Application of Genetic Disease Resistance for the Control of Fusiform Rust in Intensively Managed Southern Pine

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Fusiform rust is the most important tree disease in extensive portions of the southern pine forest and it severely limits the intensive management of slash and loblolly pine throughout much of this region. This disease occurs from southern Maryland to Florida and west to southeastern Arkansas and Texas. The highest incidence occurs in planted pine (age, 1–20 yr) in south central South Carolina, central Georgia and south central Alabama (52). Within this "rust corridor" average rust incidence (percentage of trees with at least one rust gall) in 8- to 12-yr-old plantations is 70–80%; disease incidence in some plantations is virtually 100%. Incidence of rust is also high in contiguous areas in Florida, southwestern Mississippi, and southeastern Louisiana.

Yield loss is primarily associated with stem-galled trees that succumb throughout the rotation. In addition, there are significant direct and indirect losses associated with growth reduction, reduced marketability, lost capital investment and management costs (16). Although comprehensive disease-yield-loss models are not available, annual economic losses are estimated to exceed $100 million.

The pathogen, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme* is a heteroecious macrocyclic rust fungus (4). Pycnia and aecia occur on pine and uredia and telia occur on oak. Species of the black oak group are the most susceptible (9) and of these water oak (*Quercus nigra* L.) and willow oak (*Q. phellos* L.) are epidemiologically important (53). Basidiospores produced during wet, humid weather in April–June in hairlike columns on the undersurface of oak leaves, are wind-disseminated, and under favorable conditions they infect needles and succulent branch and leader tissues of pine. The mycelium is perennial in pine, in which branch or stem galls develop within 4–12 mo. Pycnia occur on the galls in October–December and are followed in February–April by aecia. Presumably, pycniospores function as spermatia. Aeciospores are wind-disseminated and under favorable conditions infect succulent oak leaves through stomata on the undersurface. Here uredia develop within 2 wk and are followed by telia in another week or 10 days. Hardened leaves are not infected by the pathogen and only telia occur on leaves that are not succulent at the time of infection. Prodigious amounts of inoculum are produced each year on pine and also on oak when conditions are favorable.

Fusiform rust, which was reported before the turn of the century (56), was not recognized as a potential problem until the late 1920s (23). Since then the fungus has increased and spread rapidly (6). Overall rust incidence appears to be increasing 2–3% annually. In high-rust-hazard areas disease incidence in young plantings of susceptible genotypes can be nearly 100% by age 4–6 yr (14).

The rapid increase and spread of fusiform rust is, in part, synchronous with intensive forest management (37). Increased numbers of young plantations provide a large amount of susceptible pine tissue. Also, in certain instances, management practices result in increased abundance of oak (a climax species) or pine-oak associations. These conditions, coupled with very susceptible hosts, a virulent pathogen with a high inoculum potential, and a warm, wet climate favorable for the pathogen have resulted in the current pandemic.

Control of fusiform rust was confined to forest tree nurseries where the protective fungicide ferbam is regularly sprayed on pine seedlings during the period of basidiospore flight. Ideally, rust-infected seedlings are rogued when lifted and excluded from outplantings. Recently, systemic fungicides have been, and currently are being, tested. Additional control efforts are directed toward the development of rust-resistant seedlings for plantation establishment (30,60). This work is the topic of this paper.

PATHOGEN INOCULUM POTENTIAL

Role of environment. The occurrence and duration of critical meteorological variables are important for the development of the fusiform rust epidemic. In general, fusiform rust is a warm, wet-weather "foliar" disease. Temperatures ranging 15.8–27.0 C (60–80 F) favor most inoculum production, germination, and infection phenomena. Moisture is critical; 6–9 hr of a nearly saturated atmosphere is required for telia germination (basidiospore production), and a minimum 4-hr free-moisture period is required for germination and penetration by aeciospores, urediospores, and basidiospores (41,43). Therefore, rain and dew enhance inoculum production on oak and infection of pine and oak (42,47). Succulence of oak leaves is critical for infection and subsequent inoculum production (50). In the absence of critical factors, the epidemic is stopped or delayed. However, in some areas of high rust incidence such factors do not appear to limit the epidemic because conditions that favor disease increase are the rule, not the exception (17). Although years of unusually high or low rust incidence occur, these appear not to affect the overall 2–3% increase in rust incidence with each successive year of planting (14).

