# On the Origin of Fusiform Rust Resistance in Loblolly Pine[1]

R.C. Schmidtling[2], C.D. Nelson[2], and T.L. Kubisiak[2]

Abstract:-- Studies of geographic variation in loblolly pine have shown that seed sources from the western (generally west of the Mississippi River) and the northeastern part of the natural distribution are relatively resistant to fusiform rust disease, while those from elsewhere are more susceptible. The greatest problem with rust infection, on the other hand, is in the center of the distribution, exactly where the frequency of resistant genotypes appears to be lowest. One might expect that the frequency of resistant genotypes would be higher, where the disease is more prevalent, due to natural selection. It has been proposed that (1) fusiform rust resistance in loblolly pine in the west originates from hybridization with shortleaf pine. It is well known that shortleaf pine is relatively resistant to fusiform rust, and it is also known that natural hybrids between the two species exist, and they seem to be more common in the west. In the northeast, it has been proposed that (2) hybridization with pond pine is the source of resistance to fusiform rust. Once again, natural hybridization between loblolly and pond pine is known to exist in the northeast, but not much is known about the relative resistance of pond pine to fusiform rust. Allozyme and cortical monoterpene data were used to evaluate these hypotheses and the results suggest that hybridization is not the primary source of fusiform rust resistance either in the west or northeast.

Keywords: *Pinus taeda*, *Cronartium quercuum* f. sp. *fusiforme*, fusiform rust, disease resistance, evolution, hybridization, *Pinus echinata*, *Pinus serotina*.

## INTRODUCTION

Fusiform rust (caused by *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*) is the most damaging disease of southern pines in the southeastern United States (Powers and others 1981) and it causes substantial mortality in severe epidemics. In lesser, more common epidemics the disease causes relatively less mortality but moderate to severe degrade in the quality and strength of the main stem and branches. In loblolly pine (*Pinus taeda* L.), considerable geographic variation in resistance to fusiform rust disease has been found, with resistance decreasing from west to east, except in the northeastern part of the range where trees tend to be nearly as resistant as western seed sources. For the current study we reviewed the available research to evaluate the hypothesis that resistance in western and northeastern sources of loblolly pine originated in related, sympatric species known to be relatively resistant to fusiform rust.

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[1] Paper originally presented at the 27th Southern Forest Tree Improvement Conference, June 24-27, 2003, Stillwater, OK and inadvertently omitted from the Proceedings. It is published here (28th Southern Forest Tree Improvement Conference, June 20-23, 2005, Raleigh, NC) as presented in 2003 (08/29/05).

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## DISCUSSION

### Geographic Variation

In his pioneering study of geographic variation in loblolly pine, Wakeley (1944) found that a Georgia seed source was much more heavily infected with fusiform rust than western sources from Texas, Arkansas and Louisiana. This study was the first evidence for the now well-known superiority in growth and disease resistance of seed sources from Livingston Parish, Louisiana. The results of the Southwide Southern Pine Seed Source Study (SSPSSS) (Wells and Wakeley 1966) confirmed the relative resistance of the western sources to fusiform rust, and also found a great deal of resistance in a seed source from the extreme northeast of the loblolly pine range (i.e., Maryland). The results of these studies and a study by Grigsby (1973) resulted in large-scale planting of Livingston Parish loblolly pine in areas of high rust hazard in Mississippi, Alabama, Georgia, and Florida (Wells 1985).

Significant seed source-by-planting site interaction in fusiform rust resistance was also observed in the SSPSSS, although the resistant sources from the western part of the range plus the Maryland source are clearly separated from the susceptible sources regardless of the infection level (Figure 1). The eastern and western populations of loblolly pine have been considered to be distinctly different, and the isolating effect of the pine-free Mississippi River basin has been proposed as the mechanism that perpetuates these differences (Wells and Wakeley 1966). This is especially true with regard to resistance to fusiform rust. Sources from west of the river are considered resistant, while those from east of the river are considered susceptible. The one important exception has been Livingston Parish loblolly pine, which is from east of the river but is relatively resistant to fusiform rust.

Studies that have sampled the range of loblolly pine more intensively have shown that the variation in fusiform rust resistance is continuous from west to east. In a range-wide study planted in Arkansas, Grigsby (1973) found no distinct separation between western and eastern sources in rust resistance, rather there was a continuous decrease from west to east, reaching a minimum at the longitude of eastern Georgia, then increasing to moderate levels in the Maryland (MD.) and Delaware (DEL.) sources (Figure 2).

