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Long-Term Changes in Fusiform Rust Incidence in the Southeastern United States

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Fusiform rust is the most devastating disease of slash pine (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) in the southeastern United States. Since the 1970s, the USDA Forest Service Forest Inventory and Analysis (FIA) Program has assessed fusiform rust incidence on its network of ground plots in 13 states across the southeastern United States. Through analysis of the FIA data, we found that current fusiform rust incidence varied by state, forest type, and stand origin and that across all stand ages, rust incidence was approximately equal in planted and natural stands of loblolly pine but was higher for planted versus natural stands of slash pine. Decreases in rust incidence over the last 30–40 years were evident in young planted loblolly pine stands but not in young planted slash pine stands. Results for slash pine were surprising, and the reasons remain unclear but one reason may be planting stock origin, which was unknown and may be highly variable in rust resistance. These analyses of FIA rust incidence data also were used to update the original rust disease hazard maps published by Starkey et al. (1997).

Keywords: *Cronartium fusiforme*, disease incidence, forest health monitoring, Forest Inventory and Analysis data, southern pine

Selection, breeding, and deployment of disease- and insect-resistant planting stock is a preferred method for minimizing losses caused by many different kinds of endemic or introduced forest pathogens and insects (Borlaug 1972). Optimum deployment of genetically controlled planting stock requires detailed knowledge of both the geographical variation and temporal changes in the risk of disease- or insect-induced losses in forest health and productivity (Cubbage et al. 2000, McKeand et al. 2003). Because of the interaction between land cover and land-use patterns, this risk monitoring inherently involves a landscape perspective (Holdenrieder et al. 2004). Thus, large-scale forest inventory systems such as those overseen by the European Forest Inventory Network, Canadian National Forest Inventory, Mexican National Forestry Commission (Comisión Nacional Forestal), and US Department of Agriculture (USDA) Forest Service[1] provide valuable opportunities for regional-, national-, and even continent-scale collaboration among forest pathologists, entomologists, geneticists, and inventory specialists (Cowling and Randolph 2013). This article, examining the distribution and hazard of fusiform rust in the southeastern United States based on data collected by the USDA Forest Service Forest Inventory and Analysis (FIA) Program, is one such effort.

Southern Pine and Fusiform Rust

Currently there are >60.3 million acres of slash and loblolly pine timberland in the southeastern United States (Miles 2013) (Tables 1 and 2). These lands are some of the most productive forests in the world (Fox et al. 2007). Management in these forest types ranges from natural regeneration with few subsequent management inputs to careful matching of species and genotypes to site and silvicultural treatments (Allen et al. 2005). Commonly used methods of artificial regeneration include mechanical, chemical, and prescribed fire site preparation treatments (singly or in concert) followed by the establishment of genetically improved material through direct seeding or the planting of seedlings. Herbaceous and woody vegetation control, fertilization, and precommercial and commercial thinning are characteristic treatments once stands, both planted and natural, are established.

During the last half of the 1900s, fusiform rust became the most devastating disease of slash pine (*Pinus elliottii*) and loblolly

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Table 1. Current area of slash pine timberland, by state and stand origin.

State	Year[a]	Natural		Planted		Total	
		Thousand acres	SE%[b]	Thousand acres	SE%[b]	Thousand acres	SE%[b]
Alabama	2012	234.9	13.92	160.3	17.31	395.2	10.59
Florida	2011	1,655.5	5.37	2,999.3	3.81	4,654.8	2.96
Georgia	2012	755.7	7.93	2,321.1	4.29	3,076.8	3.59
Louisiana	2012	110.8	22.16	491.5	10.23	602.3	9.16
Mississippi	2012	378.0	11.51	201.2	16.11	579.2	9.14
North Carolina	2012	12.1	76.51	51.1	42.55	63.2	38.09
South Carolina	2012	35.0	50.08	29.6	48.19	64.6	34.91
Texas	2010	29.7	41.36	87.5	24.54	117.3	21.05
Total	2010–2012	3,211.7	3.89	6,341.8	2.66	9,553.5	2.11

Source: Forest Inventory and Analysis Database (Miles 2013). Columns may not sum to totals due to rounding.
[a] May include data collected in years before the one listed.
[b] SE%, sampling error percent.

pine (*P. taeda*) in the southeastern United States (Dinus and Schmidt 1977). Fusiform rust, caused by *Cronartium quercum* f. sp. *fusiforme*, requires both pine and oak (*Quercus* spp.) species to complete its life cycle. Infections on pine trees typically result in spindle-shaped galls on the branches and stems (Phelps and Czabator 1978), although galls can be round, oval, or odd-shaped as well (Figure 1). Stem infections that occur before 5 years of age typically result in tree mortality, whereas infections on older trees create open cankers that continue to enlarge and degrade stem quality and often become points of breakage during storms (Anderson et al. 1986).

Fusiform rust existed at endemic disease levels across the southeastern United States before the 1930s, but increased to epidemic proportions in the mid-1900s (Dinus and Schmidt 1977). Much of this transformation from an endemic to an epidemic disease was induced by changes in forest management practices that included (1) widespread planting of infected nursery stock (Hodges 1962); (2) establishment of susceptible pines (i.e., nonresistant genotypes) over large areas of land that frequently included sites to which the species were not well adapted (Siggers and Lindgren 1947); (3) increased populations of oak due to wildfire suppression (Schmidt 2003); and (4) intensive management practices such as site preparation (Miller 1970) and fertilization of forestlands (Boggess and Stahelin 1948), which stimulated growth and increased susceptibility. Annual southwide stumpage losses due to fusiform rust were estimated to be $28 million, excluding mortality, in 1972 (Powers et al. 1974). This very large estimate of disease loss was part of the justification used by the USDA Forest Service to establish a Resistance Screening Center (RSC) in Asheville, North Carolina, with the primary purpose of rapidly and consistently testing slash and loblolly pine seedlots for rust resistance (Cowling and Young 2013).

In 1997, Starkey et al. published a forest health protection report detailing the then-current status of fusiform rust incidence in the southeastern United States based on an analysis of FIA data. The most valuable results of the report were as follows: maps showing the locations of FIA measurement plots where fusiform rust galls were observed on 10% or more of the trees on each plot; a series of graphs showing trend lines for changes in acreage of planted and naturally regenerated slash and loblolly pine stands with at least 10% fusiform rust infection; and isopleth maps showing areas of high, moderate, and low disease hazard across the southeastern United States. The hazard zone maps for both slash and loblolly pine were widely used by forest pathologists, tree improvement specialists, and managers of both private individual and commercial forestland in making decisions about deployment of planting stock with various degrees of fusiform rust resistance.

In 2003, Schmidt asserted that rust incidence and mortality had been "significantly reduced, especially in high-rust hazard areas" (p. 1050). More recent anecdotal evidence suggests that, in some areas, rust galls suitable for collection of *C. fusiforme* aeciospores for use at the RSC "are much harder to find than they once were" (Josh Bronson, USDA Forest Service, pers. comm., Sept. 10, 2011), especially on commercial ownership lands where the best available genetic sources of resistance to fusiform rust are most likely to have been planted. Prompted by these statements and related questions raised at a June 2012 IEG-40 (Information Exchange Group) meeting involving the leaders of three university-industry cooperative tree improvement programs in Texas, Florida, and North Carolina, the manager of the RSC, forest pathologists, geneticists, and other scientists (Cowling and Randolph 2013), a reexamination of southwide rust incidence seemed timely and worthwhile.

