Risk Assessment with Current Deployment Strategies for Fusiform Rust-Resistant Loblolly and Slash Pines

Floyd Bridgwater *and* **Tom Kubisiak,** *USDA-Forest Service, Southern Institute of Forest Genetics, Harrison Experimental Forest, Saucier, MS 39574-9344;* **Tom Byram,** *Texas Forest Service, Texas A&M University, College Station, TX, 77843-2585; and* **Steve McKeand,** *North Carolina State University, Raleigh, NC 27695-8002.*

ABSTRACT: *In the southeastern USA, fusiform rust resistant loblolly and slash pines may be deployed as 1) ulked seed orchard mixes, 2) half-sibling (sib) family mixtures, 3) single half-sib families, 4) full-sib family mixtures, single full-sib families from 5) "bulking up" or producing large numbers of controlled cross seeds, or as 6) clones of individual genotypes. These deployment types are respectively less genetically variable and less well buffered against environmental stress, but provide respectively greater genetic gains from higher selection intensity. Currently, bulked seed orchard mixes are deployed by all state organizations and many smaller companies, but about half the 1.1 billion loblolly and slash pines deployed annually are planted in half-sib family blocks. The most aggressive landowners plant virtually all of their land with a small number of half-sib families. Full-sib families and/or clones are currently planted on a small fraction of the total area regenerated, but research and development seeks to make the deployment of full-sib families and clones economical to increase the genetic gains from applied tree improvement programs. Resistance to fusiform rust currently being deployed is likely due to resistance based on both major genes and genes of small, cumulative effects. However, major genes for resistance to fusiform rust have been discovered using molecular genetic techniques, and deployment strategies are currently being developed. "Boom and bust" cycles of pathogens on other crops when major genes were deployed against them create concerns that these same problems might arise when deploying major genes for resistance against fusiform rust. We assessed the risk that fusiform rust might overcome one to few major genes for resistance if they are deployed widely and strategies to mitigate the risk that this will occur. We concluded that the deployment strategies currently in widest use (bulked seed orchard seedlings and half-sib family blocks) robustly resist fusiform rust infection. Plantations are probably sufficiently genetically buffered to present little risk of cataclysmic failure, as current resistance is likely to be based on both major and minor genes. Furthermore, these same deployment strategies are likely to provide robust protection against risk factors other than fusiform rust. We concluded that deploying pine cultivars with known genes for major resistance to fusiform rust in regions where their associated virulence genes are absent or in low frequencies is a practical near term strategy and that deploying a mosaic of different resistance genes may mitigate the presumed greater risk of deploying full-sib family blocks or clones. South. J. Appl. For. 29(2):80–87.*

Key Words: *Pinus taeda, Pinus elliottii, Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme, Fusarium subglutinans* f. sp. *pini*, deployment strategy, risk management.

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The discovery that there are several major genes for resistance to fusiform rust, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiform*, and developing technology for deploying more genetically uniform loblolly, *Pinus taeda* L., and slash, *Pinus elliottii* Englm., pines has led to a concern that these major genes for resistance might fail under certain deployment strategies. Our objective herein was to assess the risk of plantation failure under current and possible future deployment strategies and to consider alternative strategies for deployment that might mitigate against failure.

Deployment Strategies

Fusiform rust resistant loblolly and slash pines may be deployed as 1) bulked seed orchard mixes of open-pollinated half-sibling (sib) families, 2) selected half-sib family mixtures, 3) single half-sib families, 4) full-sib family mixtures, single full-sib families from 5) "bulking up" or producing large numbers of controlled cross seeds, or as 6) clones of individual genotypes. These deployment types are respectively less genetically variable and less well buffered against environmental stress factors but selection intensity and expected genetic gains increase, respectively. Currently, wind-pollinated seed orchards produce the bulk of genetically improved seedlings of both loblolly and slash pines. Beginning in the 1970s, many organizations seized the opportunity to deploy only the few best half-sib families from first-generation seed orchards when seed yields from younger orchards eased the demand for seeds from older seed orchards (Gladstone 1981, Duzan and Williams 1988, McKeand et al. 1997). Some of these organizations planted bulked mixtures of the best half-sib families while others planted single half-sib families to specific sites. With the development of controlled mass pollination (CMP) (Bramlett 1997), it became practical to produce full-sib families from seeds, and a few organizations are deploying these singly and in mixtures.

