DIFFERENTIAL SUSCEPTIBILITY OF WHITE FIR PROVENANCES TO THE FIR ENGRAVER AND ITS FUNGAL SYMBIONT IN NORTHERN CALIFORNIA

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INTRODUCTION

The fir engraver, *Scolytus ventralis* LeC., attacks white fir, *Abies concolor* (Gord. and Glend.) Lindl., and other true firs, *Abies* spp., in western North America. The biology, attack behavior, and ecology of this bark beetle were recently summarized by Berryman and Ferrell (1988). During the summer flight season, the attacking beetles bore into the cambial zone of fir boles, introducing a pathogenic brown-staining fungus, *Trichosporium symbioticum* Wright. Resistant firs react to the invasion by forming a resinous necrotic wound in the phloem and outer sapwood, which contains the spread of the fungus and repels or kills the beetles. In such interactions, the tree usually survives. This reaction is less intense or absent in susceptible firs, resulting in reproductive success of the beetles, and severe damage or even death of the fir. Sporadic outbreaks of the fir engraver, associated primarily with droughts, have caused widespread mortality of true firs in nearly every decade of this century in western North America.

In the drought years of 1987-88, four 26-year-old white fir provenance test plantations at Camino, California, located at 1028 m elevation in the central Sierra Nevada, sustained considerable levels of mortality. Subcortical examination of a subsample of the dead firs indicated that all had reproductively successful gallery systems of the fir engraver. Drought continued until winter 1992-1993. Surveys beginning in fall 1988 revealed pronounced differences in this mortality, among both plantations and provenances, and also within plantations.

This paper describes the observed patterns of susceptibility and resistance in relation to known patterns of geographic variation in white fir in western North America and discusses studies underway to understand the mechanisms responsible for these patterns.

METHODS

The adjacent provenance test plantations represent two studies. The "geographic range" plantations (1 and 3) consist of 39 provenances from throughout most of the western portion of white fir's natural geographic range in western North America. Each provenance was originally represented by three replications, each of three seedlings. One replication was removed by thinning in 1970. The "elevational transect" plantations (2 and 4) contain only four provenances representing a west-east elevational transect across the Sierra Nevada at the latitude of Camino. Each of these provenances is represented by 10 half-sib families, each originally with nine trees, since thinned to six. In all four plantations, provenances were planted in an interlocked randomized non-contiguous plot layout designed to minimize effects of microsite variation (Libby and Cockerham 1980).

Beginning in August 1988, trees in these plantations were surveyed annually in summer or early fall for mortality and susceptibility to fir engravers. Surveys were conducted after trees attacked and killed by fir engravers the previous year had faded crowns, but before trees killed by current attack had faded crowns. During these surveys, trees topkilled by the previous year's attack were also noted.

Mattson, W.J., Niemelä, P., and Rousi, M., eds. 1996. Dynamics of forest herbivory: quest for pattern and principle. USDA For. Serv. Gen. Tech. Rep. NC-183, N.C. For. Exp. Sta., St. Paul, MN 55108.

Patterns of tree resistance were surveyed in December 1989; numbers of pitch streamers indicating unsuccessful fir engraver attacks were classified as 0, < 5, 5-10, and > 10 on stems of all live trees.

Distributions of trees classified by status (live, dead) and number of pitch streamers were compared among provenances by Chi-square Contingency Test (SAS Institute Inc. 1988). Data from the two replicates of each type of plantation (geographic range, elevational transect) were similar and were pooled for analysis. In the geographic range plantations, provenances were combined according to Hamrick and Libby (1972) as modified by Libby *et al.* (1980). The latter authors divided white fir in the western part of its range into five major geographic groups based primarily on needle morphology: (1)"Northern"— central Oregon and northwestern California; (2) "Central"— south-central Oregon, central and northeastern California; (3) "Southern California"; (4) "Interior South"— Arizona; and (5) "Interior North"— eastern Nevada and western Utah.

