

# SLASH PINE TREE IMPROVEMENT

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**Abstract**—Slash pine breeding programs in the southern USA began more than a half century ago and are conducted in two tree improvement cooperatives: Cooperative Forest Genetics Research Program, CFGRP, housed at the University of Florida in Gainesville, and Western Gulf Forest Tree Improvement Program, WGFTIP, centered at the Texas Forest Service, Texas A&M University, in College Station. These tree improvement cooperatives consist of private companies, state agencies and university personnel all working together to conduct selection, breeding, progeny testing and research to genetically improve slash pine. The CFGRP consists of 10 members improving slash pine in its native range. Six of the 14 members of the WGFTIP participate in the tree improvement program of slash pine as an exotic for the lower coastal plain areas of TX, LA and MS. Members of both cooperatives are: (1) In the second generation of breeding and testing; (2) Focusing on improvement of a few key traits, the most important of which are volume yield and resistance to fusiform rust; (3) Maintaining large breeding populations, consisting of several hundred selections, to sustain genetic diversity of the species; (4) Establishing operational plantations with expected genetic gains in total yield of more than 30 percent above plantations established with unimproved material; and (5) Making genetically-improved slash pine available to non-members and small private landowners through seed and seedling sales. Nearly 100 percent of all new plantations of slash pine are being planted with genetically-improved material, although the degree of improvement varies.

## INTRODUCTION

Large-scale tree breeding programs (also called tree improvement programs) began in the 1950s. Zobel and Talbert (1984) cite 23 papers from 14 countries published in the 1950s that advocate or describe tree improvement programs. Today, there are breeding programs for nearly all commercially-important tree species and multiple programs sponsored by different organizations for some species in different regions or countries. Breeding of slash pine (*Pinus elliottii* Engelm.) also started in the 1950s.

Early on, slash pine was recognized as being second in importance to only loblolly pine as a target for tree improvement in the southern USA. This was despite the fact that it has the most restricted range of the four major species of southern pines (Dorman 1976). Slash pine is adapted to a variety of difficult sites in the southern most part of the commercial pine range and has been planted extensively. It is generally acknowledged to be more resistant to fire and tip moth than loblolly pine, and to be as well suited for naval stores production, as is longleaf pine. Its good stem form and wood quality traits make it extremely valuable for solid wood products as well as also being an excellent feedstock for pulp production.

Slash pine tree improvement in the southern USA is mainly conducted by the members of two regional cooperatives in which private industry, state agencies and university personnel all work together cooperatively. The purposes of this report are to: (1) Describe the nature and infrastructure of these two tree improvement cooperatives; (2) Summarize the first-generation tree improvement programs of both cooperatives, which have been completed; (3) Highlight key

features of their on-going second-generation programs; and (4) Document the genetic gains and genetic diversity in the operational plantations currently being established by members of these two cooperatives.

## TREE IMPROVEMENT COOPERATIVES OF SLASH PINE

### Organization and Activities of Slash Pine Cooperatives

Slash pine breeding programs in the southern USA are conducted cooperatively through two regional tree improvement cooperatives: Cooperative Forest Genetics Research Program (CFGRP) housed at the University of Florida in Gainesville, FL and Western Gulf Forest Tree Improvement Program (WGFTIP) centered at the Texas Forest Service, Texas A&M University, in College Station, TX. These tree improvement cooperatives consist of private companies, state agencies and university personnel all working together to conduct selection, breeding, progeny testing and research to genetically improve slash pine. The CFGRP was initiated in the 1950s and has been conducting slash pine tree improvement continuously ever since. Tree improvement started at Texas A&M University in the early 1950s as a cooperative program between the Texas Forest Service and several organizations in East Texas. Soon after, there were several other independent programs operating in the area. WGFTIP was formally founded in 1969 when several of these former programs agreed to join forces and new members were added to the effort.

The CFGRP and WGFTIP have similar organizational structures and these structures have changed little since

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the inception of the cooperatives. Each cooperative has a small staff (3 to 4 people centered at the University of Florida for the CFGRP and at the Texas Forest Service in College Station for the WGFTIP) which performs the following functions: (1) Provides scientific leadership in developing and implementing breeding strategies; (2) Conducts research and development in both basic forest genetics and applied tree improvement; (3) Provides technical support to cooperative members; and (4) Carries out data management and data analysis of all cooperative experiments and genetic tests. The latter function is especially important because both cooperatives have hundreds of field experiments with data collected every few years. With personnel changes and corporate mergers, a key function of the cooperative staff is to provide institutional memory about when, where and how to measure cooperative field tests.

The private companies and state agencies that are the members of the tree improvement cooperatives are active participants in every phase of cooperative activity. The members: (1) Set policy and direction of the cooperative through participation in advisory councils and executive committees that meet as often as needed, but at least annually; (2) Provide financial support to the cooperative in the form of annual dues and in-kind contributions; and, most importantly, (3) Conduct all field activities of the tree improvement programs using their personnel and their equipment on their timberlands (for example, selection, field testing and breeding). It is an understatement to say that the southern USA owes much to the foresight of the founding and continuing members of tree improvement cooperatives. The private companies compete in most every other aspect of their business, but decided long ago to cooperate in the long-term efforts to genetically improve southern pines for the betterment of the entire region.

### **Magnitude and Impact of Slash Pine Tree Improvement Efforts**

The CFGRP consists of 10 members improving slash pine in its native range, principally in the lower coastal plain regions of GA, FL and AL. These members own or lease 2.7 million acres of slash pine plantations. They produce 50 million genetically-improved slash seedlings each year that are used to reforest 110,000 acres of their own timberlands. In addition to the seedlings produced for reforestation of their own timberlands, CFGRP members sell 70 million genetically-improved slash pine seedlings and 4,000 pounds of genetically improved seed each year to non-members.

Six of the 14 members of the WGFTIP (3 private companies and 3 state agencies) participate in the tree improvement program of slash pine as an exotic for the lower coastal plain areas of TX, LA and MS. These six WGFTIP members own or lease 0.7 million acres of slash pine plantations. They produce 6.5 million genetically-improved slash seedlings each year that are used to reforest 10,000 acres of their own timberlands. In addition to the seedlings produced for reforestation of their own timberlands, WGFTIP members sell 13.5 million genetically-improved slash pine seedlings and 1,500 pounds of genetically improved seed each year to non-members.

