlings from each pot were then placed in polyethylene bags and stored in a refrigerator until measurements could be made. The measurements were made over a period of approximately sixty days.

At the time of measurement, the seedlings were removed from the bags, and the root systems were further cleaned by gentle agitation in water. Shoot and root length were then measured to the nearest cm. and the number of lateral roots greater than ten cm. in length were counted. Following these measurements, the seedlings were cut at the root collar and both the roots and shoots were oven dried at 105°C for 48 hours. Upon removal from the oven, the root and shoot of each seedling was weighed to the nearest 0.001 gm.

Table 1. Correlations between seed weight and seedling variables and ratios of seedlings approximately 150 days old.

Trait	r values
Shoot length	0.34*
Root length	0.08
Shoot weight	0.35*
Root weight	0.23
Number of lateral roots	0.27
Shoot length/root length	0.08
Shoot weight/root weight	0.11
Root length/number of lateral roots	-0.24

* Significant at 0.05 level.

Statistical Analyses

Because of poor germination and survival, only 39 of the original 50 full-sib families were complete enough to be included in the analyses. Because of the unequal numbers of seedlings in some pots, all analyses of variance and covariance were performed on plot means and the within plot variances were calculated separately for each plot. Robinson et.al.(1949) used a similar method for estimating the within plot variances in corn. Although, as Snedecor (1946) points out, this method is not exact, it was felt that reasonably accurate estimates of the parameters desired could be obtained for this root study.

In addition to the five traits measured (see Table 1), ratios of shoot weight to root weight, shoot length to root length, and root length to number of lateral roots were included in the analyses. Plot means and within plot variances were calculated for each trait as well as for the three ratios. Prior to performing the analyses of variance and covariance, correlations between seed weight and the eight variables were computed. It is commonly believed that size of seed has a direct effect upon size of shoot of the seedling and perhaps on the root characteristics. If this effect were large, it could result in an upward bias of the variance due to female differences. Therefore, seed size of the various crosses were measured, and the correlations of the traits are presented in Table 1.

It is obvious that because of the general low correlation between seedling size and seed size relationships, no adjustment for seed weight was necessary in the subsequent analyses.

Analyses of variance and covariance were performed on plot means first separately for soil A and B followed by the pooled analyses for both soils as illustrated in Tables 2 and 3.

All analyses and computations were performed on an IBM computer[1/] with machine programs which were specifically designed by the senior author for the analyses of data for all phases of the control pollinated heritability study.

Estimation of Genetic and Environmental Components of Variance and Covariance.

The mean squares for the analyses of the eight traits were determined by separate soils and combined for both soils. The pooled error terms were obtained by combining the replication by males and replications by females in males interactions. In addition to the analyses of variance, analyses of covariance for the 28 relationships among the traits were performed.

Estimates of components of variance and covariance were obtained from the means squares and mean cross products of the analyses of variance and covariance. In the case of the components of variance, difficulties arose because in several cases the estimates obtained were

[1/] Grateful acknowledgement is made to Messrs. L. W. Brown and Graham E. Abbott of International Paper Company's Southern Kraft Division's Engineering Computer Facility, who provided computer time and helped in "debugging" the program used to analyze the data of this study.

Table 2. Form of analysis of variance and covariance used for analyses by separate locations.

Source	d.f.	m.s.	Expected mean squares[a]
Replications	2	m.s.1	$\frac{\sigma^2 w}{k} + \sigma^2 p + 39\sigma^2 b$
Males	15	m.s.2	$\frac{\sigma^2 w}{k} + \sigma^2 p + 3\sigma^2 f + 7.28\sigma^2 m$
Females/males	23[c]	m.s.3	$\frac{\sigma^2 w}{k} + \sigma^2 p + 3\sigma^2 f$
Pooled error	76	m.s.4	$\frac{\sigma^2 w}{k} + \sigma^2 p$
Within plot	[b]	m.s.5	$\underline{\sigma^2 w}$

[a] k = Harmonic mean of plants per plot = 4.13 for soil A and 4.25 for soil B.

$\sigma^2 w$ = Variance due to differences among plants in plots.

$\sigma^2 p$ = Variance due to differences among plots.

$\sigma^2 f$ = Variance due to differences among progenies from females mated to the same male.

$\sigma^2 m$ = Variance due to differences among progenies from the same male.

$\sigma^2 b$ = Variance due to differences among replications.

[b] Within plot degrees of freedom for soil A and soil B was 396 and 407, respectively.

[c] Ten male groups had two females per male, five had three, and one had four.

negative. Anderson (1960) discusses this problem and gives two alternative methods for estimating components from expected mean squares which contain negative component estimates. He points out that the biased procedure of pooling the sums of squares, assuming the true value of the component which had a negative estimate of zero, gives more precise estimates. This biased procedure was followed in estimating the components of variance from the mean squares (see Tables 4 and 5). The genetic correlations were estimated from the male components for the relationships between four of the five traits which had non-negative male components in the pooled analyses (Data are shown in Table 6).

Genetic Interpretation of the Components of Variance and Covariance.

The necessary assumptions for the genetic interpretation of components of variance estimated from Design I have been presented by Comstock and Robinson (1948). These authors further show that the male component ($\hat{\sigma}^2 m$ or $\hat{\sigma}^2 m'$ in Table 5) estimates one-quarter of the additive genetic variance, and the female component ($\hat{\sigma}^2 f$ or $\hat{\sigma}^2 f'$ in Table 5) estimates one-quarter of the additive plus one-quarter of the dominance variance. Similarly, the components of covariance have the same genetic interpretation as the components of variance (Falconer, 1960). For example, the component of covariance for males estimates one-fourth of the covariance of the additive values of two traits.

Heritabilities, such as those reported in Table 6, were estimated from the following formula:

$$h^2 = \frac{4(\hat{\sigma}^2 m')}{k' \frac{(\hat{\sigma}^2 w')}{k'} + \hat{\sigma}^2 p' + \hat{\sigma}^2 fs + \hat{\sigma}^2 ms + \hat{\sigma}^2 f' + \hat{\sigma}^2 m'}$$

The genetic correlations, which are reported in Table 6, were estimated by the following formula:

$$\hat{r}g = \frac{\hat{\sigma} mxy}{(\hat{\sigma}^2 mx' \hat{\sigma}^2 my')^{\frac{1}{2}}}$$

Where:

$\hat{r}g$ = genetic correlation estimate

$\hat{\sigma} mxy$ = additive genetic covariance for traits x and y

$\hat{\sigma}^2 mx'$ = additive genetic variance for trait x

$\hat{\sigma}^2 my'$= additive genetic variance for trait y

Table 3. Form of analysis of variance and covariance used for analyses which were pooled over soils.

Source	d.f.	m.s.	Expected mean squares[a]
Soils	1	m.s.1'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho' + 3\sigma^2 fs + 7.77\sigma^2 ms + 39\sigma^2 b' + 117\sigma^2 s$
Replications/soils	4	m.s.2'	$\frac{\sigma^2 w'}{k'} + \sigma^2 p' + 39\sigma^2 b'$
Males	15	m.s.3'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho' + 3\sigma^2 fs + 7.28\sigma^2 ms + 6\sigma^2 f' + 14.56\sigma^2 m'$
Females/males	23	m.s.4'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho' + 3\sigma^2 fs + 6\sigma^2 f'$
M x S	15	m.s.5'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho' + 3\sigma^2 fs + 7.28\sigma^2 ms$
F/M x S	23	m.s.6'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho' + 3\sigma^2 fs$
Pooled error	152	m.s.7'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho'$
Within plot	803	m.s.8'	$\frac{\sigma^2 w'}{k'} + \sigma^2 \rho'$

[a] k' = Harmonic mean of plants per plot = 4.19

$\sigma^2 w'$, $\sigma^2 \rho'$, $\sigma^2 f'$, and $\sigma^2 m'$ are due to the same sources as indicated in Table 3.

$\sigma^2 fs$ = Variance due to the interaction between paternal half-sibs and soils.

$\sigma^2 ms$ = Variance due to the interaction between progenies from the same male and soils.

$\sigma^2 s$ = Variance due to differences among soils.

TABLE 4. Mean squares for the analyses of variance by separate soils and combined for soils

Source	d.f.	Shoot Length	Root Length	Shoot Weight	Root Weight	No.Laterals	Shoot Length Root Length	Shoot Weight Root Weight	Root Length No.Laterals
SOIL A:									
Replications	2	18.08250	412.71500	0.12340	0.00850	55.31975	0.05957	2.76295	166.19400
Males	15	20.25040	30.40333	0.01178	0.00149	3.11790	0.06972	1.12195	20.85806
Females/males	23	27.03691	43.62608	0.00829	0.00082	2.27847	0.09649	0.58949	15.36526
Pooled error	76	2.89643	24.14683	0.00940	0.00075	1.39883	0.02192	0.45248	11.90062
Within plot	396	40.05710	76.21543	0.01610	0.00141	3.24310	0.22359	0.74775	35.18589
SOIL B:									
Replications	2	68.04000	740.03000	0.47190	0.03986	23.70740	0.04339	0.69855	55.00650
Males	15	11.78473	103.27733	0.05278	0.00421	3.79877	0.05717	0.58986	12.54226
Females/males	23	13.34130	106.31043	0.05717	0.00461	2.83559	0.02267	0.40910	3.94652
Pooled error	76	8.17396	45.50302	0.04295	0.00368	1.84585	0.01306	0.44511	5.68951
Within plot	407	20.50335	113.40839	0.05098	0.00387	3.38304	0.08147	0.87080	17.11010
COMBINED:									
Soils	1	788.39900	579.36000	3.36600	0.25654	20.07220	0.29333	0.20510	117.10000
Reps/soils	4	43.06125	576.37000	0.29765	0.02418	39.51355	0.05148	1.73072	110.60025
Males	15	19.56193	72.52733	0.02818	0.00350	4.86603	0.08170	1.19634	16.54073
Females/males	23	17.18491	92.35608	0.02919	0.00230	1.77164	0.07803	0.67352	8.88713
Males x soils	15	12.47320	61.15266	0.03638	0.00220	2.05063	0.04519	0.51546	16.85960
Females/males x soils		23.19330	57.58043	0.03626	0.00313	3.34242	0.04113	0.32506	10.42465
Pooled error	152	5.53520	34.82499	0.02617	0.00222	1.62235	0.01750	0.44880	8.79506
Within plot	803	30.14630	95.06666	0.03378	0.00266	3.31403	0.15156	0.81012	26.02419

TABLE 5. Estimates of components of variance by separate soils and combined for soils

SOIL A	Shoot Length [1/]	Root Length	Shoot Weight	Root Weight	No.Laterals	Shoot Length Root Length	Shoot Weight Root Weight	Shoot Length No.Laterals
$\hat{\sigma}^2 m$	N.C.	N.C.	0.00036	0.00009	0.26360	N.C.	0.07314	0.75450
$\hat{\sigma}^2 f$	6.14440	6.49308	N.C.	0.00002	0.29321	0.01585	0.04567	1.15488
$\hat{\sigma}^2 p$	N.C.	5.69274	0.00551	0.00041	0.61358	N.C.	0.27143	3.38104
$\frac{\hat{\sigma}^2 w}{k}$	9.69905	18.45409	0.00389	0.00034	0.78525	0.05413	0.18105	8.51958
SOIL B								
$\hat{\sigma}^2 m$	N.C.	N.C.	N.C.	N.C.	0.13230	0.00473	0.02103	0.99693
$\hat{\sigma}^2 f$	1.72244	20.26913	0.00474	0.00031	0.32991	0.00143	N.C.	N.C.
$\hat{\sigma}^2 p$	3.34964	18.81871	0.03096	0.00277	1.04984	N.C.	0.08007	1.66361
$\frac{\hat{\sigma}^2 w}{k}$	4.82432	26.68131	0.01199	0.00091	0.79601	0.01917	0.20489	4.02591
COMBINED								
$\hat{\sigma}^2 m'$	.08723	N.C.	N.C.	0.00006	0.16713	N.C.	0.03021	0.30951
$\hat{\sigma}^2 f'$	N.C.	5.79594	N.C.	N.C.	N.C.	0.00615	0.04016	N.C.
$\hat{\sigma}^2 ms$	N.C.	0.49069	0.00001	N.C.	N.C.	0.00055	0.01139	0.88392
$\hat{\sigma}^2 fs$	4.71899	7.58514	0.00336	0.00030	0.57335	0.00264	N.C.	0.51349
$\hat{\sigma}^2 p'$	N.C.	12.13605	0.01811	0.00158	0.83141	N.C.	0.25545	2.58404
$\frac{\hat{\sigma}^2 w'}{k'}$	7.19482	22.68894	0.00806	0.00064	0.79037	0.03617	0.19334	6.21102

[1/] N.C. = negative estimate of component

TABLE 6. Estimates of heritability and genetic correlations

Estimates of Heritabilities [1/]

Trait	Shoot Length	Root Weight	No. Laterals	Shoot Weight Root Weight	Shoot Length No. Laterals
Heritability:	0.01	0.05	0.14	0.11	0.04

Estimates of Genetic Correlations

Traits	Root Weight	No. Laterals	Shoot Weight/Root Weight
Shoot Length	3.18	2.97	0.36
Root Weight		2.37	-0.78
No. Laterals			-0.50

[1/] $\hat{\sigma}^2 m'$ for shoot weight, root length, and shoot length - root length ratio, were negative and, therefore, no additive variance was indicated for these traits.

RESULTS AND DISCUSSION

A total of 1,037 seedlings were measured in this study. Considerable within plot differences were found as can be seen from the estimates of the within plot components of Table 5. In the case of two traits (shoot length-root length ratio, and shoot length) the estimate of the within plot component was larger than the plot to plot component.

Male group mean values for the eight traits analyzed are given in Table 7. Also in

TABLE 7. Male group means averaged over both soils and means for both soils for the eight variables used in analyses

	No. of Female	Shoot Length CM.	Root Length CM.	Shoot Weight GMS	Root Weight GMS	No. of Lateral Roots	Shoot Length Root Length	Shoot Weight Root Weight	Root Length No. Lateral Roots
Male #									
10	2	15.4	34.8	0.45	0.13	4.8	0.46	3.5	8.3
12	3	17.8	35.4	0.50	0.14	4.7	0.56	3.4	9.0
14	3	18.3	32.0	0.41	0.11	3.6	0.34	3.6	10.0
16	3	16.6	30.3	0.43	0.11	4.2	0.61	4.0	9.8
19	2	15.4	37.8	0.48	0.14	4.7	0.45	3.4	10.3
20	4	15.9	37.1	0.45	0.14	4.8	0.45	3.3	9.5
28	2	15.0	32.6	0.40	0.10	3.3	0.51	3.9	12.4
30	2	16.6	33.9	0.43	0.11	3.7	0.52	3.7	11.1
34	2	15.6	34.3	0.42	0.11	3.8	0.50	3.8	10.5
37	2	16.7	33.0	0.38	0.11	3.8	0.56	3.5	10.0
39	2	17.3	30.7	0.46	0.11	3.2	0.59	4.4	12.0
40	2	15.6	33.0	0.44	0.12	3.9	0.49	3.9	9.8
43	3	17.5	36.0	0.52	0.13	4.8	0.50	3.9	9.5
46	2	15.9	34.9	0.43	0.13	4.7	0.52	3.7	9.4
49	2	16.2	36.5	0.53	0.16	5.2	0.48	3.5	8.3
50	3	13.9	35.1	0.40	0.11	3.9	0.41	3.4	10.6
TOTAL	39								
Averages:									
Soil A		14.4	32.7	0.33	0.10	4.0	0.49	3.6	10.7
Soil B		18.1	35.9	0.57	0.16	4.6	0.56	3.7	9.3
Both Soils		16.2	34.3	0.45	0.13	4.3	0.52	3.6	10.0

Table 7 are the average values for each of the traits by soils. As mentioned earlier, laboratory analyses of the physical and chemical properties of the two soils used showed the soils to be quite similar. However, it is obvious from the mean values presented in Table 7, that the growth response of the seedlings was quite different in the two soils. The F test of soil effects was significant at the five percent level for three of the eight traits analyzed, viz., shoot length, and shoot weight, and root weight.

Of the eight traits presented in Table 7, the greatest difference among male group means is for number of lateral roots greater than ten cm., followed by root weight and the ratio of shoot weight to root weight in order. Only one of the traits analyzed (number of lateral roots) showed a significant difference for male effects.

Although there was no evidence for differences among male groups in the case of root length, there was evidence for differences among females mated to the same male. Even more striking in the case of root length,is the evidence for a large female by soil interaction effect. If an F test for females effect on root length is applied to the mean squares of separate soils in Table 5, we find that there are significant differences among females mated to the same male. If, however, we apply an F test to the combined mean squares, we find that the test for root length difference among females is non-significant if the female by soils interaction is used as the denominator for the test.

Such genotype by environment interaction effects are of great importance to the tree breeder. For example, the breeder who wanted to increase root length would be forced to decide whether to concentrate on producing types with an increased root length for a specific soil and thereby possibly obtain greater improvement, or to concentrate on producing types which had longer roots in a variety of soils with a possible resultant lesser degree of improvement. It would seem, at the present time, that the forest tree breeder is more interested in producing types which are fairly widely adapted to a variety of site conditions. However, the possibility of selecting genotypes for specific environmental and cultural situations should not be overlooked by the forest geneticist. More important, tests of superior tree progeny as well as experiments designed to estimate genetic variances in forest trees should be planned so that some measure of the magnitudes of genotype-environment interactions can be obtained.

The F test for the presence of a significant female by soil interaction effect showed that shoot length, number of lateral roots, and the ratio of shoot length to root length were significant at the 0.01 level, and root length was significant at the 0.05 level (see Table 4).

The estimates of narrow sense heritability reported in Table 6 are on an individual basis, and were obtained from the components of variance derived from the combined analyses.

As can be seen in Table 6, the heritability estimates are generally low. It is encouraging, however, that root weight, shoot weight-root weight ratio, and number of lateral roots, show some evidence for presence of additive variance in these young seedlings. It appears that some gains could be obtained by selecting within a population for more fibrous or spreading root systems resulting in a production of seedling types which have a greater ability to survive outplanting as well as to more fully utilize soil nutrients.

In order to examine the possible relationships between these three root traits and ability to survive outplanting, an examination of values obtained from the field planting of 31 full-sibs, which were common to both the large field study and the root study, was made. There were no significant correlations between number of laterals or root weight and survival, but there was a small but significant negative correlation between the shoot weight-root weight ratio and first year survival. Since the seedlings of the field planting were carefully handled and environmental conditions were such as to maximize survival, the value of the correlation obtained could be conservative. More rigid tests of survival ability might possibly show much better relationships to root traits.

Of the traits analyzed in this study, three (root length, shoot length/root length, and shoot weight/root weight) show evidence of dominance variance. This is particularly strong in the case of root length as can be seen by the estimates of the female components in the combined analyses of Table 5. As mentioned above, the estimates of the female in male components of variance $\hat{\sigma}^2_f$ contain one-fourth of the additive plus one-fourth of the dominance variance if the assumption of no epistasis is made. Therefore, if the estimate of the female component of variance is larger than the male component there is evidence for the presence of dominance variance.

If an appreciable portion of the genetic variance of a characteristic is the result of dominance variance, then methods of selection used should be altered in order to make maximum gains. A simple selection system will not give maximum gain and only specific crosses, progeny tested under proper conditions, would enable the breeder to take advantage of dominance variance.

Estimates of genetic correlations, which are reported in Table 6, are of interest to the breeder for the following two reasons: 1. They indicate how selection for one trait will change another trait, and 2. They indicate if a secondary trait which might be relatively easy to evaluate can be used to select for a primary trait which might be more difficult to evaluate. For example, if an above ground seedling characteristic had a high genetic correlation with a root characteristic, the former more easily measured trait could be used to select for the root trait.

The genetic correlations in Table 6 were estimated from the combined covariance analyses and the variance analyses for four traits which contained non-negative male components. Theoretically, these genetic correlations should be less than or equal to one. The fact that the correlations were estimated from components of variance and covariance which had rather large standard errors resulted in values greater than one. The exact values of the correlations reported in Table 8 should not receive great emphasis. However, it is of interest to examine the sign and general degree of relationship between the traits.

The two correlations of most interest are those which show the relationships between shoot length and the root characteristics of weight and number of lateral roots. The indication from the correlations calculated is that selection for increased shoot length would also result in an increase of root number and size.

It is important to emphasize that this study used families which were derived from randomly selected parent trees which were growing in the same locality under quite similar environmental conditions. Whether the estimates obtained in this study are similar to natural loblolly pine growing under more varied environmental conditions is debatable. However, it seems logical that the heritability estimates obtained in this study are conservative when compared to estimates which might be obtained from populations growing under more varied environmental conditions which, for example, exist over an area serviced by a loblolly pine seed orchard.

Summary

The estimates of additive variance and, therefore, the narrow sense heritabilities obtained from the characteristics observed in this study were generally quite low. Of the five root and shoot traits and three ratios analyzed, number of lateral roots greater than 10 cm., root weight, and the ratio of shoot weight to root weight gave the highest estimates of narrow sense heritability. Although the heritability estimates were fairly low for number of laterals and root weight, their values indicate that there is usable genetic variance present in a local population for these two root traits.

The results indicated that the genetic variances of three traits analyzed in this population are the result of dominance variance. Although dominance variance can be utilized in a breeding program, the evaluation of specific crosses becomes necessary.

Four characteristics and ratios analyzed showed evidence of quite large variances caused by genotype by environment interactions. These interaction estimates were particularly strong in the case of the female by soils effects. The possibility of presence of such genotype by environment interactions should be strongly considered in planning progeny tests as well as experiments designed to estimate genetic variances in forest trees. If such effects are ignored, serious over estimates of gains or poor evaluations of genotypes could result.

The standard errors of the estimates of the components of variance, particularly the male components, were disappointingly high. It appears that if reliable estimates of genetic and environmental components of variance for forest tree population grown under field conditions are to be made, large amount of experimental material will have to be used.

The standard errors of estimates of components of variance, obtained from traits measured in the extensive field plantings involving 51 male groups at Southlands, are of acceptable magnitudes. These larger studies are yielding reliable estimates of genetic variances for many important tree characteristics.

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Evidence of Inherent Resistance to Dioryctria Infestation in Slash Pine

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INTRODUCTION

Tree improvement workers are interested in developing strains of pines resistant to destructive insects. The objectives, methods, possibilities, and limitations of pest-resistance improvement in trees have been discussed thoroughly by Holst and Heimburger (1955), Schreiner (1960), and Soegaard (1964). We shall present evidence of resistance of individual slash pines, *Pinus elliottii* Engelm., to cone and stem infestation by *Dioryctria* spp. Lepidoptera: Phycitidae. In these studies, mature cones were attacked by *Dioryctria abietella* (D. & S.) and *D. amatella* (Hulst), whereas stem infestation was by the latter species only.

Dioryctria larvae are very destructive to the seed crops in southern pine seed orchards and natural seed-production areas. Annually they destroy from 20 to 50 percent of the slash pine seed crop in such areas in north Florida, where chemical control is not used. Although extensive reliable data on the economic importance of stem attacks is lacking, *D. amatella* is known to cause serious damage to young plantations of either seedlings or grafted trees. Larvae bore meandering galleries in the phloem of the main stem and eventually enter the xylem, particularly in tissues infected with southern fusiform rust. The larval galleries frequently girdle young trees resulting in their death; whereas larger stems often become weakened and break during high winds. Crooked trees may also result from larvae destroying the terminal shoots.

CONE ATTACK

Evidence of inherent resistance of mature cones to infestation by *Dioryctria* coneworms

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Table 1. Record of mature cones harvested from 10 slash pines and the incidence of infestation by *Dioryctria* spp. -- Olustee, Florida, 1956-1958.

Tree Number	1956			1957			1958			3-year weighted average infestation
	Total cone crop	Total cones infested		Total cone crop	Total cones infested		Total cone crop	Total cones infested		
	Number	Number	Percent	Number	Number	Percent	Number	Number	Percent	Percent
10	244	70	28.7	180	15	8.3	178	23	12.9	17.9
14	465	207	44.5	239	61	25.5	410	121	29.5	34.9
23	78	44	56.4	409	16	3.9	508	66	13.0	12.7
30	373	164	44.0	205	14	6.8	185	64	34.6	31.7
34	225	88	39.1	329	17	5.2	196	70	35.7	23.3
35	307	179	58.3	199	41	20.6	366	87	23.8	35.2
50	204	81	39.7	172	31	18.0	151	43	28.5	29.4
59	266	83	31.2	421	36	8.6	401	31	7.7	13.8
61	149	99	66.4	283	60	21.2	23	14	60.9	38.0
75	385	181	47.0	343	46	13.4	379	111	29.3	30.5
Totals	2,696	1,196		2,780	337		2,797	630		
Averages	270	120	44.4	278	34	12.1	280	63	22.5	

Table 2. Percent[1] mature slash pine cones infested by Dioryctria spp. expressed as departures from yearly averages at Olustee, Florida.

Year	Tree number									
	10	14	23	30	34	35	50	59	61	75
	Percent									
1956	18.4	+12.1	-2.2	+5.4	-1.4	+15.2	-10.2	-14.6	+12.6	+1.2
1957	7.1	+10.3	-5.0	-8.5	-6.2	+3.4	0.2	+1.8	+8.5	+3.6
1958	-18.6	+10.7	-2.1	+1.4	+5.2	+1.8	-6.2	-14.6	+16.4	+8.5
	R[2]	S[3]						R	S	

1/ Adjusted for cone crop size by analysis of covariance

2 R = apparently resistant tree

3. S = apparently susceptible tree

was obtained in a 4-acre, 21-year-old, natural slash pine-seed production area at Olustee, Florida. The area had been thinned to 33 seed trees per acre in late 1953. For 3 consecutive years, starting in 1956, all mature cones were harvested from 10 trees, and total numbers of cones attacked by coneworms were determined (table 1).

It should be noted that our recorded data for Dioryctria cone attack represent only that portion of the second-year cones infested during the period from early June through cone harvest time (mid-September). Second-year cones attacked prior to June have usually dried up and dropped off the tree by cone harvest. Coneworms also kill many first-year cones.

RESULTS AND DISCUSSION

Correlation analysis of data in table 1 showed that the number of Dioryctria attacks on mature slash pine cones were positively correlated with the total mature cone crop. The pooled correlation coefficient (0.62), within years, was highly significant. Covariance analysis showed that the numbers of cones attacked among trees, after adjusting for the effect of cone-crop size, was highly significant.

Further analysis showed that percent cones infested was also related to the size of the mature cone crop per tree. The within-years pooled correlation coefficient (-0.51) was negative but still highly significant. As in the case of numbers of cones attacked, covariance analysis of percent infestation (transformed to arcsin angles) showed highly significant tree effects.

It is difficult to explain the biological significance of the negative relationship between percent infestation and size of mature cone crop. Hansberry and Richardson (1935) found a similar relationship between the percent apples infested with codling moth larvae and the total apple crop per tree.

The apparent resistance and susceptibility of certain trees to cone attack by Dioryctria spp. is shown in table 2. The data in table 2 were computed by adjusting the percent cones infested for cone crop size by covariance analysis and expressing the adjusted percent as a departure from the yearly average percent infestation for all trees. On this basis, trees 10 and 59 showed fairly consistent below-average coneworm attack for 3 consecutive years and might be judged relatively resistant. Conversely, trees 14 and 61 demonstrated consistent susceptibility to attack.

Although inherited resistance of cones to Dioryctria attack is not proven by these data, it is strongly suggested. Progeny tests are needed to verify or nullify this hypothesis.

STEM ATTACK

Evidence of inherent differences among trees in susceptibility to stem attack by Dioryctria amatella was obtained in three plantations at Olustee, Florida. These plantations are briefly

Table 3. Degree of stem attack by Dioryctria amatella in 4-year-old planted slash pines (Progeny Planting G-48-A), Olustee, Florida--1964.

