TREE IMPROVEMENT ACCOMPLISHMENTS IN THE SOUTH

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Abstract.-- Tree improvement progress in the South during the past 40 years has been very significant, with 85 % of seedlings currently being planted coming from genetically-improved seed. Realized genetic gains in stand volume resulting from use of improved seed vary greatly, but average about 6 % for unrogued first generation loblolly and slash pine orchards and 17 % for rogued orchards. Appreciable gains in other traits, especially fusiform rust resistance, have also been attained. Many improved techniques, which are briefly discussed, assure that gains will continue to increase. The problem of decreased funding and manpower for research is pointed out along with possibilities for alleviating it.

Keywords: Forest genetics, tree improvement, southern pines, hardwoods

INTRODUCTION

It would be difficult to discuss our progress in all phases of tree improvement in a half-hour. Without attempting complete coverage, I shall first point out our progress in developing and employing superior trees and present evidence of genetic gains. Then I shall briefly discuss progress of some phases of research and techniques of special interest. Finally, I shall bring up the recent problem of decreased funding for research.

DEVELOPMENTAL PROGRESS

Accomplishments in developing superior trees during the past 40 years in the South have been tremendous. As of 1987 almost 10 thousand acres of seed orchards have been established (Table 1). Seeds from these orchards are producing 1330 million seedlings per year, sufficient for planting 1.9 million acres of forest land. This acreage planted with superior seedlings represents approximately 85 % of all trees currently being planted in the South.

Progress in the South has been considerably greater than in other major regions of the U.S. Data on production of superior seedlings by State nurseries in 1982 (Risbrudt and McDonald 1986) provide an approximate comparison. About 32 % of seedlings produced by southern state nurseries in 1982 were grown from genetically-improved seed, compared to an average of only 4.3 % for state nurseries of other regions.

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Table 1. Development and utility of genetically-improved forest trees in the South as of 1987. 1/

Item	Organizations involved	Acres of seed orchards established as of 1987	Seedlings produced annually	Acres planted annually
	(no.)	(no.)	(millions)	(thousands)
NCSU	28	4000	630	900
WGFTIP	17	2050	350	500
CFGRP	15	2300	300	400
USFS	1	1400	50	60
Totals	2/	9750	1330	1860 3/

1/ Adapted from a report by Tim White in the Spring 1988 newsletter of the SAF Tree Genetics and Improvement Working Group.

2/ A total of 45 different organizations (one federal, eleven state, and thirty-three private) are involved. Some state and private organizations are members of more than one cooperative.

3/ This figure represents 85 % of all southern reforestation.

NCSU = North Carolina State University Tree Improvement Cooperative, N.C. State University, P.O. Box 8002, Raleigh, NC 27695.

WGFTIP = Western Gulf Forest Tree Improvement Program, Texas Forest Service, College Station, TX 77843.

CFGRP = Cooperative Forest Genetics Research Program, University of Florida, N-Z Hall, Gainesville, FL 32611

USFS = USDA Forest Service, Southern Region, 1720 Peachtree Rd, Atlanta, GA 30367

The excellent progress of tree improvement in the South is admittedly partly due to the extensive forest planting and demand for seeds. However, it is also undoubtedly due to the cooperative nature of our tree improvement activities, which was stimulated by the formation of the Southern Forest Tree Improvement Committee in 1951. About 33 private organizations work through one or more of the southern tree improvement cooperatives listed in Table 1. There are, in addition, 12 state and federal organizations involved. Organizations within each of the major forest areas of the South cooperate very closely, freely exchanging superior material (seeds, scions, etc.) and sharing technical knowledge. The progress is, of course, also due to the efforts of many individuals.

But I wish to mention five who were especially outstanding for both their promotional and research efforts, namely, Philip Wakeley, Keith Dorman, Bruce Zobel (unquestionably, the "Father of Southern Forest Tree Improvement"), Hans van Buijtenen, and Ray Goddard.

So much for developmental progress. How about the extent of genetic gains being made? Many researchers have predicted genetic gains on the basis of progeny tests. These are fairly suitable for some traits, such as fusiform rust resistance. But they usually are not considered highly reliable for estimating gains in wood volume per acre, because they do not adequately take into account effects of survival and competition. The most reliable estimates of such gains are based on large-block plantings of improved vs. unimproved seed using operational procedures (realized gain tests). These will be summarized later. But first note results from two exceptional predicted gain studies for loblolly and slash pine, based on many progeny tests and which give estimates for several orchard types in Table 2. Predicted gains in stand volume for unrogued and rogued first-generation orchards of loblolly pine (6.4 and 12.7 %, respectively) agree very well with those for slash pine (7.0 and 13.2 %). The estimate of no appreciable gain in fusiform rust resistance for unrogued first-generation orchards is typical--selections made in early years were not from highly-infected stands, and hence not resistant. But, the predicted gains of 18 and 30 % for rogued first-generation orchards and 1 1/2-generation orchards are very appreciable.

