ACCELERATED BREEDING AND TESTING OF LOBLOLLY PINE IN THE SOUTHERN U.S.A.

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Abstract.--Progress on accelerated, advanced generation breeding of loblolly pine in the southeastern U.S. is described, including use of indoor breeding orchards and the status of early testing. An accelerated breeding and testing scheme, applicable to any tree breeding program is discussed, which could also be the basis for an operational tree improvement program with significantly shortened generation turnover.

INTRODUCTION

Large-scale genetic improvement of loblolly pine (Pinus taeda L.) began in the early 1950's. Flowering was slow to start in most orchards and some clones flowered very late. Consequently, it was not unusual for the breeding phase of the first generation of tree improvement to require 13 years for completion. Failures due to poor controlled crossing techniques and lack of insect control also caused delays. Because of the long time needed for breeding in production orchards, considerable research has been aimed at reducing the time to complete a generation of breeding and testing. The first breeding efforts to produce seed for genetic tests were in production seed orchards which had been established on sites of largely unknown flower production potential.

In the past 2 decades breakthroughs have resulted in techniques which can reduce breeding time for operational size populations to only 5 years (or perhaps 4) under the best greenhouse circumstances and experience has shown that the proper choice of orchard site and good management can result in commercial seed quantities in less than ten years. These breakthroughs can be of great value since many economic analyses indicate that anything that reduces the time needed for generation turnover or time to seed orchard production will dramatically increase the value of a tree improvement program.

The choice of whether or not to accelerate breeding is driven by an analysis of whether the benefit of getting a fixed gain earlier outweighs the costs. Unfortunately, the decision to reduce selection age is more complex. Not only must the cost of earlier evaluations be considered but also the degree of risk associated with earlier genetic evaluations. Early selection is a complex issue because some of the parameters which would determine its potential benefits are not well understood: juvenile-mature correlations (genetic), heritability as a function of age (or size), impact of genotype-environment interaction when testing in atypical environments, and risks of large-scale planting of a family based on early performance. Nonetheless, there are many results which suggest that even imperfect early selection could yield greater gains in the long term than selections at

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older ages. For the purposes of this paper, early selection will refer to evaluations at age 2 years or less. In most operational loblolly pine tree improvement programs, selections are currently made at age 5 years or older. Orchard establishment and roguing decisions are more often based on 8- to 10-year measurements.

In this report we will describe recent applications in accelerated breeding and testing of loblolly pine. Finally, a long-term tree improvement scheme which employs accelerated greenhouse breeding and early selection with some control of risk is described.

ACCELERATED BREEDING

Greenhouses.--Accelerated breeding of loblolly pine using specially designed breeding greenhouses has been going on since 1978 when Weyerhaeuser's tree improvement facility in Hot Springs, Arkansas, became operational. Since then, 3 more facilities have been constructed by other companies and other organizations are planning to build their own breeding greenhouses. These facilities are similar in design and operation (see Table 1). All rely on indoor, potted breeding orchards, housed in approximately 1000-square-meter (floor surface area) fiberglass greenhouses consisting of 3 bays each with a 7.6M peak and 5.5M eaves. During the summer,

Table 1.-- Operational tree breeding facilities in southeastern U.S.

Company, Location	Comments
Weyerhaeuser Co. Hot Springs, Arkansas	Operational in 1978. Over 20 diallels (6 parent disconnected) have been completed since then, followed by progeny test establishment.
Westvaco Corporation Summerville, South Carolina	Grafts are pruned; 2-year-old ramets average 34 female strobili each, which average 80 sound seed/cone. Irrigation water is very basic and is treated by a reverse osmosis facility.
Union Camp Corporation Belleville, Georgia	In 1985, 11,000 female strobili produced. Instead of Osmocote®, liquid fertilizer is injected through the drip irrigation. They claim Osmocote burned some trees. Irrigation water has a pH of 8, so sulfur is added to pots to lower it.
Catawba-Bowater Corp. Rock Hill, South Carolina	Are currently trying to complete 40 6-parent diallels in their facility. First year grafts of 83% of all clones produced males in response to out-of-phase dormancy.

evaporative cooling is used to keep maximum temperatures 3° to 9° C below ambient, while during the winter, temperatures are kept just above freezing mainly to protect the plumbing. No supplemental lighting is used at any time so that bud development occurs in response to natural photoperiod.