Progeny	Trees infested	Progeny	Trees infested
	Percent[1]		Percent[1]
G-1 x G-196	10.0	G-148 x W	2.5
G-1 x G-202	27.5	G-151 x W	7.5
G-10 x W	5.0	G-153 x W	10.0
G-11 x W	10.0	G-155 x W	7.5
G-27 x W	7.5	G-156 x W	10.0
G-29 x W	.0	G-157 x W	5.0
G-105 x W	5.0	G-159 x W	7.5
G-107 x W	15.0	G-160 x W	15.0
G-108 x W	12.5	G-162 x W	5.0
G-109 x W	10.0	G-163 x W	.0
G-123 x W	.0	G-164 x W	2.5
G-126 x W	5.0	G-165 x W	5.0
G-129 x W	5.0	G-166 x W	5.0
G-31 x W	7.5	G-167 x W	7.5
G-133 x W	25.0	G-168 x W	7.5
G-134 x W	2.5	CBC[2]	5.0
G-137 x W	10.0	19-SPAC[2]	5.0
G-146 x W	5.0	NF-SPAC[2]	12.5
		Average	7.8

1/ Based on 40 trees per progeny; each tree was classified as infested if it had at least one active pitch mass on the main stem.

2/ Control lot.

Table 4. Degree of stem attack by Dioryctria amatella in slash pine progeny planting G-48-B, Olustee, Florida--1964.

Progeny	Trees infested
	Percent[1]
G-1 x G-195	20.0
G-1 x G-196	15.0
G-1 x G-197	22.5
G-1 x G-198	5.0
G-1 x G-199	32.5
G-1 x G-200	2.5
G-1 x G-201	32.5
G-1 x G-202	32.5
G-1 x G-203	15.0
Average	19.7

[1] Based on 40 trees per progeny.

described below:

1. Progeny Plantation G-48-A.--This is a 4-year-old progeny test of selections for either high gum yield or rapid growth rate. It includes 36 progenies, most of which were wind-pollinated (table 3). The design is a randomized block type, with 40 trees per progeny planted in 4-tree row-plots in each of 10 replications.

2. Progeny Plantation G-48-B.--This is also a progeny test, similar to G-48-A, excepting that there were nine progenies in all. The progenies all had a common female parent but different male parents (table 4). The plantation is located adjacent to G-48-A.

3. Clonal Plantation NS-112.--This plantation includes 24 7-year-old ramets of each of 26 trees (table 5). There are three ramets in each of eight blocks. The ortets of the clones are located in a progeny test and hence are of known parentage.

The numbers of trees with stems attacked by Dioryctria amatella in these plantations were recorded in the spring of 1964.

RESULTS AND DISCUSSION

Progeny Test G-48-A.--Percentage trees infested in this plantation varied from 0 for several progenies (G-29 x W, G-123 x W, and G-163 x W) to as high as 27.5 for progeny G-1 x G-202 (table 3). An analysis of variance of the number of trees infested per plot, showed that differences among progenies were significant at the 1-percent level. The intraclass correlation coefficient (r_I) for progenies was .09 (Snedecor, 1956, P. 282).

Progeny Test G-48-B.--In this plantation, where all progenies had a common female parent, infestation was high in seven progenies and low in two (table 4). An analysis similar to that conducted in G-48-A showed that differences among progenies were highly significant and r_I for progenies was .20.

Clonal Plantation NS-112.-- Percentage of trees infested varied from 0 for clones 1-6-4, 1-1-4, 6-4-7, and 2-9-1 to as high as 42 for clone 1-3-7 (table 5). An analysis of variance was run on the percentage of trees infested per block. (In this analysis clones 8-8-1 and 3-8-7 were omitted because they were represented on only four of the blocks.) Differences between clones were highly significant and r_I for clones was .31.

Note that some groups of clones are full-sibs, having two common parents, and others are half-sibs, having one common parent. In some of these families variation among clones was high. For example, among the 4 clones

Table 5. Degree of stem attack by Dioryctria amatella in slash pine clonal plantation NS-112, Olustee, Florida--1964.

Clone number	Parentage	Ramets per clone	Ramets infested
		Number	Percent
2-5-6	G-1 x G-2	22	4
4-2-7	G-1 x G-2	24	4
6-9-6	G-1 x G-2	21	14
8-8-1	G-1 x G-2	12	30
2-1-4	G-1 x G-7	22	36
[illegible]-3-5	G-1 x G-7	24	25
1-3-7	G-1 x W	24	42
1-6-4	G-2 x W	24	0
3-8-2	G-2 x W	24	50
4-7-5	G-2 x W	24	4
7-5-4	G-2 x W	24	12
1-1-4	G-3 x G-2	24	0
7-7-1	G-3 x G-6	20	5
7-4-3	G-3 x W	24	8
2-3-4	G-4 x G-1	23	4
3-8-7	G-4 x G-1	12	50
6-4-7	G-4 x G-1	24	0
6-9-7	G-4 x G-1	24	25
4-3-2	G-4 x W	24	17
6-2-5	G-4 x W	24	4
2-9-1	G-6 x G-5	24	0
7-[illegible]-5	G-8 x W	24	4
2-7-3	G-10 x G-7	24	21
3-9-6	G-10 x G-7	24	8
4-7-[illegible]	G-10 x G-7	24	3
4-10-5	G-25 x W	24	4
Average			[illegible]

of the mating G-1 x G-2 stem attack varied from 4 to 30 percent. In other families, such as G-1 x G-7 and the G-3 half-sibs, consistency prevailed.

The results suggest that inherent differences occur among individual slash pines in susceptibility to stem attack by Dioryctria amatella. This conclusion is based mainly on the fact that significant differences due to clones or progenies were found in all plantations. However, further evidence is apparent in the degree of infestation of progenies of G-1, which are represented in all plantations. Although progenies of this tree varied considerably within plantations, the plantation averages were consistently high, as indicated in the following tabulation:

Average stem attack by D. amatella

Plantation	Progenies having G-1 as a parent	Progenies not having G-1 as a parent
	Percent	Percent
G-48-A	18.8	7.2
G-48-B	19.7	---
NS-112	20.0	8.9

Thus, G-1 seems to be relatively susceptible. Among other parents involved in plantation NS-112, G-7 also seems to be relatively susceptible, while G-3 is relatively resistant.

Note also that G-1 x G-196 and G-1 x G-202 were represented in both plantation G-48-A and G-48-B. In both plantations the latter cross had more stem attacks than the former.

SUMMARY AND CONCLUSIONS

Cone infestation by Dioryctria amatella and D. abietella were studied on 10 mature slash pines over a period of 3 years. Covariance analysis revealed that some trees experienced either consistently low or consistently high cone attack from year to year independent of the total mature cone crop per tree. This suggests that inherent differences in resistance to cone worm attack exist in slash pine.

Stem infestation of young trees by Dioryctria amatella was studied in a clonal plantation and two progeny tests. Large differences in the degree of infestation occurred among clones or progenies, suggesting some degree of genetic control over this trait also.

Results point to the possibility of selection and breeding for resistance to Dioryctria spp.

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Variation in Resistance of Slash Pine to Southern Fusiform Rust[1]

J. T. ARNOLD AND R. E. GODDARD[2]

Southern fusiform rust caused by Cronartium fusiforme (Hedgc. & Hunt) is widely recognized as the most serious disease of slash pine. The widespread incidence of this disease throughout the species range, and its reduction in timber production, leaves no doubt of the economic importance of fusiform rust.

Although most southern foresters can easily cite cases of plantations with 90% or more of the trees infected, natural selection for resistance to fusiform rust does not appear to be very strong. Some reasons for this condition are: (1) many diseased trees live long enough to pass on susceptible genes, (2) presence of alternate hosts is required and (3) weather conditions must be favorable for disease spread. These afford ample opportunity for highly susceptible trees to escape infection.

Thus, it appears that the most promising procedure for developing strains of slash pine with improved resistance to this disease is to artificially induce disease epidemics to locate resistant types.

This paper concerns early results of procedures used in the University of Florida Cooperative Forest Genetics Research Program to screen slash pine selections for resistance to fusiform rust.

In the Florida program, as in others, selections with observable disease were rejected. However, in a few cases small branch cankers were found in crowns of selected trees after they were established in seed orchards. But even if these trees are thrown out, there is little reason to suspect that the selected trees as a group have greater or less susceptibility than average dominant slash pines, i.e. they are probably representative of the general slash pine population in this respect.

PROCEDURES AND INOCULATION TECHNIQUES

In the spring of 1964 both seed and one-year-old progenies from 40 open-pollinated lines of slash pine selections were chosen for intensive testing. Seedlings of 90 additional lines were retained for limited tests.

For each of the 40 mother tree lines, 20 one-year-old seedlings were potted during January. In March, 30 seeds from each line were planted in 4-inch pots, six seeds per pot. (Germination within lines varied from 20 to 87 per cent, yielding from 6 to 26 cotyledon stage seedlings per line.)

Aeciospores were collected from slash pine cankers in the early spring and stored in a refrigerator. This material produced heavy infection when placed on new leaves of small oaks potted for this purpose. Within two to three weeks, numerous telial columns developed on plants dusted with aeciospores. The pathogen remained in the telial stage for an extended period. Extensive sporidial development was stimulated by keeping infected oak leaves on moist filter paper in Petri dishes at approximately 70°F for 24 hours. This procedure made sporidia production possible at any time desired.

A humidity chamber - a wooden frame covered with canvas - was constructed. A mist

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[1] This paper is based on a thesis submitted by the senior author to the Graduate School, University of Florida, for partial fulfilment of requirements for the degree, Master of Science in Forestry.

[2] J. T. Arnold is now Research Forester, West Virginia Pulp and Paper Company. R. E. Goddard is associate professor, School of Forestry, University of Florida.

system inside and an external sprinkler maintained high humidity and provided some cooling by evaporation.

In late April, approximately six weeks after germination, the newly germinated seedlings were placed in the humidity chamber during late afternoon. A section of an oak leaf having abundant sporidia was placed between cotyledons on the apical meristem of each seedling. The mist system was turned on for approximately one hour. The external sprinkler was started and maintained for the entire 48-hour inoculation period.

Second-year-potted seedlings of the same lines were inoculated using the same procedures except that it was necessary to divide the 800 seedlings into four blocks for inoculation in four consecutive periods (five trees of each line per block).

Supplementary trials of inoculation procedures on one-year-old potted seedlings were conducted. The techniques included wrapping moist cotton around infected oak leaves placed on succulent new growth, and inserting leaf sections in incisions made in new growth. Jewell (1960) has used these methods successfully.

Seedlings in the nursery were shaded with a light cotton cloth. Entire infected oak leaves were attached to new growth of each of 10 trees from 31 lines. Of these, five trees of each line were encased in polyethylene bags for two days and the other five were left open. On a number of other lines in the nursery, only the open treatment was attempted.

The nursery bed treatments were applied last and were not completed until May 20. Local inoculum was exhausted by that time, and infected leaves from the vicinity of Albany, Georgia, were used for this phase. The oak leaves were transported in a styrofoam cooler with a thin layer of ice on the bottom. Sporidial development under these cool, moist conditions was excellent.

A tally of infection from cotyledon stage inoculation was made in July and again in late October. The first tally was based primarily on needle symptoms but some galls were forming already. In the second tally, only seedlings with actual galls were classed as diseased.

Infection of seedlings one-year-old at inoculation time was recorded in November and rechecked the following April (disease development progresses more slowly in the older material).

RESULTS

Cotyledon stage inoculations

Seedlings inoculated during the cotyledon stage showed symptoms of infection in July; the different mother tree lines varied from 42.9 to 95.7 per cent infected. Chi-square analysis indicated highly significant heterogeniety of infection rates. Individual lots with infection rates of 50 per cent or less were significantly lower, and those with infection rates above 90 per cent were significantly higher, than the general population tested. Thus, three of the 40 lines of 7.5 percent had a significantly lower incidence of initial infection by fusiform rust (higher resistance) than other lines tested.

The second tally in October showed that some of the seedlings which had definite symtoms including needle lesions and red coloration in July had failed to develop a gall and were apparently healthy. This occurred in 13.7 per cent of initially infected seedlings and was noted in as high as 45.0 per cent of the infections in some mother tree lines. The correlation coefficient for July and October determinations was 0.823. There were significant differences among lines in what might be termed secondary resistance following initial needle infection. Ten per cent of the lines tested had significantly higher resistance of this type.

In July, mean infection rate was 71 per cent. Because of the secondary resistance, only 62 per cent of the seedlings developed galls; rates of galling ranged from 31.6 to 91.3 per cent.

For "all or none" traits such as this where measurement of character expression on an individual plant is not feasible, Robertson and Lerner (1949) and Dempster and Lerner (1950) have proposed these statistical methods for heritability calculations. The formula,

$$\text{heritability} = \frac{\text{genetic improvement}}{\text{phenotypic selection differential}}$$

may be expressed in statistical terms as:

$$\text{heritability} = \frac{\text{heterogeniety Chi square} - (N-1)}{r\,N_o}$$

where N is the number of families, r is the genetic relationship within families, and

$$N_o = \Sigma n - \frac{\Sigma(n^2)}{\Sigma n} - (N-1),$$

n being the total individuals per family. The application of this method to fusiform rust resistance was discussed previously by Arnold (1964) and Goddard and Arnold (1964). Heritabilities calculated were:

Resistance to initial infection--.199 ± .092

Resistance to disease development after infection--.253 ± .121

Combined resistance to gall formation--.237 ± .100

Table 1. Comparison of fusiform infection rates on seedlings of two ages and with various inoculation techniques.

Inoculation Method	No. of Plants	Per cent Infected
Cotton-wrap (year old)[5]	50[1]	16.0
Oak leaf insertions (year-old)[5]	50[1]	24.0
Humidity Chamber (year-old)[5]	800[2]	8.75
Humidity Chamber (cotyledon stage)[5]	719[2]	62.30
Nursery bed, polyethylene bag[6]	156[3]	15.40
Nursery bed, unbagged[6]	582[3]	27.30
Humidity Chamber[1]	100[1]	7.00
Nursery bed, polyethylene bag	151[4]	15.20
Nursery bed, unbagged	151[4]	27.80

[1] Seedlings of mixed origin.
[2] Seedlings of 40 mother tree lines.
[3] Seedlings of 133 mother tree lines.
[4] Seedlings of same mother tree lines.
[5] All inoculated in April with same inoculum.
[6] All inoculated in May with same inoculum.

Table 2. Infection rates of 22 progeny lines inoculated with fusiform rust at two ages.

	Cotyledon stage in humidity Chamber	Year-old in Nursery bed	Year-old in Humidity Chamber
240-55	43.7	20.0	15.0
270-55	71.4	40.0	00.0
283-55	61.1	00.0	10.0
284-55	81.8	40.0	10.0
289-55	81.8	00.0	10.0
78-56	57.1	80.0	15.0
80-56	42.9	00.0	15.0
106-56	50.0	00.0	00.0
108-56	85.7	00.0	05.0
110-56	55.6	00.0	00.0
116-56	83.3	20.0	10.0
216-56	60.0	33.3	25.0
235-56	70.8	60.0	20.0
269-56	36.4	20.0	20.0
339-56	41.7	40.0	05.0
345-56	90.0	20.0	10.0
18-57	83.3	40.0	10.0
21-57	87.0	60.0	15.0
51-57	64.7	100.0	05.0
65-57	52.6	80.0	05.0
67-57	57.9	20.0	00.0
93-58	61.1	20.0	05.0
Mean	64.9	31.9	9.5

Inoculation of year-old seedlings.

Inoculations of year-old seedlings were not nearly as successful as inoculations during cotyledon stage. Potted seedlings of the same parentage and inoculated with the same inoculum in the canvas chamber in the same manner as the newly germinated ones had an average infection rate of only 8.75 per cent. Because of the spotty infection rates, no differences among lines could be detected.

Both the cotton wrap and oak leaf insertion techniques gave a somewhat higher infection than the humidity chamber. However, resistance to penetration is eliminated by the incision and for that reason the insertion method is inferior.

Nursery bed inoculation is more promising for testing year-old seedlings. The overall infection rate for seedlings not bagged with polyethylene was 27.3 per cent. Nursery bed seedlings bagged had an infection rate of 15.4 per cent. Several comparisons of techniques used on progenies of the same lines and inoculations made during the same period are possible. Although these data do not lend themselves to statistical analysis, comparisons of interest are presented in Table 1.

A detailed listing of infection rates in progenies of 22 lines which were inoculated at two ages and in both the humidity chamber and nursery bed are presented in Table 2. Insufficient trees per line were inoculated in nursery beds for a good definition of line differences although an indication of trends was expected. Correlations between infection rates within lines under these various conditions were extremely low and nonsignificant.

DISCUSSION

It is very obvious that infection rates were far higher when inoculations were made on cotyledon stage seedlings than when made on year-old seedlings. Jewell (1960) reported infection rates on one-year-old seedlings higher than obtained here, perhaps because he worked with smaller numbers and was more experienced with inoculation techniques. Of the methods tried on older seedlings, the most successful was inoculation of seedlings retained in nursery beds even without means of maintaining high humidity.

Work with cotyledon stage seedlings indicated highly significant differences in rates among progenies of the various selections in both initial infection and actual gall formation. However, a continuous variation of the quantitative type was suggested by these data rather than simple major gene differences as may explain species differences (Jewell, 1964).

There appeared to be a reduction in susceptibility of older seedlings and a lack of correlation between relative infection of lines inoculated at both ages. Possibly improved techniques would increase the infection of older seedlings. Year-old seedlings potted a few months prior to inoculation attempts had a less vigorous growth and, consequently, less susceptible tissue than either cotyledon stage seedlings or nursery bed seedlings one year old. Humidity and temperature conditions during the nursery bed inoculations were not ideal for the pathogen.

On the other hand, it is entirely possible that resistance increases with seedling age and that the mechanism of resistance changes. With proper attention to fungicide application, fusiform rust can be almost completely eliminated from a southern pine nursery. However, protection of plantations is not practical. If the mechanism of resistance is different with older seedlings, selection of a strain resistant during the cotyledon stage could be of little value in combating plantation infection.

Future plans in the Florida program include development of methods and testing of year-old progenies. In the spring of 1965 additional nursery bed inoculations were applied. To obtain conditions more favorable for the pathogen, a portable humidity chamber was prepared. It consists of a light metal frame and mist system covered with canvas and an external sprinkler hose to keep the canvas wet. Approximately 25 seedlings per line of 50 mother tree lines were inoculated. In addition, seedlings of 50 crosses between select trees were inoculated to gain more insight into the inheritance of resistance. Definitive data on fusiform resistance should be obtained. If the 1965 inoculations are successful, these tests will be expanded in the future to determine relative susceptibility or resistance of progenies of all selected slash pines used in the program. This would provide a basis for development of a clonal orchard for resistant types and for a breeding program to obtain greater resistance.

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The Efficiency of Photosynthesis and Respiration in Loblolly Pines: Variation [1]

C. FRANK ROBERTSON AND M. REINES [2]

INTRODUCTION

Four questions govern our investigations concerning the variation and inheritance of photosynthetic efficiency and its association with vigor: (1) Is there variation in photosynthetic efficiency? (2) Is vigor an attendant quality? (3) Does photosynthetic efficiency, as measured, reflect a peculiar genic inheritance? (4) Can this measure of photosynthetic efficiency be used as a method of selecting superior vigorous strains?

During the past year several trials have been carried out to study the variation in rates of photosynthesis and respiration in pines. One of these trials involving eight one-parent progeny groups of loblolly pine seedlings will be discussed in this paper.

Carbon dioxide absorption and emission were measured to determine rates of apparent photosynthesis and respiration, respectively. Measurements of photosynthesis are complicated by the fact that respiration occurs simultaneously. Therefore, photosynthesis as measured in this study actually represents apparent photosynthesis. Respiration was measured because it is an indicator of metabolic activity and may prove to be a better way of expressing efficiency.

METHODS

The loblolly pine seedlings sampled in this trial were selected from eight one-parent progeny groups. Each progeny group was composed of ten one-year-old seedlings. These seedlings were removed from the greenhouse and placed in a controlled environmental room approximately three weeks prior to sampling.

The uptake of CO_2 during photosynthesis and the release of CO_2 during respiration for each seedling were measured by a model 15A Beckman/Liston Infra-Red Analyzer. At the beginning of each sampling the system was flushed with fresh air after which the system was closed. The absorption curve for photosynthesis and the emission curve for respiration were produced on a recorder chart for a 5-minute time interval with constant recycling of the used air through the analyzer. As the purpose of the study was to make comparisons of gas exchange rates among progeny groups and not to determine absolute amounts of CO_2 absorption and emission, the numerical recorder readings were used directly in the statistical analysis.

An inverted battery jar with inlet and outlet for circulating air was used as the plant chamber. The chamber, resting upon plates of aluminum, was sealed around the base of the seedling to be measured. Each seedling enclosed in the chamber was placed under a light bank in the controlled environment room for the measurement of photosynthetic rates. The seedling chamber was draped with a black plastic cover before recording the rates of respiration.

Environmental conditions inside the control room were approximately constant at all times and were conducive to sustaining a healthy state of all seedlings. Control room conditions were maintained at 40% of full sunlight, relative humidity at 80%, temperature at 85°-90° F, and a 12 hour photoperiod. During the dark period temperatures were 15°-20°F cooler. Seedlings were watered daily and fertilized weekly with Hyponex.

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[1] This work was done under Regional Project S-23 Hatch 359 in cooperation with the School of Forestry, University of Georgia.

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The size of all seedlings were measured after sampling. The various measurements of seedling size included total seedling dry weight, needle dry weight, and stem dry weight.

Seedlings were placed in a randomized complete block experimental design inside the control room. An analysis of variance and an analysis of covariance were used to test for significant differences in rates of photosynthesis and respiration among progeny groups. The analysis of covariance adjusted the mean rates of photosynthesis and respiration for differences in total seedling dry weights, needle dry weights, and stem dry weights. The analysis of variance was used to determine if significant differences existed among progeny groups for unadjusted mean rates of photosynthesis and respiration, for rates of photosynthesis and respiration on a per unit dry weight basis, and for dry weights of the loblolly pine seedlings.

RESULTS AND DISCUSSION

In analyzing for performance, mean rates of photosynthesis and respiration among the eight progeny groups when adjusted for seedling dry weight and needle dry weight by the analysis of covariance were not significantly different. The anlysis of variance for unadjusted mean rates of photosynthesis did not reveal any significant differences, but the unadjusted mean rates of respiration among the progeny groups were significantly different at the 5 percent level. In analyzing for variation in size, significant differences occurred among the progeny groups for seedling dry weights, needle dry weights, and stem dry weights. The differences in respiration among progeny groups may, therefore, be due to the larger size of seedlings in some of the progeny groups. However, the significant differences in seedling sizes among progeny groups had no affect on the rates of photosynthesis.

An analysis of variance of photosynthesis per unit seedling dry weights showed no signigicant differences, but photosynthesis per unit needle dry weight among the progeny groups was significantly different at the 1 percent level. These results tend to show that the rates of photosynthesis may not depend on the mass of green plant tissue alone, but that these seedlings may differ in their genetic capacity for rates of photosynthesis. However, volume measurements for seedling size, which were not available for this trial, may have been more preferable as a measure of functional green tissue. The significant difference of photosynthesis per unit needle dry weight may be due to an unrealistic quantification of photosynthesis. The process of photosynthesis occurs in hydrated green tissue which would be more accurately measured by volume or surface area.

The analysis of variance for respiration per unit seedling weight, per unit needle weight, and per unit stem weight revealed no significant differences among progeny groups. These findings furnish further evidence that significant differences among progeny groups for unadjusted mean rates of respiration were due to seedling size.

In general the results as presented for this trial agree with the results of other trials in this study using loblolly pine seedlings. In another trial, rates of photosynthesis and respiration of detached branches from slash pine clones were measured with similar results. However, the mean rates of photosynthesis and respiration for each of these clones will be compared with various morphological traits.

The use of covariance analysis methods may prove to be an important statistical tool in analyzing real differences in rates of photosynthesis and respiration among pine seedlings. In this trial photosynthetic and respiratory rates were adjusted for differences in seedling sizes, and no differences in performance were observed. Better parameters of functional tissue may be needed to relate gas exchange rates to the efficiency of these processes. The number of stomates per unit needle area or the concentration of chlorophyll in functional green tissue may provide such useful parameters.

Genetic Variation in Ability to Withstand Transplanting Shock

WALTER F. BEINEKE [1] AND THOMAS O. PERRY [2]

INTRODUCTION

Is there genetic variation in ability to withstand transplanting shock? If there is, this would be of extreme importance in tree improvement programs. A fast growth rate strain that survives poorly is useless. There have been many articles that have considered survival in connection with racial variation studies. However, most of the survival assessments were made at the end of the growing season and there is no record of attempts to follow survival of individual tree progenies. Langdon in 1958 reports on the early survival of different seed sources of slash pine in South Florida and Minckler reported on genetic differences in survival of one parent progeny tests with loblolly pine in the Journal of Forestry in 1942. However, his survival estimates were determined at the end of the fourth growing season and involved only one planting date on one site.

A study of genetic differences in ability to withstand transplanting shock was made with slash pine at the University of Florida in 1956 by the junior author. Differences in survival amongst half-sib progenies ranged between 90% and 15%. However, because of variability between blocks the results would be explained by chance alone in one out of ten similar experiments. These results justified a more exhaustive study of the possible significance of genetic differences in transplantability for tree improvement. For this purpose we collected seed from thirty open-pollinated mother trees located in 3 stands in the Piedmont of North Carolina. The seed from each mother tree was kept separate and planted in 5 replicated blocks in the nursery in accordance with the procedure recommended by Wakely et al in 1962. Wakely's nursery planting design is arranged so that the nursery effects are preserved in the outplanting design and hence can be removed from the total sums of squares in experimental results. The field design consisted of 5 randomized blocks with each of the 30 mother trees represented by one row of 20 seedlings in each block, thus a total of 100 seedlings were represented for each mother tree. This design was replicated in one location on 5 planting dates six weeks apart from December to June. A separate planting was made in the N. C. sandhills to test survival ability under stress conditions.

The planting site near Raleigh, North Carolina was a good bottom-land site with abundant moisture; the soil of the planting area was primarily a clay--loam. Seedlings were outplanted in this area at 1 ft. x 1 ft. spacing. A total of 15,000 seedlings were set out on the 5 planting dates in the Raleigh nursery. From the bundle of seedlings listed from each block on each planting date 2 seedlings were chosen at random for root-shoot ratio and height measurements and 2 others were chosen for root regeneration potential studies. Twenty remaining seedlings from the bundle were selected for field planting. Planting was so arranged that 2 or 3 men crew planted all seedlings in one block. Thus the differences due to planting technique were the same within each replication. The time required to plant 3000 seedlings on each planting date varied from 3 to 7 hours except on the first planting date which required parts of three days.

RESULTS

Except for the first planting date all observations on survival were made within 30 to 60 days after the planting. About six weeks are required before dead and dying seedlings show distinct moribund symptoms. A second survival observation was made at the end of the growing season. Significant differences were generally the same for both observation times, but greater variation occurred within blocks in the winter measure of survival due to the severe weed competition that had developed during the summer season. This paper reports on the observations of mortality to 60 days after outplanting. Fig. 1 illustrates the variation in survival for 4 of the progenies on the various planting dates. For simplicity only four progenies are included in figure 1, although thirty progenies were included in the test.

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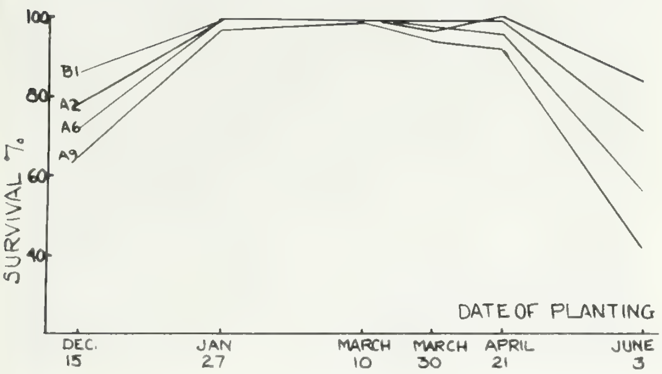

Table 1 -- % Survival of all progenies.