"Bulking up" is another strategy for deploying full-sib families. This strategy deploys rooted cuttings derived from young (circa 1- or 2-year-old seedlings) and has resulted in the implementation of several pilot-scale programs to bulk up full-sib families for operational deployment (Frampton et al. 2000). There is no difference between CMP and bulking up in terms of expected genetic gain; however, bulking up will reduce genetic variability as clones are replicated across the landscape. If rooting potential is strongly biased, genetic variability will decrease and may approach the limits that would be achieved with clonal deployment. Deploying single full-sib families capitalizes on substantial portions of both the additive and nonadditive genetic variances and promises the greatest genetic gains from traditional tree improvement without deploying clones of single genotypes.

Deploying mixtures of full-sib families or polymix crosses among a few elite females and males seeks to increase genetic gains by capitalizing largely on the good general combining ability of a few parents while minimizing perceived risk by deploying them in mixtures or as polymix crosses. The fundamental biological problems of maturation and its effects on rootability and growth have long been recognized as limitations to the deployment of rooted cuttings of individual selected genotypes (Stelzer and Goldfarb 1997). If maturation of hedges can be delayed until clones of individual full-sib seedlings can be evaluated in clonal trials, then genetic gains can be increased by within-family selection and deploying single genotypes as rooted cuttings. The ultimate goal of true clonal forestry depends on being able to vegetatively propagate any single desirable genotype. This may become reality for loblolly pine and slash pine through cryopreservation of tissue cultures and the deployment of somatic seedlings, products of tissue culture (somatic embryogenesis). Somatic seedlings are currently being deployed by a few organizations on a trial basis. Improvements in the process of producing somatic embryos for loblolly offer great promise for the future of clonal forestry (MacKay et al. 2001).

Current Deployment Practices

An informal survey was conducted among the 31 state and industry members of three tree improvement cooperatives in the southeastern USA: the Cooperative Forest Genetics Research Program at the University of Florida, the North Carolina State University-Industry Cooperative Tree Improvement Program, and the Western Gulf Forest Tree Improvement Program at Texas A & M University. Complete results of the survey are provided elsewhere (McKeand et al. 2003b), but a summary of the averages for 2000–2002 is provided in Table 1.

Over half of all genetically improved loblolly pine propagules are currently deployed as open-pollinated family block seedlings (59%) and fewer for slash pine (43%). Currently, all of the state and a few of the private tree improvement programs deploy seedlings only as bulked seed orchard seedlings. Since private industry produces the greatest proportion of propagules (85 and 83% of loblolly and slash pines, respectively), the proportion of seedlings deployed in family blocks on industry lands is greater than presented in Table 1. About 80% of loblolly pine and about 51% of slash pine regeneration on company lands is currently with half-sib families. An additional 33% and 32% for loblolly and slash pines, respectively, is market sales of half-sib families. It is clear that mitigating risk related to deployment strategy will apply primarily to the deployment of half-sib families until the technology to deploy full-sib family blocks and/or clones is further developed. Assessing risk from deploying half-sib family blocks is especially important to privately owned companies.

Table 1. Average annual deployment (2000–2002) for loblolly and slash pines in the southeastern USA.[a]

	Loblolly pine	Slash pine
Annual seedling production (MM)	1,137	150
Open-pollinated family blocks (%)[b]	59.0	43.0
Full-sib family blocks (%)[b]	0.4	1.7
Selected clones (%)[b]	0.0	0.0

[a] After McKeand et al. 2003b.

[b] Percentage of annual seedling production.

