Forest Pathology for the Last Century: A Retrospective and Directions for the Future

Fusiform Rust of Southern Pines: A Major Success for Forest Disease Management

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ABSTRACT

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The effective management of fusiform rust in slash and loblolly pine plantations is a major success story for disease management scientists and practitioners in the southeastern United States. This disease, which reached epidemic proportions by the 1960s, resulted from anthropogenic causes associated with intensive pine culture and greatly inhibited the optimum management of slash and loblolly pine throughout extensive areas of the southern pine region. Successful management of this disease was made possible by the combined resources and personnel of federal and state agencies, universities, and the forest industry. Chief among these personnel were research pathologists, geneticists, and silviculturalists.

Following early studies on the biology of the fusiform rust pathosystem, research on epidemiology, host resistance, and pathogen variability slowly but steadily progressed. Testing of pine selections for resistance was facilitated by the establishment of a rust screening center. Fortunately, genetic rust resistance is relatively abundant in both slash and loblolly pines and has become the foundation for the management of the disease. Rust resistant half- and full-sib progeny from resistant parents established in seed orchards are routinely planted, especially in high-rust-hazard areas. Several important lessons in disease management have been learned or remembered during the progress of this research. Perhaps the ecologically fit fusiform rust pathogen will have additional instructions for us in the future, but for now resistance is an effective management strategy.

Fusiform rust, caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*, has increased to epidemic proportion in slash and loblolly pine plantations throughout extensive areas of the South since the late 1950s and early 1960s (14). Previously this disease, first reported near the turn of the last century, was neither widespread nor prevalent. There is evidence the disease spread and intensified from Mississippi to the Atlantic coast and south to Florida (6). The pathosystem is indigenous to the southeastern United States, which is likely the center of origin and a region of great genetic diversity in host and pathogen (44). The pathogen is not known to occur naturally outside the southern United States, although some species of pine-oak rusts occur elsewhere. The increase in fusiform rust incidence and therein its role as a major limiting factor in the management of slash and loblolly pines over extensive areas resulted from changes in the forest ecosystem that accompany intensive pine management, principally plantation culture (33). The pathogen is not favored nor abundant in old growth natural stands but is greatly favored in young, rapidly growing pine plantations, especially those established in high-rust-hazard areas, where 90% or more of rust-susceptible trees can be infected by age 5 (14).

Current comprehensive losses caused by fusiform rust are not known. In 1972 estimates were 28 million dollars annually to stumpage, excluding mortality (30). The most recent estimate (1986) was 35 million dollars annually in five states (Florida, Georgia, North Carolina, South Carolina, and Virginia) (1); losses also

occur in Alabama, Arkansas, Louisiana, Mississippi, Oklahoma, and Texas. Losses occur mostly as mortality to young pines. When 1- to 5-year-old trees develop stem galls, they often die before harvest age or become deformed and unmerchantable. Trees with severe stem galls may die throughout the rotation, especially if to high-velocity winds. Forest inventory data (1987 to 1993) from 11 southeastern states estimate that 1.2 million acres of planted slash and loblolly pines had $\geq 50\%$ of trees with potentially lethal infections (52).

Fusiform rust has affected nearly all forest management practices, some quite significantly. Forest managers are faced with the dilemma—more growth, more rust. Nursery management, site preparation, species selection, fertilization, thinning, pruning, controlled burning, and rotation length are impacted by the disease. Inventory procedures and growth and yield modeling (26) must consider the disease. Perhaps the most significant impact has been on tree improvement programs in which new emphasis was placed on the selection, testing, and deployment of potentially rust-resistant families. The continued improvement and stability of rust resistance remains a concern of these programs.

Biology. *C. quercuum* f. sp. *fusiforme*, pathogenic on slash pine (*Pinus elliotii* Engelm. var. *elliotii*), loblolly pine (*P. taeda* L.), and longleaf pine (*P. palustris* L.), is one of four form species of the pine-oak rusts in the United States (5). Other form species are *banksianae* on jack pine (*P. banksiana* Lamb.), *virginianae* on Virginia pine (*P. virginiana* Mill.), and *echinatae* on shortleaf pine (*P. echinata* Mill.). Another pine-oak rust pathogen, *C. strobilinum* Hedgc. & Hahn on slash pine (cone rust), is also recognized. *C. quercuum* f. sp. *fusiforme* is a macrocyclic heteroecious biotroph producing spermatia and aecia on pine galls and uredinia and telia on the undersides of oak leaves. The pathogen is perennial on pine and annual on oak. The pathosystem is discontinuous; pine-to-pine infection does not occur. Aeciospores from

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pine galls are wind-disseminated to infect succulent oak leaves in the spring. Several weeks later, wind-disseminated basidiospores from oak infect succulent pine shoots, resulting in branch and stem galls after 6 to 9 months (7,15,27,34).