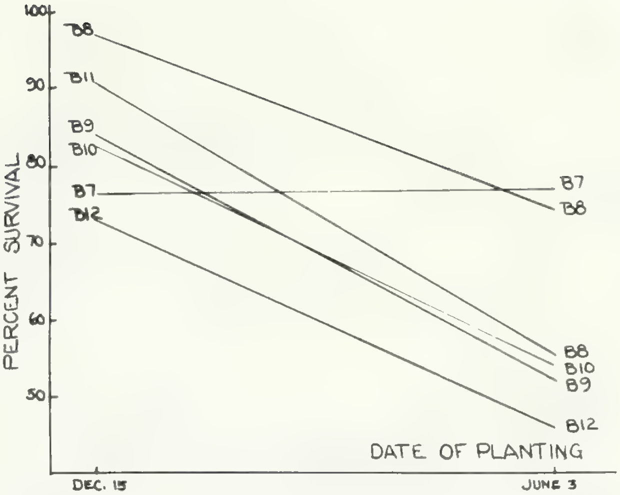

Figure 2 -- Percent survival of selected progenies planted December 15 and June 3. Note the change in rank of some progenies on the two planting dates.

Table 1 gives the percent survival for all progenies on all planting dates.

On planting date one, two and five, the differences in survival were too great to be explained by chance along. Hence the conclusion that there are genetic differences in ability to withstand transplanting shock is most reasonable. Note that progeny A-9 gave an inferior survival performance on all planting dates recorded. The probability that the low survival rank of progeny A-9 on all planting dates can be explained by chance or sampling error is infinitesimally small. Correspondingly, the consistently superior survival rank of other progenies is equally impressive.

Figure 2 illustrates the shift in position of rank in percentage of survival for a number of progenies for the first and fifth planting dates. There were other shifts in survival percent with time. Evidently factors which favored survival for one genotype at one time of the year were disadvantageous at another in some instances. The spring of 1964 was one that was highly favorable to survival of transplanted material, and, for most planting dates, the survival of all progenies was between 94 and 96%. However, for the December and June planting dates survival ranged between 40 and 77% for individual progenies. In spite of the favorable season we found distinct differences in ability to withstand transplanting shock. A more adverse transplanting season would have resulted in significant differences in survival on all planting dates. The second phase of these investigations was centered on attempting to develop an explanation for the observed genetic differences in ability to survive transplanting.

Table 1.

SURVIVAL BY PLANTING DATES

Planting Date	A2	A6	A9	A10	A12	A13	B1	B2	B3	B4
PD1	77	72	65	91	66	62	86	77	70	92
PD2	100	100	97	99	100	100	100	100	100	100
PD3	100	100	99	100	98	100	100	100	98	100
SH	99	99	94	99	98	95	97	98	97	100
PD4	96	99	92	95	100	97	100	99	98	99
PD5	56	71	41	48	53	61	84	59	52	72
	528	541	488	532	515	515	567	533	515	563
Av.	88.0	90.17	81.33	88.67	85.83	85.83	94.5	88.83	85.83	93.83
	B5	B6	B7	B8	B9	B10	B11	B12	C1	C2
PD1	80	68	76	97	84	83	91	73	88	83
PD2	100	100	100	100	100	100	100	96	100	100
PD3	100	100	98	100	100	100	100	98	99	100
SH	97	99	96	99	99	97	100	95	98	99
PD4	97	98	97	99	97	98	98	96	98	96
PD5	49	39	77	74	52	54	55	46	50	54
	523	504	544	569	532	532	544	504	533	532
Av.	87.17	84.0	90.67	94.83	88.67	88.67	90.67	84.0	88.83	88.67
	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
PD1	66	77	85	81	71	79	77	78	61	75
PD2	100	100	99	98	100	99	100	100	100	100
PD3	100	100	100	99	100	100	100	100	100	100
SH	97	99	97	99	99	98	97	98	98	100
PD4	98	99	100	100	96	93	100	99	98	96
PD5	48	81	43	40	54	45	50	61	77	71
	509	556	524	517	520	514	524	536	534	542
Av.	84.83	92.67	87.33	86.17	86.67	85.67	87.33	89.33	89.0	90.33

PD planting date

	% Survival Range	Average		Range	Average
PD1 = Dec. 15	61-97	77.7	SH(sandhills)		
PD2 = Jan. 27	96-100	99.6	March 30	94-100	97.8
PD3 = March 10	98-100	99.6	PD4 = April 21	92-100	97.6
			PD5 = June 3	40-77	57.2

We found no correlation between the percentage of survival and date of flushing. We did find a correlation between root regeneration potential and ability to survive. Root regeneration potential was measured after the method of Stone (1955) at the University of California: The roots on several seedlings were removed at the time of transplanting and the number of new roots at the end of the 30 day period was recorded. There was a fair correlation between the number of new roots formed in

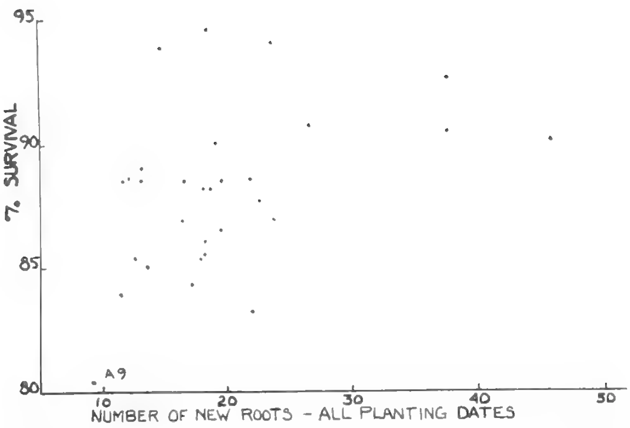

Figure 3 -- Note the fair correlation between percent survival and the number of new roots formed by the different progenies.

Figure 4 -- Representative root system of progeny A 9. Note the contrast in the fleshy but sparse root systems of progeny A 9 with the fibrous root system of progeny C

30 days and the percent survival. This is illustrated in Fig. 3

An attempt was made to correlate the percentage of survival with the root-shoot ratio; that is, the ratio of the dry weight of the roots to the dry weight of the shoot. A slight correlation was found. This does not mean that there is no correlation between survival and the balance between root and shoot. The measurement of root-shoot ratio by the methods we used leaves much to be desired. Heavy, fleshy, tap roots with few laterals and little absorptive ability may weigh as much or more than fibrous root system as illustrated with progeny A-9, a poor survivor, and progeny C-12, a good survivor, figures 4 and 5. Progeny C had average root-shoot ratio, but the root system was generally more fibrous than others investigated. In the process of lifting the plants in the nursery, all were pruned back to 8 inches and this, too, may have lessened the correlation between root-shoot ratio and survival. Root pruning at lifting time may also explain the negative correlation between height of the plants and percent survival (See figure 6). Percent Survival = 112.3-1.259 height, r = 0.59. It should be noted again that root-shoot ratio is correlated with the size of the plant per se, and undercutting nursery beds before lifting in the nursery has the effect of creating a severe imbalance of root-shoot ratio for large seedlings.

The results of the studies on genetic differences in transpiration rate are most interesting. Ten seedlings from each of the 30 mother trees were placed in pots. After the plants were well established, the pots were wrapped with polyethylene, so that any loss of water was through the plants themselves. The plants were weighed in 4-day intervals and the amount of loss per day was calculated. The results were recorded for 20 days, since, as indicated in figure 7, the transpiration rate becomes low under the conditions of severe stress that prevail after 20 days without water. The plants were ranked according to their transpiration loss in grams per day and these were correlated with the ability to survive transplanting shock. It is interesting to note that when we plot percent survival versus grams of transpiration per day for a plant that we have a negative correlation without too good a fit

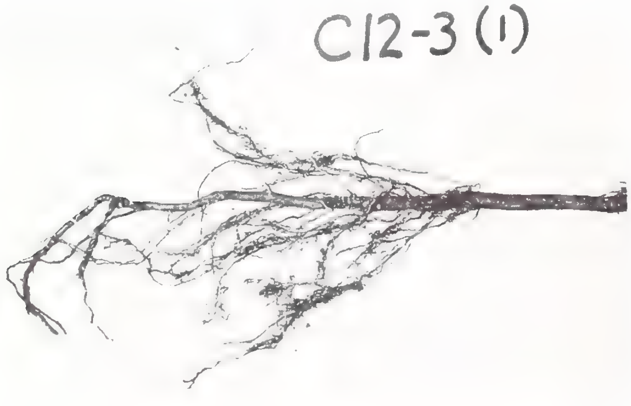

Figure 5 -- Representative root system of progeny C 12. Compare with root system of progeny A 9 (figure 4).

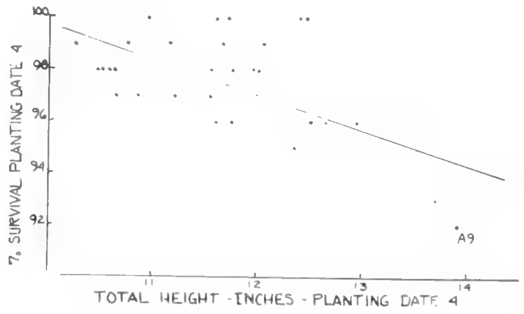

Figure 6 -- Negative correlation between total plant height and percent survival—is possibly the result of root pruning at lifting time.

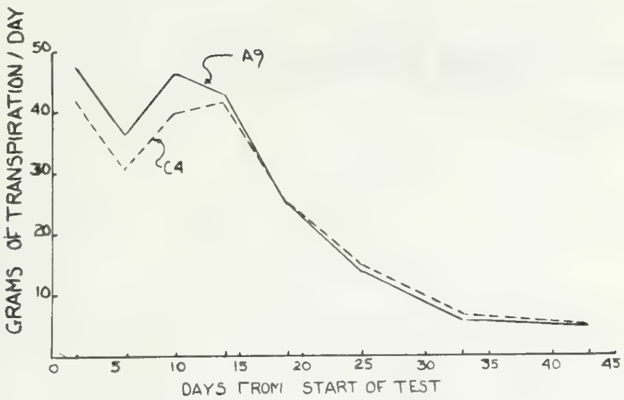

Figure 7 -- Variation in rate of transpiration per day with time since last watering (moisture stress).

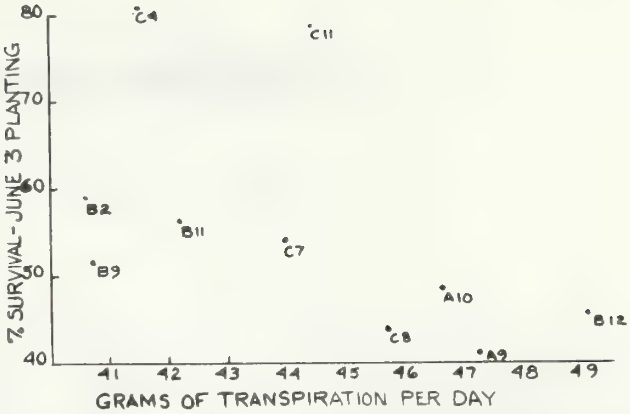

Figure 8 -- Note the slight negative correlation between grams of transpiration per plant per day and percent survival.

to the data as per figure 8. However, when this data is converted to transpiration per gram needle weight, we see that there is positive correlation for transpiration per needle weight and percent survival (See Figure 9). Perhaps these results can be explained in terms that transpiration is dependent upon the development of an effective root system. In those plants that are able to develop effective root system we are able to have good survival percentages. Dr. Maki working in the Southern Forest Experiment Station found that the transpiration in plants bore a direct linear relationship to the size of the root system of the plants.

SUMMARY

The results of this series of investigations show clearly that there are genetic differences among progenies in ability to withstand the shock of transplanting. Progeny A-9 of the thirty plants investigated is an example of a plant that characteristically has low survival percentages on all planting dates studied, while progeny B-8 gave a superior planting survival on all dates studied. Attempts to find physiological bases for some of these observed differences in ability to withstand transplanting shock showed that there are genetic differences in plant size, plant height and root-shoot ratio, root habit and root regeneration potential. All of these characteristics are correlated with ability to withstand transplanting shock. There are genetic differences in transpiration rate on a per plant basis and on a per gram of needle weight basis. The general evidence indicates that the factors that cause some progenies to survive well at one time of the year are not correlated with the good survival at other times of the year. One surprising observation is the positive correlation between transpiration per gram of needle weight and percent survival, while there is a negative correlation between the total transpiration per plant and percent survival.

LITERATURE CITED

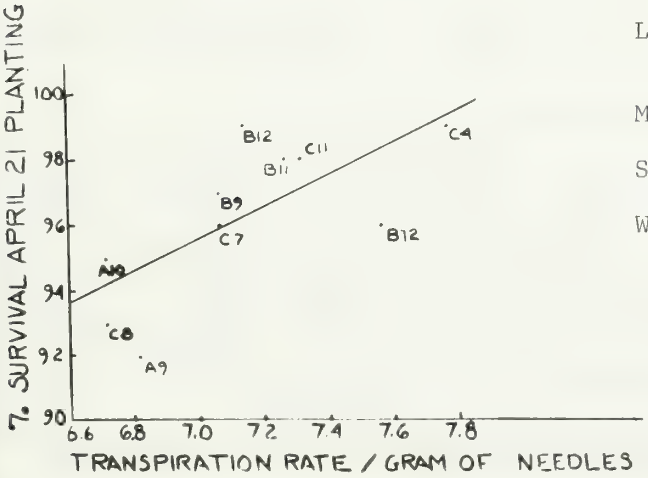

Figure 9 -- Note the strong positive correlation between grams transpired per cm of leaf surface and percent survival.

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Hybridizing Pines with Diluted Pollen [1]

R. Z. CALLAHAM [2]

When pollen is limited or expensive to collect, tree breeders should use diluted pollen so long as seed production is not affected. Duffield and I looked into the feasibility of using pollen dilution at the Institute of Forest Genetics at Placerville a number of years ago (Callaham and Duffield, 1961). Our first results were promising. Since then diluted pollens are used occasionally in research breeding at Placerville. The California Region of the U. S. Forest Service uses them in mass-production of pine hybrids. Diluted pollens might be used advantageously in breeding southern pines in seed orchards. This report gives results of the most recent experience at Placerville with diluted pollens.

Our first studies at Placerville showed that viable pollen can be diluted with dead pine pollen without ill effects. Dilutions to 50 percent live pollen did not affect cone set, total seeds per cone, or the proportion of sound seeds. Unresolved were questions of how far can we dilute and what is the effect of using pollen of different species as the diluent. A comprehensive series of interspecific hybridizations was made in 1962 to learn more about possibilities of diluting pine pollen.

PROCEDURE

We were primarily interested in three hybrids having commercial possibilities. These were Pinus attenuata x P. radiata, P. monticola x P. strobus, and the backcross hybrid P. jeffreyi x (P. jeffreyi x P. coulteri). Trees for breeding were selected in natural stands on the Eldorado National Forest near Placerville and in the Institute's arboretum. Mixtures of pollen from 2 or 3 trees of each pollen parent species were prepared and diluted with heat-killed pollen. Pollen lots were used a few days later to pollinate receptive conelets on bagged branches. Each lot was used to pollinate three bags on each of three trees of the seed parent species.

Ten pollen lots were used on each tree. Seven lots contained increasing amounts, 10, 20, 30, 40, 50, 70, and 100 percent, of live pollen of the desired pollen parent. The diluent in this case was dead pollen of the seed parent. A control pollen lot was live pollen of the seed parent species. To determine the influence of the species used as the diluent, pollen of two species known to be genetically incompatible with the seed parent were used separately as 50 percent diluents.

For each cross the cones were harvested in 1963, and the seeds were extracted, winnowed, and counted. Percent of all seeds that were sound was calculated.

RESULTS AND DISCUSSION

Pollen dilution did not affect cone set. About the same proportion of pollinated conelets developed into cones regardless of pollen dilution. This confirms our earlier finding.

However, total seeds per cone was significantly reduced at the greatest dilutions. This contradicts our earlier conclusion which was based on fragmentary data. Analysis of variance showed a significant effect of dilution on number of seeds per cone when data were combined for all nine seed trees. Dilutions having only 10 and 20 percent viable pollen combined significantly fewer, 60 and 59, seeds per cone, but 30, 40, 50, 70 and 100 percent viable pollen resulted in 72, 81, 88, 82, and 81 seeds per cone. These results suggest that dilution

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1/ Research reported here was done while the author was Leader of the Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, Placerville, California.

2/ Chief, Branch of Forest Genetics Research Forest Service, U. S. Department of Agriculture Washington, D. C.

to less than 30 percent live pollen may reduce total seed yield.

Pollen dilution had a significant effect on the proportion of seed that were sound. The sound seed percent varied with the hybrid being produced as follows:

Hybrid	Viable pollen - percent			
	100	50	20	10
attenuata x radiata	72	68	62	64
monticola x strobus	33	43	25	15
jeffreyi x (j. x cl.)	54	52	47	36

The two species involved in the hybrid P. attenuata x radiata are highly compatible, and even 10 percent viable pollen gave high proportions of sound seeds. Pinus monticola and strobus are less compatible, and dilutions containing only 10 percent viable pollen gave few sound seeds. Results for the three P. monticola seed trees were variable, so the reduction was not quite significant at the 5 percent confidence level. A highly significant reduction in proportion of sound seed occurred when dilutions to 10 percent were used to produce P. jeffreyi x (jeffreyi x coulteri). The high degree of genetic incompatibility between the species involved in this hybrid may have influenced the result.

The species of pollen used as diluent at the 50 percent level did not significantly alter total seed yield or proportion of seed that were sound. The average seed yields were as follows:

Seed parent	Diluent species		
	at.	jef.	mon.
attenuata	59	75	68
jeffreyi	148	160	188
monticola	27	43	45

These results suggest that dead pollen of any pine species can be used as a diluent with equal results.

These results show that it is safe to use pollen dilutions having only 30 percent of live pollen. Strictly speaking, the results pertain to interspecific hybridizations, but I believe they can be extrapolated to hybridization within species where highly compatible parents are being crossed. In your southern pine seed orchards excellent sets of sound seeds probably can be obtained with only 10 percent viable pollen in the pollination syringe. You might be able to reduce your "stud fee" by 70 percent or more by diluting valuable pollens.

SUMMARY

Interspecific pine hybridizations at Placerville show the extent to which viable pine pollen can be diluted with dead pollen. Valuable lots of pine pollen can be diluted generally to 30 percent live pollen and in certain cases to 10 percent with no effect on the proportion of seeds that are sound. Dilutions having only 10 or 20 percent viable pollen did produce significantly fewer total seeds per cone. Varying the species of pollen used as diluent did not affect seed production. In breeding southern pines pollen probably can be safely diluted with dead pollen to only 30 percent live pollen without effect on seed production.

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Progeny Tests of Slash Pine (Pinus elliottii Engelm.) in Queensland, Australia

D. G. NIKLES [1]

INTRODUCTION

Slash pine (Pinus elliottii Engelm.) was first planted in Queensland some 40 years ago, the original seed source being northern Florida. Stocks from the first introductions grew rapidly, and younger plantations descended from the original material through mass-selected local parents remain free from serious diseases and pests and are unsurpassed by other provenances introduced at a later date. Because of its good performance, slash pine will surely play a major role as an exotic species in Queensland, probably along with Pinus caribaea Mor. from several sources being tested.

The progeny tests planted prior to 1948, mainly from wind-pollinations, were reported by McWilliam and Florence (1955). These and more recent tests were reviewed by Haley (1957) and Nikles (1962) and are referred to in some issues of the Annual Report of the Conservator, Department of Forestry.

The objectives of the progeny tests described here are:

1. to determine the accuracy of mass-selection as a means of identifying phenotypes with good breeding characteristics;

2. to measure the gains from both open and controlled pollination of mass-selected parents;

3. to identify the most valuable parents for propagation in clonal seed orchards and for future breeding work.

The present paper summarizes assessments made in 1962 and 1963 and certain remeasurements made in 1965 of well replicated and controlled progeny tests established in the period 1952 to 1957. In addition, some older tests were examined to add to the information available on several parents being evaluated. The report given here is preliminary in nature since the data have not been exhaustively analyzed; a full study of the 1952-58 series of progeny tests is expected to be completed in approximately two years.

TEST MATERIALS AND PROCEDURES

The parent trees used in the tests were chosen from plantations 10 to 16 years old and established at a 7' x 7' or 8' x 8' spacing. Forty trees were selected from approximately 2000 acres of plantations for superiority in a combination of bole straightness, crown form, and vigor. The present appearance of two of the trees selected is illustrated in Figure 1. Open-pollinated cones were collected from all selected trees, and as many crosses as possible and numerous selfings were made among them over a period of several years. This gave unequal numbers of families per parent and for the full-sibs there was no regular mating design. The seeds available each year from each type of pollination were used to establish a test; hence wind-pollinated, selfed and full-sib progeny tests were separately planted each year. In the 1952-57 plantations 59 full-sib, 42 wind-pollinated, and 20 selfed families were available in all.

Seed for the control stocks (checks) was the same as that used commercially and in the local reforestation program. For these purposes cones are collected in plantations of the Department of Forestry from the 160 most vigorous, well-formed trees per acre. Such trees are selected at approximately ten years of age, are then pruned, and will finally yield the crop of trees harvested at the end of the rotation.

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Figure 1 -- Plus trees G20 (left) and G40 (right), now 23 and 32 years old, respectively, which were selected at 10 and 12 years of age for superiority in a combination of bole straightness, vigor and crown characteristics. Progeny of these trees are shown in other figures.

Table 1. Age and composition of principal[1] progeny tests studied.

Year when planted	Age when assessed	Type of Pollination Involved Control-cross #parents	#families	#sections	Open #families	Self #families
1952	10	3	2			
1953	10	4				
1954	8	8	[illegible]		4	
1955	7	11	[illegible]		26[2/,3/]	[illegible]
1956	6, 9	10	1	[illegible]	6[6/]	[illegible]
1957	6, 8	9	[illegible]			

[1] Other tests planted 1946-1949 inclusive examined also to supplement data from principal tests, involved additional 11 control-cross and 20 self-pollinated families

[illegible] No checks included in these t[illegible]

[illegible] Less than four replications per family in these tests

[illegible] Vacant cells indicate no t[illegible]

[illegible] This test assessed at nine years

6/ This test not reassessed at nine years.

Check and pedigreed seedlings were handled in the same way in the nursery. In the field, planting locations of average site quality were chosen, a separate progeny test experiment being planted each year in the area cleared for routine departmental planting. Square multi-row plots of both check and pedigreed progeny were planted at 10' x 10' spacing, with up to 64 trees per plot, replicated up to four times. The blocks of randomized complete-block designs were restricted to 1.5 acres in the full-sib progeny tests to minimize heterogeneity of site within blocks. Thus, no more than eight families plus checks were included in any section of the experiments established each year; in any one year, from one to four such sections, each a randomized, complete-block experiment, were planted, accommodating all the families available. The progeny test areas received standard fertilizer and tending treatments, the same as did the routine plantations. Open-pollinated families were treated similarly to the controlled crosses, except that spacing was 8' x 8' and the block size sometimes reached two acres. The self-pollinated progenies were established in separate blocks adjacent to the other material at 10' x 10' spacing in multi-row plots; a few had enough seedlings to allow replication within years and several selfs were replicated in time. Relevant details of the experimental material are summarized in Table 1.

Figure 2 -- Portion of a nine-year-old progeny test plantation. On the right is check material in which most trees scored 6 or 7 points for straightness, only 26 per acre scoring 8 or more points out of a possible 10; average total volume per acre inside bark was 1075 cu. ft. The plot on left contains full-sib progeny of mass-selected parents; in it 135 trees per acre scored 8 points or more for straightness; volume per acre in this plot, adjacent to the check, was 1204 cu. ft. The average gain in volume of the 21 families in the nine-year experiment was 243 cu. ft. per acre.

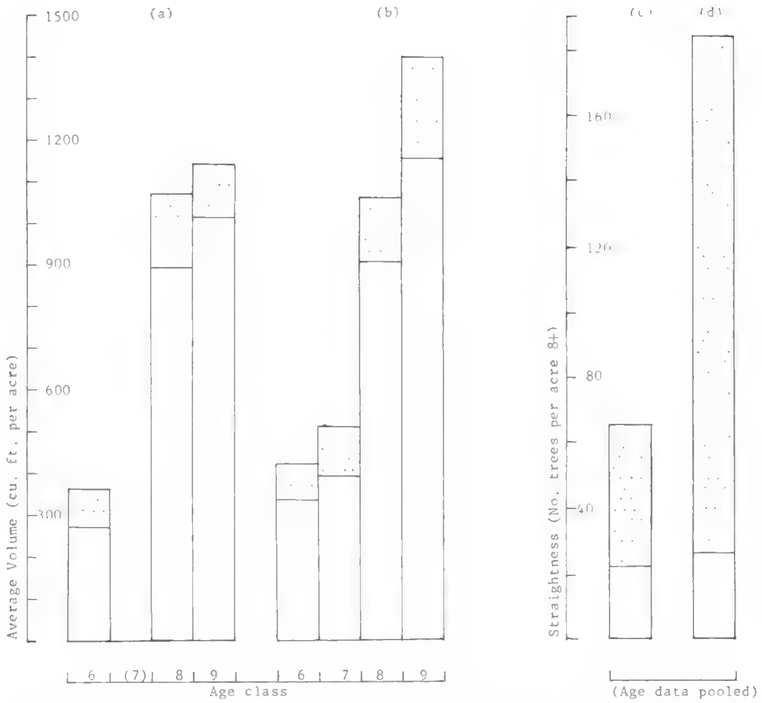

Figure 3. Histograms (a) and (b) show by type and age of progeny test the average volume per acre of checks (basal rectangles), the gains realized (stippled), and the average volume per acre of progenies of mass-selected parents (entire diagrams) after (a) open and (b) controlled pollination. Refer to Table I for details of the individual progeny tests.

In histograms (c) and (d) straightness data are pooled and averaged across age classes, within type of progeny: (c) open, (d) controlled pollination. Again, bases of rectangles represent checks, stippled areas the gains, and entire diagrams the average absolute values for the progenies.

Prior to the assessments of the progeny in 1962 and 1963 all trees were pruned to the height of approximately 8' to facilitate measurement and scoring. The following measurements and assessments were made on the interior 36 trees of each plot:

1. The diameter at breast height
2. Total tree height
3. Bole straightness.

Straightness was scored on a scale from 10 (no visible defect) to 6 (serious defect, affecting sawn recovery). The assessors (the present author and an assistant checked themselves occasionally by reassessing several trees at the beginning of and during the day. Examples of the appearance of trees with various ratings for straightness may be seen in Figure 2. Full-sib progenies average approximately 40 feet in height at 10 years of age.

Bole straightness of selfed progeny was scored in the same way but height and diameter measurements were not made, vigor being scored subjectively in relation to adjacent outcrossed progeny on a scale from 1 (equal to outcrosses) to 4 (virtual failure).

RESULTS

The numbers of trees scoring 8 or better for straightness were enumerated for each plot and converted to a per acre basis; the plot mean diameter breast height and mean total height values were used to obtain the volume inside bark of the mean tree in each plot. It was then possible to calculate volume per acre for both wind-pollinated and full-sib progeny. Statistical analyses of the significance of differences between individual crosses and checks were made.

The data were first examined for superiority of selected tree progeny over checks, which were progeny of the best 160 trees per acre in the older plantations. These data are summarized in Figure 3.[1] In calculating the gains for each experiment, account had to be taken of the fact that the 1955-57 experiments each comprised from two to four sections with relatively large numbers of families per experiment. These numbers of families differed from those in the 1952-54 experiments, each of which comprized a single section. However, sections were reasonably equal in numbers of families, so it was decided to derive mean straightness and volume gains for each. The mean gains for the sections were then used to derive the mean for each experiment; from these data were computed means for each age class, which are presented in Figure 3. It must be

Table 2. General combining ability for straightness and volume of several parents tested in one or more years.