Risk Factors

There are many kinds of risks to plantations. They may be damaged or destroyed by environmental catastrophes, insects, diseases, animals (including humans) and errors such as planting an ill-adapted seed source. In the present analysis, we considered risks that managers can hope to mitigate by appropriate selection, breeding and/or deployment of genetically improved propagules. If risks are to be addressed in the breeding population, they must be anticipated and therefore exclude erratic and unpredictable events such as environmental catastrophes, animal damage, and insect and disease pests that are not yet attacking forests. Furthermore, the agent causing risk must be sufficiently widespread to justify using genetic improvement to mitigate risk. Currently, the only agent causing risk to loblolly and slash pines that meets the criteria of predictability and ubiquity is the fusiform rust fungi, *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*. Thus, resistance to fusiform rust is currently a major selection criterion in all of the loblolly and slash pine tree breeding programs in the southern United States. Although there are apparently inherent differences in susceptibility to other kinds of risk agents including the southern pine beetle, *Dendroctinus frontalis* Zimm. (Strom et al. 2002) the pitch canker fungi, *Fusarium subglutinans* f. sp. *pini*. (Rockwood et al. 1988), and ice damage (Schmidtling and Hipkins 2001), none has been included as a selection criterion in loblolly or slash pine breeding programs to date. However, when formerly unknown risks arise, or it is not justified to include them as selection criteria in a breeding program (e.g., pitch canker), they may be mitigated by appropriate deployment of propagules if variation in susceptibility to the risk factor has been included in a breeding population by chance (Rockwood et al. 1988). Thus, for purposes of this discussion, risk is defined in terms of the potential for damage or loss to fusiform rust or to other less important or as yet unknown factors.

Fusiform Rust Hazard

Information on rust hazard has been available since the early 1970s (Phelps 1973). These surveys continue today and are available to the public (Anderson et al. 1997). While fusiform rust incidence in plantations increased from the 1970s to the 1980s, there was a decline thereafter to the 1990s (Figure 1). Several factors contributed to this decline, but it occurred during the period when most plantations of loblolly and slash pines in the South arose from genetically improved planting stock from open-pollinated seed orchards (Pye et al. 1997). There is no doubt that efforts to reduce fusiform rust incidence by genetic selection have been effective for both species (Hodge et al. 1990, Lambeth 2000). Should we expect these populations to remain resistant to fusiform rust in the presence of a genetically variable pathogen population?

Early trials suggested that inocula collected from resistant trees of slash pine were four times more virulent than wild-type inocula (Snow et al. 1976), but a similar trial showed only small increases in the virulence of inocula from resistant loblolly pine (Powers et al. 1978). However an elegant analysis of the risk to improved populations o trees concluded that "biological risk has often been overestimated for many of today's improved forests" (Carson and Carson 1989). Their analysis was based on data from sources other than loblolly and slash pine, but their conclusion is supported by more recent data on half-sib families of loblolly pines.

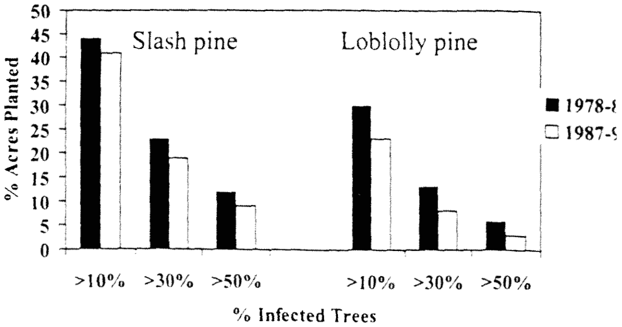

Figure 1. Percentage of acres of planted slash and lobloll pines at three infection levels for eleven southern state Adapted from Anderson et al. 1997.

