Developing Fusiform Rust-Resistant Loblolly and Slash Pines

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ABSTRACT

Powers, H. R., Jr., and Kraus, J. F. 1983. Developing fusiform rust-resistant loblolly and slash pines. Plant Disease 67:187-189.

Fusiform rust-resistant selections of loblolly and slash pine have been planted in a seed orchard for production of seedlings with high levels of resistance to the disease. Half of the orchard consists of grafted trees of superior clones and the balance is designed as a seedling seed orchard made up of survivors of artificial inoculation tests. Eventual production should exceed 15 million seedlings annually for use in areas subject to high hazard from fusiform rust.

Additional key words: *Cronartium quercuum* f. sp. *fusiforme*, disease resistance, *Pinus elliottii* var. *elliottii*, *Pinus taeda*

Fusiform rust caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* is the most serious disease of loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* Engelm. var. *elliottii*) pines in the southern United States (9,12). Recent estimates of financial loss attributed to tree mortality and lumber degrade caused by this disease exceed $100 million annually (13). In many areas, management decisions such as intensity of site preparation, choice of species for planting, planting density, and even the final product are determined by the severity of this disease (4). Because of the impact of this disease on forest industries in the southern United States, large research programs have been initiated to produce rust-resistant strains of both slash and loblolly pine. Genetic resistance has been demonstrated in both species (1,6,14), and progeny from individual tree selections of both loblolly and slash pine have shown high levels of resistance compared with nursery-run seedlings.

In 1967, the USDA Forest Service and the Georgia Forestry Commission initiated a cooperative program to develop rust-resistant southern pines. Before this time, many phenotypically superior pine selections had been made and put into first-generation seed orchards. These selections were made primarily with regard to growth and yield; rust resistance was only one of the many factors considered. Many of the selected trees were in older stands that had developed before rust incidence had increased to its present high level so selected trees may not have been exposed to strong natural-selection pressure for rust resistance. In addition, branch infections had been lost due to self-pruning and were no longer visible when the selections were made. As a result, many of the selections did not have high levels of disease resistance.

This large reservoir of superior genetic material, however, made it possible to

Accepted for publication 12 July 1982.

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begin the rust-resistance program with second-generation selections from progeny test plots. Information was available not only on disease resistance but also on growth and yield characteristics of the progenies produced by crossing the first-generation selections. Initial evaluations were made to select the best families for all characteristics, and within this group, individual trees from families with outstanding rust resistance were selected. Scions were obtained from these selections to produce grafted trees, which were placed in clone banks for evaluation of rust resistance. The best of these trees eventually provided the material for the formation of rust-resistant seed orchards.

Nearly all of the rust-resistant orchards in the southern United States have been developed by the standard practice of making grafts from selected apparently rust-resistant trees. Unfortunately, the number of proven rust-resistant clones is relatively low, particularly in the case of loblolly pine. In 1976, it was estimated that there were about 50 highly rust-resistant slash pine selections available in the entire South but less than 30 loblolly pine selections of this caliber (H. R. Powers, Jr. *unpublished*). Other selections classified as intermediate in resistance to rust could be added to these numbers. This, however, is a very limited genetic base from which to produce seedlings to be distributed over the large area where rust is a critical problem.

Research on rust resistance was accelerated in the early 1970s by the development of a large-scale carefully controlled artificial inoculation system for evaluating resistance to the disease (7). This inoculation procedure, called the Concentrated Basidiospore Spray (CBS) system, screens large numbers of seedlings by uniformly inoculating them with a specific inoculum density of basidiospores. Field progeny tests are still basic to resistance evaluation, but the artificial testing provides results in a fraction of the time required for field tests. The CBS system also gives good correlations with field tests and is quite efficient in selecting the most resistant families (8). The survivors from these tests, especially from the more resistant families, are obviously valuable plant material for breeding programs (2,3).

This paper outlines a procedure for using rustfree survivors from inoculation tests in an orchard designed for the large-scale production of rust-resistant seed. A preliminary report covering some aspects of this research has been published (10). This paper presents family-by-family data from both 5-yr-old slash and loblolly seedling seed orchard blocks.

MATERIALS AND METHODS

As soon as the selections in the clone banks began producing cones, the resulting seedlings were tested with the CBS system. By 1974, it was obvious that many of these selections were producing seedlings far superior in rust resistance to commercially available seedlings. Therefore, in cooperation with the Georgia Forestry Commission, we decided to establish a 24.3-ha (60-acre) production orchard of disease-resistant material equally divided between slash and loblolly pine. Because of the relatively low number of resistant selections available, half of the acreage for each species was designed as a standard clonal orchard and the other half as a seedling seed orchard. One completely new aspect was the use of survivors of the CBS tests to form the seedling seed orchard.