Other biotic or edaphic factors may affect the rust epidemic, but their impact is thought to be slight. There are insects and fungi, including rust mycoparasites, which inhabit rust galls on pine

(20,21). Increased pine growth often results in increased rust incidence; eg, site preparation and fertilization also can result in increased rust incidence.

Quantity of inoculum. Given appropriate environmental conditions, prodigious amounts of inoculum are produced by the pathogen during the disease cycle. Although quantitative data are not available, the following observations are generally accepted as fact: tens-of-millions of aeciospores can be produced on a pine gall; each successful aeciospore infection in a succulent oak leaf can result in a uredial sorus containing hundreds of urediospores; urediospores can infect succulent oak leaves and theoretically produce several generations of inoculum, and infections initiated by aeciospores or urediospores result in a telial column that produces thousands of basidiospores.

In theory, each basidiospore is capable of producing on pine a lesion that can eventually become a gall. Screening trials for rust resistance indicate that, in an environment favorable for infection, large numbers of basidiospores are required to induce galls on a high percentage of inoculated seedlings (45). Inoculum dosage-response curves indicate that the percentage of seedlings infected increases with the amount of inoculum, and that 50,000 spores per milliliter of aqueous suspension are required for adequate testing of pine genotypes (24). Fewer spores allow susceptible genotypes to escape and larger spore concentrations mask useful field resistance.

Preliminary studies (40) indicate that dispersal gradient curves for aeciospores (average size 14×27 μm) are relatively steep as are the resulting disease gradient curves on oak. Thus, local sources appear to be very important even though aeciospores are released during periods of wind turbulence, can travel long distances, and are capable of initiating secondary cycles. Basidiospore (average size $8-11 \times 10-14$ μm)-produced disease gradients appear less steep (R. A. Schmidt, *unpublished*) and through time are often obscured in the field. Although disease gradient data suggest that local inoculum is most important, significant long-distance dispersal also is thought to occur.

Pathogenic variability. Similar forms of *C. quercuum* (Berk.) Miyabe ex Shirai occur on more than 30 species of oaks and at least 20 species of pines in North America, extending from the Gulf of Mexico to Canada (15). Because there is a large amount of heterogeneity in the host populations, it is not surprising that *C. quercuum* possesses a large amount of pathogenic variability. Initially, species of pines were inoculated to distinguish pathogenic forms (19,26) which were subsequently classified as: *banksianae*, *virginianae*, *echinatae*, and *fusiforme* (3). Within the latter form significant pathogenic variation is identified among inocula from diverse geographic areas, among galls within the same geographic area, and within a single gall (28,34,44). Also, there is evidence (46) that in one resistant family of slash pine (family 8-7) there is selection for increased virulence in the pathogen. These results were confirmed on family 8-7 (48), but other resistant slash pine families did not produce inoculum that was more virulent on these same resistant families. Similar studies with resistant loblolly families indicated only a slight increase in virulence of inoculum collected and tested on the same resistant loblolly families (35). Although no increase in virulence was evident between inocula collected on pines infected in 1945 and those infected in 1970, the latter inoculum expressed greater pathogenic variability (29). Rust-resistant selections in first generation loblolly seed orchards appeared more susceptible to current naturally produced inocula than was previously indicated (32). Conflicting evidence exists with respect to the virulence of different geographic sources of inocula. Artificial inoculation studies indicate that local inoculum is more virulent on pine seed sources from that same area (33,34). Yet both loblolly and slash pines appear to have a higher incidence of rust when planted either south or north of their natural ranges (36). As noted in other plant populations, a heterogeneous host population has conditioned a similar situation in the pathogen population (5,7). Because the pine and oak host are highly heterogeneous, pathogenic variability in *C. quercuum* f. sp. *fusiforme* may exceed that in the cereal rusts.

The evolution of the pathogen has implications for pine management. Presumably the pine-oak rusts have a common ancestry of long duration in North America; nevertheless, *C. quercuum* f. sp. *fusiforme* is unique to the southern pine region even though pines and oaks in other regions of the U.S. are susceptible (10). There is evidence that the pathogen is of more recent occurrence on slash than on loblolly pine (13) because the former appears to be less tolerant than the latter (27). Also, resistant loblolly pine provenances exist, but resistant geographic sources of slash pine are not known (58). Further evidence that slash pine-oak associations are relatively recent suggests that the pathogen is more recent on slash pine. Prior to intensive management, slash pine was most abundant in wet areas not favorable for oak.