Deploying Half-Sib Families

Half-sib families are usually deployed with one of two strategies in mind. Families with the greatest expected growth rates are often assigned to the best sites to maximize yields, but some organizations make site assignments based on the belief that some families are better adapted to specific sites (usually based on soils) (Gladstone 1981, Bridgwater and Stonecypher 1978). A more recent analysis recommended that the strategy of assigning the best loblolly pine families to the best sites be adopted rather than site-specific assignments since large genotype x environment differences are not common for loblolly (Duzan and Williams 1988). These authors further suggested that planting half-sib family blocks may be an economically viable way to deal with risk as damaged or destroyed blocks could be salvaged more easily than the same families in genetically mixed stands. Deploying half-sib families of slash pine resistant to pitch canker to high-risk sites has been used as a strategy to mitigate damage to that disease in Florida (Rockwood et al. 1988). Half-sib families of loblolly pine carrying genes for resistance to fusiform rust are also being deployed on high-risk sites. Some of these families have major genes for resistance (Wilcox et al. 1996). Field-testing is underway to determine if these resistance genes confer resistance on a few or many sites. Half-sib families that are more resistant to fusiform rust also have greater interaction across sites (McKeand et al. 2003a). These families are still resistant relative to the population of loblolly pine as a whole. However, their predicted susceptibility is not reliable given the expected nature of the pathosystem, i.e., a gene-for-gene system where resistance/susceptibility in the host is due to the interaction between resistance gene alleles in the host and corresponding avirulence/virulence gene alleles in the pathogen. This lack of reliability can be mitigated by deploying mixtures of these most resistant families (McKeand et al. 2003a). Deploying mixtures of seedlings from seed orchard bulks through mixtures of a few to several half-sib families appears to be a very conservative strategy for deployment with respect to both known and unknown risks.

Deploying Full-Sib Families

Full-sib families are being deployed on an operational scale for both loblolly pine and slash pine (Table 1), though on a small scale at present. Large numbers of controlled-pollinated seeds may be produced economically by using controlled mass pollination (Bridgwater et al. 1998) or by bulking up using rooted cuttings (Goldfarb et al. 1997). There is some evidence that we should be more concerned about deploying full-sib families than other, more diverse populations. Based on an analysis of 171 slash pine progeny tests with a wide range of fusiform rust infection percentages that estimated that dominance x environment interaction was 64% as large as the dominance variance, Dieters et al. concluded that an interaction this large could have important implications in full-sib family deployment. Full-sib families of slash pine have also been demonstrated to show significant differential interactions with single-urediniospore cultures of the rust fungi (Stelzer et al. 1999). Based on our current understanding of the fusiform rust-southern pine pathosystem (i.e., a gene-for-gene model), the dominance x environment interaction observed in Dieters et al. (1996) is most likely the direct result of the host families being exposed to populations of fusiform rust that differ in their frequency for particular virulence alleles.

Deploying Clones of Selected Genotypes

If problems of maturation of hedges (Goldfarb et al. 1997) or initiation rates of somatic embryos (MacKay et al. 2001) are solved, then single, tested genotypes can be deployed. Deploying clones of selected genotypes increases yields, but also increases the risk of loss, particularly to unknown risk agents, and this risk is likely to increase with the size of the plantings. Theoretical studies offer some guidance with regard to managing for such risks (Libby 1982, Huhn 1986, Foster 1993, Bishir and Roberds 1995). Individuals within full-sib families interact with single-urediniospore cultures of fusiform rust (Kuhlman et al. 1997), which implies that vegetatively propagated clones of loblolly pine may also interact if propagation effects are not great enough to negate the interactions (Foster and Anderson 1989).

Potential for Fusiform Rust to Evolve in the Presence of Resistance Genes

Although there is very little direct information that fusiform rust would evolve to overcome resistance, that risk may be real, especially for resistance due to major genes. The population genetic structure of an organism reflects the sum of the evolutionary events that shaped it: mutation, genetic drift, gene and genotype migration, the reproduction and mating system, and selection. Population genetics principles can be used to infer the evolutionary potential of an organism, which, in turn, can be used to guide resista breeding strategies (McDonald and Linde 2002).

Although we know nothing about mutation rates in f form rust, mutation is likely to be important for patho that exist as large populations in individual plants whe is more likely that virulent genotypes will arise, multipl the susceptible host genotype and spread before they are to genetic drift, i.e., chance. Deploying the same resista gene in many individuals of the pine host will gre increase the exposure of a single resistance genotype to fusiform rust population and increase the opportunity for pathogen to evolve a virulent mutation or to increase frequency of a previously existing virulence allele. Si fusiform rust galls may live for several years, especially loblolly pine (Walkinshaw and Barnett 1995), the likeliho of a virulent mutation is further increased.