Pot Culture.--All breeding orchard trees are grown in galvanized steel or plastic containers, which are light weight, durable, and relatively cheap. Two sizes are commonly used, 91 and 205 liters; the latter are only used for trees which will remain in the facility for long periods. The growing medium consists of 2 parts each of coarse (builder's) sand and shredded pine bark, and 1 part each of peat and vermiculite. Hardwood bark must be avoided, especially if it has been composted, since it can cause severe chlorosis which is related to an increase in pH. If these symptoms appear, they can be relieved by applications of ferrous sulfate. Fertilization is accomplished initially by incorporation of Osmocote® 18-6-12 timed-release fertilizer at a rate of 6 grams per liter. Good quality water is of vital importance (see Table 1).

Water stress is a vital part of the flower stimulation process but is somewhat difficult to manage. Severe stress is not needed; a level sufficient to cause bud set is all that is required. Higher levels will inhibit male flowering (although female flowering is still promoted) and may affect the development of second year cones already present on the tree. For best results, the stress is applied episodically with thorough watering after the stress has passed 1000kPa (150psi) as measured predawn with a pressure bomb. Water stress is applied from mid-June through early September. If applied properly, water stress can approximately double female strobilus production. Other devices can also be used to measure water stress such as tensiometers or moisture blocks, but they should be calibrated with a pressure bomb, especially if trees vary widely in size or if container size varies.

Flower Stimulation Treatment. -- Biweekly application of a mixture of gibberellins 4 and 7 ($GA_{4/7}$) from mid-June to mid-September can increase female strobilus production by a factor of 2 to 3. Effectively applied water stress will provide an additional doubling of response. While $GA_{4/7}$ does not affect male strobilus production, the greenhouse environment favors their formation for reasons at present unknown. In addition, a treatment called out-of-phase dormancy is successful on 60 to 80% of the trees treated. This treatment will cause trees to produce males when they are most needed (at the beginning of the third growing season from grafting). At this time, the trees have produced enough female strobili to begin breeding. For further information, see Greenwood (1981 and 1982).

EARLY TESTING

Unfortunately, early testing, when defined as selection at age 1 or 2 years, has not been applied as widely as accelerated breeding. The primary reasons are: 1) early evaluation techniques have not been worked out for all traits of interest in loblolly pine, and 2) early evaluation is seen as entailing greater genetic risk in spite of the fact that greater genetic gain per year may result. Whether or not to accelerate breeding is purely an economic question with no genetic risk. One of the primary reasons that implementation of early testing will be slow is the fact that most organizations in the southeastern U.S. have their tree improvement schedules mandated through large cooperatives. The leaders of these cooperatives emphasize their responsibility to conduct programs which will result in increased genetic gain at low genetic risk. While certain organizations may be willing to incur a higher risk for the potential of higher gain per unit time, they are reluctant to bear the added expense of running an additional accelerated breeding and testing program on their own.

Nonetheless, because an increasing body of research results show that earlier evaluations are possible, selections are being made at younger ages in cooperative programs. Western Tree Improvement Cooperative leaders are confident with a 5-year evaluation (Lowe and van Buijtenen, 1980) and North Carolina State University - Industry Tree Improvement Cooperative leaders are leaning toward a 6-year evaluation in the next generation (Steve McKeand, personal communication, N.C. State Tree Improvement Cooperative, Raleigh, N.C., 1986). Most geneticists agree that quality of a given genetic test must dictate the selection age for that test. Selection may be postponed in tests where establishment difficulties result in slow early growth and/or a high degree of variability.

There are some instances where early evaluation as defined above is being practiced. One company is attempting to develop a fusiform rust resistant population employing laboratory evaluations of families at the Forest Resistance Screening Center and short-term evaluations in very uniform field trials. The Western Gulf Tree Improvement Cooperative is also using the Resistance Screening Center results to aid in roguing decisions in production seed orchards.

A 1-year drought resistance testing system has been developed by Weyerhaeuser Company for screening families for use on rocky and mountainous sites in Arkansas and Oklahoma. There is particular interest in screening families from non-local provenances. The local provenance is very slow-growing but has good drought resistance. Weyerhaeuser has been planting North Carolina families on the better sites for some time but there is the potential to reduce the risk of this type of seed source transfer by selecting families that have the greatest drought resistance potential as well as excellent growth.

Weyerhauser is also interested in developing an accelerated generation turn-over program for developing drought resistant strains of nonlocal seed sources. The Texas Forest Service is working on techniques for the development of drought resistant strains of loblolly pine through early testing (Hans van Buijtenen, personal communication, Western Gulf Tree Improvement Cooperative, College Station, TX, 1986). These would be used on low rainfall sites near the western fringes of the natural range of the species.