For members of both cooperatives, the relative importance of slash pine has diminished through the years as loblolly pine (*Pinus taeda* L.) has become more important, and both cooperatives also have tree improvement efforts for loblolly pine. Therefore, it is useful to estimate the total size of the plantation estate of slash pine being supported by the breeding efforts of the two cooperatives. One way to measure this is simply the sum of the slash pine plantations currently owned or leased by the members (2.7 and 0.7 million acres by the CFGRP and WGFTIP members, respectively). However, these figures suffer in two ways: (1) Current ownership reflects historical patterns of plantation establishment, not current or future trends (for example, members could be converting these plantations to loblolly pine as they reach harvest age); and (2) These ownership figures do not include slash pine plantations managed by non-members who purchase genetically-improved seed or seedlings from cooperative members. For example, small, non-industrial landowners who purchase genetically-improved seedlings directly benefit from the efforts of the two cooperatives.

Another way to estimate the current size of the slash pine plantation estate being supported by the breeding efforts of the cooperatives is to assume that annual reforestation rates and seed and seedling sales have reached equilibrium values that are not changing through the years. Then, if all of the seed and seedlings are being planted in the southern USA (we ignore the small fraction of seed being sold internationally), we can calculate the "regulated" plantation estate assuming a 20-yr rotation. For example, for the CFGRP, there are 50 million seedlings planted annually on member timberlands and 70 million seedlings sold to non-members. In addition, the 4,000 pounds of seed sold to non-members equates to another 32 million plantable seedlings (assuming 8,000 plantable seedlings per pound of seed). Therefore, total annual reforestation of genetically-improved seedlings of slash pine supported by CFGRP members is 152 million seedlings (50+70+32) which means approximately 215,000 acres of annually reforestation (assuming 700 trees planted per acre). Assuming a regulated forest with a 20-yr rotation, the total plantation estate of slash pine being supported by the CFGRP tree improvement cooperative is 4.3 million acres (215,000 \* 20). Similarly for the WGFTIP, internal seedling use, seedling sales and seed sales sum to 32 million seedlings annually which supports a regulated plantation estate of slash pine of approximately 1 million acres.

To put these numbers in perspective, there were a total of 1.7 billion forest tree seedlings planted in the entire USA in 1999 and 1.2 billion of these were loblolly pine in the southern USA (<http://www.afandpa.org/forestry/forestry.html>). Slash pine reforestation with seedlings bred by the two cooperatives totals 180 million seedlings each year (150 and 30 for the CFGRP and WGFTIP, respectively) which is approximately 15 percent of the reforestation of loblolly pine and 10 percent of all tree seedlings planted nationwide. To our knowledge, these figures account for nearly all slash pine reforestation in the southern USA.

## FIRST-GENERATION IMPROVEMENT OF SLASH PINE

Genetic improvement programs capitalize on the facts that there is tremendous genetic variation within most tree species and that family members resemble each other more closely than do unrelated individuals. One of the oldest and historically most successful schemes to take advantage of these facts is the method of genetic improvement referred to as recurrent selection (RS). Recurrent selection uses repeated cycles of breeding aimed at the gradual and cumulative improvement of a few traits in a population (Shelbourne 1969, Namkoong and others 1988 Chapter 3). The benefits of breeding accumulate in each cycle or generation as improvement builds upon advances made in prior generations.

The oldest form of RS is called simple recurrent selection in which each cycle of breeding involves: (1) Mass selection of individuals based solely on phenotypic appearance; and (2) Breeding of these phenotypically-superior individuals to produce the offspring available for selection in the subsequent generation. In this form, the selected and breeding populations are identical and there is no genetic testing or pedigree control. Simple recurrent selection was the method used more than 10,000 years ago by ancient farmers to improve their field crops (Briggs and Knowles 1967): seed from phenotypically-superior individuals was retained for next year's crop. Simple recurrent selection is what landowners practice when they leave the best trees to seed in the next generation.

Simple recurrent selection is rarely used in modern tree breeding programs, because it is less efficient at achieving genetic gains than forms of recurrent selection that incorporate genetic testing and pedigree control. The vast majority of conifer breeding programs employ recurrent selection for general combining ability (RS-GCA) (Shelbourne 1969, Namkoong and others 1988). In RS-GCA, genetic testing follows selection. This generally takes the form of progeny tests where the breeding values of parents are evaluated by tracking the performance of their offspring. Selections with high GCA values for any trait are those that produce top-performing offspring. To start the next cycle, parents with high GCAs and their offspring are selected for further breeding and testing, while poor-GCA selections are eliminated from the program. Genetic testing greatly increases the genetic gain above that possible from mass selection. This is especially true for traits with low heritabilities which, unfortunately, account for most economically-important traits of conifers.

This section documents the first-generation tree improvement programs of slash pine in the CFGRP and WGFTIP. These programs began in the 1950s and the CFGRP first-generation cycle was completed in the 1980s. The first-generation cycle for the WGFTIP is currently being completed. Both cooperatives employed similar breeding strategies involving: (1) Mass selection of outstanding trees from natural stands and plantations based solely on outward appearance; (2) Grafting a portion of those trees in clonal seed orchards to produce genetically-improved seed for operational reforestation, while establishing the remainder in scion banks for preservation and breeding;

(3) Establishment of progeny tests to rank the selections based on GCA; and (4) Breeding together of first-generation selections to create new combinations of genes and planting of these seedlings in tests to make second-generation selections. Details of the first-generation slash pine tree improvement programs are in tables 1 and 2 for the CFGRP and WGFTIP, respectively, and the highlights are summarized below.

### Breeding Zones and Base Populations

Tree improvement programs are organized around geographic areas known as breeding zones. These are deployment areas where important economic traits are similar and in which the performance of the outplanted trees can be accurately predicted. Thus, the breeding zone is the geographical area for which an improved variety is being developed. Determining breeding zone boundaries is a critical decision in tree improvement programs, because each breeding zone requires a separate improvement program with its own distinct base, selected, breeding, and propagation populations. The tendency in conifer breeding programs is to develop large breeding zones to minimize costs associated with multiple programs and to breed improved varieties that have broad adaptability. This approach is suitable when genotype x environment interaction is not important for most traits across the edaphoclimatic region in the breeding zone and when conserving natural patterns of geographic variation is not a primary concern.