Many species of southern red oaks (*Quercus* spp.) are susceptible and their epidemiological importance varies with location (9). In the Coastal Plain, water oak (*Q. nigra* L.) and laurel oak (*Q. laurifolia* Michx.) are important alternate hosts; further north, red oak (*Q. rubra* L.) becomes important. Of the commercial southern pines, slash, loblolly, and longleaf are susceptible, whereas shortleaf is considered immune (7,27). Although fusiform rust is known only to occur in the southeastern United States, several species of pine from western United States, Central America, and Mexico are susceptible when artificially inoculated, as is at least one species of oak from California (10,23).

It is a concern that significant gaps exist in our knowledge of fundamental biology, e.g., pathogen life history and genetics and host-parasite interactions. Many details of biology were bypassed since the early promise of resistance focused research on the applied aspects of host-pathogen relations and epidemiology.

Epidemiology. In the natural forest, with limited human activity, indigenous pathosystems usually reach a balance at endemic disease levels. Such was the case historically (at least in the recent past) with fusiform rust in natural pine forests, where this disease was of rare occurrence at the turn of the 20th century (14). However, in our desire (and need) for more productive forests, requiring more intensive forest management, we have created conditions very favorable for the increase and spread of fusiform rust (33).

Since World War II, intensive planting efforts replaced natural regeneration and resulted in extensive areas of young, rapidly growing susceptible slash and loblolly pine plantations. This most successful regeneration effort significantly altered the species composition, but especially the age composition of the preexisting forest, in favor of the rust pathogen and the resulting disease. Old growth forests—often of the more rust-resistant longleaf pine—were replaced by young plantations of susceptible slash and loblolly pines. For example, in Florida, pine plantations increased from an estimated 291,000 acres in 1952 to 5.59 million acres by 1990 (52). In the Southeast, pine plantations increased from 1.0 to 22.6 million acres. The shift to younger age-classes accompanying the increase in plantations has contributed greatly to the increase in rust incidence. Silvicultural practices that improve pine growth, e.g., fertilization, vegetative competition control, genetic growth rate improvement, and intensive site preparation, result in rapid and succulent growth of young trees and favor rust development, both infection and sporulation (8,24,41,42).

The alternate oak hosts, the source of basidiospore inoculum for the infection of pine, are critical for disease development. The potential for rust on pines increases with the abundance and nearness of infected oaks (51). Basidiospores are transported over long distances (at least 1/2 mile) to infect pine (11). On the better-drained upland sites, where oaks can flourish in the absence of fire, reduced prescribed burning and absence of wildfires, which has occurred over the last 50 to 70 years, have favored oak regeneration and allowed oaks and rapidly growing young pines to occur in close proximity. Then too, some silvicultural practices favor oak regeneration, e.g., wind-rowing and chopping. Forestry incentive programs have resulted in an increase of planting on former agricultural sites (i.e., better-drained soils with abundant oaks). In contrast, the poorer-drained coastal flatwood sites do not support the abundance of oaks (7,41).

Temperature and moisture requirements for infection of pine and oak were determined early (45,46) and greatly aided our understanding of rust incidence in the natural and plantation ecosystem. Most important is surface moisture in the form of rain or dew on succulent oak leaves and pine shoots. Unfortunately, over extensive areas of the Southeast, both moisture and temperature are not limiting. This is especially true in young pine plantations

in which abundant plant surface moisture occurs almost daily for long periods during the critical spring season when sporulation and infection occur. Fusiform rust may be limited by climatic factors on the northern and western extremities of its geographic range (7). It is also apparent that rust incidence varies among years and locations (14,35,40) depending, in part, on favorable or unfavorable weather at critical periods in the disease cycle. Determining the optimum temperature and moisture conditions for the successful inoculation of pine and oak seedlings was a critical step in the search for rust resistance.

Regional rust hazard maps (52) and guidelines for predicting rust incidence on land management units (34) were developed to aid forest managers in making a priori decisions, especially decisions of where to deploy rust-resistant and rust-susceptible planting stock (40). Resistant seedlings were deployed to high-rust-hazard areas, and growth-improved seedlings with little or no rust improvement were deployed to perennially low-rust-hazard areas.