The clonal orchards were established with a standard spacing of 9.1 × 9.1 m (30 × 30 ft) with each 0.4-ha (1-acre) block containing 49 grafts. Most trees were grafts of second-generation selections, but a few of the best first-generation selections were included to produce 49 different clones per block.

Seedling seed orchard blocks contained 50 replicates. Each replicate included a randomly placed single tree of each family included in the block. All seedlings used in these plantings were survivors of artificial-inoculation tests and were gallfree 9 mo after inoculation. Seedlings of 12 to 16 families were usually included in each block, and 93 and 76 families were represented in the loblolly and slash orchards, respectively. These families were rated as resistant after inoculation tests and in some cases also on the basis of field progeny test data. Seedling seed orchard trees are spaced closely; in our case, they were 1.5 × 4.6 m (5 × 15 ft). As selection proceeds, it is necessary to thin heavily in order to reach an eventual spacing of about 9.1 × 9.1 m (30 × 30 ft). More than 90% of the seedlings originally planted must be removed, leaving about five seedlings of the original 50 of each family as crop trees. The first removals were trees that became diseased by natural infection. Subsequent removals were based on growth and form characteristics and on family histories of rust resistance. Data on rust infection, height, and growth characteristics were taken the third year after planting and every year thereafter. Percent infection data were based on the number of trees of each family within a block that became infected in the field.

RESULTS

The first loblolly pine seedling seed orchard blocks, planted in 1975, were survivors of greenhouse inoculation tests from 16 wind-pollinated families rated intermediate to good for rust resistance. After 5 yr of exposure to natural field infection, the seedlings in these families ranged from 2 to 56% infected (Table 1). A similar block of slash pine ranged from 21 to 44% infected (Table 2). No susceptible checks were included in the orchard blocks, but adjacent plantings of nursery-run trees had 78% infection at 5 yr of age. Therefore, the incidence of rust in this particular area is moderately heavy.

There was a good correlation (r = 0.755) between the results from the artificial inoculation tests and subsequent natural infection on the survivors in the orchard. For example, the first 10 families listed in Table 1 have been consistently among the more resistant in several artificial inoculations and all of these families had 16% or less infection after a 5-yr exposure to natural infection. The next five families have been intermediate in resistance in greenhouse tests and ranged from 18 to 48% infection in the orchard. Family 10-31, the most heavily infected family in the orchard, was a marginal candidate in this planting

Table 1. Fusiform rust infection and height of 16 loblolly pine families in a rust-resistant seedling seed orchard after 5 yr

Family	Rust infection (%)	Height[a]	
		Meters	Feet
SML-9	2	4.7	15.5
29-RX1495-35	4	5.0	16.5
10-6	4	4.8	15.7
TDR	6	5.1	16.7
TFS	8	5.3	17.4
1495-35	9	4.5	14.9
11-9	10	4.8	15.9
11-20	11	4.8	15.8
42-R	13	4.8	15.7
10-5	16	5.5	17.9
15-42	18	5.3	17.3
2318	28	5.0	16.4
T-605	32	5.3	17.3
T-601	41	5.7	18.6
29-R	48	4.6	15.0[b]
10-31	56	5.0	16.4[c]
$\bar{x}$	19	5.0	16.4

[a] Mean height of tallest 10 trees.
[b] Based on six remaining trees.
[c] Based on nine remaining trees.

Table 2. Fusiform rust infection and height of 16 slash pine families in a rust-resistant seedling seed orchard after 5 yr

Family	Rust infection (%)	Height	
		Meters	Feet
J-18	21	4.5	14.9
2882-23	21	4.3	14.2
2905-5	21	4.8	15.9
2792-14	21	4.6	15.0
2737-11	21	4.5	14.9
2797-10	22	4.8	15.7
2788-8	23	4.8	15.7
2907-5	24	4.7	15.4
2882-1	33	4.5	14.8
2965-12	35	4.7	15.3
3016-1	35	4.6	15.2
2972-1	36	4.7	15.3
2936-5	41	4.5	14.6
86	42	4.6	15.0
10-226	43	4.1	13.4
3302-21	44	4.6	15.0
$\bar{x}$	30	4.6	15.0

because in two artificial inoculation tests it had only 25% less infection than susceptible checks.