Management and Policy Implications

Slash pine (*Pinus elliottii*) and loblolly pine (*Pinus taeda*) are the two most important commercial timber species in the southeastern United States, and millions of research dollars have been spent over the last 40 years in selecting, breeding, and out-planting rust-resistant slash and loblolly pine planting stock. One of the long-term objectives of these endeavors has been to minimize disease losses and thus increase pine timber harvests. Although fusiform rust incidence in planted loblolly pine stands is generally lower now than 30 years ago, no reduction was evident among planted slash pine stands. Because rust hazard remains moderate to high throughout much of the southeastern United States for both slash and loblolly pines, continued deployment of rust-resistant seedlings is recommended. Moreover, continuation of rust research and monitoring programs is imperative so that the gains in genetic resistance achieved to date are not lost.

Table 2. Current area of loblolly pine timberland, by state and stand origin.

State	Year[a]	Natural		Planted		Total	
		Thousand acres	SE%[b]	Thousand acres	SE%[b]	Thousand acres	SE%[b]
Alabama	2012	2,420.3	4.29	5,688.4	2.65	8,108.6	2.06
Arkansas	2012	1,690.6	5.14	2,712.4	4.21	4,403.0	2.89
Florida	2011	285.4	13.24	637.9	8.91	923.3	7.30
Georgia	2012	2,770.5	3.95	4,275.1	3.19	7,045.6	2.28
Kentucky	2011	29.6	37.03	8.3	76.27	37.8	33.34
Louisiana	2012	1,906.4	4.82	3,139.9	3.56	5,046.2	2.49
Mississippi	2012	2,402.2	4.23	4,636.7	2.97	7,038.9	2.19
North Carolina	2012	2,017.6	6.25	2,507.7	5.80	4,525.3	3.85
Oklahoma	2012	109.0	22.45	506.8	9.86	615.8	8.85
South Carolina	2012	2,441.4	5.10	2,856.3	4.62	5,297.7	3.06
Tennessee	2011	129.5	18.45	488.8	9.89	618.3	8.65
Texas	2010	2,227.7	4.44	2,525.5	4.18	4,753.2	2.73
Virginia	2012	367.3	14.58	2,018.6	5.70	2,385.9	5.08
Total	2010–2012	18,797.5	1.65	32,002.4	1.24	50,799.9	0.90

Source: Forest Inventory and Analysis Database (Miles 2013). Columns may not sum to totals due to rounding.
[a] May include data collected in years before the one listed.
[b] SE%, sampling error percent.

Figure 1. Multiple branch cankers such as the ones on this pine tree are symptomatic of infection by *Cronartium quercum* f. sp. *fusiforme*, the pathogen that causes fusiform rust disease. Photo by Robert L. Anderson, USDA Forest Service, Bugwood.org.

Using the Starkey et al. (1997) report as an inspiration and model, the objectives of the present study were to estimate the current incidence of fusiform rust in states across the southeastern United States from measurements made by the USDA Forest Service FIA Program, update the rust hazard maps for slash and loblolly pine published originally by Starkey et al. (1997), and evaluate changes in regional fusiform rust incidence between the late 1970s and the early 2010s.

Methods

Background

The FIA Program maintains the most extensive, long-term data on regional fusiform rust incidence in the United States. The FIA Program began tracking fusiform rust incidence during the 1970s when inventories were conducted periodically on a whole-state basis. At that time, field crews completed statewide inventories one state at time, typically within 1–4 years and then returned to the same state on a cyclical basis 6–8 years later (Gillespie 1999, McRoberts 2005). In the southeastern United States, trees ≥5 in. dbh were measured on plots made up of a cluster of 10 variable-radius subplots, and smaller trees (1 to < 5 in. dbh) were measured on fixed-radius microplots centered around the variable-radius subplot points (USDA Forest Service 1985a, 1985b). The 10 subplot points were required to fall within the same forest condition,[2] and reconfigurations to the 10-point plot layout were allowed to ensure that this was so. In addition, all subplot points were required to be located on land not administratively withdrawn by written statute from timber production (i.e., not "reserved" forestland). The presence of fusiform rust galls directly on the main stem or on branches within 12 in. of the stem was noted for all live slash and loblolly pine trees with dbh ≥ 1 in. as part of a multiagent damage variable, i.e., fusiform rust was one of many possible agents that could be recorded under a single categorical damage variable. If a tree showed symptoms of damage by more than one agent, field crews were instructed to record the agent considered to be most serious (USDA Forest Service 1985a, 1985b).

With the passage of the 1998 Farm Bill (Agricultural Research, Extension, and Education Reform Act of 1998 [Public Law 105-185]), the FIA Program transitioned to an inventory system in which 20% of each state would be measured each year after 1999 (Bechtold and Patterson 2005). This new system known as the Enhanced FIA Program, or more commonly as the "annualized inventory," was introduced in 1999 and gradually implemented across the United States. When the annualized inventory was implemented, three important changes took place: the 10 variable-radius subplots were replaced with a cluster of 4 fixed-radius subplots; the single-condition requirement was replaced with mapping procedures that allowed multiple conditions on a single plot; and reserved forestlands were added to the sample (USDA Forest Service 2000). In addition, some plot locations from the periodic inventory were dropped and some new plot locations were added to accommodate a standardized national sampling framework (Bechtold and Patterson 2005, Brand 2005).

Collection of fusiform rust incidence data continued after the transition from the periodic inventory to the annualized inventory, but the size of trees on which fusiform rust symptoms were recorded by FIA field crews was changed. When the Enhanced FIA system was introduced, data collection protocols were revised so that fusiform rust symptoms would be noted as a stand-alone damage variable but only on trees ≥ 5 in. dbh rather than ≥ 1 in. dbh.

Data

FIA Periodic Inventory Data. FIA tree and plot data from the late 1970s through the mid-1990s were obtained from the FIA database (O'Connell et al. 2010) for Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia. Only data from timberland plots with the slash or loblolly pine forest type and live slash and loblolly pine trees ≥ 5 in. dbh were kept in the data set. Timberland is defined as forestland capable of producing in excess of 20 ft^3 of industrial wood per acre per year and not withdrawn from timber utilization (USDA Forest Service 2006). The rationale for focusing on the slash and loblolly pine forest types was twofold. First, the disease is primarily a management issue in stands dominated by slash pine and loblolly pine. Second, rust incidence calculations were thought to be most meaningful when an abundance of host trees were present and available for infection. The oak-pine forest type was not included because a rather small number of host pines on a mixed-species plot could yield a high rust incidence rate that in terms of management would be rather unimportant.

Stand age was included in the plot-level data obtained from the FIA database. In Florida, Georgia, North Carolina, South Carolina, and Virginia, stand age was determined by averaging the age from three or more increment borings of representative trees in the manageable stand (USDA Forest Service 1985a). In Alabama, Arkansas, Kentucky, Louisiana, Mississippi, Oklahoma, Tennessee, and Texas, stand age was based on increment borings of five dominant growing stock trees located on the plot (USDA Forest Service 1985b).