There is still considerable interest in early testing in southern pine species even though there are few large-scale operational applications. Some major universities, the U.S. Forest Service and some forest products companies are conducting research to work out early evaluation techniques. Both cooperatives are supporting research on making selections at ages 1-2 years using retrospective tests, where families of known performance are greenhouse grown, and the results compared with those from field tests established 8-20 years previously. It is generally recognized that the potential economic benefits of early selection are great and that results to date are generally positive though not always consistent. Research efforts in early testing for growth rate, fusiform rust resistance, pitch canker resistance, drought and cold resistance and specific gravity are under way. For further information see Lambeth (1980 and 1983).

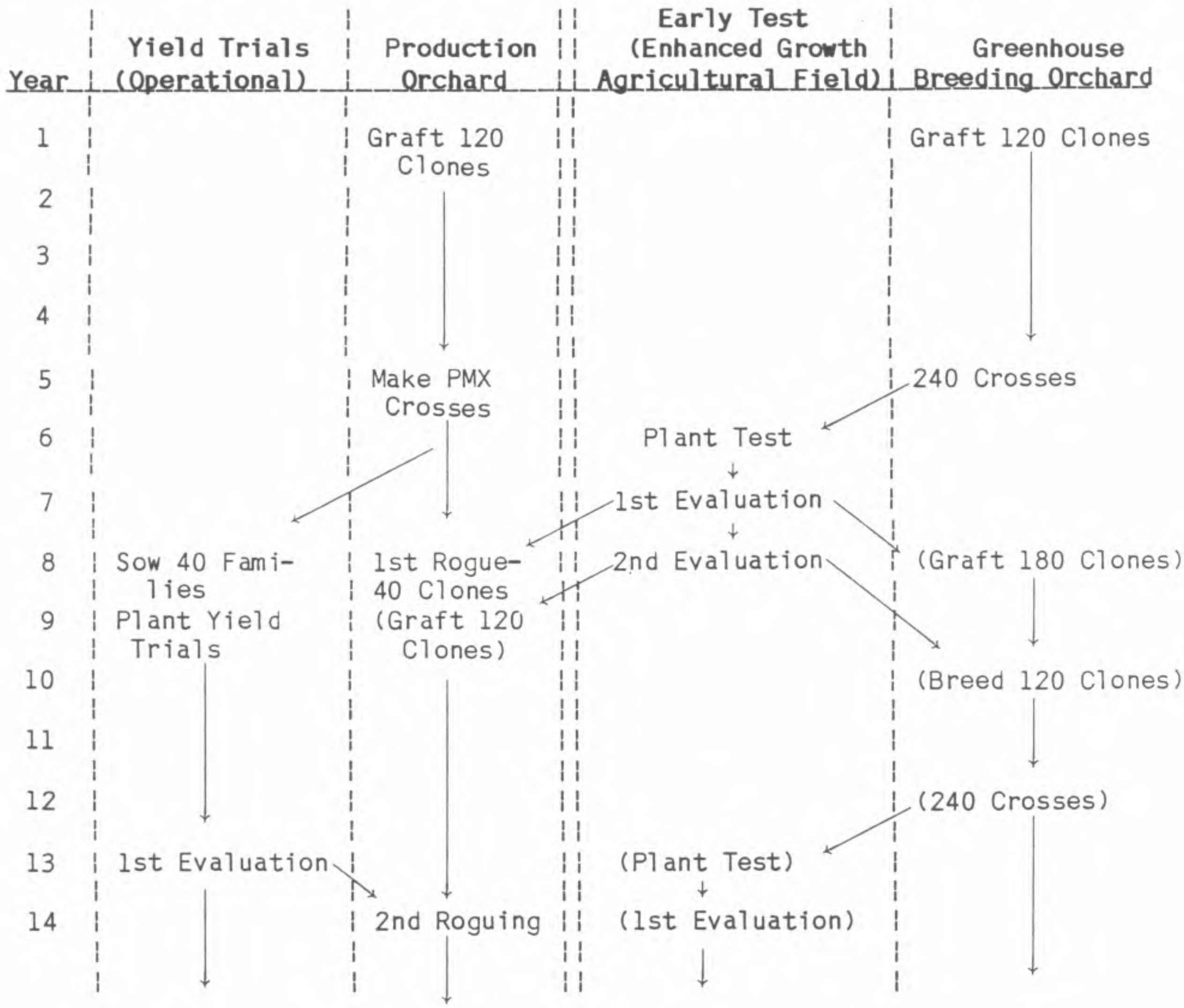
AN ACCELERATED BREEDING AND TESTING SCHEME

We feel that it is time for more application of recent findings in accelerated breeding and testing. Questions on the validity of early evaluation will not likely be completely resolved unless it is tried on experimental populations designed for rapid generation turnover. These populations should not replace conventional cooperative tree improvement programs but rather should be tried on a small operational or research scale. One of us (Lambeth) has started such a research population with loblolly pine and the other (Greenwood) plans a similar research program for larch. The loblolly pine population will use well established accelerated breeding techniques to attempt completion of the breeding in 5 years and a 2-year test on uniform agricultural sites with high growth potential will hopefully provide a 7-year generation cycle. Generations will be cycled as rapidly as possible and improved material will be periodically tested against material from the conventional program. The larch population will consist of Japanese, European and North American selections and clonal propagation will be used for augmenting progeny test material. Such programs are necessarily long-term in nature but the information is badly needed and there is a good chance that material developed in this manner could have a high level of genetic gain and could be fed into operational programs.

Accelerated breeding programs need not be experimental. For those willing to take the risk, we propose an accelerated tree improvement scheme which would work for loblolly pine (Figure 1). To meet the time lines in this scheme, one must have 1) a production orchard site with early flowering potential, 2) a uniform agricultural field with early growth potential, 3) a breeding greenhouse, and 4) competent, dedicated personnel. The details of how the time lines are achieved will not be covered here. A key component of this scheme which makes it an acceptable operational program is the 2-stage testing system. On the right-hand side of the chart is the accelerated breeding and testing. The left-hand side shows how the production population is further tested operationally to offset the risk of early evaluation without slowing the generation turnover of the breeding population. All components of this scheme are on a 7-year cycle.