Mean heights of the tallest 10 trees in each family are shown in Tables 1 and 2. These trees are most likely to be the group from which eventual seed producers will be selected. The average height for loblolly families ranged from 4.5 m (14.9 ft) for an open-pollinated family from an Arkansas seed source growing in central Georgia to 5.7 m (18.6 ft) for another open-pollinated family from Marion County, FL. The mean height for all loblolly families was 5 m (16.4 ft) and the correlation between levels of rust resistance as expressed by percent infection and the mean height of the 10 tallest trees was not significant ($r = 0.185$). The mean height for the slash pine families was 4.6 m (15.0 ft) with a range of 4.1–4.8 m (13.4–15.9 ft).

Because the oldest seedling seed orchard blocks are now only 6 yr old, they are not yet producing many cones and it is still too early to determine the overall level of rust resistance of seedlings from this orchard. Only four open-pollinated loblolly families from the seedling seed orchard have been tested to date, and they had 58% as much infection as the susceptible checks in the inoculation tests, very similar to the maternal parents of these families.

DISCUSSION

All of the data from the seedling seed orchard show that survivors from the most resistant families in the artificial inoculation tests also had the fewest infections in the field. This correlation was also noted by Dinus and Griggs (3). This indicates that resistance detected in the juvenile stage is often maintained in older trees under natural conditions. It is also obvious that not all survivors of inoculation tests are resistant in the field, even among the most resistant families. However, individuals selected as final crop trees in the seedling seed orchard, having survived a relatively severe artificial inoculation in the juvenile stage and from 6 to 10 yr of exposure to natural infection in the field, should be some of the most resistant material currently available for breeding programs. Seedlings from these same families have also been planted in survivor progeny tests at several locations. In every case, the survivors from the more resistant families have held up best under field conditions, but strains of the pathogen that are highly virulent on otherwise resistant selections have been found in specific geographic areas (11), again emphasizing the need for a broad genetic base of resistance.

Many of the progenies initially tested for rust resistance by artificial inoculation were from open-pollinated seed obtained from seed orchard trees. It is likely that the pollen parents of these seedlings were also seed orchard trees with favorable growth characteristics. The remainder of the progenies were from open-pollinated seed from trees in clone banks or progeny tests. The possibility that seedlings in this group have an unselected male parent is higher than for those from seed orchards, but the relatively high intensity of selection practiced in the development of the maturing seedling seed orchard should eliminate the least desirable genetic material, leaving trees with a potentially broader genetic base than those in clonal orchards. The seedling seed orchard approach also avoids some problems inherent in clonal orchards, such as the mechanics of producing grafts, incompatibility, and the adverse effects of the understock on the scion portion of the graft (5). Most important, the seedling seed orchard design is very compatible with breeding programs utilizing survivors of artificial inoculations.

A few forest industries in the southern United States have developed seedling seed orchards, but none are designed as rust-resistance orchards or use survivors of rust inoculation tests. Our orchard is the first of this type, and along with the production of resistant seed, we hope to get a comparison of resistance levels from clonal vs. survivor seedling seed orchards. Eventual production from the entire 24.3-ha (60-acre) seed orchard should exceed 15 million seedlings annually for use in high rust-hazard areas. The test results to date are encouraging because the relatively few seeds produced thus far in these orchards have produced seedlings with about the same levels of rust resistance as their mother trees. These seeds have resulted from fertilizations by pollen from sources outside of the orchard because very few orchard trees are producing any pollen. As the trees mature and begin producing both male and female flowers, levels of resistance should be increased because the seed will then be formed largely as a result of resistant × resistant crosses. In a nearby second-generation slash pine seedling seed orchard established by the Georgia Forestry Commission with full-sib crosses from progeny-tested first-generation trees, there was significantly less fusiform rust infection after 4 yr in 16 crosses of resistant × resistant trees than in 17 crosses in which only one parent was classified as resistant ($P = 0.05$) (J. F. Kraus, *unpublished*).

Original estimates of gain from the rust-resistant orchard were an average reduction of 50% in rust incidence in slash pine and 40% in loblolly pine. This is a conservative estimate, and controlled pollinations of resistant parents indicate that we will produce seed with better levels of resistance than predicted. Future generations of selections from these orchards should bring the incidence of rust down to less than 33% of that in currently available seedlings.

The most obvious immediate use for the best individuals among the trees in the seedling seed orchard would be as new selections to provide scion material for grafting and inclusion in new clonal orchards. In addition, as these trees mature and begin to produce seed, their progeny can again be screened for resistance and the cycle repeated with a new generation of survivors.

Because the oldest orchard blocks contain some trees producing cones, limited production should begin within 2 yr. At that time, about one-half million rust-resistant seedlings will be produced for use in high rust-hazard areas.

ACKNOWLEDGMENT

We wish to thank the Georgia Forestry Commission for supplying land and personnel to help carry out this study.

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