RUST RESISTANCE IN PINE

Tree improvement, primarily via seed source trials, was in evidence in the USA near the turn of the century. Seed source studies in southern pine were in progress by the 1920s; however, enhanced and organized efforts on tree improvement began in the early 1950s. Centers for improvement of southern pine arose within the USDA Forest Service at the Southern and Southeastern Forest Experiment Stations, in the Georgia Forestry Commission, and the universities of North Carolina, Florida, and Texas. Aggressive and rapid development in these programs was and is aided and implemented by a progressive forest industry committed to improvement and intensive management of the southern pine resource.

Selection and screening. Initially, many hundreds of "superior" pines were selected and scions were grafted to rootstocks to form first-generation seed orchards. In 10–15 yr seeds from wind-pollinated trees were collected and extensive field progeny tests were established. The results of these progeny tests were used to rogue first-generation seed orchards and to establish successive-generation orchards via scion grafting or from seedlings resulting from wind or controlled pollination. The progeny resulting from wind pollination of female parents in these orchards are designated as a "family." Families presumably are heterozygous for various traits since individual progeny can contain different genomes, contributed by various male parents.

Initially, the emphasis in tree improvement programs was on growth and yield traits and gains of 10–29% were realized. However, in extensive areas planted to slash and loblolly pines these gains, and more, were lost to fusiform rust. The need arose to incorporate rust-resistant genotypes into the existing tree improvement program. Unfortunately, even though rust-infected phenotypes were discriminated against in the original selection process, subsequent testing indicated that only an occasional selection contained rust resistance (11). Originally trees were not selected in high-rust-hazard areas; in fact, often such areas were purposely avoided. Also, selection was among older trees from which branch galls could have been naturally pruned. Even more disconcerting, initial progeny tests most often were not established in high-rust-hazard areas; such areas were avoided since growth and yield data were preeminent at that time (39). Therefore, it was necessary to reevaluate all initial selections for rust resistance by establishing progeny tests in high-rust-hazard areas (51) and via artificial inoculation tests. The latter were begun in order to standardize test conditions and to reduce the expense and time involved in extensive field progeny tests. Also, because of the variability in rust incidence among years and locations, useful comparisons were often difficult to obtain from previously established field tests.

The earliest artificial inoculations with *C. quercuum* f. sp. *fusiforme* were accomplished at the Southern Forest Experiment Station (18) at Gulfport. Telia-bearing oak leaves were suspended above pine seedlings in a double tent sprayed with water to maintain a high relative humidity. Results indicated that rust-resistance existed in slash pine and, in general, confirmed earlier conclusions drawn from field data (1). Jewell's inoculation procedures were used successfully by others (11) to screen progeny, but the method did not provide adequate control of conditions, especially inoculum concentration. As with field tests, family

comparisons within and among the early artificial inoculation tests often were difficult. Subsequently, Snow and Kais (49) and Dwinell (8) developed modified artificial inoculation systems that provided better control of inoculum concentration. These were useful for specific research studies, but not for mass-screening tests. In the early 1970s the concentrated basidiospore spray (CBS) system was developed for screening trials (25). In this method greenhouse-grown oak seedlings are inoculated with a water suspension of aeciospores under conditions favorable for abundant production of telia. Basidiospores are collected on acidified water, concentrated on Millipore pads and stored at cool temperatures. This inoculum is resuspended in water and its concentration is standardized via an electronic particle counter prior to the spray inoculation of 4- to 6-wk-old pine seedlings. The CBS system was adapted to large-scale mechanized screening trials at the USDA Forest Service Resistance Screening Center in Asheville, NC. Here, under standard conditions of host, inoculum potential, and environment, candidate seedlings are evaluated against specific sources of inocula. Generally, results are in good agreement with field data; very resistant and very susceptible families are appropriately identified. However, due to the very favorable conditions for infection at the Resistance Screening Center, some families judged relatively resistant in the field are classified as susceptible. Recently, the use of other traits, in addition to gall occurrence, has significantly improved correlations between results at the Resistance Screening Center and those of field progeny tests (57). Because of known genotype-environment (site) interactions, field testing of progeny continues.