Several regional studies with intensive geographic sampling verified the continuous variation model of Figure 2. Across southern Louisiana, Crow (1958) and Dyer and others (1977) found that resistance to fusiform rust disease decreased from west to east in a continuous manner, with no apparent discontinuity at the Mississippi River. Wells and others (1991) also found that variation in rust resistance across the Mississippi River was continuous, and that there was no distinct separation between western and eastern sources in rust resistance. In a study in Georgia, Sluder (1980) showed a decrease in resistance from west to east across Georgia, reaching a probable low point at the longitude of eastern Georgia. The performance of Livingston Parish is not anomalous when the variation is assumed to be continuous.

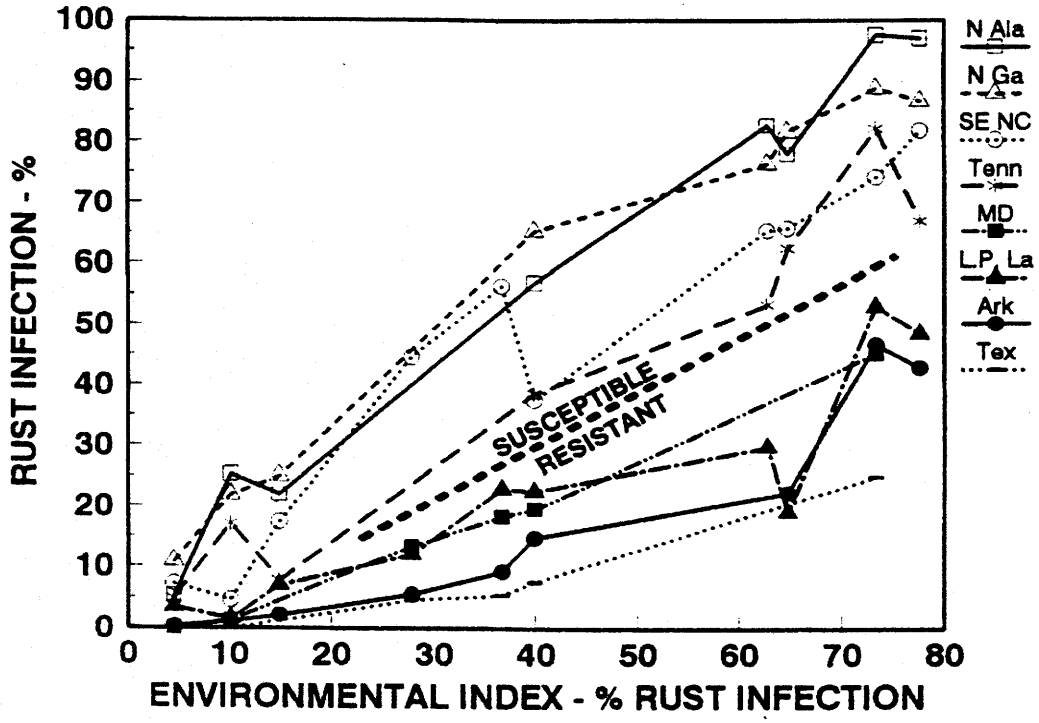


Figure 1. Fusiform rust infection (% galled trees) in eight seed sources of loblolly pine plotted against average rust infection for each planting (adapted from Wells and Wakeley 1966).

Several other studies verify the pattern of fusiform rust resistance of Figure 2. Wells (1966) compared infection of nine Texas seed sources with a source from Livingston Parish, Louisiana and central Georgia. The Texas sources averaged 12% infected, the Livingston Parish source 10% and the Georgia source 32%. Pait and Draper (1983) included sources from east Texas, Maryland and Livingston Parish as well as Florida sources in several plantings in Florida and south Georgia. In all plantings, the Maryland and east Texas sources suffered less infection than the Florida sources. The performance of the Livingston Parish source was comparable to that of the Texas and Maryland sources in all plantings except for one. Other studies further verify the model of Figure 2, for example, Cole (1973) found only minor differences among sources from Georgia and South Carolina, where only small differences might be expected.

The geographic pattern for fusiform rust resistance is difficult to explain, since the lowest concentration of resistant loblolly genotypes occurs exactly where rust infection levels have been the highest, that is, in central Georgia and adjoining Alabama and South Carolina (Squillace 1976). Since fusiform rust infection often causes reduced growth and mortality, natural selection should favor the more resistant genotypes in areas of high infections (Kareiva 1999).