Year of test	Parent tree #	# of 1/ families	General combining ability 2/ Straightness in trees/ac. 8+	Volume per ac. cu. ft. at age 6	7	8	9
1949	16	4	215	3/			
1954	15	4	215			903	
1955	16	2	105		589		
	15	6	193		572		
	14	6	60		473		
	6	3	45		600		
	7	4	64		473		
	8	3	143		533		
	19	3	77		461		
	26	5	112		389		
1956	16	5	193	383			1367
	15	7	146	413			1423
	14	5	69	456			1479
	9	4	181	375			1249
	12	3	64	400			1419
	13	4	150	374			1428
	20	3	400	376			1247
	24	6	146	447			1505
1957	15	3	215	412		1075	
	5	3	300	410		989	

1/ Parent may have been male or female. Each parent not necessarily mated to same testers.
2/ By way of comparison, checks averaged 26 trees per acre 8+ for straightness, volume production of checks at various ages are given in Figure 3.
3/ Vacant cells indicate data not taken.

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[1] The 1952 and 1953 full-sib and 1955 open-pollinated tests did not include check plots, so no estimation of gain in volume was attempted. However, gains in straightness were estimated on the basis of the over-all means of checks.

Table 3. General combining ability[1] and designation[2] for straightness, and score[3] for volume production of parents involved in three types of tests.

Tree No.	General combining ability, designation, and score by test								
	Selfed progeny			Full-sib progeny			Open pollinated progeny		
	Straightness		Volume	Straightness		Volume	Straightness		Volume
	mean	designation	score	g.c.a.	designation	score	g.c.a.	designation	score
1	129	[4]	B	206	+	B	72	+	B
2	241	+	C	189	+	C	72	+	B
3	49	-	A	86	-	B	26	-	B
5	396	+	C	206	+	C	103	+	C
6	N[5]		N	95	-	B	26	-	B
7	21	-	C	52	-	C	21	-	C
8	215	+	C	215	+	B	77	+	B
9	35	-	C	215	+	B	47	-	B
11	228	+	B	120	-	B	73	+	B
13	168		B	172		B	60		B
14	56	-	B	73	-	B	17	-	B
15	130		B	181		B	77	+	A
16	215	+	C	172		B	90	+	B
17	34	-	C	N	N	N	47	-	B
19	73	-	B	77	-	C	17	-	B
20	380	+	C	400	+	B	170	+	B
24	N		N	146		A	142	+	A
26	N		N	129	-	A	56		A
27	86	-	C	172		B	N		N
29	52	-	C	N	N	N	69		B
33	26	-	A	180		A	50		A
TEST MEANS (15 parents)	157[6]			176			65[6]		

[1] Straightness for all families in each type of progeny test pooled and averaged for each parent. G.c.a. expressed as number of trees per acre scoring 8 points or better.

[2] Parents with all-family averages well above mean for type of progeny test, designated "+"; well below designated "-". Such parents would be selected for and against respectively with confidence.

[3] Parents scored subjectively as A, B, or C according to the relative performance of all their families within each type of progeny test. Parents scoring A or C would be selected for or against respectively with confidence; those scoring B are about average in breeding potential.

[4] Absence of designation for straightness indicates all-families mean is about average.

[5] N=No progeny test of this type with this parent. [6] Both test means (157 and 65) significantly different from 176 and from each other.

realized, however, that this information came from a diversity of material in different experiments, not from the same material in one experiment over several years.

The data were also examined with a view to evaluating the breeding qualities of individual parents. Problems were immediately apparent because of inequality of test intensity for each parent and incompleteness of their representation over years. However, within the more comprehensive 1954-57 full-sib test, estimates of general combining ability (g.c.a.) were possible for 14 parents. Each parent was represented by at least three families; in some cases, many more. The mean values for straightness and volume of the groups of families associated with each of the 14 parents, that is, general combining abilities, are given in Table 2.

Specific combining abilities (s. c. a.) for straightness and volume of 30 crosses in the 1955 and 1956 experiments at ages 7 and 9 years were derived as:

s.c.a. A x B = observed value A x B - g.c.a. A - g.c.a B + mean for the experiment [1]

The results can be summarized as follows:

Figure 4 -- Nine-year-old full-sib families; on left G40 x G20, much more vigorous than G16 x G20 on right. In this case both families had the same exceptionally high value for straightness.

With regard to straightness, specific combining ability was large for ten of the crosses. However, only four specific combining abilities for volume differed markedly from zero. The crosses with large, positive specific combining abilities were not outstanding in absolute terms. Moreover, none of these crosses combined a higher gain for both traits than several other families which showed no marked specific combining abilities. In other words, the most productive full-sib families with respect to straightness and volume individually, and to a combination of these traits, resulted from combinations of parents of high general combining abilities.

Analyses of the less comprehensive older experiments were attempted also to effect comparisons among an additional seven parents. The data on straightness for all full-sib, wind-pollinated, and selfed progeny tests were pooled within test types on the assumption that direct comparisons could be made across types of test and experiments. These data yielded mean straightness values for the progenies of 21 parents well represented in at least two of the three types of progeny test; families of 15 parents were so represented in all three types of test. The relative merit of all 21 parents, judged by vigor of progeny, could not be determined directly in this series of tests because of the

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[1] Mean value for straightness and volume of all families involved in the particular experiment.

Figure 5 -- A nineteen-year-old plantation from controlled crossing of superior parents G2 and G3. Note the excellent straightness and fine short branches in this family. The stand was thinned commercially in 1963. Several trees have been artifically pruned as high as 30 feet.

Figure 6 -- Eighteen-year-old progeny from selfing good phenotypes; on left a family from parent G2 showing excellent bole straightness but poor vigor; on right a family from parent G40 with poorer straightness but outstanding vigor. Performance of selfed progeny of a parent was highly indicative of its general combining ability.

haphazard distribution of families among experiments. But an attempt was made to differentiate two extreme groups on the basis of each type of test in the following way: within experiments, parents were ranked according to the mean performance of their families; across experiments, judicious comparision were made utilizing the facts that check material was common to all experiments and that some families were common to two or more tests. Parents were then scored according to their apparent potential for producing progeny of class:

A = exceptionally high volume production
B = intermediate volume production
C = very low volume production

Similarly, parents with high potential for straight offspring were designated "+" and with low potential, "-." It was considered that parents scoring +, A or -, C could be selected for and against, respectively, with confidence. Results of these further parental evaluations are presented in Table 3. Variation in performance among different families is illustrated in Figures 4 and 5 (full-sibs) and 6 (selfs). Among 20 families resulting from selfing, three showed no observable reduction of vigor compared to outcrosses, and two had straightness values as high as the best full-sib families.

DISCUSSION

1. Gains from selection and controlled breeding.

Complete control of pollination among mass-selected parents gave spectacular improvement in both volume and straightness, while open-pollinated progeny yielded useful gains (Figures 2 and 3). This confirms the results obtained by McWilliam and Florence (1955).

With regard to full-sib progeny, considerable gains in both traits occurred in all sections of the six full-sib experiments from which data were obtained to produce Figure 3. The check sources averaged only 26 trees per acre, scoring 8 or better (hereafter designated

8+) out of a possible 10 points for straightness; the very best check plot gave only 52 trees per acre, scoring 8+, while the mean gain for all 59 crosses was 158 trees per acre, rating 8+. Only in six families were there absolute gains of less than 100 per cent. For volume, there is a clear trend of increasing gain values over and above a steeply rising rate of volume production with age in the checks. It is probable that larger volume gains will yet accrue as the plantations get older. [2] Only two families out of 50 produced less volume in absolute terms than did the checks with which they were compared. In the nine-year 1956 full-sib test which comprises 21 families involving 10 parents, the average gain was 243 cu. ft. per acre (approximately 2.7 cords), a figure significant both practically and statistically. The 21 families are nearly a 50 per cent sample of all possible family combinations which could result from random pollination in a clonal orchard composed of the same 10 parents. Therefore, the realized gain quoted is likely to be a very good estimate of that available from such an orchard. Greater improvements are possible for slash pine, since the other experiments revealed parents surpassing in general combining ability many of the 10 used in the 1956 test.

The gains from wind-pollinated progeny of the mass-selected parents were also considerable (Figure 3). On a basis of 650 trees/acre (equivalent to the standard 8' x 8' spacing) the gain in straightness was 65 trees per acre 8+; real gains in volume were obtained from some families. Since the nine-year-old 1953 test involved as many as 21 families and is well replicated and controlled, results from it are of special interest. Analyses showed eight families had volumes exceeding checks by at least two standard deviations, and none of the open-pollinated families was significantly inferior to the checks. With respect to straightness no selected parent gave progeny significantly poorer than the checks, while ten families were markedly superior, with gains of at least 40 trees per acre 8+. In the check plots only 22 trees per acre rated 8+ for straightness. These results indicate that use of wind-pollinated seed from selected parents can be beneficial, but a high intensity of selection such as was used here is necessary for really worthwhile gains.

2. Evaluation of parents.

The general combining ability values given in Table 2 are based on four or more families in 12 of the 20 crosses, while the remainder are based on three families. Although each parent was not crossed with the same group of testers, the families of many parents did have some testers in common. Thus, direct evaluation of parents using these general combining abilities must be done with caution. The following points do, however, emerge:

a. There is considerable variation among general combining abilities for straightness[3] for some parents in different experiments, for example:

Parent	g.c.a. for straightness in different tests
16	215, 103, 193
15	215, 193, 146, 215

Possible sources of this variation are: (1) effects of specific crosses, since means for most parents represent somewhat different sets of testers; (2) genotype by environment interaction; (3) error in the subjective assessments.

b. Tentative ranking of parents in respect to breeding potential for straightness and vigor might be made on the basis of Table 2 as follows:

Year of Test	Ranking of parents[4] as breeders		Year of Test	Ranking of parents[4] as breeders	
	Straightness	Volume		Straightness	Volume
1955	8 15	26	1956	20	14 20 24
	6 16 26	6 8 15 16		9 16	9 12 13 15 16
	7 14 19	7 14 19		13 15 24	
				12 14	

[2] Results just received of the remeasure of the 1955 full-sib test show an average gain for the 12 families involved in two well replicated sections of 260 cu. ft. per acre over the check plots which produced 1050 cu. ft. per acre.

[3] Volume comparisons not attempted because of varying ages.

[4] Ranked in descending order of value; parents of equal value on same line.

It is of special interest to note that tree 15 shows a reversal of ranking for straightness in 1956, but the 1954 and 1957 tests (Table 2) suggest the 1956 result is atypical; and tree 14 shows a reversal for volume. Other than these two instances, most likely effects of specific crosses, parents common to both tests are similarly placed for the different years. It is evident that for precise evaluation of parents a tester system with perhaps a minimum of five testers is highly desirable. Further, the duplication of tests over years and the development of an objective assessment method for straightness appear to be necessary.

c. A further point worthy of note is that tree number 24 displays high combining ability for volume production and a very acceptable standard for straightness. This tree was selected for its outstanding vigor and good straightness within an open-pollinated family with high performance in these traits. Other examples of the efficacy of second-cycle selection within the progeny tests were noted in the 1955 open-pollinated trial. Twelve of the parents included were selected at eight years of age in two full-sib families outstanding for straightness. The open-pollinated progeny of six of the 12 selections displayed exceptionally good straightness, equivalent to the performance of open-pollinated progeny of tree number 20 (shown in Figure 1, left), which had the highest general combining ability of all trees in the whole series of progeny tests.

d. Another important point which emerged from the results in Table 2, and indeed from the whole series of tests, was that phenotypic selection of the parent trees was generally very accurate. Only rarely did mass-selected parents produce progeny without significant gains over the checks, and in no case did they give progeny significantly poorer than the checks.

The information in Table 3 represents an attempt to utilize the data collected throughout all the experiments for evaluation of a maximum number of parents. This further illustrates variation of breeding value among parents and points up a general coincidence of parental ranking in all three types of progeny test. Thus, with respect to breeding value for straightness, of the 15 parents common to all three types of test essentially the same groups of parents would be chosen by positive selection in each of the three types of progeny; in only two cases (parents 9 and 11) are there conflicting indications. In addition, the same parents (trees 3, 7, 14, 19) are selected against on the basis of each test method. With respect to vigor there appears to be very substantial agreement among the three methods in indicating the best and the poorest parents. Exceptions to the rule that parental evaluation can be made on the basis of either type of progeny test might be explained on the basis of the particular sample of pollen parents involved in the full-sib or wind-pollinated families. Thus for example, all the full-sib families available of tree 33 (the selfed progeny of which is crooked - Table 3) involved pollen parents known to have high general combining ability for straightness; this would bias the result of full-sib tests.

It appears, therefore, that provided the full-sib and wind-pollinated progeny tests represent several families of the parent in question (perhaps a minimum of five) then all three progeny test methods will give very similar evaluations of the breeding quality of the parents. However, more precise experimentation is necessary to determine the real relationship of the three types of test, and particularly if selfed progeny alone can be relied upon to indicate the breeding potential of a parent. As is discussed more fully below, this phenomenon involves the relative amount of additive gene action for the trait concerned. From personal correspondence with several other conifer breeders, four researchers have reported evidence of a fair relationship between self- and cross-pollinated progeny performance. This was also reported by Diechert (1964) for spruce and larch and has been found also in corn (Koble, 1964; Lonquist and Lindsay, 1964).

There are indications in Table 3 of negative phenotypic correlations between straightness and vigor. For example, trees 2, 5 and 20 gave straight progeny of average vigor, while trees 3 and 33 gave vigorous but relatively crooked progeny. However, progeny of tree 7 showed a positive correlation. Clearly, more studies are needed to determine this point and to investigate the genetic correlation between the two traits.

3. Possible gene action; choice of breeding methods.

Although the experiments discussed in this paper were not designed to yield information on gene action <u>per se</u>, some evidence on it can be obtained and is discussed here because of its importance in determining the most efficient breeding method.

It is generally recognized that complex traits such as yield (for example, volume production) are not controlled by simple Mendelian inheritance but are quantitative in character. Quantitative inheritance is best considered in terms of the relative magnitude of the three major kinds of associated genetic variance - additive, dominance and epistatic. Explanations of the nature and sources of these variances are beyond the scope of this paper; for a general treatment of this subject, reference may be made to a standard text such as Falconer (1964). An attempt will be made here to indicate evidence on the relative magnitude of these variances in the breeding population of slash pine which was studied.

Considerable additive variance for both straightness and volume is manifested by the large gains realized (Figure 3) from the simple selection schemes used. Estimates of realized narrow sense heritabilities are obtainable from these experiments but were not calculated for the present paper [5]. However, such values will surely prove to be relatively high since phenotypic selection was very accurate and the mass-selected parents gave progeny much superior to the base population.

Further evidence of the importance of additive variance in straightness in this population is provided by the facts that the selfed and the full-sib progeny tests yielded similar values and essentially the same ranking of parents for this character (Table 3). Finally, the occurrence of specific combining ability effects for both straightness and volume, though evidence of dominant gene action, was such that the level of dominance and the amount of dominance variance appeared to be low. This conclusion was arrived at as follows:

Apparently real specific combining ability effects, though not statistically tested, were present for straightness in 10 out of 30 crosses (p. 5), but none of the families involved had outstanding straightness while all the families with outstanding straightness had parents of very high general combining ability. Hence the level of dominance in the alleles controlling straightness appears to be low. As regards vigor, there were only four out of 30 crosses with apparently real specific combining ability effects (p. 5). Further, inbreeding depression of growth (and effects on straightness) were very variable in expression (Table 3). Although mean straightness of 15 selfed families was significantly depressed compared to the controlled crosses, it was not markedly reduced (Table 3). These points suggest that dominance variance for vigor and straightness in this population may be low. A large proportion of additive variance for yield, though it is a complex character, is not without precedence in other crops (Gardner, 1963). However, in other samples of slash pine or even in later selection cycles of this population, non-additive genetic variance may increase in importance. Clearly, a breeding procedure enabling utilization of both general and specific combining ability would be optimum.

To sum up the discussion on gene action and breeding methods it appears that additive variance is of greatest importance for both volume growth and bole straightness but that larger non-additive effects may become apparent in other populations of slash pine or in later selection cycles of the material studied or with greater tree age. It is evident that for precise estimation of the relative magnitude of the different components of genetic variance use of improved mating and field designs will be necessary. In the meantime, selection with major emphasis upon general combining ability combined with restriction of interbreeding to the trees selected appears to be by far the best approach. For example, a seed orchard might be developed, composed of clones of the best individual tree in each family of a best fraction of all families available as indicated by Squillace and Dorman (1961) and Johnsson (1964). Since the full pedigree of each family is known, it would be possible to ensure that all clones to be retained permanently were unrelated, thus minimizing inbreeding. Gains can be expected to accrue for several cycles of selection, and they may in fact improve, since heritability should increase when selections are made within rather uniform progeny test areas and when the more accurate combination of family and mass selection is applied. If a particular cross were found to out-yield all others to a large enough extent to warrant its mass production, then the specific combining ability demonstrated might be so utilized.

SUMMARY

Progeny tests of slash pine (Pinus elliottii) established in Queensland between 1952 and 1957 were studied when six to ten years of age to determine the gain in volume and bole straightness over commercial stock, resulting from mass-selection of parents combined with controlled and open pollination. Progeny resulting from the selfing of many parents were also available and, together with the cross-pollinated material, were examined to evaluate the breeding qualities of the parent trees. The results also provided a basis for some speculation on the

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[5] The raw data from the assessments were not available to the writer at the time of preparation of the paper; it is planned, however, to make a fuller analysis later.

relative importance of types of genetic variance present in the population and hence on the optimum breeding procedure.

The replicated and controlled full-sib experiments involved 59 families from 25 parents. Subjective assessments of bole straightness revealed on the average seven times the number of trees of a defined high standard (8+) in these progeny as compared to the checks of commercial stock, which averaged 26 per acre 8+. The gain in volume per acre increased with age, reaching 243 cu. ft. per acre (approximately 2.7 cords solid wood per acre) at nine years and appeared to be still rising. Gains realized in the wind-pollinated progeny tests were smaller but considerable. Twice as many trees scored 8+ for straightness compared to checks which averaged 22 per acre 8+, and in one large experiment the gain in volume was 123 cu. ft. per acre at nine years of age.

Evaluation of the breeding qualities of parent trees was attempted by comparison of their general combining abilities for straightness and volume. Estimates for 14 parents involved in the more comprehensive full-sib tests showed great variation in their capacities to produce superior offspring, indicating progeny test selection to be potentially of great benefit.

When all the data within each of the three types of progeny test (full-sib, wind-pollinated, and selfed progeny) were pooled, 15 parents were found to be represented in all types of test. A significant difference between the means for straightness of the full-sib and self-pollinated progeny was found; the respective means were 176 and 157 trees per acre 8+. The wind-pollinated progeny mean was 65. The three types of progeny test differentiated the same trees, with few exceptions, into groups of parents characterized by: excellent and very poor straightness; very high and about average vigor.

Specific combining abilities for straightness and volume were calculated for 30 crosses, resulting in high values in 10 and 3 cases, respectively. However, the most outstanding single crosses encountered did not show high specific combining ability, and those with high specific combining ability were relatively poor in absolute terms.

The test results provided indirect evidence on the relative magnitude of components of genetic variance for straightness and volume; additive variance appeared to predominate in the breeding populations studied. Consequently, the breeding procedure recommended was one with major emphasis on general combining ability but which also allowed utilization of any worthwhile specific combining ability effects.

ACKNOWLEDGMENT

Tree breeding work in Queensland, in which the progeny testing described here is a major element, was initiated by Mr. V. Grenning, then Director of Forests, and has continued under the direction of Mr. A. R. Trist, formerly Deputy-Director and now Conservator of Forests. The demonstrated success of the work is a tribute to the foresight of these foresters. Several research officers have been involved in the work over the years, in particular Messrs. C. Haley, J. J. Smart, J. R. McWilliam, R. G. Florence, and M. U. Slee. Mr. T. R. Chard has been an invaluable technical aid throughout the program. Photographs used in the paper are due to Mr. G. Trinder. Permission to use the data accumulated by myself and these workers was kindly given by the Conservator, Department of Forestry, Brisbane. Finally, I wish to thank Dr. B. J. Zobel for encouragement to prepare this paper and for his criticisms of an earlier draft.

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Sweetgum Seed Quality and Seedling Height as Related to Collection Date

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Viability of most tree seed is highest at the time of dispersal. In practice, collections normally precede dispersal either to increase efficiency or insure seed of known parentage.

The study reported here was made to determine the effect of collection data on germinability of sweetgum seed and on seedling height growth in the nursery. A secondary objective was to learn if specific gravity of the seed head is an indicator of seed maturity.

METHODS

Collections were made from six trees in Harrison County, Mississippi, at 2-week intervals from September 5 to November 28, 1962. By the latter date, some heads were open and beginning to disperse seed. All trees were in different stands, therefore probably not closely related.

On each date a sample of 20 seed heads were collected from each tree. The heads were placed in sealed containers, and immediately taken to the laboratory. Five representative heads from each sample were weighed to the nearest 0.01 gram. Volume of each head was determined by water displacement to the nearest 0.5 milliliter.

The entire sample from each tree was air-dried in the laboratory until the heads opened. The seeds were extracted, cleaned, counted, and stored for 4 weeks at 5°C and 12 percent relative humidity. Following storage (which permitted moisture contents to come to equilibrium) all samples were weighed to the nearest 0.001 gram.

Following 30 days' stratification, 100 seeds from each sample were sown on filter paper in petri dishes. Germination was recorded daily. Total germination was computed as a percentage of sound seed, and number of days for each sample to attain 90 percent of total germination was calculated.

In the spring of 1963, 37 stratified seeds per sample were sown in each of four replications of a split-plot test in the nursery. The main plots consisted of seed from individual trees, the subplots represented collection dates. The number of emerged seedlings was recorded 3 weeks after sowing. At the end of the growing season the heights of the five tallest plants in each 4-foot row were measured to the nearest centimeter.

RESULTS

Specific gravity of the seed heads decreased markedly between the first and second collection dates (fig. 1). Although subsequent fluctuations varied significantly, the value at the final collection date, when natural dispersal had begun, was not significantly different from that on October 3. In contrast to the data reported for the southern pines (McLemore 1959; Wakeley 1954), sweetgum seed heads will open naturally when collected prior to seed maturity.

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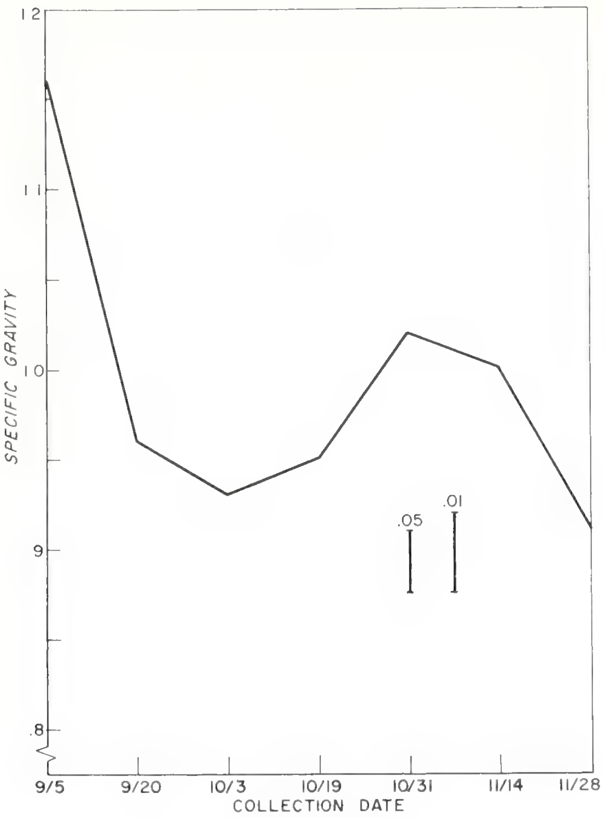

Figure 1 -- Specific gravity of sweetgum seed heads. Vertical lines indicate the minimum range of mean values for significance at the 0.05 and 0.01 levels according to Duncan's test (1955).

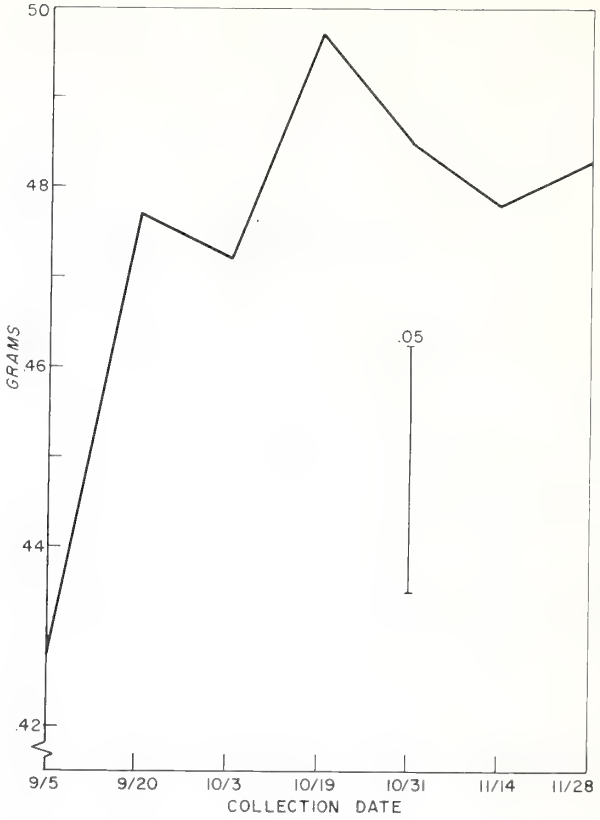

Figure 2 -- Weight per 100 sweetgum seeds.

test (1955).

Seed weight and rate of germination were related to time of collection. Weight per hundred seeds (fig. 2) was significantly less on the first collection date than subsequently, but did not differ significantly among collections after September 5. The marked increase in weight between the first and second collections suggests that the seed was not fully developed until mid-September.

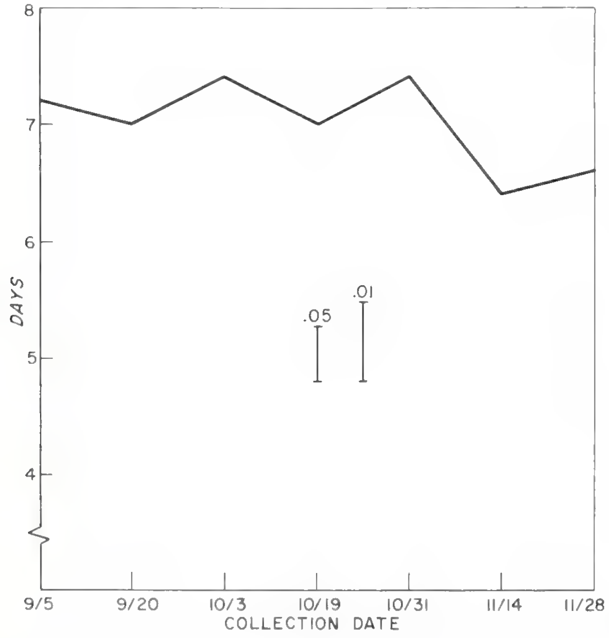

Figure 3 -- Time required to attain 90 percent of total germination.

The number of days required to attain 90 percent germination (fig. 3) was about constant until November, when it decreased slightly--indicating an increase in rate of germination. The increase was so small and came so late that for practical purposes it would be overbalanced by seed losses through dispersal.

Total germination did not differ significantly among collection dates. In several coniferous species, by comparison, a progressive increase in germination was associated with decreases in cone specific gravity (Eliason and Hill 1954; Maki 1940; McLemore 1959).

In the nursery, neither the proportion of emerged seedlings nor the seedling heights differed significantly among collection dates. The percent of emerged seedlings was consistently about half the total laboratory germination. Mean heights ranged from 72 to 75 centimeters and showed no consistent change with collection date.

The Woody Plant Seed Manual (1948) reports that sweetgum seed heads turn yellow between September and November as the seed matures. In this study it was not possible to distinguish any color change that could be used as an index of either seed maturity or time of dispersal.

Specific gravity of the head appeared to be a good indication of seed weight. This same relationship between specific gravity and seed weight has been reported in ponderosa pine (Maki 1940).