During the 1960s and 1970s, selection and testing for fusiform rust resistance were intensified. Current efforts include second-generation selections from among progeny of the original selections; controlled pollination among resistant parents, including hybridization; and selecting and testing new resistant phenotypes from high-rust-incidence areas. Concurrent research on indirect selection, tissue culture, and the role of inoculum potential (both quality and quantity) in field resistance is in progress.

Available resistance. At present there are several opportunities to use rust-resistant materials to mitigate the fusiform rust epidemic in intensively managed southern pine forests. The amount of resistance among parents or progeny often is not optimum and in some instances growth and yield traits are not maximized, but the use of these rust-resistant materials will aid significantly (30,60).

Species. Among the major pine species, slash is the most susceptible; loblolly is nearly as susceptible, but appears to have some tolerance to stem infections; longleaf is relatively resistant; both sand and shortleaf are very resistant and perhaps immune to the special form *fusiforme* (27). These resistant host species should be favored on appropriate sites and where rust is a problem. Shortleaf pine offers an alternative to loblolly in the northern portion of the disease range; longleaf and sand pines are viable alternatives for slash pine on the drier sites in the southern portion of the disease range.

Provenances. Within loblolly pine, specific geographic seed sources contain useful levels of rust resistance (58). These resistant provenances occur on the periphery of the natural range of loblolly pine; eg, the eastern shore of Maryland, southeastern Arkansas, east Texas, central Florida, and Louisiana (13). Currently, the Louisiana provenance (Livingston Parrish) is extensively planted for rust resistance along the Gulf Coast and into central Georgia. The Maryland provenance, which appears most resistant in artificial inoculation trials (33), may prove useful in the northern portion of the disease range. Resistant provenances appear not to exist in slash pine (55).

Families. Within slash, loblolly, longleaf, and pond pines, individual families or clones possess resistance to the rust pathogen (1,31,54,59). In loblolly and slash pine the frequency of resistance is relatively high. Among the slash pine families tested, 5% possess a useful level of resistance. Among the first-generation selections, rust-resistant families showed about 30% improvement (reduction in rust incidence) compared with unimproved seed. Second- and third-generation selections, including new selections from high-rust-

incidence areas and those resulting from controlled pollination, are expected to double this improvement. First-generation orchards are producing seed in quantity and progeny from second-generation orchards are being tested (30).

Rogued seed production areas. Until rust specialty orchards produce enough seed, one immediate solution is the creation of natural seed-production areas in 15- to 20-yr-old plantations in which rust frequency and severity are high. When such areas are rogued of rust-infected trees, the remaining trees provide a ready-made, rust-resistant seed production area (12). Provided trees are stimulated to flower, improved rust-resistant seed can be obtained in a few years.

Hybrids. Progeny resulting from natural as well as controlled crosses between pine species were examined for rust resistance. Some crosses possess the rust resistance of the more rust-resistant parent and maintain the good growth and yield characteristics of the slash or loblolly parent. Of those tested, shortleaf × loblolly, shortleaf × slash, and longleaf × slash progeny appear to hold the greatest promise for rust resistance (13,22). Since shortleaf × loblolly hybrids occur naturally, certain provenances of rust-resistant loblolly may be the result of natural hybridization and backcrossing to loblolly (58).

In Table 1, we provide some information on available rust resistant materials. These data are estimates and do not identify all agencies or include all resources; eg, provenances and hybrids are excluded.

STRATEGIES FOR RUST MANAGEMENT

There are several unique aspects of developing and using genetic disease resistance in a perennial forest crop. These aspects must be considered in a management strategy for fusiform rust.

On the negative side, minimum rotation length (age at harvest) is 20–30 yr; pathogenic variability in *C. quercuum* f. sp. *fusiforme* appears quite large; and selection, breeding, screening, and orchard establishment require large investments of time, labor, and money.