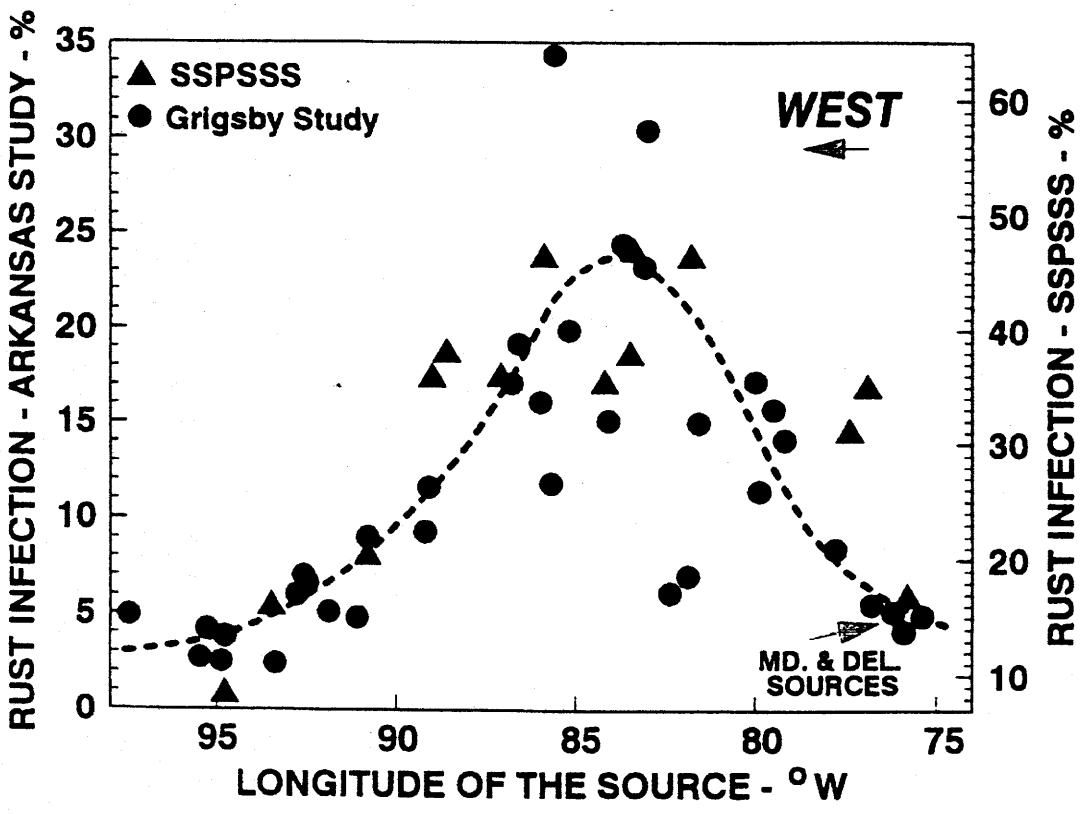


Figure 2. Fusiform rust infection in loblolly pine seed sources from across the natural range, when planted in south Arkansas, plotted against longitude of the seed source (adapted from Grigsby 1973). Also shown is the average infection of SSPSSS seed sources over 10 plantings (adapted from Wells and Wakeley 1966).

One could argue that infection levels are lower in the west and northeast, because that is where the more resistant genotypes are found. That would logically require greater selection for resistance in these areas now or at some time in the past. Warm temperatures and very high humidity at the time of infection of the pine host is a requirement for successful infection (Snow and Froelich 1968). Currently, however, the climate in the central part of the range is more favorable for infection than in the colder northern portions (Arkansas and Maryland) and drier western portions (Texas and Arkansas) of the loblolly pine range.

One popular explanation for the geographic pattern of fusiform rust resistance in loblolly pine involves hybridization with shortleaf pine (*Pinus echinata* Mill.) in the west and pond pine (*Pinus serotina* Michx.) in the northeast (Wells and Wakeley 1966).