FIA Annual Inventory Data. Under the annualized FIA system, all plots within each state are divided into spatially balanced "panels." Each panel of plots is measured on a rotating basis so that, under ideal conditions, data for each panel are collected once every 5 years in the eastern United States and once every 10 years in the western United States. However, because of the nature of the forest resource, the window of opportunity for data collection, and fiscal constraints, some states in the eastern United States collect data on a 7-year rather than a 5-year cycle. Estimates of current conditions are made using a temporally indifferent method that pools a complete set of panels into the equivalent of one large periodic inventory (Patterson and Reams 2005). Although measurements are spread over multiple years, the inventories are dated with the year of the most recently collected panel. For this analysis, the most recently collected FIA tree-, condition-, and plot-level data were obtained from the FIA database (O'Connell et al. 2010) for Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, and Virginia. The assigned inventory years for these data sets were 2010 for Texas, 2011 for Florida, Kentucky, and Tennessee, and 2012 for all other states.

Partially forested plots or plots that straddle heterogeneous forest conditions are subdivided by a procedure known as "condition mapping" (Bechtold and Patterson 2005). Multiple conditions known as condition classes are distinguished on the basis of reserved status, owner group, forest type, stand size class, regeneration status, and tree density, and any number of condition classes may be recorded for each plot (USDA Forest Service 2011). As was done for the periodic inventory data, only data from timberland plots with the slash or loblolly pine forest type and live slash and loblolly pine trees ≥ 5 in. dbh were kept in the data set.

Under the annual FIA system, stand age is an ancillary attribute used to further describe each condition class but is not used to delineate a new class. Stand age for naturally regenerated stands was determined by taking increment cores from two or three dominant or codominant trees from the overstory of each condition and calculating a weighted average of the tree ages based on the percentage of overstory trees represented by each cored tree (USDA Forest Service 2011). Stand age for planted stands was estimated based on the year the stand was planted and does not include the age of the planting stock.

Data Analysis

Primarily because of the change in the size of trees on which observations of fusiform rust are made, it was not possible to make estimates of timberland area damaged by fusiform rust that were directly comparable to those reported by Starkey et al. (1997). Therefore, although some of the constraints used by Starkey et al. (1997) were retained, all analyses presented here are based on estimates of percent rust incidence at either the state or plot level.

Current Status of Fusiform Rust Incidence. Data from the annual FIA inventory were used to estimate the current status of fusiform rust in each of the 13 southern states. Estimates of current percent rust incidence ($\hat{R}$) were calculated for each condition class of interest using the ratio of means (ROM) estimator (Cochran 1977, Zarnoch and Bechtold 2000)

$$\hat{R} = \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} x_i} = \frac{\bar{y}}{\bar{x}} \qquad (1)$$

where $\hat{R}$ is the percent rust incidence for a state, inventory year, and condition class of interest, y_i is the number of rust-damaged slash and loblolly pine trees per acre in the condition class of interest on plot i, x_i is the total number of slash and loblolly pine trees per acre in the condition class of interest on plot i, and n is the number of plots containing at least one condition class of interest. The condition class of interest was defined by forest type (slash or loblolly) and stand origin (natural or planted[3]). The variance of the ROM estimator is

$$\hat{V}(\hat{R}) = \frac{1}{n(\sum_{i=1}^{n} x_i/n)^2}(S_y^2 + \hat{R}^2 S_x^2 - \hat{R} S_{yx}) \qquad (2)$$

where S_y^2 and S_x^2 are the typical sample variances of y and x, respectively, and S_{yx} is their covariance. The SE was estimated as the square root of $\hat{V}(\hat{R})$.

Temporal Changes in Rust Incidence. To estimate the magnitude of changes in rust incidence over time, $\hat{R}$ was calculated for each state by forest type and stand origin for the FIA inventories conducted in the late 1970s or early 1980s and the 2010s. For this analysis, the condition class of interest was defined by forest type (slash or loblolly), stand origin (natural or planted), and stand age. Only plots in stands age 5–15 years were included in these estimates in an effort to capture the level of rust incidence before rust-damaged trees succumbed to mortality.

The difference in $\hat{R}$ between the oldest and most current inventory was calculated as

$$\hat{R}_{\text{diff}} = \hat{R}_{\text{current}} - \hat{R}_{\text{oldest}} \qquad (3)$$

with variance

Table 3. Inventory years included in the rust hazard mapping, by state.

State	Year[a]
Alabama	1990, 2012
Arkansas	1995, 2012
Florida	1995, 2011
Georgia	1989, 2012
Kentucky	1988, 2011
Louisiana	1991, 2012
Mississippi	1994, 2012
North Carolina	1990, 2012
Oklahoma	1993, 2012
South Carolina	1993, 2012
Tennessee	1989, 2011
Texas	1992, 2010
Virginia	1992, 2012

[a] May include data collected in years before the one listed.

$$\hat{V}(\hat{R}_{\text{diff}}) = \hat{V}(\hat{R}_{\text{current}}) + \hat{V}(\hat{R}_{\text{oldest}}) \tag{4}$$

and 95% confidence interval

$$\hat{R}_{\text{diff}} \pm 1.96(\hat{V}(\hat{R}_{\text{diff}}))^{0.5} \tag{5}$$

Note that the covariance between $\hat{R}_{\text{current}}$ and $\hat{R}_{\text{oldest}}$ is assumed to be zero in Equation 4. $\hat{R}_{\text{current}}$ and $\hat{R}_{\text{oldest}}$ were considered significantly different from one another ($\alpha = 0.05$) if the 95% confidence interval for $\hat{R}_{\text{diff}}$ did not include zero. $\hat{R}_{\text{diff}}$ was calculated only if n plots ≥ 30 for both inventories.

Rust Hazard Mapping. To map the current rust hazard, plot-level percent rust incidence (p_i) was determined for each FIA plot inventoried from 2010 to 2012 (hereafter referred to as the "2010s") (Table 3). Because the condition mapping used by FIA allows for more than one forest type or stand origin at a given plot location and because hazard maps were desired for the slash and loblolly pine forest types separately, percent rust infection was calculated for each condition class on each plot as

$$c_i = 100 \times \frac{n_{inc,c}}{n_{t,c}} \tag{6}$$

where $n_{inc,c}$ is the number of live slash and loblolly pine trees $\geq$ 5 in. dbh with symptoms of fusiform rust per acre on condition class c, $n_{t,c}$ is the total number of live slash and loblolly pine trees $\geq$ 5 in. dbh per acre observed on condition class c, and condition class is defined by forest type and stand origin. Then the data set was subdivided by forest type, and p_i was assigned to each plot location according to the following criteria:

- If only one stand origin was observed at the plot location, then p_i was assigned to equal c_i if for natural stands, stand age was 5–15 years old or if for planted stands, c_i was $\geq$30%. Otherwise, the plot location was not assigned a p_i value.
- If both stand origins were observed and c_i for the planted origin was <30%, then p_i was assigned to equal c_i for the natural origin if stand age was 5–15 years old. If the natural stand origin was not 5–15 years old then the plot location was not assigned a p_i value.
- If both stand origins were observed and c_i for the planted origin was $\geq$ 30% and stand age for the natural origin was not 5–15 years old, then p_i was assigned to equal c_i for the planted stand origin. If stand age for the natural origin was 5–15 years old, then the plot location was assigned a p_i value equal to the larger of the two c_i values.