For slash pine in the southeastern USA (table 1), the CFGRP defined a single breeding zone consisting of the entire natural range of the species, approximately 10 million acres of timberlands (White and others 1986). A single program with its base, selected and breeding populations is being conducted for this zone. Similarly for slash pine in the Western Gulf, the WGFTIP defined a single breeding zone consisting of the flatwoods sites that stretch across the southernmost parts of the coastal plains in Mississippi, Louisiana, and Texas (table 2). Much of this area is outside the natural range of the species, but includes large areas in which slash pine has been planted as an exotic since the 1930s.

While there are many similarities between the two breeding zones of the CFGRP and WGFTIP, there are also some significant differences. In the southeastern USA slash pine is frequently found on well-drained sandy soils, while in the Western Gulf region it is favored for planting on poorly-drained, phosphorous-deficient silty clay soils. In the southeastern USA, there are areas where fusiform rust (*Cronartium fusiforme*) and its obligate alternative host, the red oaks, are present at only low levels. In these areas, growth rate is the most important economic trait. In the Western Gulf region, where slash pine has not coevolved with the endemic pathotypes and red oaks are plentiful, improving resistance to fusiform rust is the single most important goal of the tree improvement program.

The base population of a given cycle of improvement consists of all available trees that could be selected if desired (Zobel and Talbert 1984). It is the population of trees that will be improved upon through selection and breeding and

**Table 1—First- and second-generation breeding programs for *Pinus elliottii* as conducted by the Cooperative Forest Genetics Research Program<sup>a</sup>**

Category	First generation	Second generation
Breeding objectives	Increase volume yield, resistance to <i>Cronartium fusiforme</i> (rust) and stem straightness.	Increase volume yield, resistance to <i>Cronartium fusiforme</i> (rust), stem straightness and wood specific gravity.
Breeding unit	One large breeding unit encompassing the natural range of slash pine.	One large breeding unit encompassing the natural range of slash pine.
Base population	Ten million acres of predominantly natural stands encompassing the entire native range.	(1) Field tests containing 2,700 FS families and 200,000 trees available as forward selns; (2) 1,200 FG selns plus 1,250 FG infusions available as backward selns.
Selected population	1955–65: 1,200 intensive selns made by comparison tree method: volume, stem straightness, freedom from disease, crown form.	1987–88: 965 selns: (1) one-third are backwards selns of top first-generation parents; (2) one-third are forward selns; and (3) one-third are untested infusions not bred in FG.
Propagation population	1955–70: 2,500 acres of clonal SO established by CFGRP members. Each member's SO contained their 25 to 150 original selns. Bulk collections of wind-pollinated seed used for reforestation.	1990–95: 600 acres of clonal SO established by CFGRP members. Each SO contained the best 20 to 40 backward and forward selns from the selected population. Single-family collections of OP seed are used for reforestation.
Progeny testing	1965–80: 350 OP field tests (325,000 trees) to rank 1,200 selns. Seed collected from selns grafted in SOs.	No separate progeny testing to rank selns prior to breeding and testing described below.
Infusions	1970–85: 1,250 infusions: (1) 850 rust-free selns in highly-infected stands; (2) 125 selns from the southern part of the range; (3) 115 selns for high yield of oleo-resin; (4) 60 selns free of pitch canker fungus; and (5) 100 others.	1995: 85 infusions: (1) 70 selns obtained as top forward selns from USDA Forest Service field trials upon closure of USFA program; and (2) 15 new backward selns of top first-generation parents after reanalysis of data.
Breeding population	1970–85: 820 top selns (600 of 1,200 original selns plus 220 of 1,250 infusions) bred together in 6 parent disconnected diallels and factorials to create 2,700 FS families planted in 225 field tests containing 200,000 trees.	1995–2001: 1,050 selns in 24 BGs with 44 selns/BG. Complementary mating designs: (1) for ranking, polymix mating of 325 poorly-tested selns planted in 16 replicated tests containing 55,000 trees; and (2) for forward selection, breeding among all 1,050 selns use to create 1,500 FS families planted in unreplicated plots in 12 locations with 100,000 trees.

BG = breeding group; FG = first generation; CP = control-pollinated; FS = full-sib; OP = open-pollinated; seln = selection; SO = seed orchard.

<sup>a</sup> The generation intervals were: 1955 to 1985 for the first generation and 1987 to 2003 for the second generation.

Source: White and others (1986), White and others (1993).

hence is also called the foundation population. In first-generation conifer breeding programs, the base population is typically very large consisting of many thousands or millions of trees. In the case of the CFGRP, any tree growing in natural stands within the native range was, at least in concept, a potential candidate for selection and therefore inclusion in the program.

The WGFTIP base population drew on native stands of slash pine from southeastern MS and planted stands in MS, LA and TX. The intent was to capitalize on the beginnings of a land race that was created when slash pine was established as an exotic in the Western Gulf region.

However, as most of the WGFTIP first-generation selections originated from populations that were, at most, only one generation removed from the native range, both programs originally sampled the same genetic resource.

### Selected Population

In the first generation, both the CFGRP and WGFTIP used a process called mass selection to select outstanding trees based on their phenotypic, outward appearance. For both cooperatives, first-generation selections were identified by comparing growth rates and other characteristics of candidate trees to five comparison trees chosen among the candidate's neighbors. The selection procedure emphasized

**Table 2—First- and second-generation breeding programs for *Pinus elliottii* as conducted by the Western Gulf Forest Tree Improvement Cooperative**

Category	First generation	Second generation
Breeding objectives	Increase resistance to <i>Cronartium fusiforme</i> (rust), volume yield, and stem straightness. Maintain regional averages for specific gravity.	Increase volume yield, resistance to <i>Cronartium fusiforme</i> (rust), stem straightness and wood specific gravity.
Breeding unit	One large breeding unit encompassing the flatwoods of MS, LA, and TX.	One large breeding unit encompassing the flatwoods of MS, LA, and TX.
Base population	Natural stands in MS and plantations in MS, LA, and TX where slash pine was planted as an exotic. Most of these plantations were of unknown origin, but came from seed collected in the native range.	(1) Field tests containing 712 FS families and 168,000 trees available as potential forward selns; (2) 500 FG selns.
Selected population	1955–83: 1,000 intensive selns made by comparison tree method: volume, stem straightness, freedom from disease, crown form. This was reduced to 500 selections based on performance at the Resistance Screening Center.	Target of 550 selns: (1) 90 will be backwards selns of top first-generation parents; (2) 460 will be forward selns; currently 166 second-generation selections have been identified. The remainder of the second-generation selns will be identified by 2010.
Propagation population	Six organizations currently manage 200 acres of first and 1.5 generation orchards. Bulk and family collections of wind-pollinated seed used for reforestation.	130 acres of advanced-generation SO established by WGFTIP members. Each SO contained the best 20 to 40 backward and forward selns chosen for disease resistance and volume growth. Bulk and family collections of OP seed are used for reforestation. Control-mass pollinated seed and rooted cuttings will also be used.
Progeny testing	120 progeny tests established to evaluate 367 parents in CP tests and 22 parents in OP tests. The last remaining first-generation progeny tests should be established in 2003.	Currently 3 polymix tests established to evaluate 37 second-generation parents. Eventually there will be approximately 550 parents evaluated in polymix tests.
Infusions	None	None