Management of rust. There are several pest management strategies that mitigate losses caused by fusiform rust depending on landowner objectives and rust hazard (2,31,34,36). There are guidelines to reduce potential losses in infected stands (4) and tactics to avoid severe losses in newly established plantations. The latter include site preparation techniques that reduce oak abundance, delaying fertilization in very young plantations, culling rust-infected seedlings from the nursery, and pruning branch galls, which could later grow into the stem. An important research contribution was the development of Bayleton® to control fusiform rust in nurseries (19,49), but most important, and the primary reason for success, was the development of rust-resistant planting stock (12,16,29,32,37,39,43,50).

Development of rust-resistant planting stock. In the mid-1950s forest scientists recognized that progeny of some open-pollinated pine selections remained rust-free when planted in field tests (3). This began the successful research and development programs on genetic resistance of southern pine to fusiform rust. Plant pathologists, geneticists, and others in federal and state agencies, and in private industry in the southeastern United States, were involved. Cooperative tree improvement programs (Florida, Georgia, North Carolina, and Texas) selected and field-tested improved varieties (families) of slash and loblolly pines throughout the region. For example, the cooperative tree improvement program at the University of Florida established over 800 field progeny tests, many of which were scored for fusiform rust at multiple ages (37). Promising families were further tested in high-rust-hazard areas (50) and new selections were made in plantations where rust incidence was $\geq 90\%$. One innovative approach was the creation of special seed production areas from plantations that were severely ($>90\%$) infected. Infected trees were rogued from these plantations and rust-free phenotypes produced seed with significant rust improvement within 3 years (13). Methods were developed to artificially inoculate pine seedlings (17). Tree improvement efforts were greatly facilitated when a screening center was established by the U.S. Forest Service at Bent Creek near Asheville, NC (20). This facility provided a standard method to screen 6-week-old seedlings for rust resistance for tree improvement programs and also aided research pathologists and geneticists to study the nature of rust resistance. A performance index was developed at the center based on resistant reaction types, e.g., hypersensitive-like lesions and small galls, which greatly improved the correlation between greenhouse inoculations and field progeny tests (53). Research on the morphology and histopathology of pine host reaction types led to a better understanding of host-pathogen relations (18,25). Studies of pathogen variability showed *C. quercuum* f. sp. *fusiforme* to be quite variable (21,28,47,48). Major genes have been identified that are associated with pine host resistance (22,54) and components of partial resistance have also been reported (38). Studies on pathogen genetics and frequency of and selection for virulence have only begun. Of course, the long-term

stability of host resistance is a continuing concern, especially in view of the abundance of pathogenic variability and the specter of clonal plantations. But early results are promising with regard to family stability, at least in the present management scheme.

In the meantime, rust incidence and mortality have been significantly reduced, especially in high-rust-hazard areas. Millions of acres of industrial and nonindustrial lands are being planted with improved seedlings, most containing some level of rust resistance. A recent benefit/cost analysis estimated that research on fusiform rust returned \$5 to \$20 for each dollar invested, depending on management objectives and strategies (32).

Lessons learned. In pursuit of fusiform rust resistance in southern pines, many lessons have been learned, relearned, or at least exemplified, especially those lessons pertaining to an indigenous endemic forest pathosystem. A few of these lessons related to disease resistance and epidemiology are described below. (i) An indigenous endemic pathosystem can rapidly become epidemic with changes in forest management practices. Plantations stripped of natural defenses became vulnerable to an "r"-type pathogen as the balance was shifted in favor of *C. quercuum* f. sp. *fusiforme*. (ii) Rust resistant slash and loblolly pine genotypes are not rare in this center of origin and, of course, neither are pathotypes. (iii) Even though rapidly growing phenotypes were most susceptible to fusiform rust, both rust resistance and rapid growth occur in specific genotypes. (iv) Genetic rust resistance is a useful and valuable disease management strategy in a plantation ecosystem, even in the face of an r-type pathogen. (v) The fusiform rust pathosystem, likely because of its discontinuous epidemiology (no pine-to-pine infection), appears to be buffered against strong selection pressure for virulence in the pathogen.

Future prospects. Beginning in the 1950s, fusiform rust was a major priority of state, federal, and industrial forestry research programs in the southeastern United States. Since the mid-1990s, with retirements and changes in programs, research on fusiform rust has decreased. However, rust still remains an important component of several biotechnology research programs and tree improvement cooperatives. To date, more than 1,000 research papers on fusiform rust have been published.

Future research will focus on questions of the stability of resistance in pine and virulence in the pathogen. Despite the present success there are reasons for concern: (i) pathogen variability is abundant, (ii) temporal and spatial interactions (genotype by environment) occur among resistant pine genotypes, and (iii) major genes in pine are associated with resistance. In addition, clonal forestry is a goal of intensive plantation culture. Surely it is prudent to maintain a viable proactive fusiform rust research program.

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