CONCEPTS RELATED TO INCREASED SUSCEPTIBILITY OF LOCAL SOURCES OF LOBLOLLY PINE TO SOUTHERN PINE BEETLES

H.R. Powers[1], R.P. Belanger,[1] W.D. Pepper,[1] and F.L. Hastings[2]

Abstract.--In a planting near Aiken, SC, loblolly pine saplings from an eastern seed source were significantly more susceptible to the southern pine beetle (SPB) than were loblolly saplings from western sources. In California, heavier infestations of the fir engraver beetle were reported on local than on distant sources of white fir. Such results conflict with the notion of native hosts and pests evolving together and developing mutual tolerance. The SPB case and the general concept deserve additional attention.

Keywords: Southern Pine Beetle, resistance, loblolly pine, fusiform rust

INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimm.) (SPB) is one of the most devastating pests of southern pines. Silvicultural guidelines have been developed to recognize high-risk stands and to provide growing conditions that promote resistance to insect damage (Belanger 1980, Nebeker et al. 1985). Another approach, which has received relatively little attention, is to plant stock that has inherent resistance to SPB damage. It is well known that southern pine species differ in their susceptibility to SPB attack. Since there are differences in susceptibility among southern pine species, there also could be differences within a species.

Genetic selection in tree improvement programs has increased individual tree growth, stand yield, and product quality in pine plantations. In addition, highly fusiform rust resistant seedlings are now available that

---

[1] USDA Forest Service, Southeastern Forest Experiment Station, Athens, GA 30602;

[2] Department of Entomology, North Carolina State University, Raleigh, NC 27695.

reduce losses to fusiform rust, caused by Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme. While certain families of loblolly pine (Pinus taeda L.) have potential resistance to SPB attack (Nebeker et al. 1991), there are no SPB-resistant seedlings available for planting, nor have means been developed for large-scale testing for resistance to the SPB. There appear to be opportunities for making genetic gains through indirect selection, since oleoresin properties of individual trees vary within species as well as between species (Hodges et al. 1977, Nebeker et al. 1988, Nebeker et al. 1991). Proposals have also been made to study seasonal variations in resin flow from bark wounds as indicators of resistance to SPB (Lorio et al. 1990). In this paper, we report findings which indicate that the susceptibility of loblolly pines to SPB attack varies among seed sources and/or geographic provenances (Powers et al. 1992), and discuss their implications related to other insect problems.

MATERIALS AND METHODS

Design

The study area, a 7-acre tract in Aiken County, SC, was divided into 28 quarter-acre plots. Each plot was assigned one of seven geographic seed sources of pine. This area was originally a study designed to evaluate the resistance of various seed sources to fusiform rust. Five of the sources were loblolly pine and two were slash pine (P. elliottii Engelm. var. elliottii). Three of these seed sources from the western part of the loblolly range have been shown to be resistant to fusiform rust (Wells and Wakeley 1966): Clark County, AR; Angelina County, TX; and Livingston Parish, LA. The two eastern sources of loblolly pine were: (1) a mix of the most rust resistant families from the cooperative USDA Forest Service-Georgia Forestry Commission (USFS-GFC) rust resistant orchard in Milledgeville, GA, and (2) a control lot from a first-generation production orchard in central Georgia. Most of the parents providing seed for the latter two loblolly sources originated in Georgia and South Carolina. Two eastern sources of slash pine were also included in the study. They were a rust-resistant mix of seed from the USFS-GFC orchard, and a control lot from a first-generation production orchard in central Georgia.

The study design was a randomized complete block with four replications. Each replication contained 7 treatments (seed sources), each with 120 trees. Trees were planted in 1978 on an 8 x 10 ft spacing (544/ac). There were no border trees between the four blocks or the treatment plots. No silvicultural treatments, such as thinning or fertilization, had been carried out on these plots.

The relative rust resistance of these sources was reported 7 years after planting by Powers and Matthews (1987). When the trees were 11 years old, several SPB infestations were observed in the study area. Numbers of living and dead trees on each plot and the mortality caused by the SPB were recorded. No information was available on the origin or sequence of SPB attack, spot proliferation, or spot spread. Detailed information was taken on the rust infections on a subsample of 30 trees within each quarter-acre plot to evaluate potential correlations between susceptibility to fusiform rust and SPB mortality.