The early test consists of planting at 1x1m spacing, complete competition and insect control for quick early growth and uniformity. It is desired (and possible) to produce trees of over 2m average height at the end of the second season. This scheme is designed for a program where growth rate is of primary importance. Note that the first evaluation is at age 2, but there is opportunity for a second screening at age 4 just before the crosses are made in the greenhouse. Breeding is accomplished by the techniques described earlier in this paper; details of the 5-year breeding schedule are shown in Table 2. We emphasize the optimistic, experimental nature of the proposed 7-year cycle; failure of either scions from 1-year-old selections to flower well or unreliable selection at test age 1 or 2 may add 1-2 years.

Figure 1.--An alternative tree improvement scheme for growth rate in loblolly pine. Activities in parentheses occur in the second generation. (PMX = POLYMIX)



The yield trails consist of large block plantings of a few families that have shown potential in the early test. There should be several of these tests in the region where improved material will be used commercially. They are designed for yield estimates and to test for pest resistance, adaptability and growth under operational conditions. Yield trials are important but they are nearly impossible to conduct on a large number of families.

In effect, this system replaces conventional progeny tests, which usually consist of row plots and conventional spacing on commercial forest settings, with early testing and yield trials. The advantages are the quick generation turnover made possible by early testing and good estimates of operational yield in the second stage of testing.

Table 2.--Proposed accelerated breeding and testing schedule for loblolly pine. Out-of-phase dormancy activities can be used to augment pollen inventory. These activities are described in the text.

Year	Activity	Season	Generation
1	Graft Selections	Spring	1
	Promote Growth	Summer	1
2	$GA_{4/7}$, Water Stress	Summer	1
3	First Crosses Made	Spring	1
	$GA_{4/7}$, Water Stress	Summer	1
4	Last Crosses Made	Spring	1
	Collect First Crosses	Fall	1
5	Collect Last Crosses	Fall	1
	Grow Crosses in Plugs	Winter	1
6	Plant Tests (Agricultural Site)	Spring	1
7	First Test Evaluations	Winter	1
8	Graft Selections	Spring	2
	Promote Growth	Summer	2
9	$GA_{4/7}$, Water Stress	Summer	2
	Second Test Evaluations (Weed Out Losers)	Winter	1
10	First Crosses Made	Spring	2
	$GA_{4/7}$, Water Stress	Summer	2
11	Last Crosses Made	Spring	2
	Collect First Crosses	Fall	2
12	Collect Last Crosses	Fall	2
	Grow Crosses in Plugs	Winter	2
13	Plant Tests (Agricultural Site)	Spring	2
14	First Test Evaluations	Winter	2

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