In conclusion, seed weight and rate of germination differed among lots collected from mid-September until late November, but establishment and growth in the nursery were not affected. Apparently, in south Mississippi sweetgum seed can be collected safely over a 6-to 8-week period beginning around October 1. The changes in weight and rate of germination suggest that, if comparisons are to be made for these characters among seed lots, collections should be as near simultaneous as possible.

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Propagation of Sweetgum by Softwood Stem Cuttings

ROBERT E. FARMER, JR. [1]

Sweetgum (Liquidambar styraciflua L.), a species difficult to propagate by mature-wood cuttings, is capable of regenerating from stump sprouts and root suckers (Johnson 1964). Brown and McAlpine (1964) have propagated 3-year-old seedlings and 20-year-old trees directly from root cuttings. This paper reports the successful rooting of softwood sweetgum cuttings taken from (1) suckers cultured on excised roots and (2) naturally occurring root suckers in a recently clearcut stand.

METHODS

Lateral roots for culturing suckers were excised in May. In previous tests, roots collected in November, December, and early April failed to develop suckers after one to two months in the greenhouse. The roots were from 23 trees varying in d.b.h. from 3 to 34 inches. They were immediately cut into sections 40 to 80 cm. long; diameters ranged from 10 to 60 mm. They were then planted horizontally 1 to 2 cm. deep in nursery beds and watered daily. Suckers were first observed in mid-July and suckering continued into early September. Production ranged from 0 to 27 suckers per meter of root length. Roots from large trees generally produced fewer suckers than did those from small trees, but the relationship was not consistent; roots from some of both large and small trees completely failed to sucker.

Naturally occurring suckers were collected directly from root systems where a mixed hard-

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[1] The author is stationed at the Southern Hardwoods Laboratory, which is maintained at Stoneville, Mississippi, by the Southern Forest Experiment Station, Forest Service, in cooperation with the Mississippi Agricultural Experiment Station and the Southern Hardwood Forest Research Group.

wood stand had been recently clearcut.

Softwood stem cuttings were made from apical portions of suckers when they were 5 to 10 cm. high. Approximately one-half came from field-grown suckers and one-half from suckers on root cuttings. These cuttings were paired with regard to source, size and clone, and one member of each pair was treated with 50 ppm IBA (24-hour water soak); the second member of the pair served as a control. Paired cuttings were planted in clay pots filled with either sand or a 1:1 sand:peat mixture and placed in a chamber under a mist of distilled water (Farmer 1963).

Five tests were initiated between August 18 and September 2. In each, an approximately equal number of pairs was propagated in sand and sand:peat; the number of pairs varied from 12 to 34 depending upon the amount of material available. Rooting was determined 6 weeks after the cuttings were placed under mist. Arc-sin transformations of rooting percentages were analyzed as for a split-plot design with five replications in time.

RESULTS AND DISCUSSION

Of the cuttings in sand:peat, 67 to 100 percent developed roots, while 0 to 67 percent rooted in sand (table 1). The effect of medium was significant at the 0.01 level of probability. IBA did not increase rooting. Field-collected suckers rooted as readily as those cultured in nursery beds. Suckers from roots of the larger, older trees and those from small trees rooted equally well. Some rooted cuttings were fertilized (soluble NPK 10:10:10 and micronutrients) and placed in the greenhouse under a long photoperiod; they resumed apical growth and developed extensive root systems within 3 weeks.

Table 1. Rooting of greenwood sweetgum root suckers at 6 weeks as affected by rooting medium and IBA.

Test number	Sand: peat		Sand	
	Control	IBA	Control	IBA
	- - - Percent - - -		- - - Percent - - -	
1	100	93	0	0
2	100	100	44	67
3	83	100	0	50
4	91	91	7	7
5	67	72	0	25

These results indicate that softwood cuttings from root suckers can be vegetatively propagated with relative ease. Propagation medium appears to be a crucial environmental factor, since the sand:peat mixture was greatly superior to sand. The reasons for this superiority were not clear, but the sand:peat appeared to provide better aeration than sand under the misting system used. The lack of appreciable IBA effect may be related to existence of high endogenous auxin levels in actively growing suckers.

While nursery culture of roots is satisfactory for certain purposes, i. e., retention of selected genotypes, the wide variation in suckering indicates that the technique may not be applicable to all trees. Moreover, suckering occurred only on roots collected in late spring. These facts suggest that studies in the physiological ecology of sweetgum root suckering may be prerequisites to uniform propagation success.

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Some Morphological Variations Among Loblolly Pine Seedlings

M. VICTOR BILAN 1/

One-year-old nursery-grown seedlings of loblolly pine show much variation in the type of

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needles formed, development of the terminal winter buds, and in the formation of height-growth flushes. In east Texas, for example, 1-0 loblolly pine seedlings may represent all developmental stages from the "juvenile" type, with only primary needles and no terminal bud, to the "mature" type with abundant secondary needles and two completed height-growth flushes, possessing a well-developed winter bud.

The author observed that loblolly pine seedlings grown from locally-collected seed in the Stephen F. Austin State College forestry nursery showed a high degree of morphological variation which could not have been attributed to differences in age or microenvironment. Some seedlings stopped height growth in late August, while others grew until the first chills in October.

Also, 2 to 4-year-old loblolly pine seedlings grown in the nursery did not cease seasonal height growth at the same time: some ceased terminal elongation by the middle of August, while others grew until late September. Trees stopping elongation early terminated their growth with a conspicuous terminal bud and well-developed secondary needles on the latest flush of growth. Late-growers, however, ended seasonal height growth at any stage of flush development, thus suggesting that height growth was arrested by the unfavorable environment rather than by inherent physiological conditions.

The above supposition is supported by an experiment conducted in an air-conditioned greenhouse. Seeds collected from ten open-pollinated loblolly pines were germinated in petri dishes during the month of May and then planted in individual 2-1/4-inch square jiffy pots filled with top soil. The labeled pots were arranged in 12" x 12" x 4" wooden flats on tables. The temperature in the greenhouse ranged between 75^{o}F and 85^{o}F and the relative humidity varied between 35 and 85 percent. The light intensity was reduced by 20 percent with a nylon netting, and the photoperiod remained natural.

Morphological development of each seedling in each of the ten progenies was recorded periodically for one year. One of the conspicuous morphological variations was cessation of seasonal height growth and formation of terminal winter buds. Table 1 represents the data pertaining to winter bud development on October 15, November 21, and February 25.

Table 1. Percentage of seedlings having conspicuous terminal buds.

Tree No.	Number of seedlings in progeny	Percentage of seedlings with conspicuous terminal buds		
		Oct. 15	Nov. 21	Feb. 25
I	73	40	27	23
II	318	70	76	44
III	173	36	26	24
IV	268	29	26	20
V	467	60	60	47
VI	257	93	93	68
VII	57	88	91	53
VIII	40	73	68	43
IX	44	57	59	32
X	73	81	81	41

Most pronounced differences existed between progenies IV and VI. Most of the seedlings in progeny VI completed their height growth by the end of August; and in the middle of October, 93 percent of them had well-developed terminal buds and abundant secondary needles. Only 29 percent of progeny IV developed terminal buds by the middle of October, while the remaining 70 percent continued to grow through the entire winter. Most of the continuously growing seedlings in progeny IV had a "juvenile" appearance: very few secondary needles, bluish-green stems, and a shortleaf-like crook at the root collar. The winter-bud forming trees in progeny IV had the general appearance of progeny VI except for the shorter secondary needles and less conspicuous terminal buds.

Since seedlings of individual progenies were randomly distributed over 72 flats, and the environment was relatively uniform, the variation in the growth habits was attributed to the inherent characteristics of the individual plants. It was concluded that in central east Texas, early cessation of height growth of at least some loblolly pine seedlings might be caused by inherent characteristics of the plants themselves. It also appears that natural hybridization between loblolly and shortleaf pines might be responsible for a high degree of morphological variation in loblolly pine seedlings in eastern Texas.

Figure 1 -- Example of variation in progeny of Tree No. IV.

Effects of Fertilization Upon Wood Properties of Loblolly Pine (*Pinus taeda* L.)[1]

CLAYTON E. POSEY[2]

Intensification of forest management practices has been accompanied by increasing interest in the use of commercial fertilizers to improve productivity of forest stands. Almost without exception, the field application of fertilizers has had volume production as its main objective with little concern being given to the effects of fertilizers on the quality of wood produced. Growth increase is unquestionably important, but fully as significant is the kind of wood produced by the fertilized trees and the possible effects of such wood upon products fabricated from it.

To achieve maximum gains through tree improvement, it is essential to determine whether individual trees respond differentially to fertilizers. Maximum improvement from new genetic "strains" is possible only by taking full advantage of individual tree response to fertilization.

Previous to this a comprehensive study of the effects of fertilization on wood properties of older trees growing under normal conditions had not been conducted in North America. One preliminary study, which led to the current more intensive research, was made by Zobel, *et al*. (1961) on wood of loblolly pine fertilized at age 16. Wood formed the seven years before fertilization was compared with wood formed the seven years after fertilization. Three consecutive annual applications of 160-80-80 pounds per acre of NPK produced wood with wider annual rings, lower density, and shorter tracheids. This same general pattern of response was reported by Erickson and Lambert (1958), Seibt (1963), Pechman and Wutz (1960), and Williams and Hamilton (1961).

The primary objectives of this investigation were:

1. To study individual tree response to fertilization, especially seeking trees that respond with increased growth rate but still maintain desirable wood characteristics.
2. To determine effect of fertilizers over time, i.e. how rapidly does a change in wood appear and how long do the added nutrients affect wood characteristics.
3. To determine the correlations among specific gravity, percent latewood, ring width, tracheid length, tangential tracheid width, and radial tracheid wall thickness.

MATERIALS AND METHODS

Two loblolly pine plantations on the Hill Experimental Forest of the School of Forestry, North Carolina State University, were selected for this investigation. The plantations, one established in 1935 and the other in 1939, are on a Georgeville silt loam, a typical well-drained Piedmont soil. They were established at a spacing of 6x6 feet following a broadcast burn. Both plantations are on sites above average for the Piedmont.

Two 10 mm. increment cores were taken in 1960 from 160 trees representing eight fertilizer treatments replicated twice ranging from no fertilizer to three consecutive annual applications of 160 pounds of ammonium nitrate (33 percent nitrogen), 80 pounds of treble superphosphate (47.7 percent P_2O_5) and 80 pounds of potassium chloride (62 percent K_2O) per acre.

[1] Based on author's Ph. D. research. Funds for the study were provided by the North Carolina State - Industry Tree Improvement Program and by the Nitrogen Division of the Allied Chemical Corporation.

[2] Assistant Professor, Department of Forestry, Agricultural Experiment Station, Auburn University.

In order to determine the length of time the fertilizers were effective, each of the 320 increment cores were divided into the four following segments:

1. 1949-50 annual rings, representing the type of wood produced before fertilization.
2. 1952-53 annual rings, representing the wood formed during fertilization.
3. 1955-56 annual rings, representing wood formed after fertilization.
4. 1958-59 annual rings, representing the wood formed after fertilization.

The following measurements of each core segment were made after the removal of alcohol-benzene soluble extractives: annual ring width; proportion of latewood; specific gravity; length of 20 latewood tracheids; and tangential tracheid width and radial tracheid wall thickness of 10 latewood tracheids. The tracheid measurements were made on macerated tissue after mounting on semi-permanent slides.

RESULTS AND DISCUSSION

In the treatment combinations tested in this experiment, level of potassium had no detectable effect upon any of the wood properties studied. The lack of a potassium effect is not unexpected, since all of the soils of the slate belt, in which the experimental area lies, are relatively high in potassium. Most of the changes reported are attributable to nitrogen, although nitrogen without phosphorus gave less response than a combination of nitrogen and phosphorus.

Growth Rate

Assuming a fully stocked stand for the 10 year period 1951-1961, trees that received 160 pounds of nitrogen, 80 pounds of phosphorus, and 80 pounds of potassium per acre produced approximately 1 cord of pulpwood per acre per year more than the unfertilized trees. The year following the first application of fertilizers trees that received 160 pounds of nitrogen in any combination with phosphorus and potassium showed a 50 percent increase in radial growth rate. They were still growing faster than the unfertilized trees eight years later.

Figure 1 is a graphic representation of the effects of fertilizers on radial growth rate. As one would expect, the radial growth rate decreases with increasing age in the check trees. Those trees receiving fertilizer treatment of at least 80 pounds of nitrogen show a significant increase in radial growth at the same age where radial growth decreased in the check trees. The maximum response to fertilizer appears to occur the year after the first of the three applications.

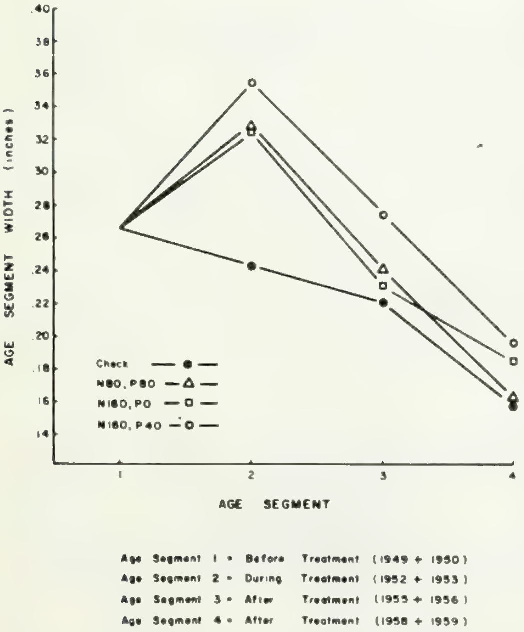

Figure 1 -- The effects of fertilizers on radial growth rate (age sgement width) in the 16-year-old plantation.

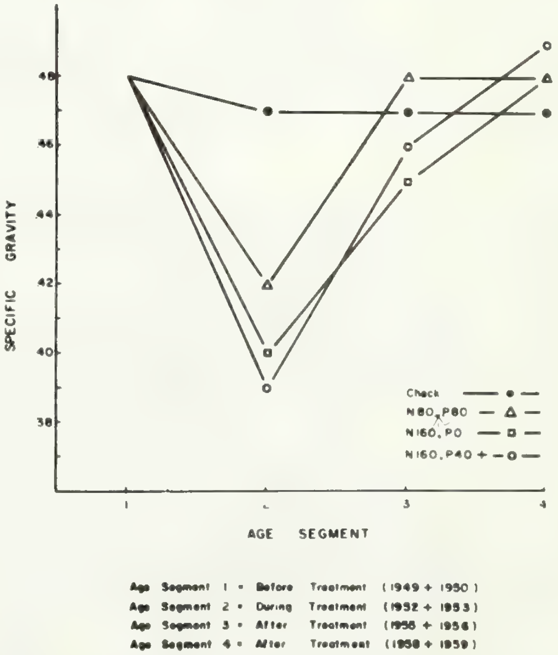

Figure 2 -- The effects of fertilizers on specific gravity in the 16-year-old plantation.

Specific Gravity and Percent Latewood

As has been pointed out by Schreiner (Zobel, 1956), specific gravity is a complex characteristic determined by several growth and physiological variables. It is affected by the percentage of latewood, tracheid wall thickness, tracheid diameter, and perhaps tracheid length.

Figure 2 shows the effect of fertilizers on wood specific gravity. The same pattern of response occurred for percent latewood. In general, wood specific gravity and percent latewood decreased as the amount of nitrogen applied increased. Treatment with 160 pounds of nitrogen, 80 pounds of phosphorus and 80 pounds of potassium caused average wood specific gravity to decrease from 0.48 to 0.39 and percent summerwood to decrease from 47 to 36. This represents a sizeable decrease in the amount of pulp obtainable from a cord of wood, but the increased rate of growth more than compensates for the decrease in density.

Without exception, the specific gravity and percent latewood of fertilized trees was greater the seventh and eighth years after the first treatment application than the check trees. This outcome was surprising, i.e., the specific gravity and proportion of latewood in the fertilized trees was expected to be equal to, or less than, the check trees. This discrepancy may possibly be explained by a study of Paul and Marts (1954). Their applications of complete fertilizer on longleaf pine (Pinus palustris) increased earlywood and decreased latewood, thus causing a reduction in specific gravity. However, when they irrigated the fertilized trees an increase in percent latewood occurred, thus probably increasing specific gravity. These trends would seem to explain the data of the current study where fertilization in dry years caused a decrease in percent latewood and specific gravity as contrasted to fertilization in years of normal or above rainfall when an increase in percent latewood and specific gravity occurred.

Tracheid Length, Radial Wall Thickness, and Tangential Tracheid Width

Without exception, in this study the average summerwood tracheid length and radial double wall thickness was less for all treatments at all periods during and after fertilization than were the tracheids of the check trees. This relationship for tracheid length is shown in Figure 3.

Trees that received 160 pounds of nitrogen with or without phosphorus and potassium showed a decrease in average summerwood tracheid length from 3.9 mm to 3.4 mm and a decrease in radial double wall thickness from 22µ to 18µ.

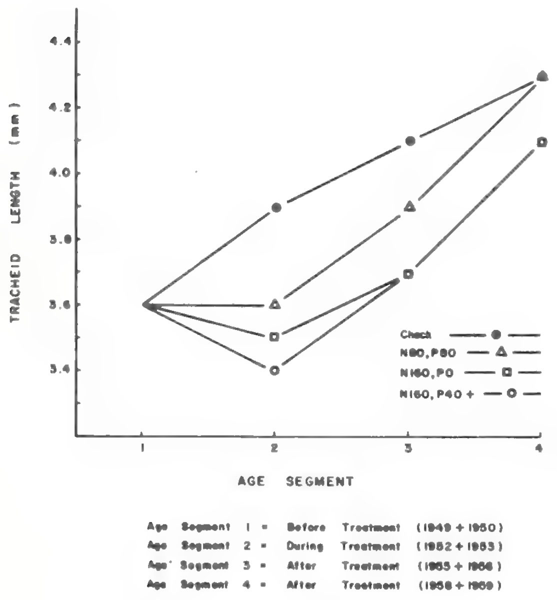

Figure 3 -- The effects of fertilizers on tracheid length in the 16-year-old plantation.

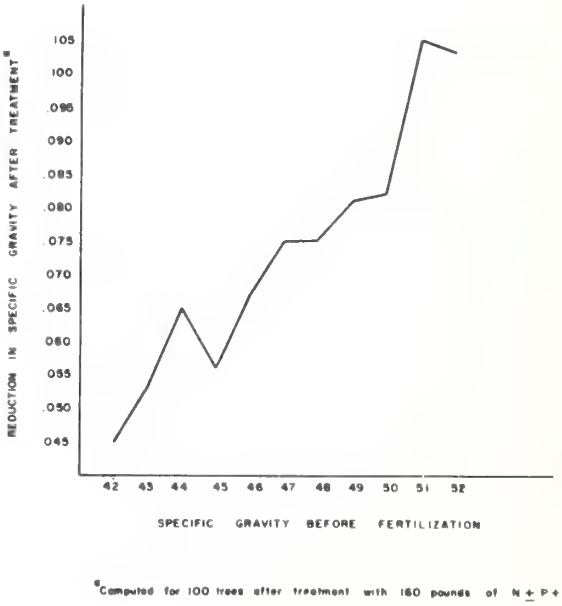

Figure 4 -- Relationship between specific gravity before fertilization and reduction in specific gravity after treatment with nitrogen fertilizers.

In contrast to all other growth and wood characteristics studied, the tangential width of summerwood tracheids failed to show any differences resulting from the several fertilizer treatments. There was a slight increase in tangential tracheid width, but this is attributable to the normal increase with age.

Individual Tree Response to Fertilizers

The possibility that individual trees within a species may react differently to a given fertilizer was discussed by York (1958) and by Maki (1959). As was shown in the previous section of this paper, the "average" tree receiving nitrogen without phosphorus or nitrogen and phosphorus responded with an increase in growth, decrease in specific gravity, decrease in tracheid length, and a decrease in radial double-wall thickness. However, of the 120 trees sampled from plots receiving at least 80 pounds of nitrogen, 30 trees failed to follow the "average" tree pattern of response.

The oft-challenged but now generally accepted concept that there is little or no correlation between specific gravity and tracheid length is supported by responses of the majority of "non-average" trees. Twenty-four of the 30 "non-average" trees showed an increase in growth rate, decrease in specific gravity, decrease in double-wall thickness, but an increase in tracheid length. Three trees showed a growth rate increase, decrease in specific gravity, decrease in tracheid length, but an increase in double-wall thickness. Such differences in response provide the basis for selection of trees to produce desired properties when fertilization is used in forest management.

In a preliminary study it appeared that the extent of changes brought about by fertilization might be somewhat associated with initial specific gravity (Zobel, *et al.*, 1961). To test this indication, the 100 sample trees from the plots receiving at least 160 pounds of nitrogen were compared for response, using the specific gravity before fertilization as a base. Results are presented in Figure 4. An initially high specific gravity tree is much more affected by fertilization than a tree with initially low specific gravity. For example, trees with an initial specific gravity of 0.52 dropped an average of 0.10, whereas trees with initial specific gravity of 0.42 dropped an average of only 0.045. The magnitude of effect does not appear to be related to growth rate.

Since there is a direct relationship between initial specific gravity and amount of response to fertilizers, progeny of seed orchards established from high specific gravity superior trees would be affected through fertilizing more than progeny of seed orchards established from superior trees selected for low specific gravity. An organization interested in low density wood could expect to reap volume gains by fertilizing plus a desired further decrease in specific gravity.

The same relationship as described above for specific gravity is true for tracheid length and double-wall thickness, i.e., the longer the tracheids or the thicker the tracheid walls the greater the reduction from fertilization.

Relationship Among Wood Characteristics

In a breeding program involving wood properties, it is essential to have estimates of relationships among different wood and tracheid characteristics.

All possible correlations among the six wood and growth characteristics used in this study were calculated. Some significant correlations are shown in Table 1.

Table 1. Correlation coefficients of several wood characteristics.

Relationship of wood characteristics		Correlation Coefficients[1]
Radial growth rate	x Tracheid length	--.61**
Radial growth rate	x Radial double-wall thickness	--.48**
Specific gravity	x Percent summerwood	.72**
Specific gravity	x Radial double-wall thickness	.65**
Tracheid length	x Radial double-wall thickness	.64**
Tangential tracheid width	x Radial double-wall thickness	.39*

[1] Based on 24 df, [illegible]

All of the important relationships found among various wood characteristics are summarized in the following list:

1. As radial growth rate increases, tracheid length decreases, radial double wall thickness decreases, and tangential lumen width increases; there is no consistent change in specific gravity or tangential tracheid width.
2. As percent latewood increases, specific gravity increases, and there is a tendency for radial

double-wall thickness to increase; but there is no important relationship between percent latewood and radial growth rate.

3. As specific gravity increases, radial double-wall thickness increases and tangential lumen width decreases. There is no consistent relationship between specific gravity and tracheid length or tangential tracheid width.

4. As tracheid length increases, radial double-wall thickness increases, and there appears to be no relationship between tracheid length and tangential tracheid width.

5. As tangential tracheid width increases, radial double-wall thickness and tangential lumen width increase.

SUMMARY

An investigation was conducted to determine the effects of fertilizers on several wood properties of merchantable loblolly pine. The wood samples were taken from two plantations 10 years after a replicated experiment in forest fertilization had been established on the Hill Experimental Forest, Durham County, North Carolina. The plantations were 16 and 12 years old when first fertilized. Eight treatment combinations were tested ranging from (0-0-0) to (160-80-80). Two 10 mm increment cores were extracted from 10 trees in each treatment, a total of 160 trees. Each of the 320 increment cores was divided into four age segments composed of two annual rings each, representing the wood formed before treatment (1949-1950), during treatment (1952-1953), and two periods after treatment (1955-1956) and (1958-1959). The length of 20 tracheids and the double-wall thickness and tangential width of 10 tracheids were measured for each segment.

The experimental design used for analysis of variance and covariance for each variable was a split-plot, split over time.

Nitrogen caused greatest differences in wood properties and growth rate, although nitrogen with phosphorus gave slightly greater response than nitrogen without phosphorus. Fertilization caused an increase in growth rate, decrease in specific gravity, decrease in radial wall thickness, and a decrease in tracheid length. All trees did not respond to fertilization in the same manner. For example, some trees decreased in specific gravity, but had increased tracheid lengths.

A comparison of the rate of change after fertilization with the initial value before fertilization showed that trees with either high initial specific gravity, or long tracheids or thick radial walls show more reduction than do those trees with initial low specific gravity or thin radial walls or short tracheids.

Meaningful correlations among several wood characteristics were also reported.

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Photogrammetric Technique for Measuring Bole Straightness[1]

C. J. A. SHELBOURNE AND G. NAMKOONG[2]

INTRODUCTION

Workers in various fields of forestry require precision in quantifying bole straightness. In wood property studies, attention is paid to the relationship between bole morphology, the development of reaction wood, and the resulting effects on wood structure and lumber and pulp properties. In tree improvement programs, bole straightness is therefore recognized as an especially important characteristic.

Bole characteristics are hard to assess using subjective indices where stand conditions, age, and height of stem vary. It is not difficult to subjectively reject stems which are not straight, or are leaning, but for precise studies such as for progeny and provenance assessments, some means of quantitative measurement of bole morphology is necessary.

Methods used in the past can be broadly divided into two types: the subjective rating method, where a tree is rated as good, fair or poor (1, 2, or 3), and the method where the assessor actually measures the deviations of the stem from straightness. The former has been widely used in the grading of select trees, and in comparing progenies, while fewer people have gone to the greater labor involved by the second [e.g. Perry (1960), Shelbourne (1963), Goddard and Strickland (1964)]. The techniques used by these authors were crude and imprecise.

The most important aspects of bole straightness from a practical point of view are the degree to which a stem deviates from straightness and from the vertical. With the technique described here, these attributes are measured on two photographs of the tree taken at right angles.

Geometrical and Statistical Basis of the Technique.

A tree can be considered to be a continuous distribution of points in space formed by the assumed pith (loci of mid-diameter points up the tree). If the points delineated by the pith in three dimensions are projected onto two vertical planes at right angles to one another, two right angle graphs may be plotted (Figure 1) with height up the stem as the abscissa and the horizontal distance of the pith from a vertical line as the ordinate. The abscissa is arranged to be vertical and is situated at any convenient distance from the tree for the two planes (A and B).

Three different models can then be fitted to these two projections of the stem in the A and B planes, by the normal statistical procedures of linear and curvilinear least squares regression. The models are: (1) A vertical straight axis (passing through the mean $\bar{A}$ and $\bar{B}$ for the A and B projections respectively; see Figure 1). (2) A straight linear regression axis. This fits a straight line to the points described by the stem in the tree's direction of lean so that the sum of squared deviations from a straight line is minimal. (3) A curved axis. The easiest curve to fit is the quadratic which gives a simple "parabolic" curve.

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[1] The computing services in this project were supported by NIH Grant No. FR-00011, held by the Institute of Statistics, North Carolina State University.

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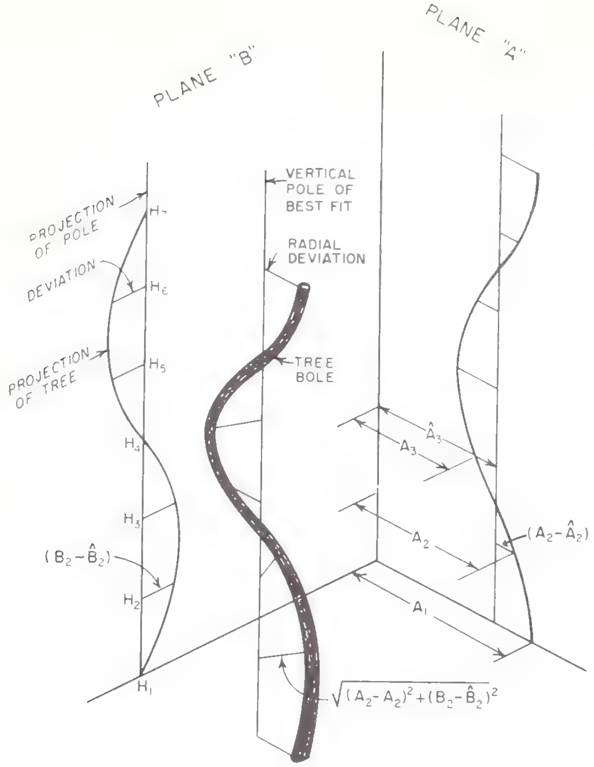

Figure 1 -- Projection of tree bole onto two vertical planes (at right angles). A vertical model is being fitted.