BG = breeding group; FG = first generation; CP = control-pollinated; FS = full-sib; OP = open-pollinated; Seln = selection; SO = seed orchard.

growth rate, wood specific gravity, stem straightness, and crown form. Selected trees were required to be free of fusiform rust, but otherwise no pressure was placed on improvement of this trait. Most selections were made in low hazard stands where rust was not prevalent; so, little advancement in rust resistance was made during the first round of selection.

From 1955 through 1965, the CFGRP made 1,200 selections in natural stands growing within the native slash pine range (table 1). These selections were widely distributed across many counties in FL, GA and AL with fewer from SC and MS. Most of the 1,000 first-generation slash pine selections by the WGFTIP were made in areas where slash pine was planted as an exotic in southern TX and LA. These selections originated from even aged plantations of unknown origin. Selection activity began in the mid 1950s by the Texas Forest Service and other organizations working independently. Selection continued from 1969

until 1983 as part of the WGFTIP cooperative. The bulk of the WGFTIP selections were made in the 1970s.

### **Propagation Populations: Clonal Seed Orchards**

Cooperators soon realized that it was critical to capture value from these selections by establishing them in clonal seed orchards. A clonal seed orchard is a collection of selections grafted in one physical location and then managed to produce genetically-improved seed for operational reforestation. By establishing the selections in a single location, both male and female parents are selected and thus theoretical genetic gains are doubled compared to collecting seed from the selections growing in the original stands. The gains from these original first-generation clonal seed orchards reflect only the gains from mass selection. That is, the seed produced from these original orchards is genetically-improved only to the extent that the mass selection was successful in identifying genetically-superior trees.

Members of both the CFGRP and WGFTIP cooperatives used similar processes to establish their clonal seed orchards involving the following steps: (1) Selections were made in the base populations as described in the previous section; (2) Many branch tips (say 100 pieces), called scion material, were collected from each selection; (3) The scion pieces from each selection were grafted onto seedling rootstock to produce the plants for establishing the seed orchard; (4) All plants originating from a single selection have the same genotype as that selection, since all branches have the same genotype, and these plants are called a clone; (5) Each first-generation seed orchard established through this means contained 20 to 200 plants of each clone (that is, grafts from each selection) from a total of 20 to 150 different selections; (6) The grafted plants were established in the orchard location at relatively wide spacing (for example, 15 ft x 30 ft) compared to plantations to provide full sunlight to the crowns to promote flowering; (7) Each plant was identified by its clone number, and ramets of the same clone were maintained at a minimum distance from each other to reduce selfing; and (8) After planting, the orchard was managed intensively to produce mass quantities of open-pollinated seed, and this seed was used for operational forestation. Cultural management of clonal seed orchards is completely different than that of plantations and genetic tests due to the very different objective: seed production.

CFGRP members established nearly 2,500 acres of first-generation seed orchards between 1955 and 1970. These mainly contained each member's selections meaning there was little exchange of selections among cooperators. In the Western Gulf, some organizations were working independently prior to the formation of the WGFTIP cooperative, while others were working together from the very beginning. Early orchards emphasized a variety of different traits. The Texas Forest Service established its first slash pine orchard in 1957 selected for growth rate and form. Small orchards were later established that emphasized high wood density (1964) and known fiber properties (1966). The Louisiana Department of Agriculture and Forestry established one of their first slash pine orchards in 1967 with clones obtained from the USDA Forest Service that were selected for enhanced naval stores properties. Crown Zellerbach (now Weyerhaeuser Company) established their first slash pine orchard in 1964 with selections made off of their own land. Organizations establishing orchards in cooperation with the Texas Forest Service or after the cooperative was formed in 1969 shared many of the same clones. All of the later orchards were established with clones selected for growth and form.

All of these first-generation seed orchards were established solely on the basis of outward appearance of the trees that were selected and subsequently grafted. That is, there was no evidence from genetic tests that the selections were, in fact, genetically superior to other candidate trees that were not selected. As data from genetic tests began to become available (described in the next section), it turned out that, in fact, some of the selections were inferior and some were superior to average, unimproved trees for the few commercially-important traits being measured. As these data became available, cooperators

rapidly eliminated poor clones (that is, clones whose offspring had performed poorly in genetic tests) to upgrade the genetic quality of the orchard seed. This process is called roguing, and roguing poor clones from a seed orchard can increase expected genetic gains by 40-50 percent over the initial mean (Talbert and others 1985; Li and others 1999).

Through the process of roguing, expected gains of CFGRP first-generation seed orchards went from an average of 9 percent volume yield above unimproved material to 14 percent gain (table 3). These values are averages over more than 20 first-generation seed orchards owned by different CFGRP members and individual orchard gains vary markedly depending on the exact composition of selections originally grafted. As more and more data became available from genetic tests, CFGRP members began to exchange clones with other members so that all could have the very best tested clones. Members established, through grafting, new seed orchards containing these very best first-generation clones obtained from the pool of 1,200 selected by the entire cooperative. These so-called 1.5-generation orchards averaged 18 percent in volume yield and also contained selections with considerable rust resistance (table 3). While many clones were common to most 1.5-generation CFGRP seed orchards, some members put more emphasis on rust resistance and others on growth rate; so, expected gains and clonal composition did vary.

