RELATIONSHIPS BETWEEN MONOTERPENE COMPOSITION AND FUSIFORM RUST RESISTANCE

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Abstract. Previous reports, dealing with the relationships between monoterpene composition and fusiform rust resistance in loblolly and slash pines, suggest that trees having relatively high ß-phellandrene are more often resistant to the disease than low ß-phellandrene trees. Although causes of the relationship are not clear, the results suggest that monoterpene composition be utilized as an early selection aid by culling low ß-phellandrene phenotypes.

Keywords: Loblolly pine, slash pine, Pinus taeda, Pinus elliottii, monoterpenes, Cronartium quercuum f. sp. fusiforme

INTRODUCTION

Development of strains of trees strictly for resistance to fusiform rust [Cronartium quercuum (Berk.) Miyabe ex Shirai f. sp. fusiforme] would be relatively easy. Selection of rust-free trees in highly infected stands can be effective. But, because most tree breeders are interested in superiority of other traits along with rust resistance, the task is more complicated. Usually selections are made in sexually mature stands with great attention paid to superiority in traits other than rust resistance. Although infected trees are avoided, more effort is required to incorporate rust resistance. Usually seeds are collected from preliminary selections and these are tested for rust resistance by artificial inoculation in greenhouse tests (Anderson 1982) or in short-term progeny tests. Several early studies suggested the possibility of using monoterpene composition as an aid in selecting trees for rust resistance. Results of these studies along with two more recent and comprehensive tests, are briefly reviewed. Implications and practical applications are then discussed.

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LOBLOLLY PINE STUDIES

Hare (1970) analyzed monoterpenes of stem xylem oleoresin in seed source plantations of loblolly pine (P. taeda L.). Trees from relatively rust resistance sources were found to contain more ß-pinene and limonene than susceptible sources.

Rockwood (1973) found no correlations between rust resistance and monoterpene composition of stem xylem oleoresin in loblolly pines. But using cortical oleoresin, he found that relatively resistant trees tended to contain less ß-phellandrene than susceptible trees. This contrasted with subsequent reports and we should note that sampling here was restricted to trees native to southwest Georgia.

Squillace and Wells (1981) studied cortical monoterpenes of loblolly pines grown from seed collected over the entire range of the species. Although results were not conclusive, trees having relatively low myrcene, high limonene, and high ß--phellandrene tended to be more resistant to fusiform rust than other trees (Table 1).

Table 1. Differences in frequencies of rust-free and rust-infected loblolly pines classified as having (1) low myrcene-high limonene-high B-phellandrene (mLP trees) or (2) all other monoterpene phenotypes (adapted from Squillace and Wells 1981).

	Rust-free trees (no.)	Rust-infected trees (no.)	Percent rust-free (percent)
"mLP" trees	297	101	74.6
Other trees	1050	680	60.7
Totals	1347	781	

Contingency test: X^2, adjusted for continuity, with 1 DF = 26.43, highly significant.

Squillace et al. (1984) studied cortical monoterpene composition of juvenile loblolly pine families having varying degrees of resistance to rust in three plantations. Trees classified as having relatively high ß-pinene, low myrcene, high limonene, and high ß-phellandrene (Squillace et al. 1980) were usually more resistant than other trees under three measures of degree infection (Table 2).

Table 2. Comparison of three measures of fusiform rust infection in BmLP[1] trees vs. other trees, in three plantations of Georgia.[2]

	Plantation No. 301 (227 trees)	Plantation No. 302 (97 trees)	Plantation No. 303 (594 trees)
	Percent Infected		
BmLP trees	31	43	12
Other trees	46	43	17
	Average Number Infections Per Tree		
BmLP trees	0.5	1.7	0.1
Other trees	1.9	2.8	1.2
	Average Number Infections Per Infected Tree		
BmLP trees	1.5	4.0	1.0
Other trees	4.0	5.8	1.3

[1] Trees having relatively high 13-pinene, low myrcene, high limonene, and high ß-phellandrene.
[2] Data from Squillace et al. (1984) in a study sponsored by the Georgia Forestry Commission.

Using data obtained by Squillace and Wells (1981), Squillace et al. (1985) showed that natural selection in loblolly pines in western and central portions of the species range tends to favor trees having high ß-pinene, low myrcene, high limonene, high ß-phellandrene. This phenotype (BmLP) presently comprises a large proportion of western populations which are relatively resistant to fusiform rust. Although the phenotype is rather infrequent in central populations it is presumably increasing with each generation. Curiously, loblolly pines in northeastern regions also tend to be rust resistant, but unlike western trees, bM1P trees were found to be favored by natural selection. In 1992 we sampled cortical monoterpenes in 38 rust resistant and 35 susceptible loblolly pine clones. Clones classified as having high ß-phellandrene were significantly more frequent in the resistant group than in the susceptible group (Table 3). Although different individual monoterpene types were too few for reliable comparisons. the BmLP clones were most often resistant while BM1p clones were most often susceptible.