**Resistance of Western Sources**

The resistance of shortleaf pine to fusiform rust disease is well known. The shortleaf-loblolly hybrid is also quite resistant (Henry and Bercaw 1956) and ample evidence for natural hybridization between loblolly and shortleaf pines exits (Mergen and others 1965). Florence and Hicks (1980) compared putative natural hybrids with loblolly and shortleaf pines and found that

these hybrids contained allozymes from both species, and that they were quite resistant to fusiform rust. However, this provides only circumstantial evidence that resistance to fusiform rust in "typical" loblolly pine comes from introgression with shortleaf pine.

Allozyme analysis provides a useful tool to look at hybridization. An interesting and rare situation exists with regard to allozymes of the isocitrate dehydrogenase (IDH) locus. Shortleaf pine is almost completely monomorphic for one allozyme variant, whereas loblolly pine is almost completely monomorphic for another variant and this variation can be used to detect recent hybrids (Huneycutt and Askew 1989). In a range-wide study of allozymes in loblolly pine, Schmidtling and others (1999) found evidence for loblolly-shortleaf hybrids based on polymorphisms at the IDH locus. The levels of hybridization were low, averaging about 1%, and were highest in the north-central part of the range, rather than in the west (Figure 3).

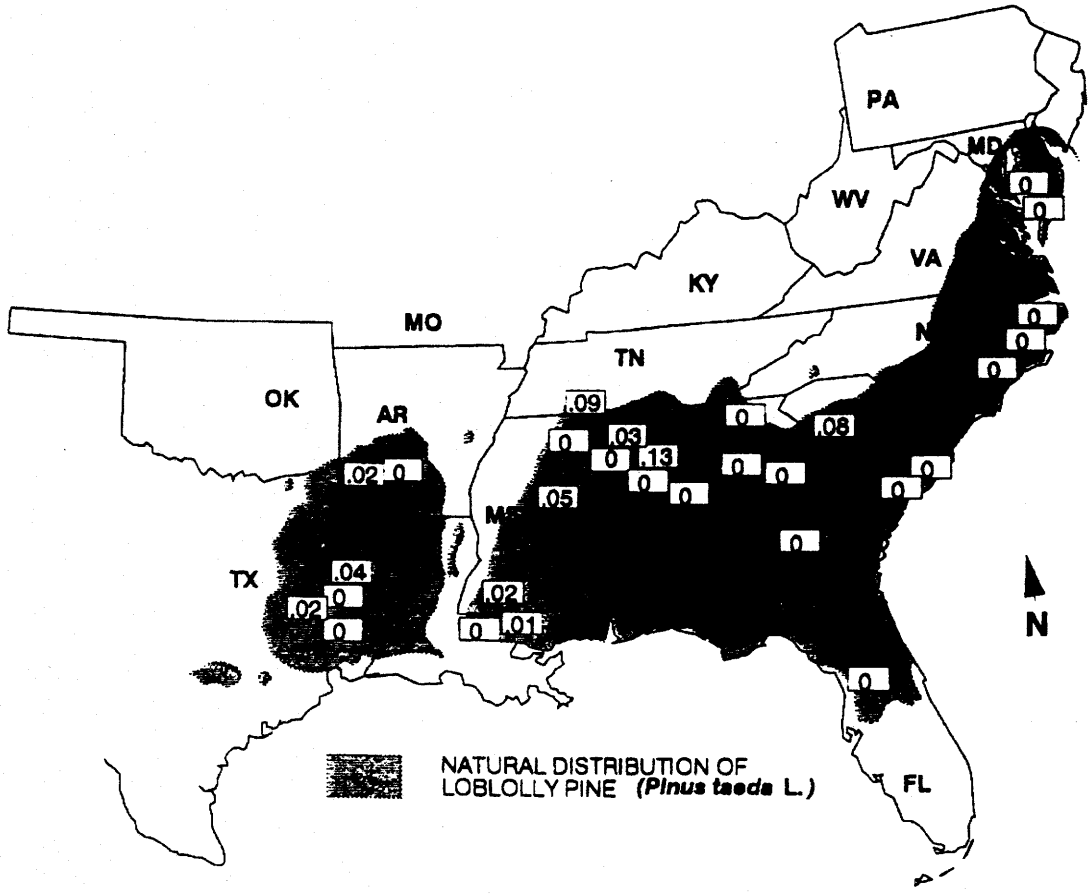


Figure 3. Map of natural distribution of loblolly pine showing the frequency of the "shortleaf" IDH allele. Numbers in the boxes are the frequencies of the allele at each sampling point (adapted from Schmidtling and others 1999).