Inverse distance weighted interpolation (ArcMap 10.0, 2010; ESRI, Redlands, CA) then was applied to the p_i values to create a grid (raster) coverage of percent rust incidence for each forest type. In accordance with Starkey et al. (1997), grid size was set to 1.9 miles square, and grid cell values were interpolated from points within 99.4 miles up to a maximum of 12 points. Each grid surface was limited (i.e., "clipped") to counties with FIA plots of the slash or loblolly pine forest type as appropriate. The resulting grid coverage was classified into categories of low hazard (0–<10% infection), moderate hazard (10–30% infection), and high hazard (>30% infection).

To estimate the change in rust hazard since the report by Starkey et al. (1997), the same interpolation methods were used to create a grid surface for each forest type based on FIA plot data from 1988 to 1995 (referred to as the "1990s") (Table 3). For these plots p_i was calculated as

$$p_i = 100 \times \frac{n_{inc,i}}{n_{t,i}} \tag{7}$$

where $n_{inc,i}$ is the number of live slash and loblolly pine trees $\geq$ 5 in. dbh with symptoms of fusiform rust per acre on plot i and $n_{t,i}$ is the total number of live slash and loblolly pine trees $\geq$ 5 in. dbh per acre observed on plot i. Plots of natural and planted origin were compiled together for each forest type and again, in accordance with the methods of Starkey et al. (1997), only natural origin plots 5–15 years old and planted origin plots with $p_i \geq 30\%$ were used in the mapping.

The classified grids from the 1990s and 2010s were compared by using map algebra (ESRI ArcMap) to classify the grid cells into categories of decreased hazard, increased hazard, unchanged low hazard, unchanged moderate hazard, and unchanged high hazard. To provide a broad view of rust hazard over time, map algebra (ESRI ArcMap) was used to create an additional grid coverage based on the average of the 1990s and 2010s surfaces.

Results

Current Status of Fusiform Rust Incidence

FIA plots of the slash pine forest type with fusiform rust incidence $\geq$ 10% were concentrated in northern Florida, southern Georgia, and western Louisiana (Figure 2), an area corresponding to the Outer Coastal Plain Forest Province (Bailey 1980). Although naturally regenerated slash pine was inventoried in eight states (Table 1), only in Alabama, Florida, Georgia, and Mississippi were there $\geq$30 plots meeting the criteria for this study. Fusiform rust incidence for naturally regenerated slash pine was 4.2% in Alabama, 3.8% in Florida, 14.0% in Georgia, and 4.3% in Mississippi (Table 4). Likewise, the planted slash pine forest type was inventoried in eight states (Table 1), but only in Alabama, Florida, Georgia, Louisiana, and Mississippi were there $\geq$30 FIA plots meeting the criteria for this study. Fusiform rust incidence for planted slash pine in these states ranged from 6.4% in Mississippi to 21.2% in Georgia (Table 4).

FIA plots of the loblolly pine forest type with fusiform rust $\geq$10% were scattered throughout the Southeast (Figure 3). Stands of naturally regenerated loblolly pine were inventoried in all 13 states (Table 2), and in states with $\geq$30 FIA plots meeting the criteria for this study, $\hat{R}$ ranged from 0.4% in Virginia to 15.9% in Georgia (Table 5). Planted loblolly pine also was inventoried in all 13 states (Table 2). Symptoms of fusiform rust incidence were not observed on any FIA plots in Kentucky, but where symptoms were observed in other states, $\hat{R}$ ranged up to 12.7% (Table 5).

Temporal Changes in Rust Incidence

The number of FIA plots in naturally regenerated slash pine stands age 5–15 years old was <30 for the oldest and most current inventories in all of the states listed in

Figure 2. Historical range of slash pine and approximate location of FIA plots in the slash pine forest type of natural (A) and planted (B) origin, by percent rust incidence. (Source of the range map: US Geological Survey 1999.)

Table 4. Current estimated percent rust incidence ($\hat{R}$) in the slash pine forest type, by state and stand origin.

State	Year[a]	Natural *n* plots	Natural $\hat{R}$	Natural SE	Planted *n* plots	Planted $\hat{R}$	Planted SE
Alabama	2012	57	4.2	2.6	34	10.1	2.6
Florida	2011	368	3.8	0.5	541	16.2	1.4
Georgia	2012	176	14.0	1.4	460	21.2	1.3
Louisiana	2012	18	—[b]	—[b]	80	12.8	1.7
Mississippi	2012	73	4.3	1.3	38	6.4	1.2

[a] May include data collected in years before the one listed.
[b] —, calculation was not performed because of insufficient sample size (*n* plots <30).

Table 4. Such low sample sizes were inadequate to confidently determine trends in rust incidence in naturally regenerated slash pine stands. For planted slash pine stands in Florida and Georgia, sample sizes were adequate for observing trends in rust incidence. In Florida, $\hat{R}$ in planted stands increased significantly from 10.7% in 1980 to 21.4% in 2011 (Table 6). In Georgia, $\hat{R}$ decreased from 25.2% in 1982 to 18.7% in 2012, but the change was not statistically significant (Table 6).

Fusiform rust incidence in naturally regenerated loblolly pine stands age 5–15 years old decreased or remained unchanged between the late 1970s and early 2010s (Table 7). Tests for change over time between the late 1970s and early 2010s were performed for Alabama, Georgia, Louisiana, Mississippi, North Carolina, South Carolina, and Texas. No significant changes were observed in Louisiana and North Carolina (Table 7). Elsewhere, $\hat{R}$ decreased significantly with $\hat{R}_{diff}$ values ranging between −6.5% and −19.1% (Table 7).

Fusiform rust incidence in planted loblolly pine stands age 5–15 years old decreased significantly in Alabama, Georgia, Louisiana, South Carolina, and Texas between the late 1970s and the early 2010s (Table 8). During the late 1970s and early 1980s, $\hat{R}$ was >18% in all of these states except Texas, and by the early 2010s, $\hat{R}$ was no greater than 12.7% (Table 8). In terms of absolute percentage points, the greatest decrease in $\hat{R}$ occurred in Georgia, declining from 45.5% in 1982 to 12.7% in 2012. No significant change in $\hat{R}$ was observed between the late 1970s and the early 2010s in Mississippi and North Carolina. An increase in $\hat{R}$ from 0.2% in 1977 to 2.0% in 2012 was observed in Virginia (Table 8).

Current Rust Hazard and Change Over Time

Currently, fusiform rust hazard for the slash pine forest type is greatest in southeastern Alabama, Georgia, northern Florida, and an area centered on the border of Texas and Louisiana (Figure 4A). These areas correspond to locations where slash pine has been planted most often (Figure 2B). Since the 1990s, rust hazard in these areas has remained high; however, in southern Mississippi, eastern Louisiana, and an area centered on the Georgia-South Carolina border, rust hazard has decreased (Figure 5).