In the Western Gulf, fusiform rust was increasingly recognized as an important problem, and all orchard clones were tested for disease resistance at the USDA Forest Service's Resistance Screening Center between 1980 and 1983 (Anderson and others 1983; Anderson and Powers 1985). These greenhouse tests, employing artificial inoculation of progeny of the orchard clones, identified susceptible selections, and existing first-generation orchards were heavily rogued based on this criterion. All subsequent orchards were established with material selected for both growth and disease resistance. The WGFTIP now has 194 acres (76 ha) of first and 1.5 generation orchards improved for rust resistance, growth, and form managed by six organizations. Gain estimates cannot be compared across the cooperatives because data summarization procedures differ. The WGFTIP breeding values for volume include a survival factor to account for less mortality due to improved rust resistance. R50s, while similar in concept, are also difficult to compare because the fusiform rust populations and environmental conditions under which selections from the two programs were evaluated also differ. Current WGFTIP production orchards, which include heavily rogued first-generation orchards and advancing-front orchards with both backward and forward selections have an estimated breeding value for volume of 30 percent and an R50 of 32. The younger advancing-front orchards that are not yet into production have an average projected breeding value for volume of 38 percent and an R50 of 25.

### **Genetic Testing and Breeding**

Genetic tests are central to all tree improvement programs and are established with pedigreed, well-labeled offspring or clonal plantlets, such as offspring from the first-generation selections planted in randomized, replicated tests

**Table 3—Genetic gains from CFGRP slash pine seed orchards in volume and rust resistance<sup>a</sup>**

Type of seed	Years seed planted	Volume gain <i>percent</i>	Rust resistance <sup>b</sup> (R50)
Unimproved	<1960	0.0	50
1.0 Generation orchard unrogued	1965–1985	9.0	49
1.0 Generation orchard rogued	1975–1995	14.0	41
1.5 Generation orchard unrogued	1985–2005	18.0	35
Advanced-generation orchard	>2002	30	20

CFGRP = Cooperative Forest Genetics Research program.

<sup>a</sup> All gains are expressed relative to plantations established with unimproved material as it existed before domestication began in 1950. Volume gain is in percent above unimproved.

<sup>b</sup> Rust resistance is expressed in R50: the percentage of trees in a stand that would be infected with rust when 50 percent would be infected in an unimproved plantation (for example, R50 = 35 means that 35 percent of the trees would be rust-infected in plantations that would have had 50 percent infection if planted with unimproved material). All gain values are averages of 10 or more seed orchards of different members, and gains of the individual orchards vary markedly depending on clonal composition.

(McKinley 1983; Zobel and Talbert 1984, Chapter 8; van Buijtenen and Bridgwater 1986; White 1987; Bridgwater 1992). The tests are usually planted in field locations on forest sites, but may also occur in nurseries, greenhouses and growth rooms. The idea of these “common garden” tests is to grow genotypes in replicated environments so that genetic effects can be isolated from confounding environmental effects.

Tree improvement programs rely on genetic testing to: (1) Evaluate relative genetic quality of selections made in any cycle of selection (that is, progeny testing to rank the GCAs of first-generation selections based on the performance of their offspring); (2) Estimate genetic parameters such as heritabilities, genetic correlations, and genotype x environment interactions for key traits; (3) Provide a base population of new genotypes from which to make the next cycle of selection; and (4) Quantify or demonstrate genetic gains made by the program.

The third function of genetic tests mentioned above involves another activity, called breeding. Some or all of the individuals in the selected population are included in that cycle’s breeding population and are intermated (cross bred) to regenerate genetic variability through recombination of alleles during sexual reproduction. Many different mating designs are used to intermate the members of the breeding population, and offspring from these intermatings are planted in genetic tests that form the next cycle’s base population. This completes one cycle of the core activities of the breeding cycle (selection, breeding and testing), and

the next cycle begins with new selections being made from these genetic tests (that is, from the new base population).

The CFGRP and WGFTIP employed different strategies for genetic testing and breeding in their first-generation slash pine programs, emphasizing the myriad of alternative methodologies available to tree breeders. In the CFGRP, the progeny testing and breeding phases (functions 1 and 3 of genetic tests mentioned above) were separated in time by 10 or so years and employed a different set of parents. Shortly after the original 1,200 selections were made, it was recognized that it was impossible to rank these selections for their genetic quality, since they were selected in hundreds of different natural stands growing in 5 states. Therefore, CFGRP members mounted a large program of progeny testing with tests established from 1965-1980. Open-pollinated (OP) seed was collected from each of the grafted selections growing in seed orchards and kept labeled by the clone (that is, selection) that produced the seed. As seed from 20 to 100 selections became available, these were planted into randomized, replicated field tests located on members’ timberlands throughout the slash pine native range. Altogether 350 separate field tests containing more than 325,000 OP progeny from the 1,200 selections were established (table 1). The performance of OP progeny was used to rank the 1,200 selections, mainly for volume growth and rust resistance (for example, a selection producing offspring that consistently grew well and were rust resistant in several replications on each of several field sites was judged as a top performer).

As soon as rankings became available from OP progeny tests (beginning in 1970 for the earliest OP tests), CFGRP members began to breed together top-ranking selections through control pollination. The idea was to increase genetic gain from the breeding efforts by eliminating poor-performing selections before breeding. The top 600 of the 1,200 original selections were combined 220 new infusions chosen as superior rust-free trees in high-hazard stands (see below) to create a breeding population of 820 parents (table 1) that were bred together to create 2,700 full-sib families that were established in 225 field tests containing 200,000 full-sib, pedigreed offspring. These tests were established from 1970 through 1985. The second generation of slash pine tree improvement began in 1987 (table 1) with selection of superior trees from top families in these selection tests.

In the WGFTIP, the plan initially adopted by the cooperative was to include each of the 1,000 first-generation selections in control-pollinated breeding where each selection would be in at least four crosses with other selections and each cross would be evaluated at three different locations for growth and form. By the late 1970s, it became apparent from analyzing the older test data that rust-related mortality was so significant that the best predictor of volume at age 15 was rust infection levels at age five. It also became apparent that parents selected only for good growth and form were frequently poor performers in the field when exposed to fusiform rust infection. This led to two changes in the WGFTIP breeding and progeny-testing programs. The first was a change in the evaluation criteria in progeny tests. The second was the adoption of a two-step screening procedure.

Rust-related mortality was the most significant factor causing changes in family ranks for volume production between ages five and 15. Therefore, the evaluation scheme was altered to use rust infection at age five as the indirect selection criterion for final volume. In order to have confidence that all families had been exposed to rust, only those tests in which the average rust infection of the test or that of the unimproved checklots exceeded 30 percent were used. At later ages (10 and 15 years), much of the rust-related mortality had already occurred, and both growth rate and infection levels were deemed to be important in determining final volume (Lowe and van Buijtenen 1991).