Reports of realized gains for loblolly and slash pines are summarized in Table 3. Gains in individual tree volumes are relatively consistent, varying from 2 to 14 % in unrogued orchards and from 14 to 21 % in rogued orchards. Gains in stand volume are highly variable, although the averages for unrogued and rogued orchards are about as expected, 6 and 17 %, respectively. The negative values are probably due to losses in survival. The losses reported by Tankersley (1983) were attributed to poor survival caused by high rust infection. The lack of gain for survival is expected in the first generation because we did not select for this trait (except that we did not select dead trees!). But losses in survival were frequent in rogued orchards also. Perhaps the reason for this is that natural selection has favored trees adapted to natural growing conditions, while our nursery and field planting techniques are far from natural. Perhaps we need to consider differences in survival more seriously in advanced-generation selection.

The very high gain in stand volume of slash pine (45%) reported by Kossuth et al. (1982) is exceptional. This is especially so in view of the fact that (1) the orchard contained only 9 clones, all of which were related to each other either as full- or half-sibs, and (2) that they were selected mainly for high gum yielding ability and to a lesser extent for rapid growth. The result tends to support previous work indicating a correlation between high gum yield and rapid growth. The apparent lack of inbreeding depression should be accepted with caution because very high wild pollen contamination was previously shown for this orchard. Further tests of seed from it would be desirable.

The Gladstone et al. (1987) report included other results of interest (not included in Table 3). They found that stand volumes were greater in single-family blocks than in mixed-family blocks, gains being 16 vs. 11 %, respectively. This apparent advantage of planting improved trees in single-family blocks should be tested further.

Table 2. Predicted superiority of loblolly and slash pine seeds from several clonal orchard types based on progeny test data.

Orchard type	Age	Gain (%) Stand volume	Fusiform rust resistance 1/
Loblolly pine (from Talbert 1982)			
First generation, unrogued	25	+6.4	---
First generation, rogued	25	+ 12.7	---
Slash pine (from Hodge et al., 1989)			
First generation, unrogued	20	+ 7.0	+ 2
First generation, rogued	20	+ 13.2	+ 18
One and one-half generation 2/	20	+ 18.0	+ 30

1/ $\frac{\text{(Percent infection of controls minus percent infection of orchard seed)}}{\text{percent infection of controls.}} \times 100$

2/ Orchards established with first-generation clones selected on the basis of progeny tests.

The average realized gains in stand volume for rogued and unrogued orchards, 6.2 and 17.1 %, respectively, are not greatly different from the predicted gains of Table 2. The lack of realized gain for rust resistance in unrogued first-generation orchards, with an appreciable average gain for rogued orchards, also agree fairly well with the predicted values of Table 2. In regards to this trait, White et al. (1989) showed a gain of 19% by selecting rust-free trees in highly-infected stands and also a gain of about 35 % by establishing seed production areas in highly-infected stands. Appreciable gains in other commercially important traits, such as wood specific gravity, stem straightness, oleoresin yield, and tall oil yield have also been shown.

Economic analyses show that, with even less than the average gains for stand volume reported above, tree improvement is an attractive investment for large forest land owners (Zobel and Talbert 1984, p. 451). Likewise, purchase of improved seed can be profitable for small landowners.

Table 3. Results of realized genetic gain tests for loblolly and slash pines.

Species	Stand age	Gains (+) or losses (-) as % of controls: Survival	Tree vol.	Stand vol.	Rust resistance	Authors
Unrogued First-generation Orchards (or Equivalent)						
Loblolly	8	-2		+2		Lowerts (1987)
	4	-2		-3		
	8	+7	+7	+13		Gladstone et al. (1987)
	22	+8	+8	+17		
Slash	5	-7	+12		-4	Kraus & LaFarge (1984)
	15	-3	+2	-1	-13	Tankersley et al. (1983)
	6	0	+14	+9	+7	Lowerts (1986)
	30	+6	+10			McReynolds & Gansel (1985)
Averages, both species		+0.9	+8.8	+6.2	-3.3	
Rogued First-generation Orchards (or Equivalent)						
Loblolly	6	-17		+20	+40	Lowerts (1986)
	8			+3		Lowerts (1987)
	8	+11	+21	+34		Gladstone et al. (1987)
Slash	6	0	+14	+6	+23	Lowerts (1986)
	10	-5		+45 1/		Kossuth et al. (1982)
	4	+4			+34	
	4	-23			+33	
Averages, both species		-5.0	17.5	17.1	+32.5	

1/ This was an unrogued 2nd generation orchard, given 1/2 weight in computing the average.