Population size is important since mutation rates generally low; thus, larger populations will also have m mutant genotypes. If population sizes were small, or if th were genetic bottlenecks that severely reduced populati size periodically, loss of these mutants would be m likely. If bottlenecks occur, they are most likely to occ when the pathogen moves from one alternate host to t other. The effect of having an obligate, alternate host population genetic structure of the fusiform rust fungi is n known. One simple genetic model that deployed one maj gene for resistance predicted that, depending on whe selection occurred in the life cycle of the rust organism a the direction of that selection, new equilibria would reached in from six to 16 fungal generations with a ne gene for virulence (vanBuijtenen 1982). Under the mo likely assumptions, 1) selection for virulence in the pathogen taking place only on the pines and not on the oaks, an 2) selection for virulence on the pines with selection f avirulence on the oaks, equilibria would be reached in fro seven to 16 fungal generations, respectively. Howeve since infection is sporadic, at least on slash pines (Froelic and Snow 1986), the number of years required to adapt ne virulence on pines might be much longer than implied b these estimates.

Gene and genotype migration also shape pathogen populations. There is a substantial amount of genetic variatio in the fusiform rust population. Evidence for variation i pathogenicity is clear from empirical trials with inocul collected from different regions (Snow and Kais 1970 Snow et al. 1975, Powers et al. 1977, Walkinshaw and Be 1981, Powers 1985, Kuhlman 1989); from different gall within regions (Snow et al. 1976, Powers et al. 1977, Powers et al. 1978, Snow and Griggs 1980, Kuhlman 1992); and from single sprores from the same gall (Powers 1980, Kuhlman and Matthews 1993, Stelzer et al. 1999). High levels of genetic variability have since been confirmed by molecular genetic analyses (Hamelin et al. 1994). However, what is more interesting than the level of genetic variability in fusiform rust is the pattern in which this variation is partitioned across its natural range. Recent evidence using microsatellite DNA suggests that regional population structure exists (Kubisiak et al. unpublished data), with at least three metapopulations of the fusiform rust fungi along the South Atlantic and Gulf Coastal plains of the U.S. Most of the genetic variation (87.8%) occurred within local populations 10 to 20 acres in size, which suggests that there is extensive gene flow between populations. Furthermore, the magnitude of a smaller, but statistically significant proportion of microsatellite variation found among populations was associated with distance among populations. Therefore, long distance migration is possible, but infrequent enough that genetic differentiation can take place (Kubisiak 2004). Although the results of this study were based on selectively neutral genetic loci, and therefore tell us nothing about the geographic distribution of pathogenicity, these kinds of data infer the relative importance of the evolutionary factors that shaped the population.

The reproductive or mating system influences the evolutionary potential of fusiform rust as regular recombination poses greater risk that new combinations of virulence genes can unite to overcome several resistance genes that may have been combined in the host. Fusiform rust is thought to undergo sexual reproduction when haploid nuclei of the pycniospores (male) and receptive hyphae (female) give rise to dikaryotic cells/hyphae in galls on pine trees (Littlefield and Heath 1979), followed by diploidization and meiosis on the oak host. However, this has not been fully verified.

Selection influences the evolutionary potential of fusiform rust when selection pressure on the pathogen population through deployment of resistance genes increases the frequencies of virulent alleles that arise in the population from mutation. There are many examples of pathogen populations adapting to overcome widely deployed major resistance genes other crops. However, the selection pressure acting on major genes for resistance to fusiform rust should not be as great as that for host:pathogen systems in other crops. The southern pines have only recently come under domestication, and resistant genotypes are being deployed in a mosaic across the landscape with natural stands. In fact, only 15% of timberland was in pine plantations as of 1992 while 18% was natural pine (greater than or equal to 50% pine) and 14% was oak-pine (between 25% and 50% pine) (Sheffield and Dickson 1998). Unless these proportions change dramatically, the selection pressure on the population of the fusiform rust fungi may remain so low that the number of generations required to overcome resistance would be increased relative to other agricultural crop:rust pathosystems. Furthermore, the complex life cycle of the fusiform rust fungi with asexual multiplication only on the oak hosts and no pine-to-pine infection may reduce selection pressure that would favor increases in virulence.