For the loblolly pine forest type, high rust hazard is currently concentrated in northern Florida and across the Upper Coastal Plain and Piedmont regions of Alabama, Georgia, and South Carolina (Figure 6A). In general, rust hazard in these areas has remained unchanged since the 1990s (Figure 7). Current rust hazard is lowest along the northern portion of the loblolly pine historical geographical range, e.g., along the southern Tennessee border and in central

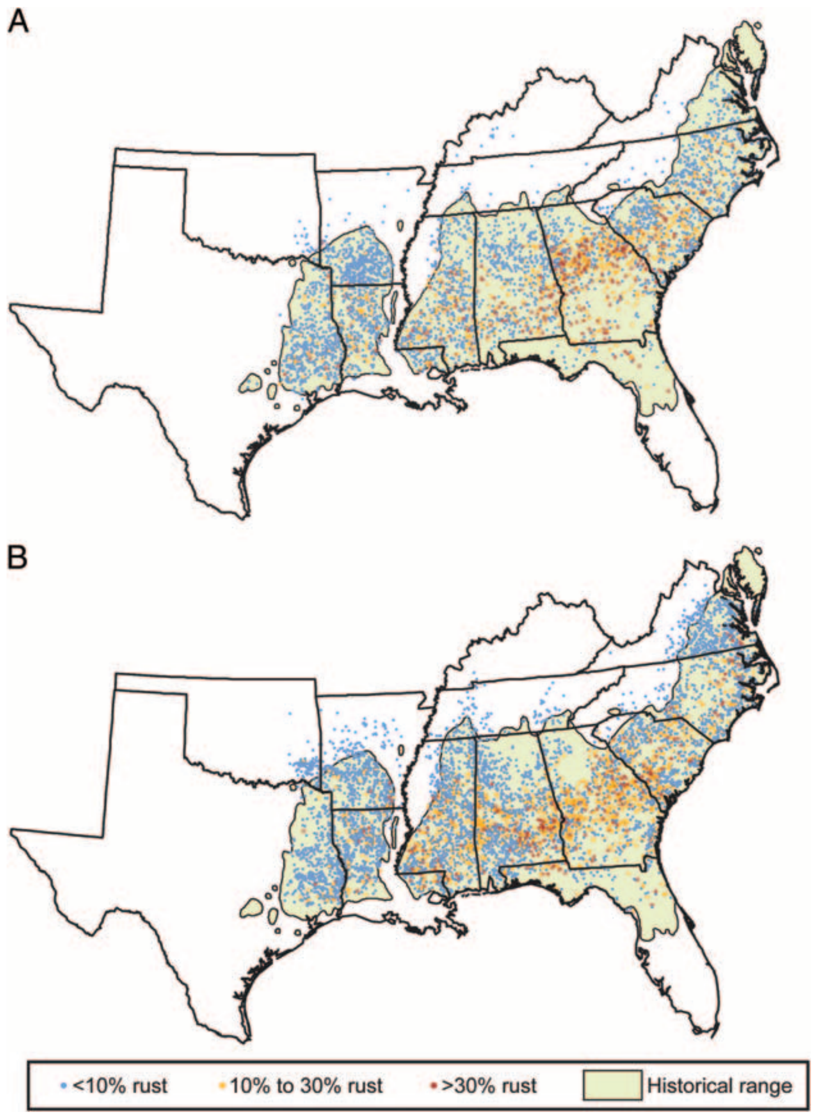

Figure 3. Historical range of loblolly pine and approximate location of FIA plots in the loblolly pine forest type of natural (A) and planted (B) origin, by percent rust incidence. (Source of the range map: US Geological Survey 1999.)

Table 5. Current estimated percent rust incidence ($\hat{R}$) in the loblolly pine forest type, by state and stand origin.

State	Year[a]	Natural			Planted		
		n plots	$\hat{R}$	SE	*n* plots	$\hat{R}$	SE
Alabama	2012	540	8.1	0.7	1026	8.7	0.5
Arkansas	2012	365	0.5	0.2	448	2.0	0.3
Florida	2011	64	11.6	3.4	119	8.3	1.7
Georgia	2012	651	15.9	0.7	840	12.7	0.5
Kentucky	2011	8	—[b]	—[b]	3	—[b]	—[b]
Louisiana	2012	395	6.0	0.8	505	5.2	0.4
Mississippi	2012	541	7.5	0.7	870	8.1	0.5
North Carolina	2012	443	4.4	0.4	461	6.4	0.6
Oklahoma	2012	20	—[b]	—[b]	86	0.5	0.3
South Carolina	2012	536	9.3	0.6	578	8.8	0.5
Tennessee	2011	27	—[b]	—[b]	105	0.0[c]	0.0[c]
Texas	2010	467	1.7	0.2	425	1.5	0.2
Virginia	2012	88	0.4	0.2	402	0.8	0.2

[a] May include data collected in years before the one listed.
[b] —, calculation was not performed because of insufficient sample size (*n* plots <30).
[c] Value is >0.0 but <0.05.

Arkansas (Figure 6A). Rust hazard in these areas has also remained relatively unchanged since the 1990s (Figure 7). Increased rust hazard was observed in Alabama, southeastern Arkansas, Mississippi, Virginia, and North Carolina, and decreases were observed in southeastern Georgia and parts of Louisiana, Texas, and Arkansas (Figure 7).

The rust hazard maps based on the average of the 1990s and 2010s data sets (Figures 4B and 6B) provide a generalized assessment of rust hazard over time. The averaged maps have fewer bulls-eye patterns near individual plot locations. Although the magnitude of percent rust is muted in the averaged maps (Figures 4B and 6B) compared with that in the current maps (Figures 4A and 6A), the two sets of maps are, in general, very similar in terms of the overall pattern of rust hazard.

Discussion

Between the years 1940 and 2000, the mean annual increment in pine plantations more than doubled, whereas rotation lengths were reduced by >50% (Fox et al. 2007). The role of tree improvement programs in this increase in productivity of southern pine plantations has been quite dramatic. Li et al. (1999) reported that seedlings from first-generation seed orchards produced volume gains of 7–12% over wild seed, and seedlings from second-generation seed orchards established in the 1980s were projected to produce an additional 14–23% gain in volume. Third-generation seedlings have been projected to increase productivity even more (Aspinwall et al. 2012). The proportion of increased productivity due specifically to increased rust resistance is substantial. Gains in mean annual increment over a 25-year rotation due to increased rust resistance in the planting stock have been estimated to be 25–30% for slash pine and 5–7% for loblolly pine (Brawner et al. 1999, Vergara et al. 2007). In terms of financial gain, fusiform rust research has estimated benefit-cost ratios of up to 6:1 (Cubbage et al. 2000).

The decrease in rust incidence was greater in the planted loblolly stands than in the natural loblolly stands, particularly in Georgia; therefore, at least a portion of the reduction in fusiform rust incidence in the loblolly pine forest type is probably due to the deployment of rust-resistant planting stock. As a result of realized gains in productivity and genetic resistance over the last 50 years (Li et al. 1999, Cubbage et al. 2000,

Table 6. Estimated percent rust incidence ($\hat{R}$) in planted slash pine stands age 5–15 years, by state and inventory year, and 95% confidence interval for the difference between the two estimates for each state.

State	Year[a]	n plots	$\hat{R}$	SE	$\hat{R}_{diff}$[b]	95% confidence interval
Florida	1980	125	10.7	2.6	10.7[c]	(3.6 to 17.8)
Florida	2011	225	21.4	2.6		
Georgia	1982	114	25.2	2.9	−6.5	(−13.7 to 0.5)
Georgia	2012	165	18.7	2.1		

[a] May include data collected in years before the one listed.
[b] $\hat{R}_{diff} = \hat{R}_{current\ inventory} - \hat{R}_{oldest\ inventory}$.
[c] $\hat{R}_{diff}$ values significantly different from zero ($\alpha = 0.05$).