Better evidence exists for introgression in the opposite direction, that is, of loblolly pine genes into shortleaf pine (Figure 4). Two range-wide studies of shortleaf pine have shown high

frequencies of the "loblolly" IDH allele in shortleaf pine, especially in the western part of the range (Edwards and Hamrick 1995; Raja and others 1997). The frequency of the loblolly allele was very high in a seed orchard population in southern Arkansas (Schmidtling and Hipkins 2001). Out of 22 clones, four (or 18%) showed evidence of hybridization with loblolly pine using the IDH locus criterion. It is interesting that high frequencies of loblolly IDH alleles occur in populations well north of the current natural range of loblolly pine (Figure 4). This suggests that there may be considerable loblolly pine pollen flow northward in the western part of the natural range.

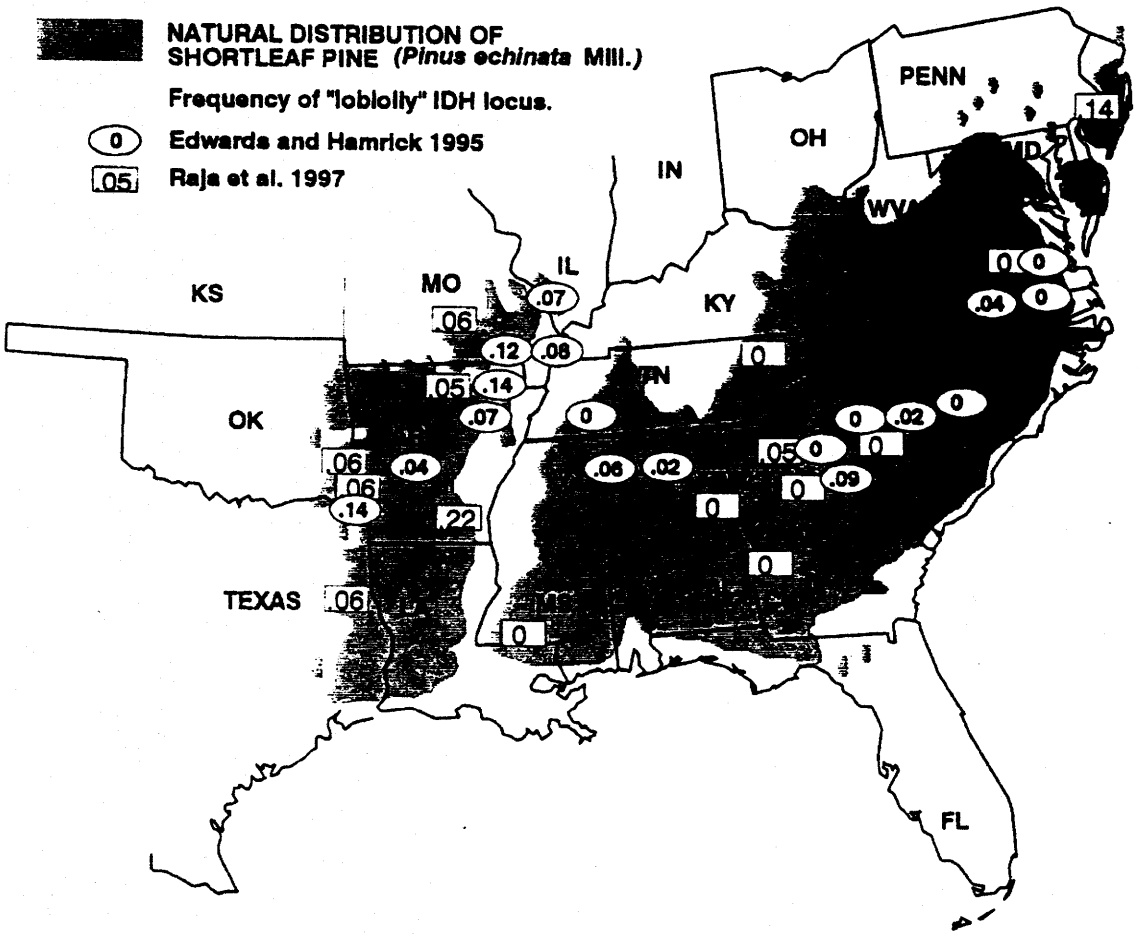


Figure 4. A map of the natural distribution of shortleaf pine showing the frequency of the "loblolly" IDH allele (adapted from Raja and others 1997 and Edwards and Hamrick 1995).