The second change in the first-generation progeny-testing program involved the adoption of a two-step screening procedure. This scheme combined greenhouse screening for disease resistance followed by breeding and testing of the most disease-resistant parents in field tests for growth and yield (Lowe and van Buijtenen 1989). All 1,000 first-generation selections were first crossed with a polymix of ten parents chosen because they lacked resistance in field tests. Rust-susceptible parents were chosen in order to ensure that any resistance apparent in the greenhouse tests would originate from the female parent under evaluation (Byram and Lowe 1987). The WGFTIP eliminated approximately half of its first generation breeding population on the basis of resistance screening at the USDA Forest Service Resistance Screening Center. The 500

remaining selections were divided into groups of six to nine parents that are being crossed in a modified half-diallel scheme in which each parent is included in four crosses. The current progeny test design consists of establishing each cross in three locations with each location containing 50 replications of single-tree plots. Growth and disease incidence are evaluated at five-year intervals. These tests are used both to rank parents and as a source for second-generation selections. To date, there have been 120 long-term first-generation progeny tests established to evaluate 389 parents. Twenty-two of these parents are only in open-pollinated tests, while 367 parents are evaluated in control-pollinated tests containing 712 full-sib families. WGFTIP anticipates that the last of the required first-generation progeny tests will be established in 2003.

### Infusions

Some years after initial selections are made, many tree improvement programs add new selections into the breeding population that were not part of the original selected population. These infusions can be aimed specifically at improving a single trait or at generally broadening the genetic diversity existing in the program. The WGFTIP did not make any infusions in the first-generation slash pine program; however, the CFGRP doubled the size of the first-generation selected population by infusing 1,250 new selections obtained through several different opportunities (table 1): (1) 850 new selections were obtained to increase rust resistance in the program by selecting phenotypically-superior trees that were free of disease in natural stands that had 85 percent or more of the trees rust infected (Goddard and others 1975); (2) 125 new selections were made in central Florida in the counties near Orlando (the southern part of the natural range of the northern variety of slash pine) to broaden genetic diversity; (3) 115 new selections were made from diallels originally established by the USDA Forest Service as part of their program for naval stores production (that is, high yields of oleoresin); and (4) 60 selections were added to increase pitch canker resistance by selecting disease-free trees in natural stands heavily infected with the pitch canker fungus (*Fusarium circinatum* which was formerly *F. subglutinans*) (Rockwood and Blakeslee 1988).

### ADVANCED-GENERATION BREEDING OF SLASH PINE

In both the CFGRP and WGFTIP, the goals of the advanced-generation breeding programs of slash pine include: (1) Achieving maximum short-term genetic gains in a few traits of high economic importance, mainly volume growth and rust resistance with less emphasis on stem form and wood specific gravity; (2) Maintaining sufficient genetic diversity in the breeding population to ensure near-optimal long-term genetic gains in the same or different traits as markets, products, technologies and environments change in the future; (3) Ensuring sufficient flexibility in program design to facilitate change in direction and incorporation of new technologies (such as biotechnologies); (4) Conserving genetic diversity in the species; and (5) Conducting all of these activities in a timely, cost-effective way that yields appropriate economic returns.



Because of the similar goals of the two cooperative programs, there are many similarities in second-generation breeding strategy and program implementation. There are also some differences. Details of the two second-generation programs are summarized in the following sections, but points of strong concurrence are: (1) Focus on improvement of two key traits, volume and rust resistance, with lesser emphasis on a few others; (2) Large selected and breeding populations designed to maintain sufficient levels of genetic diversity; (3) Use of overlapping generations in which excellent first-generation selections (called backward selections) are retained in the program and included in the selected population with forward selections of the top offspring from first-generation selections; (4) Reliance on a strategy aimed at improving the overall mean general combining ability (GCA) of the breeding population (which implies genetic testing to rank selections); (5) Subdivision of the breeding population into smaller sub-groups, called sublimes or breeding groups, to manage inbreeding; (6) Use of complementary mating designs in which a polymix design is used for progeny testing and full-sib designs are employed to create a base population in which to make third-generation selections; (7) High quality field tests employing modern experimental designs in field sites that are intensively managed to minimize competition and maximize early expression of genetic differences in growth and rust resistance; and (8) Reliance on wind-pollinated seed orchards as the principle form of producing genetically-improved seed for operational reforestation.

### Base Populations

The base population for the second generation consists of all possible selections from both the original first-generation selections that could be retained in the program (backward selections) and progeny from breeding of those selections growing in genetic tests. When the second-generation CFGRP program began in 1987 (table 1), the base population consisted of all of the following materials that could have been selected: (1) The original 1,200 first-generation selections; (2) 1,250 infusions that had been accumulated during implementation of the first-generation program and either had to be utilized or discarded; and (3) 200,000 progeny from 2,700 full-sib families growing in 225 field tests, all of which were available as potential forward selections. The base population for the WGFTIP second-generation program will include the approximately 500 first-generation parents and 168,000 progeny of those parents growing in first-generation genetic tests. Second-generation selections will be identified on the basis of rust resistance as progeny tests reach age 5 and these same tests will be screened again at age 10 on the basis of volume growth and rust resistance. The bulk of the tests will be screened during the next ten years.

For two reasons, the advanced-generation base populations for the two cooperatives will begin to diverge as the programs mature. First, each program started with a slightly different founder population, because different samples from the slash pine species were drawn for the first generation. Second, the populations will diverge as each program develops different land races as a result of testing in different environments and from selecting for slightly different traits to meet the specific requirements of their

respective breeding zones. This will be a very slow process as many similarities exist in testing and selection criteria of the two programs and many generations of breeding and selection will be required to make large genetic differences in the two base populations. Therefore, opportunities for the two cooperatives to enrich each other's breeding programs through exchange of improved material will exist for the foreseeable future.