Table 7. Estimated percent rust incidence ($\hat{R}$) in natural loblolly pine stands age 5–15 years, by state and inventory year, and 95% confidence interval for the difference between the two estimates for each state.

State	Year[a]	n plots	$\hat{R}$	SE	$\hat{R}_{diff}$[b]	95% confidence interval
Alabama	1982	96	17.7	2.3	−10.9[c]	(−16.6 to −5.1)
Alabama	2012	97	6.8	1.9		
Arkansas	1978	74	3.2	0.9	—[d]	—[d]
Arkansas	2012	28	1.6	0.8		
Georgia	1982	108	33.4	3.4	−19.1[c]	(−27.0 to −11.2)
Georgia	2012	72	14.3	2.1		
Louisiana	1984	85	6.1	1.7	0.3	(−4.3 to 4.9)
Louisiana	2012	47	6.4	1.7		
Mississippi	1977	81	13.4	2.1	−6.5[c]	(−11.1 to −1.8)
Mississippi	2012	88	6.9	1.0		
North Carolina	1974	93	9.4	1.8	0.1	(−4.6 to 4.7)
North Carolina	2012	70	9.5	1.5		
South Carolina	1978	77	19.9	3.4	−7.8[c]	(−15.2 to −0.5)
South Carolina	2012	75	12.1	1.6		
Texas	1986	39	7.9	3.3	−6.9[c]	(−13.3 to −0.5)
Texas	2010	43	1.0	0.4		

[a] May include data collected in years before the one listed.
[b] $\hat{R}_{diff} = \hat{R}_{current\ inventory} - \hat{R}_{oldest\ inventory}$.
[c] $\hat{R}_{diff}$ values significantly different from zero ($\alpha = 0.05$).
[d] Calculation was not performed because of insufficient sample size (n plots <30).

Fox et al. 2007, Aspinwall et al. 2012), we anticipated a decrease in fusiform rust in slash and loblolly pine plantations. Yet comparisons of $\hat{R}$ in stands age 5–15 years old between the late 1970s and the early 2010s produced inconsistent results. Reductions in fusiform rust incidence were evident in planted loblolly pine stands in Alabama, Georgia, Louisiana, South Carolina, and Texas, but not in Mississippi (Table 8). Furthermore, decreases in rust incidence were observed in naturally regenerated loblolly stands in all of these states except Louisiana (Table 7). Therefore, the extent to which these reductions can be attributed directly to the planting of rust-resistant seedling stock is not known with certainty. The observed decreases in rust incidence could have been influenced by other factors such as changes in the virulence of the pathogen or management of nearby oak, as well as variability in local and large-area weather conditions, which could have affected rust incidence in some or all FIA plot locations.

Unlike those in loblolly pine plantations, decreases in rust incidence were not evident in slash pine plantations. Between the 1980s and 2010s, $\hat{R}$ in planted slash pine stands age 5–15 years old increased in Florida and remained statistically unchanged in Georgia (Table 6). These results were surprising because improvements in rust resistance for planted slash pine have been documented in other studies (see Vergara et al. 2007 and the studies cited therein). Reasons for the lack of improvement and difference between slash pine and loblolly pine are unknown to us, although biological differences in the planting stock used in the late 1970s compared with that of the 2000s might have contributed to the increase in rust incidence in the newly planted slash pine in Florida. This is because, in addition to rust resistance, tree improvement programs have focused on improving volume growth, tree form, and wood quality (Fox et al. 2007). These genetic gains, along with improved site preparation techniques and better control of competing vegetation, may allow rust-infected slash pine trees to survive longer now than in the past. This possibility may partly account for the increase in percent rust over time among the planted slash pine in Florida.

Discerning the precise reasons behind the changing levels of rust incidence is difficult because the rust incidence levels recorded on the FIA plots reflect the composite effects of management intensity and planting density (Zhao and Kane 2012), as well as other factors including

- regional and local climatic and environmental conditions, which are highly variable site-to-site and year-to-year, and may even be changing slowly over time with long-term climatic variation;
- the continuing and increasing deployment of genetically improved disease-resistant planting stock and accompanying increased growth rate of genetically improved stock in general; and
- the continuing conversion of natural pine and oak-pine forests to plantation pine over large areas and the concomitant reduction in area and abundance of oaks.

Unfortunately, data to individually account for these factors on each FIA plot are not readily available. Although the widespread deployment of disease-resistant planting stock might be expected to reduce rust incidence over time, commonly used silvicultural practices of intensive plantation management tend to increase rust incidence (Zhao and Kane 2012). Thus, it is very difficult to determine the precise reasons behind changing infection levels.

Overall, the patterns of fusiform rust incidence have remained generally stable since the 1970s. Squillace (1976) used isogram charts to depict rust incidence observed among 8- to 12-year-old plantations during a 1971–1973 southwide survey. At that time, a ridge of high incidence for both species extended southwest to northeast across the region (from Louisiana to South Carolina), with the ridge of high incidence for slash pine being farther south than the ridge for loblolly pine. An examination of Figures 2B, 3B, 4A, and 6A of this article illustrate that these general patterns still hold true. Squillace (1976) also noted that the

Table 8. Estimated percent rust incidence ($\hat{R}$) in planted loblolly pine stands age 5–15 years, by state and inventory year, and 95% confidence interval for the difference between the two estimates for each state.

State	Year[a]	*n* plots	$\hat{R}$	SE	$\hat{R}_{diff}$[b]	95% confidence interval
Alabama	1982	73	24.8	3.4	−16.4[c]	(−23.4 to −9.5)
Alabama	2012	435	8.4	0.9		
Arkansas	1978	15	6.2	2.1	—[d]	—[d]
Arkansas	2012	170	3.2	0.7		
Florida	1980	9	5.9	5.3	—[d]	—[d]
Florida	2011	43	6.3	1.8		
Georgia	1982	74	45.5	3.7	−32.8[c]	(−40.3 to −25.2)
Georgia	2012	237	12.7	1.0		
Louisiana	1984	57	18.1	3.1	−12.8[c]	(−18.9 to −6.5)
Louisiana	2012	211	5.3	0.6		
Mississippi	1977	55	8.3	1.9	1.4	(−2.8 to 5.4)
Mississippi	2012	357	9.7	0.8		
North Carolina	1974	71	9.0	1.8	0.4	(−3.8 to 4.7)
North Carolina	2012	121	9.4	1.2		
South Carolina	1978	45	24.6	3.9	−14.3[c]	(−22.4 to −6.2)
South Carolina	2012	137	10.3	1.2		
Tennessee	1980	9	0.0	0.0	—[d]	—[d]
Tennessee	2011	44	0.1	0.1		
Texas	1986	64	8.2	1.9	−7.2[c]	(−10.8 to −3.4)
Texas	2010	180	1.0	0.3		
Virginia	1977	53	0.2	0.2	1.8[c]	(0.5 to 3.1)
Virginia	2012	122	2.0	0.6		

[a] May include data collected in years before the one listed.
[b] $\hat{R}_{diff} = \hat{R}_{current\ inventory} - \hat{R}_{oldest\ inventory}$.
[c] $\hat{R}_{diff}$ values significantly different from zero ($\alpha = 0.05$).
[d] Calculation was not performed because of insufficient sample size (*n* plots <30).