Phenotypic selection of hardwood species in natural stands has usually been ineffective (Purnell and Kellison 1983). But, several authors have predicted gains for selection of families (or individuals) within progeny tests and establishing orchards (Table 4). Estimated gains look good, averaging about 10, 11, and 16 % for tree height, tree diameter, and stem volume, respectively. Several authors also reported superiority of selected families over controls in progeny tests (Table 4). Although these are not genetic gain estimates, they suggest that appreciable gains might be attained.

Table 4. Predicted genetic gains for first-generation rogued orchards and superiority of selected families[1] for some hardwoods.

Species	Selection intensity	Age of test	Height	Dia.	Stem volume	Authors
		Gains or superiority %				
			Predicted gains			
Sycamore	Best 21% families	5	4	6	---	Jourdain et al. (1983)
	Best 3% individuals	5	14	18		
	Best 50% parents	8	22	24	24 -1/	McCutchan (1983)
Green ash	Best 24% families	10	5	6	12	Stauder & Lowe (1983)
Sweet gum	Best 15% families	10	6	7	20	(1985)
No. red oak	Best 50% individuals-2/	13	7	7	9	LaFarge & Lewis (1987)
Sweet pecan	Best 20% families	6	29			Toliver & Zeringue (1983)
Averages			12.4	11.3	16.2	
		Superiority of selected families!"				
Sycamore	Best 10% families	10	22	24	59	Toliver and Dicke (1987)
	Best 15% families	16			63	Byram et al. (1988)
Green ash	Best 15% families	15			40	
Water-willow oak	"	15			158	
Cherry-bark oak	"	10			62	
Yellow poplar	"	10			18	

1/ Superiority of selected families vs. controls in progeny tests.

2/ Conversion of a progeny test into a seedling seed orchard in this case.

3/ Gain based on tree dry weight rather than volume in this case. A gain of 43 % was also estimated for unrogued second-generation orchard using combined selection.

Four generations of breeding work with _Eucalyptus grandis_ in south Florida has been tremendously successful. Realized gains of 100 and 83 % for stem volume and stand volume, respectively, have been reported by Meskimen (1983) and these were for a "commercial" level of selection intensity. A higher level of selection, "Premier," resulted in gains of 164 and 159 %, respectively. The majority of the overall gains resulted from selection in the first generation (ancestral trees, which perform poorly). Additional gains from selection in subsequent generations were nearer to those being obtained in southern pines.

PROGRESS IN RESEARCH AND TECHNIQUES

General Procedures for Tree Improvement

Although some false starts were made, I believe we have ended up with the most practical procedures for most of our species. In the beginning some people felt that the best way was to select superior trees and then develop vegetative propagules from them for forest planting. This was the feeling of researchers at Olustee when high gum yielding slash pines were selected in about 1940. People there at the time felt that in order to take advantage of these it would be necessary to develop techniques for propagating them vegetatively for use in forest planting. Hence, the emphasis was on research in rooting cuttings. Soon, however, some breeding work demonstrated that seeds from crosses between high gum yielders performed well, and the approach was accordingly altered.

Another approach considered was to produce hybrids for use in forest planting, and some work was done along this line. But the problem of mass production of hybrids and other problems were soon encountered and, as Dr. John Duffield once stated, "Species hybridization has ceased, at least for the present, to be an important approach in tree improvement." In the early 1950s the seed orchard approach was begun in the South. Some variations were practiced, such as development of seed production areas and seedling seed orchards, and these have been useful in special situations. Curiously, many researchers are working on the vegetative propagation approach again, but using more refined techniques, such as tissue culture (McKeand and Weir 1984). Commercial vegetative propagation has been successful with some species and may well become the technique of the future.

Geographic variation

I believe we have pretty well learned the extent and nature of geographic variation for most of our commercially-important pines, and work is progressing well with some hardwoods. However, I believe we have been somewhat lax in delineating "planting" or "deployment" zones. Terminology is somewhat confusing, but I am here referring to areas and/or sites for which separate strains of trees may be desired now or in the future. These delineations are preferably made on the basis of local tests which reveal the best seed for each zone. But, such factors as disease hazards, climate, soils, etc., can be used in preliminary delineations. One practical approach might be for each cooperator to test seeds from orchards of other organizations, especially those in different climates, along with their own for comparison. Such plantings could be done on an operational basis, to provide information on realized genetic gain as well. I believe intensive delineations may become more important in the future. Eventually genetic gains may reach a threshold and one way to increase them will be to develop strains for smaller planting zones. In any event, if additional provenance testing is required for species that are currently widely planted, it will have to be done very soon. Pollen from the many plantations being established will often fertilize flowers on native trees, preventing forever the chance to establish reliable provenance tests for those species.