RESULTS

Of the 1,127 firs alive in all four plantations in 1987, 393 (35%) were killed by the fir engraver by 1993. Most (253) of the mortality resulted from the attack season of 1987, with an additional 121 resulting from the 1988 attack season. Relatively few (29) were killed by attack in 1989-1993. Only a few (10) trees were topkilled, two of which were killed in subsequent years. Firs on the outside edges of the plantations were infrequently killed (4/97 or 4%).

Through 1993, cumulative mortality in the elevational transect plantations (256 of 578 total trees, or 44%) was almost twice that in the geographic range plantations (137/549, or 25%). The associated Chi-square (adjusted for continuity) was 45.505, $p < 0.0001$ at 1 df.

In the geographic range plantations, mortality differed among major geographic groups of Hamrick and Libby (1972) and Libby *et al.* (1980). In both plantations, provenances of the Northern and Central groups had sustained the highest mortality, while very few of the firs of the Interior South and Interior North groups were killed (Table 1). Low levels (11 percent) of mortality occurred in southern California firs. The Chi-square associated with among-group variation was 40.631, $p < 0.0001$ at 4 df. Among individual provenances, the one from nearest Camino (AK; Omo Ranch; 32 km distant) had the highest mortality in both plantations.

Table 1.—Mortality of white fir provenances caused by fir engravers in the geographic range plantations[1] at Camino, CA 1987-1993

Group[2]	Plantation 1			Plantation 3		
	Total	Dead	Pct dead	Total	Dead	Pct dead
Northern	55	12	22	84	33	39
Central	106	22	21	124	55	44
Southern Calif.	40	3	8	47	7	15
Interior South	28	0	0	31	4	13
Interior North	14	0	0	20	1	5

[1]Each plantation contained 39 provenances from the western portion of white fir's geographic range.

[2]Provenances combined by major morphological groups of Hamrick and Libby (1972).

In the elevational transect plantations, mortality in the two lower- elevation westside provenances nearest Camino (AK, AL) averaged more than one-third greater than that in the two upper-elevation eastside provenances (AM, AN), which are only about 50 km more distant (Table 2). The among-provenance Chi-square was 24.757, $p < 0.0001$ at 3 df.

Analysis of the distribution of pitch streamers on boles of surviving firs revealed that in the elevational transect plantations, virtually all surviving firs had been attacked, and many heavily so (>10 streamers). In the geographic range

Table 2.—Mortality of white fir provenances caused by fir engravers in the elevational transect plantations[1] at Camino, CA 1987-1993

Provenance	Plantation 2			Plantation 4		
	Total	Dead	Pct dead	Total	Dead	Pct dead
AK	76	37	49	95	59	62
AL	72	30	42	72	42	58
AN	65	19	29	63	27	43
AM	61	9	15	74	33	45

[1]West-east transect across Sierra Nevada at latitude of Camino. AK, AL are lower elevation westside; AN, AM are upper elevation eastside.

plantations, however, more than 38% of Interior South and Interior North firs had no pitch streamers, and fewer than 11% had more than 10 pitch streamers (Table 3). In contrast, among Northern and Central firs, fewer than 6% had no pitch streamers while more than 24% had over 10. Distribution of pitch streamers on Southern California firs was intermediate between these two patterns. The among-group Chi-square was 128.424, $p < 0.0001$ at 12 df. The Central provenances from the Sierra Nevada where Camino is located had the lowest percentage of firs with no pitch streamers (ca. 2%) and the highest percentage with more than 10 streamers (ca. 41%).

Table 3.—Incidence of pitch streamers caused by fir engravers on boles of white fir provenances in the geographic range plantations,[1] Camino, 1989

Group[2]	Number of pitch streamers			
	0	<5	5-10	>10
Northern	5	34	31	23
Central	3	22	61	60
Southern Calif.	11	16	33	16
Interior South	27	14	8	6
Interior North	13	12	8	1

[1]Plantations 1 and 3, combined.

[2]Provenances combined by major morphological groups of Hamrick and Libby (1972).