On the positive side, there appears to be a relatively high frequency of rust resistance in the native pine populations; the economic disease threshold is relatively high and the demand for product uniformity is relatively low, thus increasing the utility of horizontal resistance and decreasing the potential of selecting virulent strains of the pathogen; resistant seedlings produced in current seed orchard programs are half-sibs that can provide gene diversity; and the extensive areas of southern pine provide

TABLE 1. Examples of some fusiform rust-resistant pine resources in the southeastern USA[a]

Tree improvement program	Total seed orchard		Seed orchard		Seed production area[b]		New phenotypic rustfree selections	
	SI[c]	Lob	Sl	Lob	Sl	Lob	Sl	Lob
	ha							
University of Florida Co-op	729	25	43	0[d]	154	0	266	0
N.C. State Univ. Co-op	164	1,219	7	45	···	···	12	66
Western Gulf Co-op	131	608	41	0	0	0	57	159
USDA Forest Service-Georgia Forestry Commission	132	53	12	12	9	0	45	57
USDA Forest Service-Region 8	43	117	···	···	···	···	···	···
TOTAL	1,199	2,022	103	57	163	0	380	282

[a]Data do not include all programs or all resources (eg, provenances).
[b]Plantations rogued of fusiform rust infected trees.
[c]Sl = slash pine; Lob = loblolly pine.
[d]0 = no materials; ··· = no information.

opportunities for genotype deployment which maximize gene diversity in time and space.

Selection, testing, and propagation. Diversity is the key to the development and use of genetic disease resistance in forest crops, generally, and in pine for fusiform rust, in particular. Appropriately, large numbers of rust-resistant pine phenotypes (and hopefully genotypes possessing different kinds of rust resistance) should be selected from areas of high rust incidence. These should be tested artificially with appropriate variants of the pathogen, but especially in the field where specific seed sources ultimately will be utilized. Propagation of resistant genotypes via the current wind-pollinated seed orchards and seed production areas is advantageous since the half-sib progeny presumably will be heterogeneous for rust resistance and other traits. Although this method of propagation is time consuming, costly, and may sacrifice some growth improvement, the resulting seedlings are genetically diverse. The consequences of mass producing a few genotypes are hazardous because of the pathogenic variability of the rust fungus and the potential for other pest problems. Tolerant varieties should not be overlooked since they offer the potential of minimizing losses.

Gene deployment. The best strategy is to maximize diversity. Within the context of sound silviculture; ie, matching species requirements with site capabilities, the less susceptible longleaf, sand, and shortleaf pines should be favored where appropriate. In addition, a viable short-term solution is to use rust-resistant provenances of loblolly pine and rust-rogued seed production areas of loblolly and slash pines. These sources will be replaced with better rust-improved materials as second- and third-generation seed orchards come into production. Regardless of their source, rust-resistant loblolly and slash pine should be mixed in time and space. This "multiline" concept (2) increases diversity and is feasible in forestry because of its expanded time and space dimensions. Further, it is especially amenable to fusiform rust management since product uniformity is not critical and some loss to disease is tolerable. A gene deployment strategy to enhance functional diversity (37) has not been tested in forestry and fusiform rust presents a special case since the pathogen cannot spread from pine to pine.

Integrated management strategy. Without question, genetic resistance of pine to fusiform rust has both proven and potential utility for forest management. However, maximizing this utility will require that resistance be employed in concert with other feasible rust-management tactics. This integrated strategy is outlined (38) and the authors' thesis is that intensive management of southern pine offers significant opportunities for complementary rust-management tactics, genetic disease disease resistance should not be the sole tactic, and the integrated strategy should be applied regionally. Specifically, proper management of the site, pine and oak hosts, and the pathogen provide ample opportunities to mitigate the current epidemic and reduce losses to fusiform rust.

Genetic resistance to the indigenous pathogen *C. quercuum* f. sp. *fusiforme* exists in southern pine, although the exact nature of this resistance is ill-understood. Rust-resistant species, provenances, varieties and hybrids are being identified, tested, propagated, and planted. These resistant genotypes currently provide the best means to mitigate the devastating rust epidemic in the intensively managed southern pine forests. Perennial forest crops offer unique opportunities and challenges for developing and using genetic disease resistance as a rust-management tactic. Wise use of this tactic necessitates ample numbers of genes for resistance and a deployment scheme to further enhance functional diversity in time and space. Just as important, genetic disease resistance must be employed in concert with other feasible disease control tactics in an integrated fusiform rust management strategy.

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