For resistance to have reached such high levels in western populations of loblolly pine, considerable hybridization would be required, along with selection for the trait. This would presumably result in the inclusion of other traits from shortleaf pine in the western loblolly pine populations. In a morphological study of shortleaf and loblolly pine provenance tests, however,

Wells and others (1977) found that resistant western sources of loblolly pine were no more similar to shortleaf pine than were susceptible eastern sources.

**Resistance of Eastern Sources**

In the northeastern portion of the loblolly pine range, pond pine is commonly associated with loblolly pine, as is shortleaf pine. There is also some evidence for introgression of pond pine genes into loblolly pine (Kang 1967; Saylor and Kang 1973). Some disagreement is found in the literature regarding the relative fusiform rust resistance of pond pine. In one manual, pond pine is listed as "moderately susceptible" compared to loblolly and slash pines (*Pinus elliottii* Engelm. var. *elliottii*), which are listed as "very susceptible" (USDA Forest Service 1972). In artificial inoculation tests, Powers (1972) found that pond pine was very rust resistant, whereas Hedgcock and Siggers (1949) found that it was nearly as susceptible as loblolly pine.

Data on cortical monoterpenes do not show any obvious relationship between pond pine and loblolly pine (Table 1). Pond pine has very high limonene content, 47.9%, whereas loblolly pine averages only 10.5%. Further, loblolly pine from the northeast has much lower limonene content than the range-wide average (Squillace and Wells 1981). If significant introgression of pond pine genes into loblolly pine was occurring in the northeast, one might expect to find a higher limonene content in northeastern loblolly pine sources.

**Table 1. Concentration of major cortical monoterpenes in buds of several southern pine species[a].**

| Species | Alpha-Pinene | Beta-Pinene | Myrcene | Beta-Phellandrine | Limonene |
|---|---|---|---|---|---|
| | % | | | | |
| Shortleaf pine | 33.2 | 11.1 | 7.8 | 38.0 | 3.2 |
| Spruce pine | 29.9 | 4.1 | 11.4 | 43.6 | 5.4 |
| Slash pine | 56.0 | 27.0 | 1.3 | 0.5 | 13.0 |
| Loblolly pine | 31.1 | 17.0 | 19.7 | 20.4 | 10.5 |
| Pond pine | 10.4 | 35.7 | 1.2 | 1.3 | 47.9 |

[a] Unpublished data on file at the USDA Forest Service, Southern Institute of Forest Genetics, Saucier, MS.

Some researchers believe that the form of fusiform rust resistance in the northeastern sources differs from that found in the western sources (Squillace and Wells 1981). An independent origin for the resistance of western sources compared to northeastern sources has been proposed based on evolutionary pressures during the Pleistocene (Wells and others 1991). Some evidence for this has been found in artificial inoculation data (Schmidtling unpublished data).

Geographic variation in fusiform rust infection from artificial inoculation tests of seedlings show a different trend than variation in field studies. It is generally acknowledged that results of artificial inoculation tests do not always conform to the results of field trials in loblolly pine (Anderson and Powers 1985). Schmidtling (unpublished data) found that the northeastern

sources tended to be resistant, as they are in field tests, but that the western sources were not, the opposite of their performance in field tests (Figure 5). This leads us to hypothesize that in field tests, several kinds of resistance, for example, physiological, morphological and phenological are expressed, but in artificial inoculation of post-cotyledon-stage seedlings possibly only one kind is expressed. Eastern sources have a relatively higher frequency of this kind of resistance than do the western sources. Thus, the resistance of the two widely separated populations may have different origins.