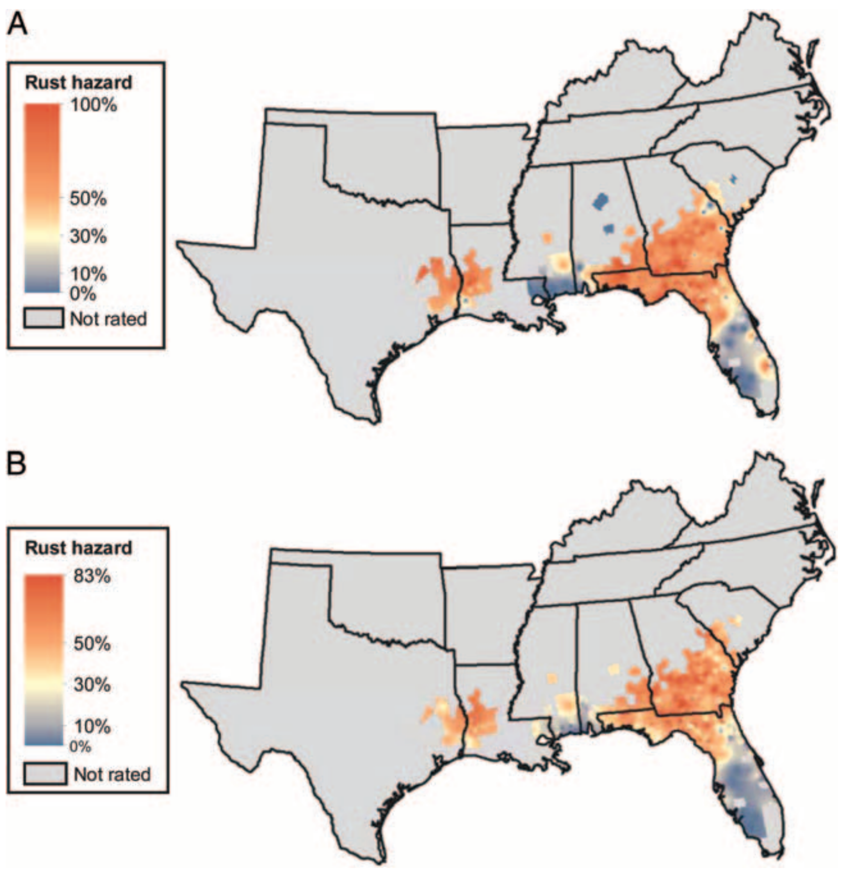

Figure 4. Estimated fusiform rust hazard for slash pine based on fusiform rust incidence assessments on FIA plots from the 2010s (A) and on the average of assessments from the 1990s and 2010s (B).

southwest to northeast ridge of high incidence was interrupted by low rust incidence in southwestern Alabama for both slash pine and loblolly pine. This still appears to be the case for slash pine (Figure 4A) but not for loblolly pine (Figure 6A).

Caveats

Although rust resistance screening at the RSC has proven successful in identifying differences in degree of rust resistance among individual seedlots in progeny tests, this study combined data from across the southeastern United States and undoubtedly included a wide selection of planting stock with varying degrees of rust resistance. Although the FIA Program keeps a record of the ownership where each plot is located, the program at present has no means to distinguish between stands established with disease-resistant and nondisease-resistant planting stock. Thus, there is probably some confounding in the change-over-time analysis because of the combining of plantations with and without rust-resistant planting stock.

Trees <5 in. dbh were excluded from this study; therefore, estimates of fusiform rust infection should be considered conservative. The change in the minimum dbh threshold in the late 1990s from 1 to 5 in. weakened the usefulness of the fusiform rust incidence data because mortality from fusiform rust typically occurs before trees reach 10 years of age (Phelps and Czabator 1978). Depending on site index, management intensity, and stand density, mortality may occur before stems reach the 5 in. dbh threshold. As a result of this study, a recommendation to reestablish the 1 in. dbh threshold for collecting fusiform rust incidence was made to and accepted by the Southern FIA Program for implementation in version 6.1 of the field data collection manual (Southern FIA Regional Management Team, USDA Forest Service, pers. comm., Sept. 5, 2013).

Future Research, Inventory, and Monitoring

Areas where slash and loblolly pine are not historically native and where one or both of these species now exists should be monitored closely for evidence of fusiform rust disease. As plantation forestry continues to expand slash and loblolly pines beyond their historical ranges, it is possible that fusiform rust will follow. Whether or not the disease will expand along with the slash and loblolly

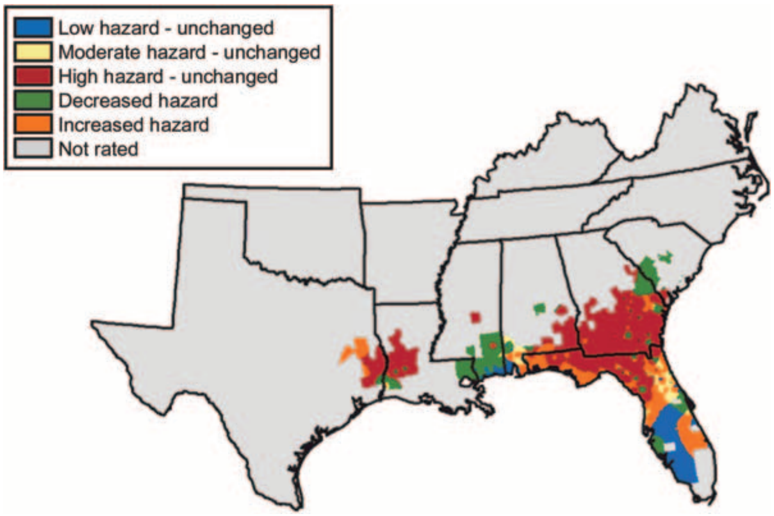

Figure 5. Estimated change in fusiform rust hazard from the 1990s to the 2010s for slash pine based on rust incidence assessments on FIA plots.