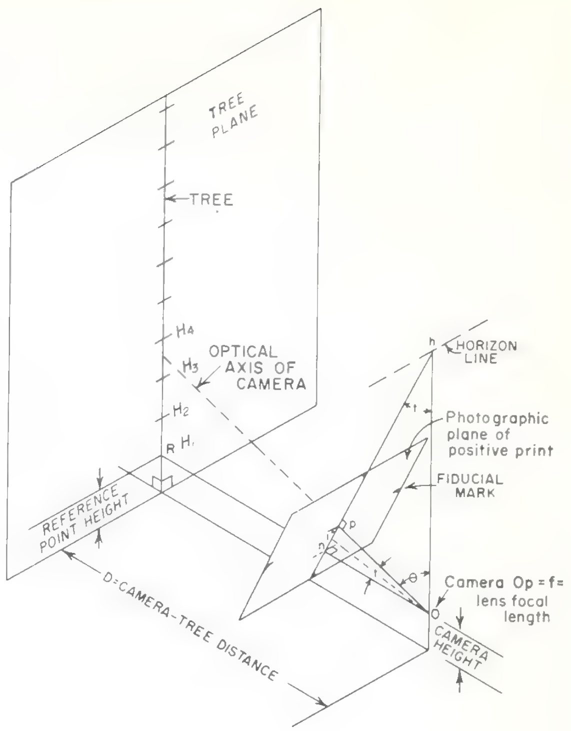

Figure 2 -- The oblique tree photograph.

After fitting these three models to the projections of the bole in the A and B planes, it is possible to compute the deviations of the location of the tree pith (as projected on that particular plane A or B) from the theoretical position of the model (vertical, leaning straight, or curved). In practice we can photographically measure $A_1, A_2, \ldots A_n$ and $B_1, B_2, \ldots B_n$ (Figure 1), and statistically calculate the expected positions of models as $\hat{A}_1, \hat{A}_2, \ldots \hat{A}_n$ and $\hat{B}_1, \hat{B}_2, \ldots \hat{B}_n$. The differences in each projection of the stem, $A_1 - A_1$, and $B_1 - \hat{B}_1$ etc., give the individual deviations from the model. Because the A and B planes are at right angles to each other, the square root of the sum of the squared deviations, $\sqrt{(A_1 - A_1)^2 + (B_1 - B_1)^2}$ is the actual radial deviation of the stem from the model "axis," at that height position. By the same procedure, the radial deviations of the stem from the three models can all be calculated. These can be presented as the sum of each deviation squared (sum of squares) or as the mean square of deviations from model.

A computer program has been written to obtain the following parameters of bole straightness:

1. Angle of lean. This is the angle made by the linear regression axis to the vertical and is calculated as:

   $$\text{tangent angle of lean} = \sqrt{b_A^2 + b_B^2}$$

   where b_A is the coefficient of the regression line in the A plane and b_B is the same for the B plane.

2. Sum of squared radial deviations from the vertical straight axis passing through the mean $\bar{A}$ and $\bar{B}$; i.e., total sum of squares, which is a measure of non-straightness and non-perpendicularity. The ideal tree, straight and vertical, would have a sum of zero.

3. Sum of squared radial deviations from the linear regression axis. This represents the deviations remaining after lean has been accounted for, and can be called non-straightness. It would be zero in the straight but leaning tree. It includes deviations caused by the curvilinearity or sweep as well as crooks (see below).

4. The sum of squared radial deviations from the quadratic curved axis. This represents

the deviations from a curved axis and corresponds to residual crook. Where there is no curvilinearity, this quantity will be the same as No. 3.

5. The additional sum of squares due to fitting the quadratic curve. This measures the extent to which the curved axis removes extra variation not accounted for by the linear regression, and as such is a direct measure of the acuteness of the curve or the incidence of sweep. The ratio of this quantity to No. 3 above represents the goodness of fit of the quadratic curve to the tree, or the proportion of the deviations from a linear regression accounted for by the quadratic curve. A high ratio would indicate that most of the deviations from linear regression are due to curvilinearity, or sweep, and that crook is not important. A low ratio indicates the converse.

All the above measures of bole straightness may be expressed as sums of squared deviations, as mean squares or as standard errors. In practice, mean squares are used for comparison.

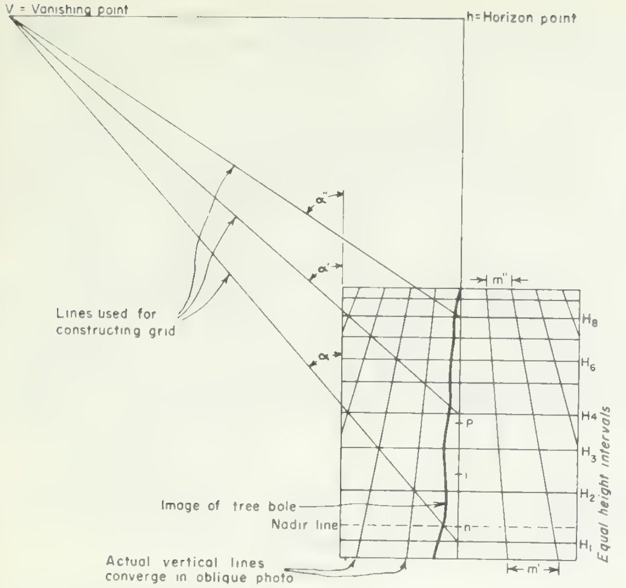

Figure 3 -- Perspective grid with tree bole photograph.

As deviations from model at each measurement point are printed out by the computer, the position of any large deviations can be located. Variation of these deviations about their mean is measured by the mean square of variation of deviations.

METHODS

There are several ways of recording the projections of the stem in two planes, but photography is the most direct and simplest. Trees must be photographed with the optical axis of the camera tilted, causing vertical lines to appear to converge on the photograph. Also, there are changes in scale with increasing height up the tree. The geometry of the oblique photograph has been fully worked out for the oblique aerial photograph and the notation of Tewinkel (1951) has been drawn on heavily for this.

The practical procedures for photography, perspective grid construction and making measurements on projected photographs together with the computer program for the analysis and also a more complete treatment of the statistical basis of the method and the photogrammetric aspects will be described in a separate publication.

The geometry of the oblique photograph of a tree is shown in Figure 2. Provided three characteristics of the oblique photograph are known, namely angle of tilt, t; tree to camera distance, D; and lens focal length, f, a perspective grid can be constructed. The photograph is then projected onto the grid (see Figure 3) and measurements of A'_i and B'_i distances are made and appropriate scales can be calculated for each height position so that actual A_i and B_i distances can be computed.

The perspective grid enables measurements of A_i and B_i to be made from the stem to a given vertical line, and horizontal lines are so spaced as to be located at equal height intervals up the tree.

In practice the photographs are projected onto a screen with a magnification of x 20 and a photographic scale of from 0.03 to 0.05 at 40 feet from the tree. A suitable perspective grid is superimposed on the screen and measurements of A'_i and B'_i (mid diameter point on stem to a given vertical line) are made there.

EQUIPMENT

A 35 mm single lens reflex camera (Pentax S.1.) with a 28 mm ultra wide angle lens has proved satisfactory for taking photographs in wild and plantation stands of southern pines of varying ages. The main problem is to get sufficiently far from the tree to include the whole of it in the photo, while being close enough to get a more or less unobstructed view.

Figure 4 -- Camera and clinometer.

The camera must be fitted with properly adjusted fiducial marks which produce images on the photograph to enable delineation of the principal line and principal point.

A Tiltall tripod Model 4602 is suitable. A special L-shaped attachment must be constructed into which the base of the camera fits snugly and which can be clamped between camera and tripod head by the tripod screw. On this L-shaped attachment a spirit level and Suunto Clinometer should be mounted (see Figure 4). The mounting must be done precisely so that, with the spirit level set, the long sides of the negative are exactly vertical. Leveling the camera and thus the photo in the horizontal plane enables the edges of the photo to be used as a vertical reference from which to measure angle of lean. The angle of tilt is set on the Suunto by adjusting the camera's tilt appropriately and the Clinometer reads zero degrees when the camera's optical axis is horizontal.

A "projection table" (see Figure 5) was devised so that a 150 watt Wollensak projector with film strip attachment projected an image enlarged twenty times, onto a mirror and through a plate glass table top onto a translucent acetate sheet on which was plotted the perspective grid. The projector was modified to take a Kodak Luxtra projection lens with short (50 mm) focal length, but this arrangement was not ideal. Better but more expensive projection equipment is on the market.

EVALUATION OF THE METHOD

Two series of tests were made of the photogrammetric method to evaluate its accuracy and to gain experience in interpreting the different measures of bole straightness.

The first test was made on a wire helix of 2.2 inches in diameter and with five full rotations in five feet of total length. This model was set up in four different configurations: vertical, leaning at an angle of 5° from the vertical, vertical but curved, and leaning but curved. Two pairs of photos were taken of each model, and measurements of A_i and B_i distances were made at intervals corresponding to three-inch intervals on the wire model.

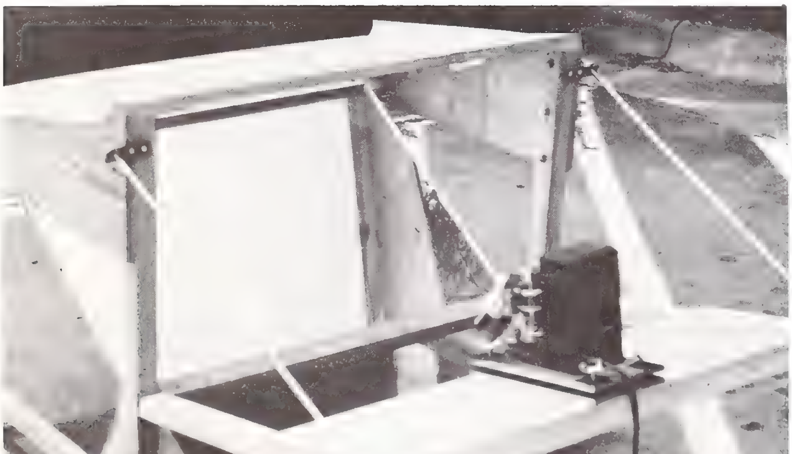

Figure 5 -- Projection table.

Repeatabilities and coefficients of variation are shown below for each measure of bole straightness:

$$R = \frac{\hat{\sigma}^2_B}{\hat{\sigma}^2_B + \hat{\sigma}^2_W} \qquad \text{and C . V.} = \hat{\sigma}^2_W / \text{ mean.}$$

	Repeat-ability (%)	Coefficient of Variation (%)
Angle of lean	98.4	10.1
Non-straightness	98.8	5.3
Sweep	99.7	6.1
Sweep ratio	99.7	8.5
Crook	56.7	7.2

The value of 56.7 for repeatability for crook can be explained by the fact that the same helix, bent in different configurations, was used for each model.

The size of the different measures and the separation between measures for different models was exactly as would be expected from a knowledge of the models' configurations. For example, Models 1 and 2 showed very slight sweep, while Models 3 and 4 showed a mean square for sweep about thirty times greater; crook showed no significant differences between the different models. Angles of lean were as expected, ± 1/2 degree. The size of the mean deviation from the best curve fitted was 1.1 to 1.2 inches in all cases corresponding closely to the actual radius of the helix of 1.1 inches as constructed.

The second test was made on a collection of eight plantation-grown trees, all aged 11 years and with heights of 55-60 feet. Three were selected for extremes of bole characteristics, while the remainder were a random sample, and of intermediate straightness. Three pairs of photos were taken of each tree and A_i' and B_i' distances were measured at intervals corresponding to two feet on the tree. (Normally only one pair of photos would be taken of each tree.) Repeatabilities and coefficients of variation are shown below for each measure of bole straightness.

	Repeatability	Coefficient of Variation
Angle of Lean	94.8	23.0
Non-straightness	99.5	12.8
Sweep	99.0	21.0
Sweep ratio	86.7	16.9
Crook	95.7	23.3

In general for all characteristics the size of confidence intervals was such that the stems picked as extremes showed wide separation and the remainder tended to show significant differences between certain groups though not between members of the same group. However, grouping of trees was not the same for every characteristic.

Coefficients of variation were about twice those for the wire models, mainly because the trees were much larger than the models and were photographed at a 40° angle of tilt under field conditions. However, repeatabilities were still high, giving confidence in the utility of the method.

DISCUSSION

The photogrammetric technique appears sufficiently reliable to provide a practicable means of measuring deviations of trees from the simple mathematical models used, i.e straight vertical, straight leaning and curved. Estimates of deviations from these models form an effective means of quantifying bole morphology. In addition to providing estimates of the angle of lean, non-straightness, sweep, and crook of the tree, the technique allows examination of the size of the individual deviations of the stem at successive height intervals.

Under reasonably favorable stand conditions, the field procedure requires only about ten minutes per tree by a technician and assistant; the time for measurement in the laboratory is approximately the same. Transfer of measurements from data sheets to IBM cards and subsequent computer time is insignificant on a single tree basis. Total time required is probably comparable to that required for other wood property measurements such as specific gravity and fiber length. Investment in equipment is not great, particularly since the three major items, single lens reflex camera, wide angle lens, and projector will have many other uses.

In addition to model fitting, errors in the technique occur at three main stages: photography, projection, and measurement.

The basic faults of the technique lie in the failure of the main assumption that the tree plane is vertical. Differences in tree-measurement-point to camera distances from those calculated on the basis of tilt and perpendicular tree to camera distance will result, and hence errors in the actual photographic scale at each H_i point will occur.

The photographic scale depends on tree to camera distance and focal length of the lens, as well as the tilt angle. Thus, the smaller the scale, the greater will be a given absolute measurement error, and so the smaller the tree to camera distance (and the smaller the tilt angle), the more accurate the measurements will be. A partial solution might be to photograph only the lower part of the bole that contains--or will eventually contain--the greatest and most valuable part of the merchantable volume. Thus it would be possible to assess progenies no later than when they had reached a height below which the bulk of the merchantable volume would be contained at maturity. An additional advantage of an assessment at a young age would be that the true configuration of the bole would be obtained before differential diameter growth obscured much of the tree's crook, as always happens as a tree ages.

Additional errors in scale can result from imprecise alignment of the camera; camera tilt angle must be the same as the tilt angle used for computing the perspective grid dimensions. Errors in leveling the camera cause errors in measurement of lean angle.

Any scale errors cause incorrect measurement of the deviation values and incorrect location of the vertical sampling points. Thus the "A" projected deviation is measured at a different height than the "B". The result is considerable error in line fitting and the location of the stem, with errors in its deviations from the model.

Measurement accuracy on the projected photograph was from ± 1/50 to ± 1/100th inch using a clear plastic rule; this means an error of from ± 0.2 to 0.7 inches at scales 0.03 to 0.05 used in the tree photographs.

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Slash, Loblolly, and Shortleaf Pine in a Mixed Stand; A Comparison of Their Wood Properties

DONALD E. COLE, BRUCE J. ZOBEL, AND JAMES H. ROBERDS[1]

INTRODUCTION

Differences have been reported among the major southern pines[2] with regard to disease resistance, form and rate of growth although there are conflicts, particularly regarding differences in growth rate. In addition, differences have been reported for such characteristics as wood specific gravity, extractive content, and total yield (see Mitchell, 1963; Johnson and Roth, 1896; Chidister et al, 1938; Robinson, 1956; and Bray and Curran, 1937). In many of the studies of growth rate and in most of the wood property and pulping studies, a direct comparison of different species has not been made in which site, age, and spacing are comparable. If one is interested in the real productive potential of slash and loblolly pine, a comparison of slash pine in north Florida with loblolly pine in central South Carolina, for example, is quite meaningless. There are many reports in the literature which do just that and often it is then concluded that species differences exist. It is essential to compare trees of the same age, growing under the same conditions, in order to make a really meaningful comparison between species.

Such a comparison, in which differences between species could be isolated from differences due to geographic origin, age, site, or other confounding variables, would be of considerable practical importance as a guide in forest management planning, in interpreting reported differences in growth rate, and in situations where a choice could be made between

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2/ Slash pine (Pinus elliottii var. elliottii Englm.), loblolly pine (Pinus taeda L.) and longleaf pine (Pinus palustris Mill.).

the species.

In order to clarify the wood property relationships among loblolly, slash, and longleaf pine, a study was initiated cooperatively by Continental Can Company, Inc., Savannah, Georgia, and the Cooperative Tree Improvement Program at North Carolina State University, Raleigh, N. C.

The present paper reports the results of the work done on the breast height increment cores; the data from the felled trees, from which wedges and cores were obtained and on some of which pulping studies were made, will be reported in a more complete paper at a later date.

The objectives of the study were:

A. To compare the wood properties of slash, loblolly and longleaf pine by analyzing wood samples from a mixed even-aged stand on a relatively uniform site.

B. To determine which species produces the most wood substance under these conditions.

METHODS

A. Field Procedures:

The study was conducted on a fifteen-acre old field stand in Bulloch County, Georgia. It is remarkably uniform with virtually no relief and less than 1% slope. It is a soil of the Kley series; after a careful examination, it was found that the soil site index for a given species varied less than five feet within the stand; site index at 50 years was 71' for longleaf and pond pine, 80' for slash pine and 90' for loblolly pine. There has been one very light improvement cut in the stand but otherwise it has been undisturbed. The stand is about 40% slash pine with loblolly and longleaf pine each making up about 30% of the volume. A very few pond pines are growing throughout the area, and nine were large enough to include in the study. Although the pond pine sample size is too small to permit us to draw definite conclusions, it does give some basis for comparing this species with the other three species. All three major species grow intermixed throughout the stand.

Fifty dominant or co-dominant sample trees were chosen for each species. Trees with excessive lean, crook, or large fusiform stem cankers were avoided. The loblolly and longleaf sample trees, being least abundant, were marked first and then the slash sample trees were chosen in the vicinity of the other two species; thus sample trees were grouped in the same areas of the stand. Each sample tree was paint-marked, bark-scribed with a number, and described externally by a series of measurements of height, diameter, crown size, and bole straightness. The mensurational data is summarized in Table 1. In addition, a record was made of all sample trees located within 50' of any other sample tree so comparisons of sample trees growing adjacent to each other could be made. A bark-to-bark 10 mm. increment core was taken at 4.5' from each sample tree. Cores which contained knots or pitch pockets or which missed the pith by more than two rings were rejected and these trees were re-bored until a satisfactory core was obtained.

These double cores were used for the determination of specific gravity, extractive contant, tracheid length, & cellulose content; this phase of the work was done during December, 1963, and January, 1964. Later it was decided that additional data on these trees was needed, including moisture content of the wood. Therefore in May & June, 1964, an additional bark-to-pith core was pulled from each sample tree and weighed in the field; these cores were obtained with an electric drill powered by a portable gasoline generator.

At the same time, ten trees of each of the three major species were felled; each bolt was weighed, and cores and wedges were taken from each bolt for the determination of wood properties. Finally, two trees from each species were sent to the Research and Development Laboratory of Continental Can Company's Paperboard and Kraft Paper Division, in Augusta, Georgia, for pulping studies; the details of this phase of the study will be reported later. To obtain moisture content of the wood, the cores were weighed in the field using the following procedure; after the reversible drill was backed out of the tree, the bit was removed from the drill and carried (with

Table 1. Mensurational Data.

Species	No. Trees	DBH	Total Height	Rings @ BH	CW Years	Cu. Vol. 2" Top*
Lob.	50	10.2"	56'	16	7	13.3
L. L.	50	10.8"	58'	21	7	11.8
Sl.	50	10.0"	54'	17	7	11.6
P. P.	9	11.0"	50'	21	7	--

* - Adjusted to a common age.

the core inside) to the field laboratory. There the core was removed from the bit, the bark was removed and the whole core was weighed. Then the core was separated into outerwood (mature wood) and visual corewood [3] and each segment was weighed separately. Next, the segments were labeled, the length and number of rings per segment was recorded, they were put into plastic bags, and sent to N.C. State University for laboratory analysis. The cores were weighed on a Mettler K7-T Balance which weighs to 1/100th gram with an accuracy of ± 3/100 grams. This accuracy corresponds to about 1/10% of the weight of the average corewood segment (outerwood segments were heavier) and about 1% of the weight of the smaller corewood segments. The accuracy of the rapid-reading balance was checked each time it was set up and it gave very little trouble in use. Cores were stored prior to analysis under running water to prevent molding. All field work was done as rapidly as possible to avoid loss of moisture by evaporation.

B. Laboratory Analysis

Wood property determinations made in the North Carolina State University laboratory included:

1. Specific gravity before and after extraction.
2. Extractive content (alcohol-benzene soluable.)
3. Moisture content.
4. Tracheid length.
5. Cellulose content.

Moisture content is the ratio of weight of water lost on drying to unextracted dry weight of the wood. It is important to note that the basis is dry wood weight because often moisture content is reported as the ratio based on wet weight.

Specific gravity is determined by the ratio of dry weight to green volume; from the difference in dry weight of the cores before and after extraction, the extractive content is calculated and expressed as a percentage of the dry weight of the extracted wood. Extractive content here refers only to those substances extractable by alcohol-benzene; this is not a complete extraction although most of the resinous materials are removed.

Tracheid lengths determined are average values for uncut tracheids. Forty tracheids were measured for each segment of each core.

Cellulose yields were obtained by a method developed by Yundt and Bradway (see Zobel and McElwee, 1958). It is a survey method, involving a chloriting procedure to obtain the water resistant carbohydrates (loosely referred to as holo-cellulose). In addition, alpha cellulose was determined. The data on cellulose content and tracheid lengths is summarized in Table 2; the data on specific gravity, extractive content, and moisture content is summarized in Table 3.

Table 2. Cellulose content and tracheid length data.

SPECIES	CELLULOSE CONTENT %				TRACHEID LENGTH	
	HOLO		ALPHA			
	CW	OW	CW	OW	CW	OW
Lob.	81.59	83.27	54.62	61.33	2.58	3.45
L. L.	74.74*	79.65	51.44	60.26	2.88**	3.81**
Sl.	78.07	81.13	55.28	62.14	2.62	3.55
P. P.	79.67	82.33	54.70	61.55	2.60	3.50
Avg.	78.13	81.35	53.78	61.24	2.69	3.60

* - Differs significantly at the 5% level.
** - Differs significantly at the 1% level.

Table 3. Specific gravity, extractive content, and moisture content data.

SPECIES	SPECIFIC GRAVITY						Extractive Content %			Moisture Content % *		
	Unextracted			Extracted								
	CW	OW	Wt'ed.	CW	OW	Wt'ed.	CW	OW	Wt'ed.	CW	OW	Wt'ed.
Lob.	.430	.553	.541	.413	.540	.527	3.06	2.67	2.71	126.8	102.0	104.5
L. L.	.503	.542	.538	.442	.529	.520	13.57	2.42	3.53	95.2	98.1	97.8
Sl.	.462	.538	.530	.439	.526	.517	4.99	1.78	2.10	99.2	97.2	97.4
P. P.	.420	.481	.475	.396	.468	.461	-	-	-	-	-	-

* - Adjusted for differences in age and extractive content.

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[3] Corewood has a characteristic "lifeless" appearance because of difference in light reflectivity. It is often "cheesy" in consistency and has very little summerwood. There is no sharp line of demarcation between corewood and outerwood, but usually the separation comes at the 7th to 10th ring from the pith. Corewood must not be confused with heartwood which may or may not be present.

RESULTS AND DISCUSSION

A. Cubic Volume

Adjustment of the volumes of the different species to a common age by co-variance analysis showed that there were differences between the species in cubic volume to a 2" top; the differences were significant at the 5% level and the average volume of the loblolly was significantly higher than either the slash or longleaf sample trees.

Rings at breast height was used to estimate age for this analysis which gives a conservative or low estimate of the age of the longleaf sample; if rings at breast height plus three had been used for the loblolly and slash sample trees and rings at breast height plus five for the longleaf sample trees, the differences in cubic volume between species would have been more marked. It is surprising, and important, that on this typical flatwoods slash pine site the average volume of the loblolly sample is 15% greater than that of the slash sample.

B. Specific Gravity

Probably the most important single finding of this study is that there were no significant diferences between the outerwood specific gravity, extracted or unextracted, of the slash, loblolly, and longleaf pine sample trees in this stand where all three species were growing together in a natural stand (see Table 3). Although the specific gravity of the loblolly pine was somewhat higher than that of the other two species the differences were not statistically significant.

These results are quite different from the idea held by most foresters and should prompt a very close scrutiny of our opinions as to the merits of these species.

There were small differences between species in corewood specific gravity but they will have only a small net effect. An average of 90% of the total merchantable volume of these trees was outerwood based on measurements of the 31 trees which were felled and sampled intensively. If a 0.02 difference in specific gravity is equal to a change of 100 pounds in the dry weight of a cord of wood (see Mitchell, 1963) the difference of 0.03 between the extracted corewood specific gravity of the loblolly sample trees and that of the slash and longleaf sample trees would indicate a difference in dry weight of only 15 pounds per cord between species.

There were so few pond pine sample trees that the data on these trees were not included in the general analyses. However, the differences in specific gravity between pond pine and the other species are so marked that there would undoubtedly be reduced yields from such wood.

C. Moisture Content Percent

Moisture content data adjusted to a common age (as measured by rings at breast height) for all species showed some differences between species (see Table 3). However, these differences were not statistically significant

D. Extractive Content

Surprisingly, all species were nearly alike in the extractive content percent of the outerwood. The corewood was much more variable with the loblolly and slash sample trees being significantly lower and the longleaf sample trees being significantly higher than the average. Total extractive content, corewood and outerwood, followed the same pattern as the corewood extractive content, with the longleaf being highest at 3.54%; this was 27% greater than the average weighted extractive content at breast height for all three species and would probably be of some economic significance.

It appeared from the samples studied that the longleaf pine had a greater amount of heartwood formation than the other two species.

E. Age (Rings at Breast Height)

The loblolly and slash pine sample trees did not differ significantly from one another in age. However, the longleaf sample trees differed significantly (at the 1% level) from the others when age was expressed as rings at breast height, being an average of 5.5 years older than slash or loblolly pines. As was noted earlier, total age would have shown even greater differences. Even though the range was from 16 to 21 rings at breast height the stand sampled was considered to be essentially even-aged.

F. Core Wood Years at Breast Height

This analysis showed no difference among the three major species in the number of years (or rings) of corewood formation at breast height; it was about seven years for all three species.

The range of years of corewood formation was also very nearly the same for all species, from a low of four years to a high of eleven years. That there were no differences between species is especially surprising because these values were based on an independent ocular estimate for every tree and it is commonly thought that the duration of corewood formation would vary considerably between species.

G. Tracheid Length, Corewood and Outerwood

Analysis of the tracheid length data showed that the longleaf sample trees had longer tracheids, both in the corewood and the outerwood, than the other species; this was significant at the 1% level. The differences in tracheid length between the slash and loblolly were not significant.

The differences between longleaf and the other species are of such low magnitude (about 3/10 mm.) that their effect on paper properties is questionable; however, this data indicates that there are real differences between longleaf and the other two species, at least in this population.

H. Cellulose Content Percent [4]

There were no significant differences between the species in alpha cellulose content, either in the corewood or the outerwood, nor in the holo-cellulose content of the outerwood.

However, the holo-cellulose content percent of the corewood of the longleaf sample trees was significantly lower (at the 5% level) than that of the other species in spite of the fact that its corewood specific gravity was higher (these determinations were made on extracted wood). But the effect of this low cellulose content on pulp yields would be negligible because of the low proportion of corewood in these trees.

I. Form Class (Fogelberg's)

There were no significant differences among the species in this stand in form class as determined on the standing trees by Fogelberg's method. This also was somewhat surprising since it is commonly felt that both slash and longleaf pine have better form than loblolly pine.