### Selected Population

In 1987, the CFGRP initiated the second-generation slash pine program by predicting breeding values for volume and rust resistance of all trees in the base population (that is, of all backward and forward candidates for selection) using an analytical methodology called Best Linear Prediction (White and Hodge 1988). Next, using a growth and yield model (Nance and others 1983), economic weights for volume and rust resistance were estimated (Hodge and others 1989). Due to the imprecision of these estimated weights and the differences among CFGRP members in the relative importance of volume and rust, 3 indices were developed for each tree:  $I_B$ ,  $I_G$  and  $I_R$  where the first index (B for both) weights volume and rust resistance according to their economic weights,  $I_G$  puts predominant weight on growth performance and  $I_R$  puts most emphasis on rust resistance. Generally, if any candidate (backward or forward) was excellent for any of the three indices, it was included in the second-generation selected population. This is similar to the multiple index selection strategy (Namkoong 1976) and aims to develop breeds for growth, rust and both within the CFGRP (Carson and others 1991).

To balance the objectives of maximizing genetic gain while maintaining adequate genetic diversity, the maximum number of relatives (full-sib, half-sib or parent-offspring) allowed in the CFGRP selected population was set at 7, and this number decreased with decreasing predicted genetic value. So, more second-generation selections were included from top families, in keeping with the principle of placing more emphasis on higher-ranking materials (Lindgren 1986). In addition, untested infusions were also included in the second-generation selected population, and many of these were infusions for rust resistance from the first generation (table 1) that had not been tested or utilized.

In summary, the CFGRP second-generation breeding population for slash pine was formed in 1987, and contained a total of 933 total selections with the following composition (White and others 1993): (1) 395 backward selections of the very best first-generation selections; (2) 318 top forward selections from the 225 field tests containing 200,000 trees from 2,700 full-sib families; and (3) 220 infusions from the first-generation. With a census number of  $N=933$  total selections, there were 850 unrelated individuals that contributed genes to the selected population and the population had an inbreeding-effective population size of  $N_e=625$  (which is lower than 933 due to relatedness, Falconer and Mackay 1996). The genetic gain for this genetically-diverse population is approximately 20 percent for volume and an  $R_{50}=35$  meaning 35 percent rust-infected trees in stands where unimproved material would have 50 percent of the trees infected. Subsequent to 1987, 30 or so new second-generation

selections were added to bring the total to 965 and 85 new infusions were added to take advantage of special opportunities (table 1).

The WGFTIP program currently has 166 second-generation selections. It is anticipated that an additional 300 second-generation selections (forward selections) and approximately 90 proven first generation parents (backwards selections) will be added to this total. The WGFTIP second-generation population will then be approximately 550. Second-generation selections will be identified based on mid-parent values for rust resistance (age 5) and a combination of volume and rust resistance (ages 10 and older). Data summarization procedures for estimating these breeding values were reported by Lowe and van Buijtenen (1991).

### **Propagation Populations: Clonal Seed Orchards**

In the second-generation, members of both the CFGRP and WGFTIP cooperatives are relying almost exclusively on open-pollinated clonal seed orchards to produce genetically-improved seed for reforestation. Control mass pollination (CMP), an alternative to seed orchards in which top parents are crossed together on an operational scale, is currently being used on a limited basis to capture additional genetic gain in the operational plantations by planting full-sib families (Bridgwater and others 1998), but plantations established through CMP account for less than 2 percent of current annual reforestation in the southern USA.<sup>2</sup> Operational planting of tested clones, produced either through tissue culture or rooted cuttings, is another alternative to seed orchards that is being explored by some companies. However, to date clonal forestry is still in the development stage. It is likely that operational deployment in the future will include all three of these options (open-pollinated seed orchards, CMP, and clonal forestry), but through 2010, the large majority of plantations will be established from seed orchard seed.

The designs and compositions of the clonal seed orchards vary between the 2 cooperatives and are described below; however, in both cooperatives a major change has occurred in how seed is collected and deployed from those orchards. In the 1970s and 1980s, most companies collected bulk seed from their orchards and, therefore, established operational plantations that were mixtures of many families. Currently, it is much more common to collect seed in one of two ways: (1) By groups of clones (for example, some organizations divide clones in the orchard into three groups, such as top growers, rust resistant and other, and collect seed according to this grouping); or (2) By clone (so if there are 20 clones in an orchard there are 20 bags of seed and each bag contains the OP family seed of a given mother-tree clone). Both options increase genetic gain in operational plantations in 2 ways. First, seed is not collected from less-desirable clones in an orchard, and second, seed is deployed to sites for which it is most suited (such as rust resistant material to high hazard sites). With the second

option, operational plantations are established with single OP families (that is, all trees in a plantation have a common female parent). Approximately half of all slash pine plantations are now established with single OP families and a given company might deploy from 2 to nearly 25 different families (see footnote 2).

In terms of the details of advanced-generation slash pine seed orchards, most CFGRP members established orchards shortly after 1987 when the second-generation selected population was formed. They employed a systematic design (Hodge and White 1993) in which 40 or so clones were grafted in the same order in each block of the orchard. Approximately half of the clones are backward, tested selections and half are forward, untested progeny. Thus, there can be parents and offspring in the same orchard. When data are available from second-generation genetic tests, the poorer clones can be rogued from orchard leaving a mix of unrelated forward and backward selections. CFGRP members currently manage about 600 acres of these second-generation clonal seed orchards, and the genetic gains are expected to be 30 percent for volume and  $R50=20$  (table 3).

In the WGFTIP program, the second-generation clonal seed orchards are designed as advancing-front orchards where blocks are established on a periodic schedule that allows new material to be incorporated from the breeding program as it becomes available. Older blocks can also be removed from management as better material becomes available. In general, blocks for these advanced-generation orchards are established on a five-year cycle with the best 20 clones currently available. This strategy was adopted because different member's programs are at different stages and as a result, advances in the breeding program occur annually rather than in evenly-timed generational intervals. The WGFTIP cooperative currently has 140 ac (55 ha) of advanced-generation orchards under management.

### **Breeding and Progeny Testing**

All advanced-generation breeding programs must cope with the fact that the number of relatives increases in closed populations through selection and breeding. This can have dire consequences in outbred species, such as pines, because matings among relatives frequently reduce family performance (called inbreeding depression) and confound the ability to accurately predict parental breeding values if families being tested suffer from different levels of inbreeding. The WGFTIP and CFGRP have adopted very similar strategies to deal with these problems. Namely, both breeding populations have been sib-divided into smaller subsets, called breeding groups or sublines, such that all relatives are assigned to and managed within the same breeding group (van Buijtenen 1976, Burdon and others 1977, van Buijtenen and Lowe 1979). This allows inbreeding to be concentrated in the breeding population by making only crosses within breeding groups to produce the next generation. At the same time, this ensures that unrelated individuals (from different breeding groups) will always be available to establish the propagation population. For example, the best selection from each breeding group could be grafted into a clonal seed orchard and

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<sup>2</sup>McKeand, S.E.; Mullin, T.J.; Byram, T.D.; White, T.L. Deployment of genetically-improved loblolly and slash pine in the Southern U.S. Manuscript in preparation.

since all breeding groups are unrelated to each other, the seed from the seed orchard would be completed outcrossed.