SPB mortality per plot was calculated as the percentage of standing trees that had been killed by SPB. The dbh of all live trees was also measured. Rust incidence on the subsample of 30 trees in each plot was calculated as the percentage of all standing trees that had at least one stem gall. The average number of stem galls per infected tree and rust severity expressed as a percentage of the stem circumference encompassed by the most severe stem gall on the tree were also measured.

Statistical Analyses

Arcsine transformations of. SPB mortality and rust incidence percentages were performed, and the six plot responses were used as dependent variables in a multivariate analysis of variance performed with SAS procedure GLM (SAS Institute Inc. 1987). This analysis simultaneously tested for the presence of a seed-source effect on all dependent variables and for the presence of partial correlations among SPB mortality and rust-related responses. Since it has not been previously demonstrated that there is a seed source (provenance) effect on resistance or susceptibility to a given SPB population, we elected to be very conservative in selecting a critical level of significance for F tests of contrasts. The comparison-wise error rate (CER) for judging F tests was calculated with Sidak's procedure (Games 1977): $CER = 1 - (1 - 0.05)^{1/c}$ where c = number of comparisons (five in this paper) and 0.05 is the maximum experiment-wise error rate. Our CER was 0.0102, rather than the traditional CER of 0.05.

RESULTS

A tree-by-tree survey for SPB mortality was made in all 28 plots of the study area during May 1990. The average proportion of trees killed by SPB varied from 5.3% for the Livingston Parish loblolly to 41.3% for the rust-susceptible check loblolly from Georgia and South Carolina (Table 1). The multivariate test of the simultaneous effects of seed source on arcsine of SPB mortality, arcsine of rust incidence, number of galls per tree, number of trees per acre, dbh of live trees, and percentage of stem girdled by most severe stem gall was significant. The approximate value of F (d.f. 36/47) was 3.84 (P = 0.0001). This statistic shows that the probability of the observed seed source effects occurring by chance is extremely small.

Table 1. SPB mortality, rust characteristics, and stand condition for seven loblolly and slash pine seed sources.

Seed source	SPB mortality	Fusiform rust[1] Incidence	Galls	Severity[2]	Stand Trees	dbh
	(%)	(%)	No./tree	(%)	No./ac	in.
Loblolly (western)						
Livingston Parish, LA	5.3	19.0	1.2	33	260	7.0
Clark County, AR	9.4	4.2	1.2	48	424	6.6
Angelina County, TX	6.5	1.5	1.0	35	416	6.9
Loblolly (eastern)						
Rust-resistant (USFS-GFC)	22.5	20.8	1.7	39	436	6.6
Commercial orchard (control)	41.3	34.2	1.5	36	432	6.8
Slash (eastern)						
Rust-resistant (USFS-GFC)	6.4	21.0	2.0	55	376	6.7
Commercial orchard (control)	6.6	51.0	2.1	50	368	6.6

[1] Value based on stem infections only.
[2] Severity based on percentage of stem circumference girdled by most severe rust infection.

Multivariate analysis of variance including all sources failed to show any significant partial correlations ($P > 0.2$) between transformed SPB mortality and any of the rust- or stand-related responses. We concluded, therefore, that differences in rust susceptibility were not responsible for the observed variations in SPB mortality among seed sources. This result permitted us to proceed with univariate analyses for the five planned comparisons among seed sources.

Mortality was less than 10% for each of the three western sources of loblolly pine (Table 1), and differences among these three were not significant. As expected, SPB mortality was also low for the two eastern sources of slash pine. In comparing each of the eastern sources individually with the average of the western sources, the eastern loblolly commercial control sustained significantly more SPB mortality than the collective western sources ($P = 0.0004$) (Table 2). There was no statistically significant difference between the eastern loblolly rust-resistant source and the western sources of loblolly pine in SPB mortality. The difference in SPB mortality between slash pine and the loblolly pine control was significant (P 0.0016). In contrast, differences between slash pine and both the rust-resistant loblolly source and the western loblolly sources were not statistically significant. These trends in SPB mortality between seed sources and species were statistically consistent among blocks according to Tukey's test of nonadditivity, F (d.f. 1/7) = 0.52 (P = 0.4942) (Tukey 1949).