CONCLUSIONS

The results of this study, based on data from 10 mm. increment cores at breast height, indicate that where loblolly, longleaf and slash pine are grown together in natural stands there are no significant differences among them in (1) outerwood specific gravity, extracted or unextracted; (2) moisture content; (3) years of corewood formation; (4) cellulose content (except for corewood holo-cellulose content); and (5) form class (Fogelberg's).

Differences were found in tracheid length, corewood specific gravity and corewood holo-cellulose content but they were of such low magnitude that they probably would have little effect on pulp yields or paper properties when total yields per acre are considered.

There were important differences between the species in rate of growth and extractive content. The loblolly sample trees were significantly larger in cubic volume (15%) than the longleaf and slash in spite of the fact that the estimate of age used in the analysis (rings at breast height) was probably biased in favor of the longleaf sample trees. The longleaf sample trees had the highest total extractive content at breast height (27% more extractives than the average of the slash and loblolly sample trees); this would probably be a factor of economic significance.

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[4] Cellulose yields are the ratio of cellulose obtained to the dry weight of the wood used.

The results cited here apply with certainty only to this particular stand and this data should not be applied to other areas until such time as these results have been tested and confirmed in other mixed stands.

However, we believe that the results are significant enough to warrant further investigation; if these results are confirmed, we should adjust our thinking about these species in the light of this new information on wood properties and growth.

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The Effect of Spacing, Fertilization, and Cultivation on Flowering and Seed Production in Loblolly Pine

J. P. VAN BUIJTENEN [1]

INTRODUCTION

The objectives of this study were:

1. To determine the best way to handle a seed orchard so as to produce the earliest, heaviest and most substained yield of seed.

2. To determine the economic feasibility of seed orchards.

3. Of secondary importance, to produce in quantity seed of drought resistance stock and to test these for their genetic worth.

The study was set up in 1954, by Zobel and Cech when virtually nothing was known about the management of seed orchards. From 1956, till 1960 the project was continued by Brown, and carried on since that time by the author. The study set out specifically to determine the effect of cultivation, fertilization, spacing and physiological age of the scion material on flowering and seed production. The literature on the subject was reviewed by Matthews (1963), Richardson (1962) and Zobel (1958).

MATERIALS AND METHODS

The materials in the orchard consist entirely of loblolly pine selected for drought resistance. The great majority of these selections were made in the "Lost Pine" areas in Bastrop and Fayette County. A few selections from Leon County and Anderson County were also included. The orchard was established over the period from 1954 through 1960. The bulk of the material was established during the period from 1954 through 1957. The soil is an extremely deep sand. The drought of 1956 and 1955 affected the orchard rather severely and caused growth during these years to be very slow. The experiment was basically set up as a

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factorial design. The following factors were tested:

1. Disking versus mowing.
2. Three levels of fertilization:
    a. Unfertilized control.
    b. A low level of fertilization consisting of two hundred pounds of phosphorous and potassium per acre plus two applications of nitrogen, each at a rate of a hundred pounds per acre and
    c. A high level of fertilization consisting of 500 pounds of P and K per acre, plus two applications of nitrogen each at a rate of 300 pounds per acre.

The fertilizer requirements were determined each year from the soil analyses of samples taken each fall. Phosphorous was given in the form of 45% super phosphate in a quantity sufficient to bring the calculated amount of phosphorous up to the prescribed level. The same procedure was followed for potassium, which was administered in the form of muriate of potash. The full amount of nitrogen was given at each application as ammonium nitrate.

3. A 30' x 30' spacing versus a 20' x 20' spacing.
4. Grafts from physiologically young material compared to grafts from physiologically mature material. The physiologically juvenile grafts were obtained from open pollinated progenies of the ortets from which the clones of mature material were derived. The orchard was not laid out according to a regular statistical design although all 24 possible treatment combinations are present. They were, however, arranged to make comparisons of most treatments feasible and a good many of combinations of treatments. An important consideration in the design was also the convenience of applying the treatments. The experimental layout is shown in Figure 1. All treatment combinations are replicated twice except the six combinations involving juvenile grafts at the 30' x 30' spacing.

The following observations were made:

1. Number of pollen clusters per graft.
2. Number of female flowers[2/] per graft.
3. Number of cones per graft.

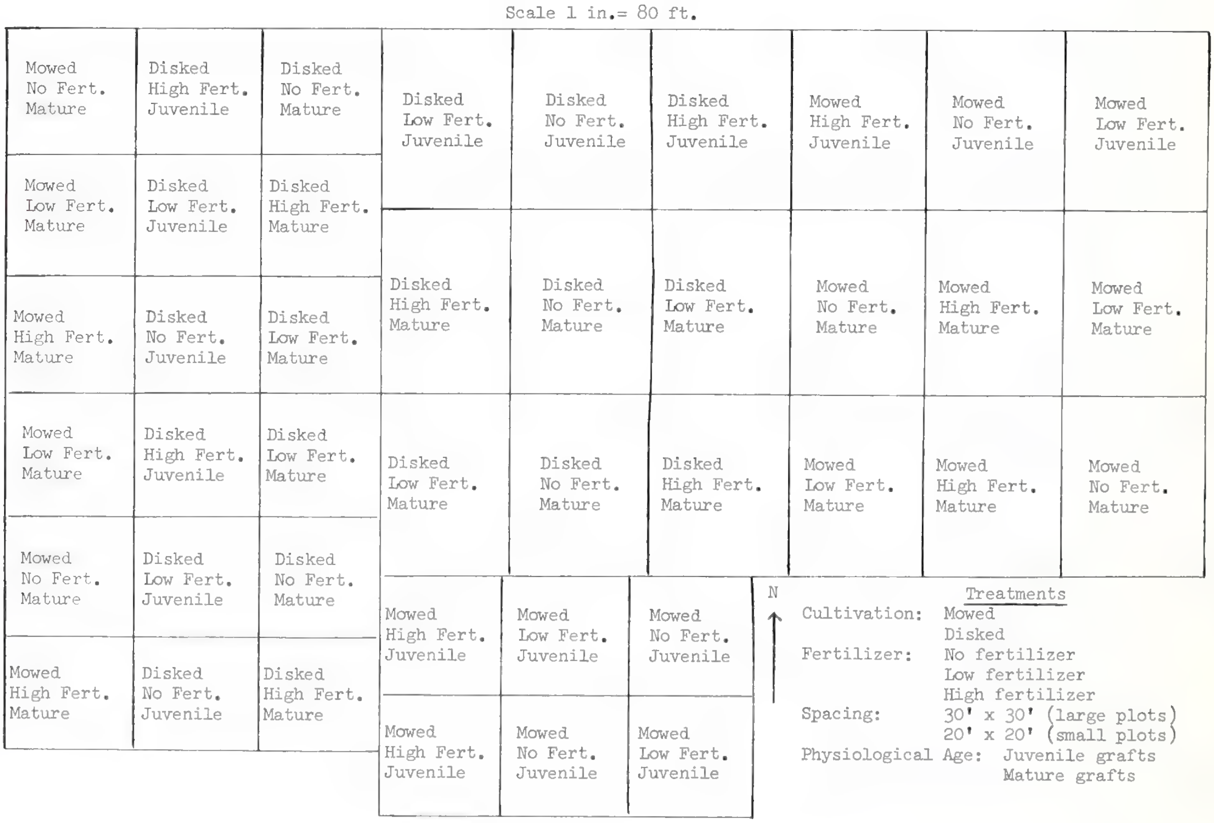

FIGURE 1. FIELD LAYOUT OF EXPERIMENTAL ORCHARD

[2/] Although botanically incorrect, the term flower has been colloquially accepted and has been used throughout this paper instead of the term strobilus.

4. Total number of seeds per graft.
5. Number of sound seeds per graft.

This paper is based on the data from 1962 and 1963.

RESULTS

Due to the unequal number of grafts in the various blocks, the different ages of the grafts and the missing replication an analysis of variance by the usual method is virtually impossible. Two approaches were taken in comparing the various treatments:

1. By grouping the data according to grafts of the same age and comparing blocks containing sufficient numbers for a statistical analysis.
2. By making an over all analysis following the method of fitting constants described by Li (1964).

Comparisons using part of the data. The results of the comparisons are given in Table 1.

Cultivation had a significant effect on the 1962 female flower production and both the male and female flower production in 1963. In all cases flower production was increased by disking.

Statistically significant effects of fertilization on male and female flower production could be demonstrated in 1962 and 1963. Fertilization apparently increases the number of female flowers, and decreases the amount of male flowers.

The number of ways in which spacing could be compared was very limited. It could be shown however, that spacing significantly increased male flower production.

It was impossible to compare the juvenile and mature grafts in this manner, since the

Table 1. Comparisons between various treatments after grouping data according to age of graft. The values given are averages per graft.

Treatments	1962 pollen clusters	1962 female flowers	1962 cones	1962 total seed	1962 sound seed	1963 pollen clusters	1963 female flowers	1963 cones	1963 total seed	1963 sound seed	Remarks
Mowed	272	131	13	480	424	476	77	22	610	151	
Disked	221	135	14	514	413	500	113	25	1843	1040	Group 1
Control	363	104	11	484	258	730**	65	29	841	553	Planted in 1954
Low fertilizer level	192	134	14	324	396	420	76	18	1237	734	30' x 30' spacing
High fertilizer level	176	164	16	710	626	290	153	23	1693	517	Juvenile scions
Control	435	90	2	7	6	388*	74	4	403	296	Group 2
Low fertilizer level	242	69	12	475	449	209	34	12	415	52	Planted in 1954 Disked
High fertilizer level	208	125	14	733	653	162	52	2	12	4	20' x 20' spacing Juvenile scions
Control	71	12	1	30	24	178	20	3	22	131	Group 3
Low fertilizer level	130	40	2	91	79	127	29	2	223	12	Planted in 1955 Mowed
High fertilizer level	115	50	1	9	7	179	25	2	50	16	20' x 20' spacing Juvenile scions
Mowed	12	7	.3	20	17	64	22	--	--	--	
Disked	24	11	-	--	--	112	56	--	--	--	Group 4
Control	3	3	.08	7	5	55	18	--	--	--	Planted in 1957
Low fertilizer level	40	10	.20	8	6	126	55	--	--	--	30' x 30' spacing
High fertilizer level	18	18	.14	13	13	109	63	--	--	--	Mature scions
Mowed	9	4**	.1	68	63	49*	19*	--	--	--	
Disked	13	13	1	40	31	83	42	--	--	--	Group 5
30' x 30' spacing	19**	9	.1	9	7	91*	41	--	--	--	Planted in 1957
20' x 20' spacing	6	9	1	82	71	52	25	--	--	--	Mature scions
Control	291*	71	5	137	109	454*	54	14	451	306	Pooled Data
Low fertilizer level	189	79	9	347	307	263	45	10	600	286	
High fertilizer level	167	114	11	495	438	195	78	9	597	182	

* The treatment effect in this group is significant at the 5 percent level.
** The treatment effect in this group is significant at the 1 percent level.

great majority of the juvenile grafts were established before the mature grafts.

Analysis using the method of fitting constants. The nature of this type of analysis is very similar to a multiple regression analysis and is particularly suited for data in which the number of observations is unbalanced. It has the additional advantage of allowing the use of a number of variables as covariates. The effect of such variables can be accounted for in the analysis of variance. In this instance, the year in which the graft was planted was used as such a variable, thus adjusting all data to the same year of planting. The results are summarized in Table 2. For the purpose of comparison the actual averages are given in Table 3.

A significant effect of cultivation could be demonstrated on the female flowers, number of cones, total amount of seed, and the number of sound seed produced. In every case the disking treatment showed an increase over mowing.

A significant effect of fertilization could be shown on male flower production, female flower production, and seed production in 1962. No effect could be demonstrated in the 1963 cone and seed data. Fertilization had a depressing effect on male flower production and increased the other factors.

Spacing had a significant effect on male flower production, female flower production, cone production, and seed production. In all cases production in the 30' x 30' spacing was highest.

Physiological age had a significant effect on male flower production and on the 1963 cone and seed production.

DISCUSSION

As shown in Table 2 disking has a considerable stimulating effect on flower and seed production as compared to mowing. An objection sometimes raised to the practical application of disking is the possibility of increased danger of infection by Fomes annosus. In our ex-

Table 2. Adjusted averages of significantly different treatments.

Treatments	1962 pollen clusters	1962 female flowers	1962 cones	1962 total seed	1962 sound seed	1963 pollen clusters	1963 female flowers	1963 cones	1963 total seed	1963 sound seed	Number of grafts in each group
Mowed							39	5	164	56	230
Disked							54	11	523	276	243
Control		35		126	99	214	36				168
Low fertilizer level		45		187	164	164	44				153
High fertilizer level		65		390	341	130	60				152
30' x 30' spacing		64	7	344	291	224	66	14	594	290	173
20' x 20' spacing		32	3	125	111	115	27	2	94	42	300
Juvenile	126					209		15	607	300	217
Mature	56					130		2	80	32	256

Table 3. Overall averages of treatments.

Treatments	1962 pollen clusters	1962 female flowers	1962 cones	1962 total seed	1962 sound seed	1963 pollen clusters	1963 female flowers	1963 cones	1963 total seed	1963 sound seed	Number of grafts in each group
Mowed	71	37	4	213	187	137	32	3	93	29	230
Disked	94	47	5	188	159	153	48	8	353	180	243
Control	91	31	3	118	94	178	33	4	148	93	168
Low fertilizer level	86	43	5	188	166	150	41	8	237	108	153
High fertilizer level	70	54	6	304	267	104	47	4	304	121	152
30' x 30' spacing	102	69	8	375	318	222	69	12	492	237	173
20' x 20' spacing	72	27	2	99	87	101	23	2	74	31	300
Juvenile	152	64	6	253	221	224	47	11	470	227	217
Mature	24	23	3	156	132	79	34	1	20	4	256

perience no adverse effect of disking on the condition of the trees has been apparent. As a matter of fact survival has been slightly better in the disked than in the mowed blocks. Another more serious objection is the danger of erosion. On many types of soil this poses a serious problem, and makes the use of disking as a method to stimulate seed production highly questionable.

Fertilization had a stimulating effect on female flower production and seed production, but a depressing effect on male flower production. Increased female flower production as a result of fertilization has been reported most recently by Goddard (1965). It is interesting to note that in 1963 the per cent sound seed in the highly fertilized blocks was considerably lower than in the controls, while the difference was much less pronounced in 1962. This is particularly meaningful if one remembers that in the spring of 1962 a severe frost did considerable damage to the pollen. This could have made the general availability of pollen so low that the reduction in the amount of male flowers in the highly fertilized blocks might have been a critical factor.

The 30' x 30' spacing seems to be much preferable over the 20' x 20' spacing. In 1962 the seed production was approximately equal on a per acre basis. In 1963, however, the seed production in the wide spacing was approximately three times as high on a per acre basis as in the 20' x 20' spacing. Visual observation of the orchard also indicates that the 20' x 20' spacing is becoming much too close.

The comparison between juvenile and mature materials was one of the most difficult to make, since the juvenile materials were predominantly established in the first three years of the experiment while the mature materials were established in the subsequent years. The statistically significant difference in pollen production appears to be rather typical. Juvenile grafts have been observed to produce abundant pollen year after year. The difference in cone and seed yields between the two groups, however, appears to be abnormally strong in 1963 and was rather contrary to expectation. The most likely explanation is that the mature grafts were more severely affected by the freeze because the flowers generally develop more rapidly than the flowers of the juvenile materials. Also the effect of the difference in age might not have been completely removed by the covariance analysis.

The study confirms the impact of cultural treatments on seed production although a good many points need clarification.

With respect to disking, it would be desirable to determine whether the effect is due to root pruning, the reduction of competition with ground cover, or both. The results might suggest better means of obtaining the same effect.

With regard to fertilization the effect of individual elements needs further study. An experiment established by Brown in 1958 on the effects of P and N is a step in this direction.

SUMMARY

1. Disking stimulates both seed and flower production. Erosion can often be a serious deterrent to its practical application.

2. Fertilization with a complete fertilizer stimulates female flower production, but has a depressing effect on male flower production. Seed production is increased.

3. A 30' x 30' spacing is preferable to a 20' x 20' spacing both with respect to flowering, and seed production on a per acre basis.

4. Juvenile grafts tend to produce more male flowers. No significant difference could be shown between the female flower production of juvenile and mature grafts. No conclusions can be drawn from the seed production in 1963 since mature and juvenile grafts were probably affected differently by the damaging freeze in the spring of 1962.

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A Report on Cone and Seed Yield in Georgia Forestry Commission Seed Orchards

SANFORD DARBY 1/

The question of prime interest to tree improvement workers is, what cone and seed yields will seed orchards produce? Do grafted trees have the fecundity of other forest trees? Are they more productive?

I wish it were possible for me to give you the answers to these questions. I feel I am safe in saying that large acreages of grafted seed orchard trees have not been established a sufficient length of time to give us yield data on which to base an answer. I was asked to report on cone and seed yields in the Georgia Forestry Commission seed orchards. To expedite our subject I am going to present orchard yield data in tabular form. The material is presented in Tables 1 through 7.

To acquaint those individuals who may not be familiar with the Georgia Forestry Commission's tree improvement activities, we will briefly review the program. Work was commenced on two orchards in 1954. The orchards are located near Glenwood and Cochran, Georgia, approximately forty miles apart. One hundred seventy-nine slash and 129 loblolly phenotypes were selected for use. Grafting was commenced in 1955. Initial ramets were planted in the orchards in 1956. Today, ten years later, we are still propagating ramets for the orchards. Currently, 26,333 slash (Pinus elliottii Engelm.) and 11,974 loblolly (Pinus taeda L.) ramets are living. The orchards are uneven aged and over 80 percent of the ramets are five years or less in age. Forty-one slash clones have produced no wind-pollinated cones. Only thirteen loblolly clones have been non-productive.

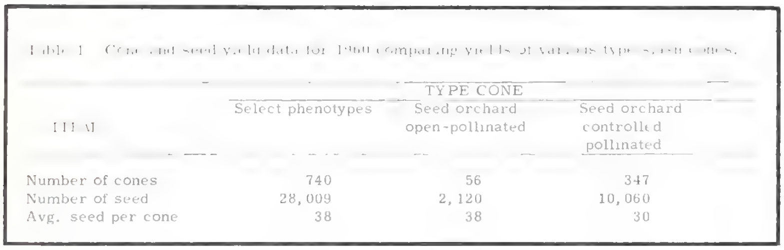


Table 1. Cone and seed yield data for 1960 comparing yields of various type slash cones.

ITEM	TYPE CONE Select phenotypes	 Seed orchard open-pollinated	 Seed orchard controlled pollinated
Number of cones	740	56	347
Number of seed	28,009	2,120	10,060
Avg. seed per cone	38	38	30

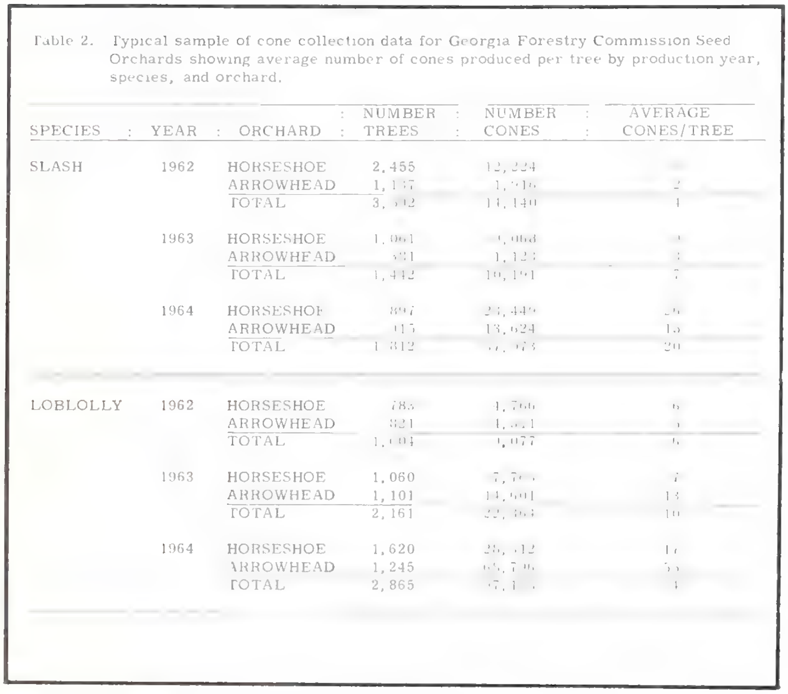
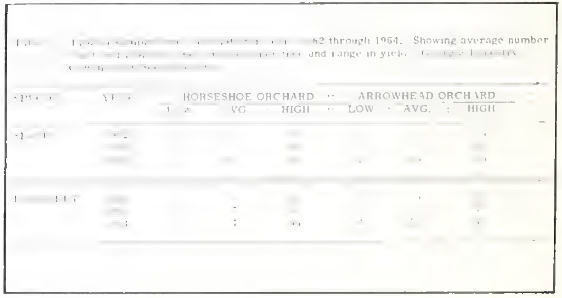


Table 2. Typical sample of cone collection data for Georgia Forestry Commission Seed Orchards showing average number of cones produced per tree by production year, species, and orchard.

SPECIES	YEAR	ORCHARD	NUMBER TREES	NUMBER CONES	AVERAGE CONES/TREE
SLASH	1962	HORSESHOE	2,455	12,224	[illegible]
		ARROWHEAD	1,137	1,916	2
		TOTAL	3,592	14,140	4
	1963	HORSESHOE	1,061	9,068	9
		ARROWHEAD	381	1,123	3
		TOTAL	1,442	10,191	7
	1964	HORSESHOE	897	23,449	26
		ARROWHEAD	915	13,624	15
		TOTAL	1,812	37,073	20
LOBLOLLY	1962	HORSESHOE	783	4,766	6
		ARROWHEAD	821	1,[illegible]1	[illegible]
		TOTAL	1,604	[illegible],077	[illegible]
	1963	HORSESHOE	1,060	7,7[illegible]	7
		ARROWHEAD	1,101	14,601	13
		TOTAL	2,161	22,364	10
	1964	HORSESHOE	1,620	28,[illegible]12	17
		ARROWHEAD	1,245	65,7[illegible]6	53
		TOTAL	2,865	[illegible]	[illegible]

Orchard cone production records are maintained on IBM cards. Seed yield records were kept on the weight of seed per cone in grams.

In an attempt to obtain preliminary information on seed yield, a small amount of data was collected during


[illegible] 62 through 1964. Showing average number [illegible] per tree and range in yield. [illegible]

SPECIES	YEAR	HORSESHOE ORCHARD LOW	 AVG.	 HIGH	ARROWHEAD ORCHARD LOW	 AVG.	 HIGH
SLASH	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
LOBLOLLY	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

1/ Chief of Reforestation, Georgia Forestry Commission, Macon, Georgia

Table 4. Comparison of slash and loblolly cone yields by clones for period 1962 through 1964 Georgia Forestry Commission Seed Orchards.

Species	Clone	HORSESHOE ORCHARD Number Trees	HORSESHOE ORCHARD Number Cones	HORSESHOE ORCHARD Average Cones/Tree	ARROWHEAD ORCHARD Number Trees	ARROWHEAD ORCHARD Number Cones	ARROWHEAD ORCHARD Average Cones/Tree
Slash	5	21	124	6	1	4	4
	18	1	2	2	9	83	9
	45	72	666	9	2	7	3
	46	1	17	17*1/	69	118	2
	80	1	1	1*	30	242	8
	85	81	179	2	4	17	4
	86	86	902	11	17	228	13
	87	4	15	4	3	8	3
	106	1	1	1	3	28	9
	119	3	8	3	6	63	10
	136	1	2	2	5	403	81
	157	17	28	2	1	27	27
	174	78	1151	15	2	71	35
TOTAL		367	3096	8	152	1299	9*
Loblolly	500	2	81	41	78	1406	18
	513	36	285	8	6	87	15
	514	1	15	.5	73	1655	23
	516	26	155	6	4	128	32
	527	29	156	5	2	117	59
	531	11	147	8	2	12	6
	538	39	148	4	78	1630	21
	546	28	229	8	1	26	26
	570	0	0	0	10	165	17
	577	65	424	7	41	1030	25
	617	77	506	7	56	2086	37
	618	44	268	6	26	659	25
TOTAL		366	2414	7	377	9001	24*

1/ * Indicates range in cone yield per tree.

Table 5. Sample seed yield data for Georgia Forestry Commission open pollinated slash and loblolly cones by production year.

Species	Year	Number Cones	Total Seed Yield Grams	Total Seed Yield Pounds	Average Seed Yield/Cone Grams	Average Seed Yield/Cone Ounces
Slash	1962	14,128	7,202.4	15.88	.510	.018
	1963	10,157	19,144.0	42.21	1.885	.066
	1964	33,361	58,668.0	129.34	1.759	.062
	Total	57,646	85,014.4	187.43	1.475	.052
Loblolly	1962	9,270	8,954.7	19.74	.966	.034
	1963	22,189	17,292.5	38.12	.779	.027
	1964	97,108	119,750.4	264.01	1.233	.043
	Total	128,567	145,997.6	321.87	1.136	.040

Table 6. Typical seed yield data for years 1962 through 1964, showing in grams range in yield per cone for slash and loblolly pine. Georgia Forestry Commission Seed Orchards.

Species	Year	Low	Average	High
Slash	1962	.05	.510	2.71
	1963	.16	1.885	6.72
	1964	.11	1.759	5.95
Loblolly	1962	.10	.966	4.21
	1963	.10	.779	2.11
	1964	-	1.233	---

1960. The interesting thing shown in this particular sample (Table 1) is that open-pollinated slash seed orchard cones produce seed equal in number to wind-pollinated cones from selected phenotypes. Controlled pollinated cones yield 21 percent less seed per cone than either of the other two types. Similar clones were not used in the comparison as clones were selected on basis of availability of cones. All clones, however, are used in the Georgia program and were originally selected using similar standards.

The important point illustrated in Table 2 is the constant annual increase in the average number of cones per tree. Annual average cone production for slash ranged from a low of two cones per tree in 1962 to a high of 26 during 1964. The average annual loblolly cone yield ranged from five in 1962 to 55 per tree in 1964. Age of ramets in sample is varied, with oldest being nine years old.

Average cone yields for slash pine shown in Table 4 are almost identical for the two orchards. One would expect this result since trees involved are similar in age. Loblolly cone yields for the two orchards are more variable. This may be explained by a difference in age as the Arrowhead Orchard loblolly trees are on an average, several years older than Horseshoe Bend trees.

Information shown in Table 5 can be used to calculate the potential yield of seed per bushel of cones.

SLASH PINE - Assuming 185[2] cones per bushel and that the average seed yield per cone is .052 ounces, cones produced have a yield of .60 pounds of seed per bushel.

LOBLOLLY PINE - Using 309[2] cones per bushel and an average seed yield per cone of .040 ounces, the seed yield is .77 pounds per bushel of cones.

Table 7 Georgia Forestry Commission 1964 seed data for open-pollinated seed orchard seed, showing total orchard yields and seed test results.

Species	Seed Size	Pounds Seed Cleaned	Germ. Percent	Purity Percent	Full Seed Percent	Seed Per Pound
Slash	Large[3]	277	84	99	92	11,139
	Medium[4]	100	84	100	97	14,153
	Small	31	75	84	91	19,560
	Total	408				
Loblolly	Large	151	65	98	94	13,337
	Medium	45	62	100	99	13,601
	Small	68	72	100	99	16,074
	Total	264				

[3] Top screen size - 11/64"
[4] Bottom screen size - 7/64" x 3/4"

It is interesting to note the variation in seed per pound for both species. Loblolly appears to be lacking in medium size seed, thus indicating lar-

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[1] Indicates range in cone yield per tree.

[2] Darby, S. P. Unpublished data collected from 1957 through 1965.

ger seed and a smaller number of seed per pound.

SUMMARY AND CONCLUSION

In summary we can say that the yield of cones per tree from Georgia orchard trees is currently considerably below that normally produced by the same species occurring in other type stands. To illustrate this point, one worker reported that an average yield of 1.85 bushels of cones per tree was collected from a loblolly seed producing area. This amounts to several hundred cones per tree compared to an average of 34 loblolly cones per tree produced in the Georgia orchards during 1964.