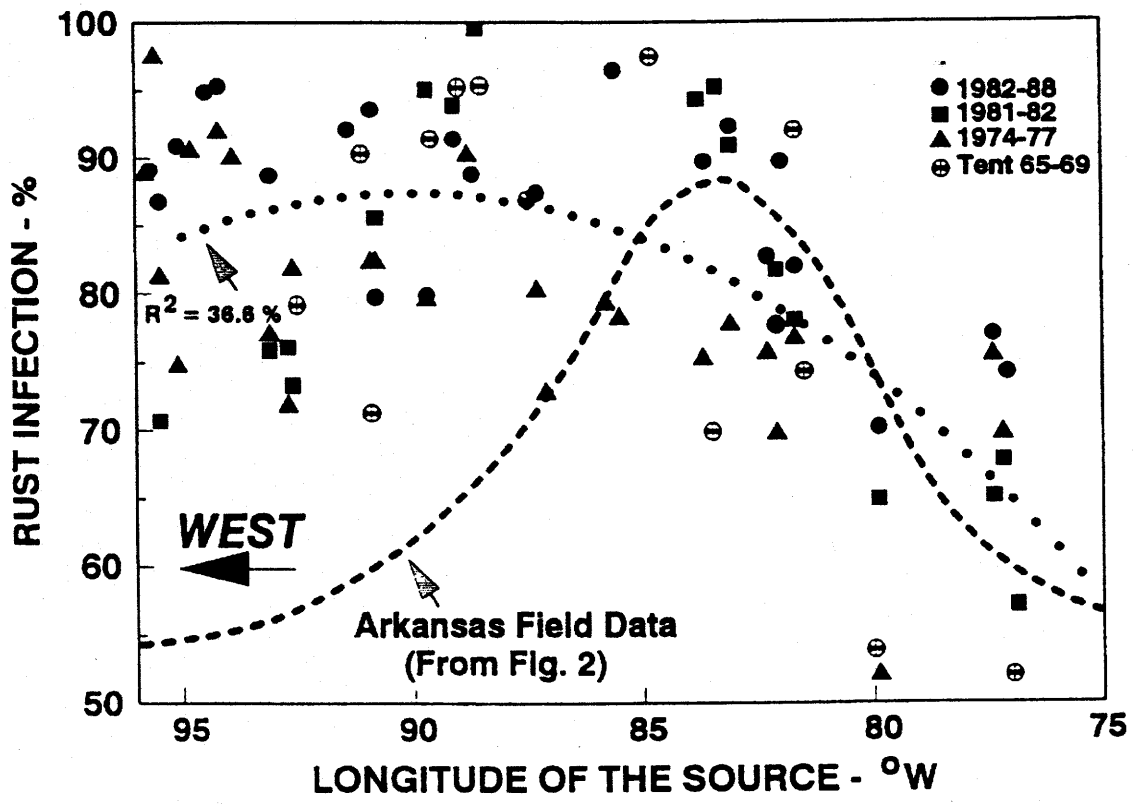


Figure 5. Infection of loblolly pine seedlings from across the natural range when inoculated with fusiform rust basidiospores. Data are from artificial inoculation trials of seedlings from seed orchard trees (Schmidtling and others 1999). The dotted line is a linear polynomial equation ($Y=X_1 - X_2^2$, where Y= % galled trees, $X_1$= longitude and $X_2$= latitude) fit to the data shown in this figure.

## CONCLUSIONS

Recent introgression of genes for fusiform rust resistance into loblolly pine from shortleaf pine in the west or pond pine in the east seems insufficient to account for the relative resistance of these seed sources. Intensive selection pressure due to optimal conditions for disease development at some time in the distant past is a more likely explanation, although hybridization during this time may have provided the genetic variation necessary for the evolution of the resistance observed today.

Schmidtling (in Wells and others 1991) proposed that loblolly pine retreated southward into two populations during the Wisconsin glaciation— Florida and south Texas or Mexico. The climate at that time was much more humid and favorable for fusiform rust infection in the western population (Texas and Mexico) and in the northern part of the eastern population (Florida) (Webb and others 1987). After the subsequent advance northward at the end of the Wisconsin, the populations merged east of the Mississippi River, creating the basis of the present pattern of geographic variation.

The lack of significant recent hybridization as a factor in resistance to fusiform rust disease may make the study of gene-for-gene interaction in host-pathogen analysis more straightforward. The possible west-east difference in resistance mechanisms also should be explored in detailed host-pathogen genetic studies and possibly exploited in breeding for rust resistance. More detailed molecular analysis of the genomes of the involved host species and the actual resistance genes will be required to completely answer this question.

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## 28th Southern Forest Tree Improvement Conference

Sponsored by

The Southern Forest Tree Improvement Committee
&
Department of Forestry and Environmental Resources
North Carolina State University
Raleigh, NC

June 21-23, 2005

Proceeding of the 28th Southern Forest Tree Improvement Conference

Edited by: Steven E. McKeand
Bailian Li
Department of Forestry and Environmental Resources
N.C. State University
Raleigh, NC 27695-8002

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