Table 2. Tests of contrasts among seed source means for SPB mortality.

Contrast	F value	PR > F[1]
Loblolly control vs. loblolly west	18.35	o.0004***2
Loblolly resistant vs. loblolly west	3.25	0.0882
Loblolly control vs. slash	13.70	0.0016***
Loblolly resistant vs. slash	1.86	0.1900
Loblolly west vs. slash	0.21	0.6558

[1] Probability of a larger value of F given that true seed source means are equal.

[2] *** significant at the 0.0102 level.

As reported earlier (Powers and Matthews 1987), rust incidence was significantly higher for both the loblolly and slash commercial controls than for either the western loblolly sources or the rust-resistant eastern sources (Table 1). There was no statistically significant difference between eastern and western sources in the average severity of stem girdling, dbh, or number of trees per acre (Table 1). Again, it is important to note that multivariate analysis failed to show significant partial correlations between rust- or stand-related responses and SPB mortality.

A check of the study area 2 years after the original collection of data found no significant changes in the number of beetle-killed trees.

DISCUSSION

On our test plots in South Carolina, loblolly commercial control trees suffered significantly more SPB-caused mortality than trees from western sources. We believe that ours is the first report of large and highly significant differences in susceptibility to SPB attack among different provenances of a pine species. Our results represent provenance responses to a single population of the beetle. Whether the susceptibility ranking would remain the same with exposure to different beetle populations is not known.

The greater susceptibility of local than western pine sources to SPB attack conflicts with a widely held concept. Many argue that hosts develop tolerance to native pests that have evolved in the same area; and that if the hosts are attacked by these pests damage will be limited. An obvious contrast is the catastrophic result when an exotic pathogen is introduced to a host that has never been exposed, i.e., white pine blister rust, chestnut blight, and gypsy moth.

We first noticed susceptibility of local hosts to local pests in a study with fusiform rust (Powers and Matthews 1980). Loblolly seedlings were grown from seeds collected in six geographic areas across the natural range of the species and were inoculated with rust spores collected from each seed source area. In each series of inoculations, the highest level of rust infection on a specific seed source was caused by the rust spores from its own area.

An additional example from entomology can be found with the fir engraver beetle (Scolytus ventralis LeConte) on white fir (Abies concolor (Gorcl. & Glend.) Lindl. **ex** Hildebr.). Otrosina and Ferrell (1992) found four times as much mortality in plantations of local provenances (northern California and Oregon) as in plantations containing 39 provenances from throughout most of white fir's range. These results were supported by cage tests where local beetles attack densities were much higher on local than on exotic (Arizona) wood bolts. In addition, the beetles successfully reproduced on the bolts from local trees. Otrosina and Ferrell conclude that local strains of these pests may be better adapted to local tree hosts. Their preliminary work with isozyme analyses and inoculations with the mycangial fungus Trichosporium symbioticum Wright support this hypothesis.

There is no direct evidence in the literature to indicate that beetle populations from various locations differ in their ability to attack pines from different geographic sources. There is, however, some indirect evidence to suggest this possiblity. In a laboratory study, Berisford et al. (1990) compared the attractancy to SPB from Texas, Georgia, and Virginia of extracts of billets of loblolly pine infested with beetles from these three locations. Beetles were significantly more attracted ($P < 0.05$) to volatiles from billets infested with beetles from their own locations. Also, loblolly pines from North Carolina were inoculated with isolates of the mycangial fungus Ceratocystiopsis ranaculosus Bridges & Perry of southern pine beetles from North Carolina and Louisiana. The spread of infection was faster for the isolate from North Carolina beetles, indicating a more aggressive fungus attack on native tree hosts. (Cook and Hain, in press). These two studies suggest that local beetle populations are more likely to be successful against native hosts.

Studies have shown differences among widely separated SPB populations in isozymes (Namkoong et al. 1979) and electrophonesis patterns (Anderson et al. 1979). While these results provide no direct evidence that beetle populations from various locations differ in their ability to attack pines from different geographic areas, they support the possibility of differences.