In regard to the number of sound seed per cone produced in the Georgia orchards, they compare favorably to that reported by other workers for Georgia. Squillace,[5] in his study of the geographic variation in slash pine, reported that the mean sound seed yield for the whole species was 51 seed per cone. Slash cones collected during 1964 from the Georgia orchards averaged 57 seed each. The seed yield per cone for slash pine averaged 1.475 grams, a potential yield of .60 pounds of seed per bushel of cones. In regard to the yield for loblolly, the average yield per cone for this specie was 1.136 grams. This is a possible yield of .77 pounds of seed per bushel of cones.

In conclusion we can safely say, based on what we now know of seed per cone, that the Georgia orchards produce seed at this time that at least equal in quantity, seed produced by the same species growing in other environments in Georgia. Additional time will be needed before trees reach maximum productivity and before we can answer the question of what cone and seed yields will grafted seed orchards produce?

5/ Squillace, A. E., 1964. Geographic Variation in Slash Pine. Unpublished Thesis - University of Florida Graduate School.

Large Scale Seedbed Grafting and Seed Orchard Development

JAMES C. WYNENS[1]

I'll re-word my subject by saying, a review of the Georgia Forestry Commission's experience in establishing seed orchards by grafting. These experiences might be mutual and, you just beginning a program may look forward to them with anticipation.

Our program began in 1954. The original mode of establishment was by grafting in February 1955, scions from initially selected parent trees on potted 1-1 seedlings. Ramets from additional selections were obtained by field grafting during the Spring of 1956.

Greenhouse or lath-house grafts on potted stock result in initially high grafting success but this is hindered by lack of grafting space and post-planting problems. Root binding (Figure 1) and wind-throw in later years are two hazards that can be overcome with intensive care such as judicious root pruning, use of large containers, and optimum soil mixes. A too friable soil mix might require extra field watering until established, due to the possible fibrous root system produced while in the container. This extra attention tends to put a higher cost on each graft.

Approach grafts on container stock and bagged seedlings gives a very high percentage take but is not feasible on a large scale due to lack of accessible scion material.

Well established transplants from containers result in a uniform, easily managed orchard (Figure 2).

Grafting in the field was performed, using a protective cover of foil and polyethylene bags on 1-1 stock planted two to the space (Figure 3). The idea being to cut one when a union was achieved. Field grafting will work well on an area that can be closely supervised,

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1/ Assistant Chief of Reforestation, Georgia Forestry Commission, Macon, Georgia provided you get a good take the first two years. Attempts were made to establish 300 acres in two grafting seasons by using a crew of fifteen school boys. A good many trees were successfully grafted but a higher percentage were not. The stock plant of these unsuccessful grafts was regrafted until the tops were too high to reach. The result, the orchard had scattered grafted trees throughout but was understocked and uneven aged (Figure 4). The graft unions were 4 to 60" from ground level. Ungrafted trees also appeared to be grafted, a new terminal shoot having sprouted at the unsuccessful graft union.

Figure 1 -- Poorly developed root system caused by plant being grown in container too long.

Grafting too high resulted in intensive pruning practices and in general; a poorly formed tree (figure 5). Over a three year period, 1957, 1958, and 1959, a total of 43,657 field grafts were made. An average of 36% take for slash and 16% for loblolly was achieved.

The low degree of success can be attributed to summer grafting and detrimental weather conditions.

In 1960 an inventory of all trees was made. Trees with no identity, diseased trees, poorly formed trees, and areas understocked to the point that inter-planting was not feasible, due to the large size of the grafts, were rogued. We began searching for methods in which we could utilize a more controlled condition of growing. Grafting on nursery seedbed seemed to be the most applicable method. 1-0 seedlings were thinned to grow approximately 12" x 12" on the

Figure 2 -- Uniform stand of grafts that were made on potted stock.

Table 1. Three year field grafting percentages. Grafts were made in February, March, June, July, and August.

Species	Year	Number Grafted	Number Lived 1 yr. from Grafting	Percent
Slash	1957	4,277	1,006	24
	1958	6,939	1,01[illegible]	15
	1959	10,144	2,[illegible]	[illegible]
	Total	21,360	7,557	36
Loblolly	1957	[illegible],265	1,90[illegible]	84
	1958	10,757	24[illegible]	2
	1959	[illegible],175	1,626	16
	Total	22,297	[illegible],750	16
	Total	43,657	11,[illegible]37	26%

Figure 3 -- Field grafted 1-1 stock.

Figure 4 -- Larger trees were field grafted and interplanted with seedbed grafts five years later.

seedbed (Figure 6). They were root pruned in September and again in December. A complete fertilizer was applied in January. This attention is necessary to achieve the largest diameter possible by early Spring.

The first discovery made in seedbed grafting was to avoid use of low overhead shade such as cheesecloth, lath or saran, together with a cover over the grafts (Figure 7). This interrupted photosynthesis during extended periods of low light intensity. Instead of dying and turning brown, the grafts died and maintained a pale green color which was misleading in casual inspections. Several combinations of protective covers or bonnets were tried during 1961. When using an unvented polyethylene bag without a cover, just a few minutes of direct sun would cause a tremendous heat build up. Grafts without any cover or poly bag didn't survive, even when grafted under continuous mist. Grafts made after April in southeast Georgia, generally were not as successful as February-March grafts.

Spring of 1962 grafting was done with only a tin foil bonnet over a vented poly bag, using cleft grafts (Figure 8). The experience gained this season was to leave some stock limbs exposed outside the cover; if not, the grafts would achieve a union and grow several inches, then flop over as if they were growing so fast they couldn't support themselves. The stock limbs would be etiolated from being under the cover. Usually the whole plant would die upon removal of the cover and exposure to the hot sun.

The Georgia Forestry Commission has successfully established 38,307 grafts, 23,524 of these are nursery bed grafts established since 1961. We feel that for successful seedbed grafting, the following general conditions must be met.

1. Root pruned 1-0 stock plants at one foot spacing and at a diameter approaching the diameter of the scion.

2. Irrigation.

3. A moisture retainer such as a poly bag, vented for heat release, covering two-thirds of the plant.

4. Outside of the poly bag, some type of shade or insulator such as aluminum foil or kraft bag should be used.

5. Begin grafting as early in the Spring as weather conditions permit and stop by the last of May.

Using grafting data of one slash orchard as an example (Table 2), the average grafting success over 64 clones, containing 9,567 seedlings grafted, is 76% for four grafting seasons Success in a clone might vary as much as 50% in two successive years. Some clones expressed a good grafting potential by having two to three years of low take then exhibiting 95% success. No more than 3% of the clones grafted successively for three years displayed a consistently below average success. Even then the low take was not so low that it was a disqualifying factor. One clone having 145 grafts made in three years resulted in 99% success. A factor that might have influenced the average percentage take could involve human skill. Over the three years a total of 25 prison inmates, with varying degrees of interest, participated in actually making the grafts.

TRANSPLANTING OF GRAFTED STOCK

Table three shows transplanting success of 5,472 grafts planted over a three year period.

Three thousand three hundred fifty-three bare root transplants (Figure 9) gave 75 and 69 percent respectively; compared to 2,119 plants balled with 87 percent transplant success. This data was taken one year from transplanting. Other test plots indicate that a 10 to 15% transplanting advantage of ball over bare root is consistent.

Table 2. Example of grafting percentages of slash in one orchard for four years. Grafting performed only in the spring.

Number Clones	Year	Number Grafted	Number Live	Percent Success
39	1961	2,421	1,437	59
58	1962	2,537	2,118	83
45	1963	2,754	2,366	86
42	1964	1,855	1,304	70
	Total	9,567	7,225	76

Table 3. Grafted slash transplanting percentages.

Year	Full Planted	Living After One Year	Percent
1961	1,437 (Bare root)	1,078	75
1962	1,916 (Bare root)	1,330	69
1963 *	2,119 (Balled)	1,842	87

* Balled and transported to field in three gallon containers.

Figure 5 -- Poorly formed field graft. Note graft union approximately 60 inches from ground.

Figure 8 -- Grafts in the seedbed.

Figure 6 -- 1-0 root stock grown 12" x 12" on nursery seedbed.

Figure 9 -- Bare root nursery seedbed graft showing root system prior to being planted.

Figure 7 -- Seedbed grafts under shade cloth.

Figure 10 -- Established ramets in the seed orchard all propagated by nursery seedbed grafting.

A consistently below average transplanting success was noticed in 20% of 34 clones transplanted to the orchard for three consecutive years. Most of these clones had a high grafting potential. All the above plants were planted in 14" auger dug holes and were watered when weather conditions made it necessary.

TIME REQUIRED FOR PROPAGATION AND VARIOUS CULTURAL OPERATIONS FOR SEEDBED GRAFTING.

The time required for making 13,771 grafts, including the various cultural operations and the lifting of 10,658 of these grafts, is 45 minutes each. Prison inmate labor was used in all operations.

Table 4. Time required by various type operations for seedbed grafting.

Item	Man Hours	Number Grafts	Time per Graft
Grafting	3,920	13,771	17 Min.
Cultural *	2,202	13,771	10 Min.
Lifting	3,172	10,658	18 Min.
Total			45 Min.

* Cultural includes spraying for disease and insect control, pruning, weeding, etc.

SUMMARY AND CONCLUSION

Establishment of seed orchards by grafting may be accomplished by using three approaches.

1. Grafting on potted or container grown stock.

This results in initially high take but the number of plants established in the field is limited by physical facilities available for propagating. Post planting problems of root-to-shoot ratio occurs in varying degrees. It is more expensive due to intensive cultural and handling practices.

2. Field grafting on planted stock.

Success depends upon ideal weather conditions. Grafting during early Spring is recommended. A full stocked stand is less likely to be achieved if repeated graft failure results at certain locations in the field. An uneven age stand is possible, complicating cultural and spraying schedules by making it necessary to continue these practices over a longer period. Continued grafting failure raises cost. Field grafting complicates supervision by increasing area to be supervised.

3. Nursery bed grafting.

This method lends itself more to mass production by concentrating efforts at one location under closer supervision and environment control. Cost of established plants are less expensive. In most cases, established plants are nearer the same age and uniform in size (Figure 10). Plants are less subject to fusiform on the stock because of protection in the grafting bed and subsequent pruning of stock limbs when planted. A higher number of plants can be established in a shorter period using the nursery bed system. It is essential when using this method of orchard establishment that stock be grafted to allow for mortality in grafting and in transplanting of low potential clones.

Cone Collecting Problems and Equipment

JAMES L. McCONNELL 1/

According to Matusz, "The collection of seeds from standing trees is perhaps one of the most dangerous and labor-intensive of all forestry operations. However, this highly complex and costly work ensures that seeds are collected from fine trees and from the best part of their crown" (Matusz, 1964). Probably the biggest engineering and mechanical problem we in the seed orchard and tree improvement business are faced with is that of collecting cones in a suitable and economic manner. Even now we have thousands of acres of seed orchards which are ready to be harvested. Each year this problem will grow larger as we put more and more acres into production as seed orchards. In many cases our funds are limited, but there is one thing we all possess in unlimited amounts which will help us overcome this and several

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1/ South Carolina Seed Orchard, U. S. Forest Service, Moncks Corner other problems. That one thing is imagination. I think we will need all the imagination we can muster to lick this problem. After all, cone collecting is one way of obtaining the end result which we all desire.

First of all, lets break the problem down into its two logical divisions. The first division will be collection from the seed production areas. The second, and probably the most important in the long run, is collection from the seed orchards. Many of the problems will be inherent to both the seed production area and the seed orchards. Usually, if we lick the problem in one area it will be solved in the other.

I once heard a forester comment that all seed production areas looked alike. This may be true until you get to working in them. All of our seed production areas were picked strictly on the quality of the stand. This certainly is an important factor. But now that we have the areas selected, cut and ready for harvest, we find that many are on rocky ground, hills, and mountain sides. Others are on swampy and unstable soil. Like people, seed production areas possess individual traits, and each must be handled as an individual. I am sure many of you have found this out already.

One of the first considerations in harvesting cones from a seed production area is topography and soil conditions of the area. These considerations will effect the method used in getting tree climbers into the trees. Depending upon the area, you may want to use Swedish ladders, rope ladders, climbing irons of various types, climbing spurs, cable hoisting equipment, nets or a variety of other equipment. On the advise of entomologists, we do not use climbing spurs on the National Forests. They state that using them is just asking for trouble. Many people prefer truck mounted ladders of various shapes and forms. Some have even used hydraulic truck mounted extension buckets. Reports are that these hydraulic buckets are too expensive unless you have an abundance of tree climbers. They are expensive to use and must be kept busy to be economical. I have reports that some have made sizable collections and prefer to use ropes to allow the climber to pull himself into the crown of the tree. The ropes are secured over limbs with a bow and arrow or fishing tackle (Thompson, 1965). Whatever the method worked out for each seed production area it must be economical, relatively fast, and safe for the tree climber.

I have seen many home-made rigs using trucks and ladders. Somehow I feel many of these outfits are not as safe as they should be. Some have taken ladders and made them fit a job for which they were never intended. Many were made under the supervision of foresters who have no idea of the different stresses and strains placed on metal fatigue after long and heavy use. I think we should take another look at some of our home-made rigs and ask advice of engineers who know just what problems are involved in this type construction.

The tree climbing business has enough risks without our helping it along.

The next consideration is the tree climbers. This falls into two categories - your own men, trained and physically able to climb, or contract professional tree climbers. This type work should be undertaken by men in good health and physical condition, 18 to 35 years of age. They should certainly want to climb and be thoroughly trained in climbing, rope handling, safety and first aid. The big problem in training your own climbers is having enough men to do the job between the time the cones ripen and the time they open and the seed falls. Unless there is enough climbing work to keep your men in good physical and mental condition, the work should be left to professional tree climbers.

The answer would seem to lay in contracting the work of tree climbing. On the surface this sounds good. Reports are that the "tree expert" companies engaged in this type of work seem to have a habit of promising more than they can deliver. I think the work is as new to them in many cases as it is to us. I hope experience and time will solve this problem to a great extent.

Another minor problem in contracting tree climbing is the method of payment. I prefer payment on a per tree basis rather than per hour or per bushel of cones collected. Costs seem to be in line with all methods used. It will just depend on which method you prefer to use. Costs for contracting tree climbing on seed production areas have varied from $3.00 per tree to $5.00 per tree. In all cases costs ran an average of one to three dollars per bushel higher for seed from the seed production areas than for seed purchased from wild collections. One important way to keep the cost per bushel of cones collected from seed production areas at a relatively low figure is to be selective in picking trees to be climbed. This is a must if we are to hold costs down. A good cone count made several months prior to collection will pay for itself several times over. We must decide how many bushels of cones we want from any one tree before we go to all the trouble of climbing it to harvest the cones. It costs almost as much to collect cones from a tree containing one bushel as it does from a tree containing five bushels. Personal experience has shown that a tree must have at least one bushel of cones to be economical for climbing. Also, along this line, "Identifying the good cone producers in an area will allow cultural operations to be concentrated on these trees and should result in a reduction in the proportional cost of such operations." (Cole, 1963).

Once we get the cones off the trees and onto the ground there are still problems. Many seed prodcution areas have good accumulations of brush and grass. Those areas that were fertilized are an even bigger problem. Intensive efforts should be made to keep brush and grass cover as low as possible. Many cones are left on the ground because crews picking them up could not find them. After we have spent considerable time and money getting cones off the trees, we should be able to collect all the cones on the ground. In many areas prescribed burning will solve this problem with little trouble. Other areas will need mowing or mist blowing at regular intervals. This is another reason why we should pick our trees to be climbed and harvested. Only those trees from which we expect to pick cones need be mowed around.

A problem that should not exist, but apparently does, is that of identifying each and every container of cones. When the cones arrive at the seed extractory, they usually are not processed immediately. Shipments of cones from several areas and sources may become mixed. To say the least, it is confusing to the nurseryman to have hundreds of bags of cones at his disposal and not know for sure from where they all came. Each bag of cones should be identified with an aluminum tag stating, at least, the seed source and species. The aluminum tags can then be transferred to the seed containers, which are usually placed in storage (King, 1965).

The biggest and most serious problem in many of our seed production areas and also in our orchards is that of taking the cone from the branch. Collection of longleaf and slash is relatively easy along these lines. Cones can be knocked from the branch with a good lick from a cone hook, pruning pole, or often shaking the limb will send them flying. It is loblolly and Virginia pine that give us the most trouble. I have reports that several individuals are working on various types of equipment to help this problem. Usually in loblolly we resort to cutting the entire branch ends in order to get the cones from the branch. In most cases this is disastrous for next year's crop. One idea is to develop a battery operated circular saw small enough for the tree climber to take into the tree. The principle is to saw as much of the cone off as possible without cutting the branch. The big disadvantage with this equipment is that it is too heavy and awkward to work with in the tree. Another idea centers around pneumatic clippers. The principle will be the same, get as much of the cone as possible without cutting the branch. Long air hoses or compressed air containers make this equipment awkward to use. Another idea is to have two or three times the area in seed production as you require for any one year. Cut the branch tips off with the cones and conelets Then give the trees a couple of years to recover. Cole indicates that two successive crops of cones may be collected from loblolly seed production area even when branch tips are clipped off (Cole, 1963). Others felled the trees from which cones were collected. This, of course, necessitates the selection and release of a new area each year for harvesting three years later (Easley, 1954).

As we move into the area of collecting cones from seed orchards, the problem changes its aspect a good deal. We will have our problems with topography and soil stability, but these should be partially solved for each orchard by the time we get into seed collection. In general, maximum flotation should be obtained for all equipment used in the orchards to minimize soil compaction.

Climbing should not be a problem, if we leave the trees with limbs close to the ground and don't prune them heavily. Most kinds of mechanized equipment and ladders can be put to full advantage when necessary. The big problem will be that of having enough people trained and ready to collect the cones in the short period of time after cones ripen and before they open.

The same problem for loblolly and Virginia pine are present in the orchard as in the seed production area - how to gather cones without "plucking" the tree. This problem reaches a more serious level in the seed orchard since we cannot afford to lose every other cone crop because of our inability to collect the cones.

One idea is to spread tarps on the ground under the trees in the seed orchards, let the seed fall, and then collecting them when they are free of the cones. Another idea is to use industrial vacuum cleaners and sweep the seed up after they fall. Foresters in Czechoslovakia and the USSR tried using a vacuum device for the collection of seed from standing trees by suction. As a rule, the methods used have not proven satisfactory. The problem lies in the fact that the seed adhere more firmly than the needles, so that suction detaches more needles than seed. As I said earlier, imagination is our biggest asset in this business.

TEN COMMANDMENTS OF CLIMBING SAFELY

1. Inspect your equipment -- take care of it -- be prepared.
2. Inspect the tree to be climbed -- plan your work.
3. Work deliberately.
4. Work in pairs.
5. Be aware of climatic conditions.
6. Use safety equipment properly.
7. Don't trust a dead limb.
8. Don't drop equipment.
9. Don't work beyond your endurance.
10. No horseplay.

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Seed Yield and Plantable Seedlings from Controlled- and Open-Pollinated Four- and Five-Year-Old Seedlings of Loblolly and Shortleaf Pine

JAMES T. GREENE [1]

The early production of strobili is highly desirable in seed orchards and especially in a program of tree breeding where early flowering of progeny and the production of viable seed are of much importance. Most loblolly pine (Pinus taeda L.) and the shortleaf pine (Pinus echinata Mill.) trees begin to produce strobili at an age of about 8 to 10 years. By selection and breeding, it should be possible to reduce "flowering" age considerably. This would save valuable years in a genetics program as well as insure early seed production in a grafted or seedling seed orchard.

Greene and Porterfield (1962) located loblolly pine trees ranging from 21 to 30 years of age on the property of the University of Georgia that produced seedlings bearing female strobili at ages of three and four years. One three-year-old loblolly pine seedling (L-81A) produced female strobili in 1959, after two years in the field. This seedling was back-crossed to one of the early cone-producing parents. Two cones from this cross were collected in late 1960 which yielded 102 seeds. These seeds produced 44 seedlings, and after three years in the field, 40 of these are making normal growth and appear exceedingly vigorous. The original parent seedling has produced female strobili during the five successive years.

RESULTS AND DISCUSSION

The following data illustrate that "flowering" age can be reduced through selection and breeding and that four-year-old parents will yield seed that will produce plantable seedlings. The term "plantable" seedling refers to a number one grade seedling with no apparent defects.

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Table 1. Open-pollinated loblolly pine cones collected in 1963 from 4-year-old seedlings.

Female	Number of cones	Number of Seeds Per Seedling	Number of Seeds Per Cone	No. and Percent of plantable seedlings	
				No.	Percent
L-72xL-78	3	119	40	71	60.0
L-72xL-78	2	111	56	6	5.0
L-79 (A)	1	62	62	20	32.0
L-65xL-64	2	129	65	6	5.0
L-65xL-64	2	64	32	11	17.0
L-65	3	98	33	11	11.0
L-65	2	78	39	5	6.0
L-64	2	139	70	94	68.0
L-64	7	208	29	7	3.0
L-64	1	62	62	19	31.0
L-64	1	107	107	2	2.0
L-64	2	109	55	11	10.0
L-78	1	66	66	16	24.0
L-64xL-78	1	77	77	1	1.0
L-64xL-78	1	78	78	27	35.0
L-64xL-78	1	83	83	12	14.0
L-64xL-78	2	140	70	52	37.0
L-64xL-78	1	62	62	44	71.0
L-64xL-78	1	92	92	43	47.0
L-64xL-78	1	24	24	11	46.0
L-64xL-78	1	53	53	35	66.0
L-64xL-78	2	120	60	36	30.0
L-78xL-77	2	73	37	40	55.0
L-72xL-64	1	109	109	56	51.0
L-72xL-72	1	69	69	36	52.0
L-64xL-64	1	47	47	1	2.0
L-69xL-64	2	111	56	3	3.0
L-69xL-64	1	25	25	2	8.0
L-69xL-64	1	78	78	43	55.0
L-69xL-64	1	47	47	17	36.0
L-69xL-65	1	97	97	44	45.0

Table 2. Open-pollinated shortleaf pine cones collected in 1963 from 4-year-old seedlings.

Female	Number of cones	Number of Seeds Per Seedling	Number of Seeds Per Cone	No. and Percent of plantable seedlings	
				No.	Percent
SH-10xSH-5	1	21	21	5	24.0
SH-10xSH-5	1	31	31	6	19.0
SH-6xSH-8	1	47	47	10	21.0
SH-5xSH-6	1	9	9	5	56.0
SH-8xSH-10	5	145	29	31	21.0
SH-8xSH-10	4	106	27	14	13.0
SH-8xSH-5	7	131	19	20	15.0

Table 3. Control and open-pollinated loblolly pine cones collected in 1964 from 5-year-old control pollinated seedlings.

Female	Male	Type of Cross	Number of Cones	Number of Seeds Per Seedling	Number of Seeds Per Cone
L-64xL-78	L-64xL-78	F_2	4	184	46
L-64xL-78	L-64xL-78	F_2	1	52	52
L-64xL-78	L-64xL-78	F_2	2	109	55
L-64xL-78	L-64	Back-cross	4	24	6
L-64xL-78	L-78	Back-cross	2	63	32
L-64xL-78	L-78	Back-cross	1	4	4
L-64xL-78	L-64xL-78	F_2	4	225	57
L-64xL-78	Wind	Open	1	62	62
L-64xL-78	Wind	Open	2	120	60
L-64	L-64xL-78	F_2	1	22	22
L-64	Wind	Open	2	151	75
L-65xL-78	L-64xL-78	F_2	1	42	42
L-65xL-78	L-65	Back-cross	2	99	49
L-65xL-78	Wind	Open	4	136	34
L-65xL-78	Wind	Open	1	32	32
L-65xL-65	L-65	Back-cross	2	19	10
L-65xL-64	L-65	Back-cross	2	12	6
L-65xL-64	Wind	Open	2	52	26
L-65	L-65	Back-cross	1	23	23
L-65	Wind	Open	5	389	78
L-72xL-78	Wind	Open	1	133	133
L-72xL-78	Wind	Open	1	102	102
L-69xL-77	L-69	Back-cross	1	22	22
L-69xL-77	L-77	Back-cross	1	14	14
L-69xL-72	L-69	Back-cross	2	102	51
L-69xL-65	Wind	Open	3	280	93
L-69xL-65	Wind	Open	1	55	55
L-79	L-79	F_2	1	47	47
L-79	Wind	Open	3	172	58
L-79xL-79	Wind	Open	1	130	130
L-78	L-78	Back-cross	1	20	20
L-78	L-78	Back-cross	1	57	57
L-69xL-64	Wind	Open	2	129	64

Tables 1 and 2 contain data relative to open-pollinated cones, seeds and plantable seedlings from young loblolly and shortleaf pine parents. The progenies had been outplanted in the field for four years when the cones were collected. This means that the progenies were producing strobili at four years from seed.

The number of open-pollinated seeds per individual seedling of loblolly pine ranged from 24 to 208. The range of plantable seedlings per individual parent was from one percent to seventy-one percent (Table 1).

Open-pollinated seeds from individual four year old shortleaf pine parents ranged from nine to 145. Range in plantable seedlings from these young parents was from thirteen to fifty-six percent (Table 2).

Tables 3 and 4 present data relative to controlled and open- pollinated cones collected in 1964 from five-year-old parents. These progenies produced female strobili in 1963 which were controlled pollinated.

Seventy-seven percent of the controlled pollinations made in 1963 on four-year-old loblolly pines were successful. These crosses were F_2 and back-crosses.

The range in number of seeds from individual F_2 crosses ranged from forty-two to 225. Backcrossing resulted in a range of seeds from four to 102 per seedling. The range in number of open-pollinated seeds for each individual parent was from 32 to 389 (Table 3).

Fifty-four percent of the controlled pollinations made in 1963 on four year old shortleaf pine parents were successful. The range of seeds resulting from the F_2 crosses for individual parents was from 14 to 762. The number of seeds for each individual parent resulting from backcrossing ranged from three to 56. One open-pollinated cone was collected which yielded 28 seeds (Table 4).

SUMMARY

These data indicate that "flowering" age can be reduced by selection and breeding. These data show that it is possible to produce F_2 seed in loblolly and shortleaf pine in five or six years from seed. In fact, we have F_2 seedlings growing in the field in a total of 5 years from seed. The next step is

Table 4. Controlled and open-pollinated shortleaf pine cones collected in 1964 from 5-year-old seedlings.

Female	Male	Type of Cross	Number of Cones	Number of Seeds Per Seedling	Number of Seeds Per Cone
SH-10	SH-10	Backcross	1	3	3
SH-10xSH-5	SH-10xSH-8	F_2	2	63	32
SH-10xSH-8	SH-10xSH-8	F_2	1	46	[illegible]
SH-6xSH-8	SH-10xSH-8	F_2	17	762	[illegible]
SH-6xSH-8	SH-10xSH-8	F_2	2	101	50
SH-6xSH-5	SH-10xSH-8	F_2	1	68	68
SH-8xSH-6	SH-6xSH-8	F_2	1	53	53
SH-8xSH-5	SH-8xSH-5	F_2	2	50	25
SH-8	SH-10xSH-8	F_2	1	14	14
SH-8	SH-10xSH-8	F_2	1	56	56
SH-8	SH-10xSH-8	F_2	1	48	48
SH-9	SH-10	F_2	1	31	31
SH-9	SH-10	F_2	1	38	38
SH-9	SH-9	Backcross	4	56	14
SH-9	SH-10	F_2	1	60	60
SH-5	SH-6	Backcross	1	37	37
SH-5	SH-6	Backcross	1	13	13
SH-5	Wind	Open	1	28	28

to find out how readily the early "flower-producing" trait found in these trees may be transmitted to the next generation, and the segregating progeny of the F_2 generation will be invaluable in this respect.

An opportunity for reducing age of "flowering" in loblolly and shortleaf pines exists in the selection and progeny testing of "early-flowering" phenotypes like the ones just described. Once tested, these genotypes can be crossed with other genotypes to produce "early-flowering" strains possessing other desirable traits. This possibility has great utility in programs of tree improvement and more especially from the practical aspect of producing commercial quantities of improved seed from seedling orchards in the future.

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