Another important commonality between the 2 cooperatives is the use of complementary mating and field designs. These schemes use one set of crosses and field designs to rank parents and another set of crosses and field designs to produce the base population from which third-generation forward selections will be made. To rank parents, selections are being bred with a pollen mix and the polymix families are being planted in well-replicated field tests planted in single-tree plots. The second type of design makes control-pollinated crosses among the selections and the full-sib families are then planted in essentially unreplicated block plots of 50 to 100 trees per family. These full-sib families are ranked for their predicted performance based on the parental breeding values obtained from polymix tests. Selections for the next cycle of breeding will then be made from within the block plots.

In the CFGRP, the breeding population consisting of 1,050 selections (table 1) was divided into 24 breeding groups with each group containing approximately 44 selections. All selections were grafted into clone banks on members' timberlands in 1988 and 1989, and members began breeding as soon as the grafts began to flower. For the polymix breeding, the CFGRP decided not to re-test backward selections that already had been adequately tested in first-generation tests. In addition, many of the 220 infusions were not included in the polymix testing. The first series of polymix tests contained 138 PM families planted in 1998 on 8 sites with 20 replications per site. The second polymix series was planted in 2001 with 177 PM families on 8 sites with 20 replications. No other polymix testing is planned for the second generation meaning that 315 (138+177) of the 1,050 selections will be ranked in these tests. In the second part of the complementary designs, members have made 1,500 full-sib families using a flexible crossing design that makes more crosses among top selections within each breeding group and crosses the lowest ranking selections only once (White and others 1993). These crosses are being planted in selection blocks of 50 to 100 trees as crosses become available from 1995 through 2003. In total, more than 100,000 pedigreed trees will be available in these selection plots to begin making third-generation selections in 2003.

The WGFTIP advanced-generation breeding population has been divided into 35 breeding groups of approximately 18 to 25 individuals. The complementary mating scheme uses polymix seedlings planted at 3 locations, each with 50 single-tree plot replications, to rank parents. Block plots of control-pedigree crosses among members from the same breeding groups are also being established. Breeding and testing for the second generation is just beginning within the WGFTIP as first-generation testing was drawn out to allow screening at the RSC. Currently, there are 3 polymix tests established to evaluate 37 second-generation selections. Three of the six slash pine members are currently producing crosses for the control-pollinated selection population.

## Genetic Gains and Genetic Diversity

Genetic diversity and gain are conflicting objectives for all tree improvement programs. In particular, it is impossible to make gains without reducing genetic diversity and genetic diversity decreases in all closed breeding populations during the course of many cycles of recurrent selection. In the current slash pine breeding population of both cooperatives, high levels of genetic diversity are being actively maintained by managing extremely large populations (500 to 1,000 selections) and by limiting the number of related selections. Since both programs are only in the second generation of breeding and both are improving only a few key traits, diversity levels have changed little in the breeding populations compared to the natural species. These breeding populations are large enough to sustain excellent genetic gains for many generations of breeding and contain sufficient levels of genetic diversity to provide considerable flexibility to changing climates, markets and technologies.

Genetic gain and diversity are also important in operational plantations. Most organizations want to maximize genetic gain in operational plantations and accomplish this by using only the best material available each generation. For example, a clonal seed orchard might contain the top 20 out of nearly 1,000 selections available in any generation, and the organization might choose to plant single OP families collected from that orchard. Most organizations are willing to take more risk in a plantation that exists for a single rotation compared with a breeding population that must sustain a program for many generations of improvement. Still, it is important to quantify the gains and risk associated with different options for operational deployment of genetically-improved material.

Genetic gains from different types of CFGRP seed orchards are shown in table 3. It is clear that steady gains have been made throughout the years as breeding technologies, data analysis methods and genetic testing have advanced. For the CFGRP, seed being planted from advanced-generation seed orchards is expected to have volume gains of 30 percent above unimproved material when planted on low hazard sites for fusiform rust. These yield gains will be enhanced on high hazard sites since the average orchard contains clones with mean  $R50=20$  (so, seedlings from these orchards are expected to have 20 percent of the trees infected in stands that would be 50 percent infected were unimproved seedlings planted).

As mentioned earlier, many organizations are now planting single OP families on portions of their timberlands to capture maximum genetic gains. Further, some organizations are piloting or developing programs to deploy single full-sib families or single tested clones to increase genetic gains still further in operational plantations. Since each of these options decreases genetic diversity to increase genetic gain, it is important to analyze the implications of these alternatives: bulk mixtures of seed from seed orchards, single OP families from seed orchards, single full-sib family from unrelated parents and single, non-inbred clone. McKeand and others<sup>2</sup> recently approached this issue through a survey of all major organizations in the south to see if any plantation failures had been reported. First, 31

state and private companies returned the surveys (100 percent of all the members in the 3 tree improvement cooperatives in the southern USA) and these companies are directly or indirectly responsible for at least 90 percent of the annual reforestation southwide. None of these organizations had experienced in unexpected environmental or pest problems in plantations established with single OP families. The only problem mentioned was that of a family being deployed that had not been adequately tested for cold or drought tolerance, but this was extremely rare. Since clonal plantations have not been planted on a wide scale, experience is limited.

Unfortunately, there is never any perfect way to assess risk (for example, how much home, car and life insurance is enough?). Extremely diverse populations of American Chestnut and American Elm were decimated by introduced fungal pathogens while Chardonnay grapes, which have very little if any genetic diversity, have been grown worldwide for over 400 years. Still, it is clear both theoretically and empirically that single OP families retain the large portion of genetic diversity in the species (75 percent of the additive genetic variance and 100 percent of the dominance genetic variance) and have been used safely for many years. As organizations employ clonal forestry, genetic diversity of the deployment population will decrease. Deployment strategies will need to balance the need to maintain genetic diversity against the desire for maximizing genetic gain in determining the number of clones to plant and their arrangement across the landscape.

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