The preliminary findings reported in this paper may provide direction for additional research. These and other seed sources should be studied to determine if the physical and chemical properties of resins are related to differences in susceptibility to SPB attack. Promising seed sources need to be field-tested within and between eastern and western provenances to determine the relative stability of SPB resistance across geographic ranges. Beetle populations need to be carefully monitored to determine the manner of spot initiation and spot growth within isolated plantings of the different seed sources. These kinds of studies would be difficult to design and conduct, but they are necessary to confirm our findings and to locate sources and genotypes that are resistant to SPB attack. Although our study did not reveal any significant relationships among fusiform rust, reduced tree growth, stand stress, and SPB behavior, we feel that a larger, more sensitive study might strengthen our findings and/or provide new insights into such relationships.

LITERATURE CITED

Anderson, W.W., C.W. Berisford, and R.H. Kimmich. 1979. Genetic differences among five populations of the southern pine beetle. Ann. Entomol. Soc. Am 72:323-327

Belanger, R.P. 1980. Silvicultural guidelines for reducing losses to the southern pine beetle. P. 165-177 in The southern pine beetle. USDA ESPBRAP For. Serv. Sci. Educ. Admin. Tech. Bull. 1631.

Berisford, C.W., T.L. Payne, and Y.C. Berisford. 1990. Geographical variation in response of southern pine beetle (Coleoptera: Scolytidae) to aggregating pheromones in laboratory bioassays. Environ. Entomol. 19:1671-1674.

Cook, S.P., and F.P. Hain. J. Environ. Entomol. (In press).

Games, P.A. 1977. An improved t table for simultaneous control on g contrasts. J. Am. Stat. Assoc. 72:531-534.

Hodges, J.D., W.W. Elam, and W.F. Watson. 1977. Physical properties of the oleoresin system of the four major southern pines. Can. J. For. Res. 7:520-525.

Lorio, P.L., Jr., et al. 1990. Modeling pine resistance to bark beetles based on growth and differentiation balance principles. P. 402-409 in Process modeling of forest growth responses to environmental stress, Dixon, R.K., et al. (eds.). Timber Press, Portland, OR.

Namkoong, G., J.H. Roberds, L.B. Nunnally, and H.A. Thomas. 1979. Isozyme variations in populations of southern pine beetles. For. Sci., 25:197-203.

Nebeker, T.E., et al. 1991. Exploring variation in the constitutive defensive system of woods run and full-sib families of loblolly pine in relation to bark beetle attack. P. 307-313 in Proc. 6th Bienn. South Res. Conf. Coleman, S.S., and D.G. Neary (comps., eds.). USDA For. Serv. Gen. Tech. Rep. SE-70. (In press).

Nebeker, T.E., J.D. Hodges, C.R. Honea, and C.A. Blanche. 1988. Preformed defensive system in loblolly pine: Variability and impact on management practices. P. 147-162 in Integrated control of scolytid bark beetles, Payne, T.D., and H. Saarenmaa (eds.). Symp. Proc. XVIII Internat. Congr. Entomol., Vancouver, B.C., Canada.

Nebeker, T.E., J.D. Hodges, B.L. Karr, and D.M. Moehring. 1985. Thinning practices in southern pines -- with pest management recommendations. USDA For. Serv. Tech. Bull. 1703. 36 p.

Otrosina, W.J., and G.T. Ferrell. 1992. Resistance of white fir provenances to the fir engraver (Scolytus ventralis) - Trichosporium symbioticum complex. P. 153-154 in Proc. N. American Forest Insect Work Conf. Denver, CO.

Powers, H.R., Jr., and F.R. Matthews. 1980. Comparison of six geographic sources of loblolly pine for fusiform rust resistance. Phytopathology 70:1141-1143.

Powers, H.R., Jr., and F.R. Matthews. 1987. Five fusiform rust resistant seed sources in coastal South Carolina: A field comparison. South. J. Appl. For. 11:198-201.

Powers, H.R., Jr., R.P. Belanger, W.D. Pepper, and F.L. Hastings. 1992. Loblolly Pine Seed Sources Differ in Susceptibility to the Southern Pine Beetle in South Carolina. South. J. of Appl. For. 16(4):169-174.

SAS Institite Inc. 1987. SAS/STAT guide for personal computers, Version 6 SAS Institute Inc., Cary, NC. 1028 p.

Tukey, J.W. 1949. One degree of freedom for nonadditivity. Biometrics 5:232-242.

Wells, 0.0., and P.C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. For. Sci. Monogr. 11. 40 p.