Mitigating Risk from Fusiform Rust

Will it be necessary to take steps to mitigate the risk of fusiform rust infection in the future? Current deployment strategies for both loblolly and slash pines are conservative with respect to risk from fusiform rust. The risk is that the frequency of virulence alleles in populations of fusiform rust may change as a direct result of the selection pressure applied (even though we expect it to be low) by the resistance genes being deployed in particular host families or individual genotypes/clones. Resistance to fusiform rust in improved loblolly and slash pines currently being deployed is likely to be based on a spectrum of resistance genes since resistant genotypes have been identified by a combination of screening at the USDA-Forest Service Resistance Testing Center (RSC) against a broad spectrum (bulked inoculum) of rust genotypes and field testing (Knighten et al. 1988). Quantitative, or "minor gene resistance," likely arises from gene effects that are small and additive and tends to be effective against all strains of a pathogen population (McDonald and Linde 2002). Quantitative resistance is sensitive to environmental conditions and more difficult to detect. The same evolutionary forces that act to produce virulence against major genes for resistance are likely to evolve to overcome resistance in quantitative resistance genes. However, this breakdown of resistance occurs more slowly.

If full-sib and/or clonal deployment strategies become more prevalent, the genetic basis for rust resistance may be narrower in the sense that only particular combinations of resistance genes are being deployed, and hence breakdown may be hastened. In fact, one current strategy for deploying loblolly pines resistant to fusiform rust is to deploy half-sib families with known major genes for resistance (Wilcox et al. 1996). If the fusiform rust-southern pine pathosystem is indeed a true gene-for-gene system, and assuming adequate selection pressure on the fusiform rust fungi, tree breeders are likely to face problems similar to those of breeders of other crops.

Growers of other crops rely on several strategies for deployment of resistance genes (McDonald and Linde 2002). The first, perhaps traditional, strategy is to deploy different, single resistance genes when the pathogen overcomes the current resistance gene under deployment. A second strategy is to deploy resistance genes over a limited time or area with replacement before the pathogen population can evolve. As a third strategy, resistance genes may also be combined into a single cultivar, i.e., "pyramided" to provide resistance to a spectrum of virulence genes. Regional deployment of different resistance genes to regions where the pathogen has no, or low frequencies of virulence genes is a fourth strategy. A final strategy is to deploy mixtures of cultivars to reduce the selection pressure on individual resistance genes.

Are these strategies appropriate for the pine:fusiform rust pathosystem? The first strategy seems the least desirable of the deployment strategies since it may lead to "boom and bust" cycles as it has in other crops, although the time frame for these cycles may be much longer for fusiform rust. The second strategy may be practical even though the southern pines are long lived and resistance genes seem to be at risk to adaptation by the fusiform rust fungi. However, most fusiform rust infection takes place during the first 5–10 years after plantation establishment (Griggs and Schmidt 1977) and alternating resistance genes every 3–5 years may effectively reduce the selection pressure applied to the fusiform rust fungi population since each resistance gene would be exposed for only a few years. The third strategy, pyramiding resistance genes, is probably impractical in the near term because of the number of breeding cycles required to combine resistance genes. If gene transformation of existing pine cultivars becomes practical, then the method of pyramiding resistance genes would be more useful. The fourth strategy is probably the best method available for deploying resistance genes in the short term. Using some method to determine where particular resistance genes should be deployed, i.e., in regions where the virulence gene for that particular resistance gene is absent or in very low frequencies, may be a practical method of deploying major resistance genes quickly. The current use of this strategy by the NCSU/Industry Fusiform Rust Program involves deploying half-sib families with known major genes for resistance in regions where previous field trials indicate that virulence genes for that particular resistant gene are not prevalent (Amerson 2002). It may be possible to achieve the same result as the fifth strategy by deploying blocks of pine cultivars with different major genes for resistance. In any case, monitoring changes in the fusiform rust pathogen is likely to be important in understanding how deployment strategies impact the fusiform rust population.