SLASH PINE STUDIES

Rockwood (1974) sampled cortical monoterpenes in relatively resistant and relatively susceptible slash pine (P. elliottii Engelm. var. elliottii) clones, families, and individuals. Although results were somewhat variable, resistant trees usually contained more ß-phellandrene than susceptible ones. Results were clear enough to suggest using monoterpene composition as an aid in selecting rust resistant trees in breeding programs.

Table 3. Numbers of resistant and susceptible loblolly pine clones classified by relative content of ß-phellandrene in cortical oleoresin. Data from Michelozzi et al. (1992).

ß -phellandrene class (percent)	No. clones resistant	No. clones susceptible	Percent resistant
	Low ß-phellandrene		
0 to 3	6	17	26.1
	High ß-phellandrene		
5 to 15	25	13	65.8
16 to 30	7	5	58.4

Results of contingency tests (adjusted for continuity): Low vs. high classes, X^2 with 1 df = 7.62, highly significant. Between the two high classes, X^2 with 1 df = 0.02, nonsignificant.

Michelozzi et al. (1990) studied cortical monoterpenes in 85 north Florida slash pine clones progeny-tested for rust resistance. Fifty-seven percent of the trees having relatively high ß-phellandrene were resistant, while only 15 percent of the low ß-phellandrene trees were resistant (Table 4). Among trees classified as having relatively high ß-phellandrene, there was no correlation with rust resistance. Thus, increasing ß-phellandrene beyond a critical level seemed to have no effect on resistance. Although high limonene trees are rare in north Florida, four of the 73 trees tested contained high limonene. Three of these were resistant, which tends to agree with earlier work, but more tests would be required to prove a relationship of limonene content with rust incidence.

Table 4. Number of resistant and susceptible slash pine clones classified by relative content of ß-phellandrene in cortical oleoresin. Data are from Michelozzi et al. (1990).

ß-phellandrene class (percent)	No. clones resistant	No. clones susceptible	Percent resistant
	Low ß-phellandrene		
0 to 3	2	11	15.4
	High ß-phellandrene		
5 to 15	12	7	63.2
16 to 25	15	14	51.7
26 to 57	14	10	58.5
Totals	41	31	56.9

Results of contingency tests: Low vs. high classes, X^2 adjusted for continuity, with 1 df = 6.04, significant at the 0.05 level. Among high classes, X^2 adjusted for continuity, with 2 df's = 0.64 nonsignificant.

Forty-six additional slash pine clones were sampled in the 1992 study by Michelozzi et al. The results showed that clones with low ß-phellandrene tend to be more susceptible to fusiform rust than trees having ß-phellandrene as found in previous data (Table 5). Unfortunately, no BmLP or BM1p types occurred among these clones.

IMPLICATIONS

Although results of the various studies are somewhat variable, high ß-phellandrene trees were more frequently resistant to fusiform rust than low ß-phellandrene trees. High limonene trees were also more often resistant than low limonene trees, but more tests are required to prove this.

Reasons for the relationships are not clear. Rockwood (1974) suggested that toxicity of the chemicals does not appear to be important. The lack of an increase in resistance with increasing content of ß-phellandrene beyond a critical level also suggests the chemical itself is not the cause. Terpenes may act in association with other important factors of resistance. Perhaps the presence of the gene (or genes) that cause high ß-phellandrene may be indicative of resistance through linkage or

Table 5. Numbers of resistant and susceptible slash pines classified by relative content of -phellandrene. Data from Michelozzi et al. (1992).

ß-phellandrene class (percent)	No. clones resistant	No. clones susceptible	Percent resistant
	Low ß-phellandrene		
0 to 3	5	14	26.3
	High ß-phellandrene		
5 to 10	18	9	66.7
Totals	23	23	50.0

Contingency test: X^2 adjusted for continuity, with 1 df = 5.74, significant at the 0.05 level.

correlations with other traits more directly related to resistance. Hare and Switzer (1969) suggested that introgression with shortleaf pine (P. echinata Mill.) may explain rust resistance in western loblolly pines. Likewise, Saylor and Kang (1973) suggest that resistance of loblolly pine in the northeastern region may be due to introgression with pond pine (P. serotina Michx.). Unfortunately, cortical monoterpenes of these pine species have not been well studied. Results also suggest that particular combinations are more indicative of resistance than a certain monoterpene alone, and this would result in more powerful predictors of field performance. More comprehensive tests would be desirable.

APPLICATION

We believe that the relationship between relative content of ß-phellandrene and fusiform rust resistance is strong enough to use as an aid in developing rust resistance strains of loblolly and slash pines. A desirable procedure would be to determine monoterpene composition of candidate trees prior to progeny testing followed by culling trees having low ß-phellandrene . Progeny testing, possibly including short-term artificial inoculation tests for rust resistance, would still be required. But sampling and analyzing for monoterpene composition can be done rapidly at relatively low cost and would greatly decrease the cost of field progeny testing. In view of Rockwood's (1973) findings, the procedure may not be effective with loblolly pine in southwest Georgia.

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