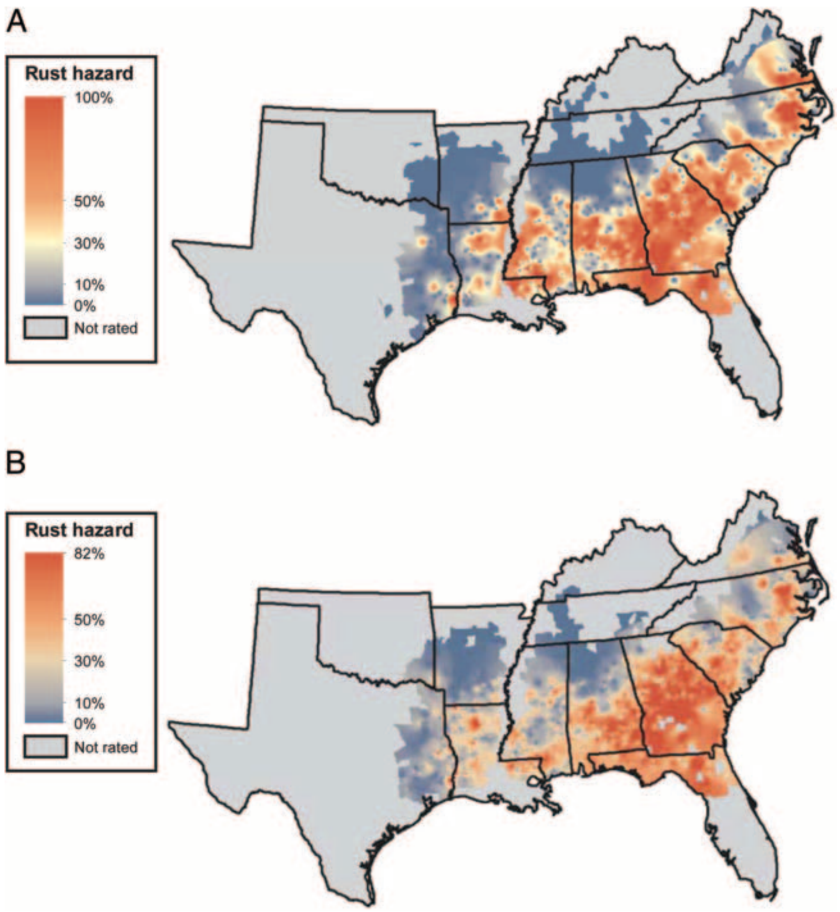

Figure 6. Estimated fusiform rust hazard for loblolly pine based on rust incidence assessments on FIA plots from the 2010s (A) and on the average of assessments from the 1990s and 2010s (B).

pines into areas where neither species is historically native, e.g., Kentucky, depends on a number of complex interacting factors, including the health and distribution of the pathogen's alternate oak host and the climatic conditions under which both the pine trees and nearby oak trees are growing.

Future monitoring of fusiform rust incidence can be enhanced by combining FIA data with data from field-based progeny tests and operational out-plantings of rust-resistant seedlots. The latitude and longitude of every FIA plot is known with an accuracy of about 50 ft. If the locations of progeny tests and operational out-plantings also were determined with similar accuracy, then rust incidence in planting stock with known degrees of genetic resistance could be compared with that in planting stock of different or unknown rust resistance on nearby plantations. In addition, recording the predicted rust resistance of the planting stock within FIA plots (when it is known) would be an additional enhancement to the future monitoring of fusiform rust. Knowledge of this predicted resistance, known as the R50 value (Hodge et al. 1989, Vergara et al. 2007), would be extraordinarily valuable in future analyses of the temporal and geographical reliability of genetic control of rust resistance.

Summary and Conclusions

The estimates presented here document conditions across the broad spectrum of site conditions, management intensities, and pine source material throughout the southeastern United States. Estimates of current fusiform rust incidence levels varied by state, forest type, and stand origin. Across all stand ages, rust incidence rates were higher in stands of planted origin than in those of natural origin for the slash pine forest type; however, for the loblolly pine forest type, rust incidence rates were approximately equal in stands of planted origin and natural origin. Decreases in fusiform rust incidence over the last 30–40 years were evident in young planted loblolly pine stands but not in young planted slash pine stands. The reason for this difference was unclear.

Despite some decreases in fusiform rust incidence over the last 30–40 years, rust hazard still remains high throughout much of the southeastern United States. Given that *C. fusiforme* is an endemic pathogen, this is likely to remain the case. The rust hazard maps created by Starkey et al. (1997) were used widely by forest pathologists and geneticists in various tree improvement programs, as well as by forest managers in making decisions about the deployment of rust-resistant slash and loblolly pine planting stock. The updated rust hazard maps presented here may be used in a like manner to guide continued deployment of rust-resistant planting stock. The average-based rust hazard maps in Figures 4B and 6B provide a broader view of hazard over time than the

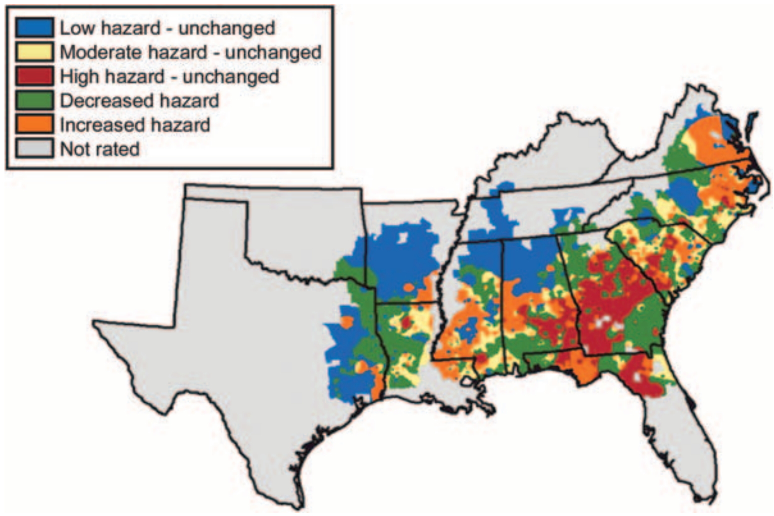

Figure 7. Estimated change in fusiform rust hazard from the 1990s to the 2010s for loblolly pine based on rust incidence assessments on FIA plots.

current-based rust hazard maps in Figures 4A and 6A and may more accurately reflect potential infection risk. Only in a few areas were there major differences between the current-based and average-based maps, and where differences exist, it seems prudent to base deployment of rust-resistant planting stock on the higher hazard.

In addition to the conclusions noted above, this research also provided a number of informative lessons that can be extended to monitoring other forest pathogens (or insects) at national and regional scales:

• Despite the relative ease of collecting disease data on field plots with host species, the number of variables influencing the disease's development contributes significant uncertainty to conclusions that can be made about changing disease levels, geographic disease hazard, and deployment of resistant host material.

• Changes in data collection methodology over the course of long-term forest inventories complicate long-term trend detection and interpretation and should be avoided when possible.

• Cooperation among forest pathologists and geneticists, as well as tree improvement and forest inventory specialists, is essential for improving scientific understanding of disease epidemics.

• Collaborative research leads to both personal and professional satisfaction for those who participate and has great potential for increasing the cost-effectiveness of both public and private forest research organizations.

• Continued monitoring is an essential component of managing fusiform rust and risks from other forest diseases and insects. National-level forest inventories, such as the one implemented by the FIA Program, are uniquely poised to conduct the systematic surveys of tree health, growth, and mortality needed to monitor changing conditions.

With the return of rust data collection on trees 1 in. dbh to <5.0 in. dbh and the continued annual measurement of FIA plots across the South, monitoring and analysis of changes in rust incidence and hazard should become more consistent, meaningful, and valuable over time. Complementary data collection efforts from progeny tests and operational plantings (as suggested earlier), if implemented, could provide a much more comprehensive and accurate assessment of the status of and change in fusiform rust incidence and hazard over time and might provide a clearer picture of the results of continued deployment of rust-resistant planting stock than can be obtained currently.

Endnotes

1. For more information, see the following websites: European Forest Inventory Network, enfin.info; Canadian National Forest Inventory, nfi.nfis.org/index.php; Mexican National Forestry Commission (Comisión Nacional Forestal), www.conafor.gob.mx/web/; and USDA Forest Service, www.fia.fs.fed.us.
2. A condition is defined by a specific combination of landscape and forest attributes, such as land use and forest type, which collectively describe a homogeneous area.
3. FIA places stands into two regeneration categories: natural and artificial. Artificially regenerated stands include stands with distinct evidence of planting or seeding. For simplicity, we use the term "planted" to refer to the artificially regenerated stands.

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