Rust Monitoring Programs

There are two major rust race-monitoring programs for cereal crops. The first is a national program that monitors cereal rusts in the cereal-producing states in the United States (National Rust Race Monitoring Program, USDA-Agricultural Research Service (ARS) Cereal Disease Laboratory, http://www.cdl.umn.edu/index.htm, Aug. 21, 2002). The second is an international program coordinated by the International Maize and Wheat Improvement Center, http://www.cimmyt.org/whatiscimmyt/AR00 2001/africa/global/global.ht, Aug. 21, 2002, CIMMYT). Both programs provide an "early warning" system for cereal growers so they can deploy cereal varieties with appropriate resistance gene(s). Both programs use seeds of varieties with known resistance to different rust virulence genes to monitor changes in frequency of virulence genes or to discover new virulence genes that the rust organisms may evolve to overcome resistance genes. These programs also serve to discover minor gene resistance that is a more durable form of resistance. The USDA-ARS program samples rust diseases in the field and screens them against a panel of varieties with known resistance genes. The CIMMYT program deploys panel(s) of varieties with known resistance genes to nurseries around the globe where they are challenged by natural inoculum. Either or both approaches might be used to monitor for changes in frequency of rust virulence genes in loblolly and/or slash pines if such a program becomes necessary.

Future Research

The implementation of a monitoring program for fusiform rust such as those described above for cereals depends on identifying genes for resistance in the host and the corresponding virulence alleles in the pathogen. Currently, eight major genes for resistance have been identified in loblolly pines using molecular markers (Amerson 2002). Screening trials by the USDA-Forest Service, Southern Institute of Forest Genetics, at the Resistance Screening Center using multiple single-urediniospore isolates and 43 half-sib families suggest that there may be at least 13 major genes for resistance in slash pines (Dr. C.D. Nelson, USDA-Forest Service, personal communication). The prospects for finding more resistance genes in both loblolly and slash pines appears to be high, and identifying more major resistance genes should receive high priority.

The presence of resistance genes in the host and virulence genes in the pathogen must be inferred from the presence of molecular genetic markers whose associations with these genes have been demonstrated in research trials. The need for such monitoring programs will not be known until empirical trials demonstrate such a need or the lack of it, or until the fundamental genetic system of the fusiform rust:pine pathosystem is understood. It may be possible to develop molecular markers to identify and track virulence genes in the fusiform rust fungi population. If molecular markers can be developed that are a part of the virulence gene itself (so that there would be no recombination between the marker and the virulence gene) or if flanking markers could be found that were very close to the virulence gene (there would be very little recombination), then the markers would be useful for developing an effective management strategy. If such markers can be developed, changes in the frequency of virulence alleles in local rust populations can be determined directly, and the appropriate resistant host genotypes could be deployed. In theory, future selection pressure put on the pathogen population due to the deployment of particular resistant genotypes/genes would no longer be an issue of concern, as the changes could be directly monitored and the appropriate resistant materials deployed.

Finally, the population genetic structure of the fusiform rust pathogen and the factors that have shaped it should receive further study since that knowledge will allow us to infer the evolutionary potential of the rust fungi to overcome resistance in the pine hosts. In particular, the effect of the alternate oak host for fusiform rust on selection for virulence on pines should be determined.

Summary

The current prevalent deployment strategies (half-sib families in mixtures or single-family blocks) for loblolly and slash pines are conservative with regard to risk from both known and unknown risk factors.

If the strategy of deploying monogenic resistance continues to gain favor, and fusiform rust overcomes those resistance genes, tree breeders may be forced to adopt monitoring and deployment strategies similar to those used by cereal breeders to mitigate the effects of fusiform rust. The population genetics structure of the fusiform rust fungi suggests that it has a moderately high potential to evolve and overcome resistance. However, mitigation of selection pressures by a complex life cycle and buffering capacity of the natural pine population may reduce this potential and hence lower the risk of resistance breakdown associated with fusiform rust disease. Continued research into the fundamental genetic basis of the pine:fusiform rust pathosystem will provide information that will improve risk assessment and management strategies for managing fusiform rust.

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EDITOR **Ian Munn**
Box 9681, Department of Forestry
Mississippi State U., MS 39762-9681
(662) 325-4546; Fax: (662) 325-8726
imunn@cfr.msstate.edu

JOURNAL PRODUCTION EDITOR **Linda Edelman**
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Ian Munn
Editor, *Southern Journal of Applied Forestry*
Box 9681 Department of Forestry
Mississippi State U., MS 39762-9681
(662) 325-4546; Fax: (662) 325-8726
imunn@cfr.msstate.edu

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