Our seed source studies have shown that local seed sources are usually safest but not always best. Seed from central positions of a species range and/or where climate is optimum will often perform better than seed from other areas, even if moved appreciable distances. For example, Lambeth et al. (1984) expect stand volume gains of 20 to 30 % from planting coastal North Carolina orchard seed in Arkansas and Oklahoma, compared to seed from local stands. Reasons for this situation may be that natural selection favors trees most suitable for performance under natural environments. But we, in planting trees, create a much different environment by growing seedlings in a nursery, preparing planting sites, etc.

Mating schemes and progeny testing

Most organizations are currently employing rather sophisticated mating schemes, such as disconnected half-diallels, for progeny testing and developing breeding populations (van Buijtenen and Namkoong 1983). These procedures have several good advantages, such as providing opportunities for capitalization of specific combining ability, increasing genetic variation and giving maximum gain per generation. Some recent reports, however, give good arguments for using simpler schemes, such as polycrossing, single-pair matings, and even use of wind-pollinated seed, which can shorten generation intervals and produce greater gains per unit of time (Cotterill 1986). Zobel and Talbert (1984, p. 430) hypothesize that a 25 % increase in genetic gain per unit of time can be made by reducing generation interval from 20 to 16 years. Possibilities for decreasing generation intervals by growing families at very close spacing over a short period of time are promising (Franklin 1983). Likewise, new flower stimulation procedures (Greenwood 1983) can greatly shorten generation intervals.

Along this line, I am wondering if progeny testing of second-generation selections is necessary. Techniques for adjusting for environmental gradients in plantations have been developed (Bongarten and Dowd 1987). Likewise, adjustments for extent of competition can also be made (Smith 1987; Land and Nance 1987). Thus, if a candidate selection is phenotypically superior after adjustment for these factors, and its siblings are at least moderately superior, and its parents are genetically superior, is progeny testing worth the effort? Omission of progeny testing would, or course, reduce generation intervals and would decrease costs considerably. Selections would still need to be interbred in order to establish the next generation, but this would be a relatively small job compared to breeding for progeny test purposes. The question certainly seems worthy of study.

Seed orchards

Many new seed orchard techniques have been or are being developed, particularly in pollen management (Franklin 1981). For example, seed yields and genetic gains can be increased and wild pollen contamination reduced by supplemental mass pollination, a technique which has been shown to be operational

(Bridgewater et al., 1987; Blush 1987). Movement of seed orchards southward is another promising technique for increasing seed yields and for avoiding contamination (McKinley 1987).

Fusiform rust resistance

Techniques for developing rust resistance have progressed rapidly after learning that phenotypic selection in the wild was effective only in highly-infected stands. Several new procedures for early assessment of resistance are now available or are forthcoming. Establishment of the Rust Resistance Screening Center of the USDA Forest Service at Asheville, North Carolina, was a very valuable development. In vitro techniques are promising (Frampton, et al., 1985) as well as indirect selection using monoterpenes [Squillace et al., 1985; Michelozzi et al. (1989)]; and use of early symptoms of the disease (Layton 1985). Delineation of rust hazard patterns (Phelps 1974, Squillace 1976) has been of great help in breeding strategy. Byram et al. (1987) recently suggested that loblolly pine selections should be mated with highly-susceptible trees to test for resistance because the trait seems to be controlled by dominant genes. This agrees with some unpublished work I did with slash pine, which showed that a large part of the variation among families of known parentage could be explained by assuming two dominant genes.

THE PROBLEM OF DECREASING FUNDING

During the 1980s both federal and nonfederal funding for forest research decreased by roughly 25 % (Giese 1988), resulting in high losses in manpower for tree improvement work. What can we do about this? Certainly we should try to avoid further losses. Better information on realized gains, especially for rogued and advanced-generation orchards will help. But perhaps we should also think about what can be done if further losses occur. The suggestions of using simplified mating and progeny testing techniques, mentioned earlier, could be considered. A methodology suggested by Franklin (1986) for use with minor species could be considered for wider application. It entails use of a single plantation per generation, which serves as a progeny test of trees selected in the previous generation, a basis for the selection and breeding for the base population of the next generation, and finally as a seedling seed orchard. An even simpler procedure was suggested for minor species by Squillace (1979). It involves the establishment of seed production areas in regions of appreciably different environments in planted stands of each generation, providing for both artificial and natural selection. The latter type of selection would be important where environments, such as virulence of fusiform rust, may change with time.

CONCLUSIONS

Our tree improvement efforts of the past 40 years have been very successful in developing superior trees with appreciable genetic gains. The many new and better techniques being developed, along with the continued high degree of cooperation among organizations involved, will help insure continued success. But we must also try to avoid further cuts in funding and may have to start employing shortcuts.

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