DISCUSSION

Results indicated that Northern (Oregon) and Central (Northern California) provenances were susceptible to the fir engraver and its fungal symbiont in the Camino plantations, while Interior South (Arizona), and Interior North (Nevada, Utah) provenances were virtually nonsusceptible. Southern California provenances demonstrated low susceptibility. These patterns agree closely with known geographic patterns of morphological and chemical (cortical monoterpenes) variation in white fir over its natural range in western North America (Hamrick and Libby 1972, Zavarin *et al.* 1975). Susceptible provenances were those characterized as green-foliaged, with needle morphology suggesting only moderate drought resistance, and low in camphene and 3-carene, consisting of California white fir (var. *lowiana* (Gord.) Lemm.) from northern California and intermediates with grand fir, *A. grandis* (Doug.), from south-central Oregon. Provenances evidencing virtually no susceptibility were blue-green foliaged with needle morphology suggesting higher drought resistance, relatively high in camphene and 3-carene, and of the Rocky Mountain variety (var. *concolor* (Gord. & Glend.) Lindl.). Southern California provenances evidencing low susceptibility were characterized as blue-green foliaged, relatively high in 3-carene but nearly lacking in camphene and thus intermediate between the Northern and Interior South groups.

In all plantations, susceptibility was always highest in provenances nearest Camino. This was evident not only on a large scale in the geographic range plantations where Central (Northern California) provenances were the most susceptible, but also on a fine scale in the elevational transect plantations where provenances 40 km distant from Camino were more susceptible than those from 80 km distant. In loblolly pine plantations in South Carolina, Powers *et al.* (1992) also found that local provenances were more susceptible to southern pine beetle, *Dendroctonus frontalis*, than distant provenances.

Mechanisms responsible for the observed differential susceptibility among provenances are under investigation. Their basis, however, is undoubtedly primarily genetic as the plantations are all adjacent with provenances planted intermixed to minimize chances that microsite would differentially affect provenances.

The very low susceptibility of trees on the outside edges of the plantations compared with those in the interior was probably primarily determined by stand factors such as differences in soil moisture or beetle pheromone dispersal rather than tree genetics because susceptibility occurred without regard to provenance. Mechanisms underlying this difference are under investigation.

We have two studies underway testing the hypothesis that observed differential susceptibility is attributable to differential moisture stress among provenances, and between firs on plantation edge versus interior. White firs with highly negative water potentials (pre-dawn in August during summer dry, and fir engraver flight, seasons) are known to be susceptible to the fir engraver (Ferrell 1978). Results to date failed to find appreciable differences among provenances in 1989, 1990, or 1993. "Edge" firs did average higher moisture stress than "interior" firs in 1992 and 1993. Both studies will continue for one more post-drought year. Results are necessarily conditioned by the fact that moisture stress can be studied only in surviving firs. Thus, parallel studies are underway to compare radial growth patterns in surviving versus killed firs, under the hypothsis that differential moisture stress should be evident in radial growth pattterns.

Differences in fir engraver attack preference and success are being investigated by reciprocally caging "local" and "exotic" populations of beetles with bolts cut from "local" and "exotic" provenances of white fir. These tests are designed to reduce or eliminate differential resistance caused primarily by differences in environmental factors such as moisture stress and to isolate for analysis differential resistance caused by factors that are primarily genetically determined such as constitutive bark chemicals. Preliminary results indicate that beetles from the vicinity of Camino initiate far fewer attacks in Arizona bolts than in "local" bolts. No such preference was evident in tests with Nevada beetles caged with bolts of firs from Nevada and the vicinity of Camino. These tests are being repeated with beetles and bolts of other provenances. Parallel studies are also under way using various geographic isolates of the *Trichosporium* fungus inoculated into stems of surviving firs in the plantations. Among-provenance variations in inoculation wound size and monoterpene composition are being studied. Thus far consistent differences in virulence have been found between isolates regardless of provenance of the fungus or the fir. Studies continue to explore seasonal and yearly variations and to analyze monoterpene composition.

Results indicate that local populations of host conifers can be more susceptible to local populations of bark beetles and their fungal symbionts while exotic host populations can be less susceptible. If generally true, this phenomenon may have to be taken into account in tree improvement programs, most of which prefer to utilize local genetic material as planting stock because this material is preadapted to the growing site. If results at Camino are any indication, however, exotic seed sources may be less susceptible to local bark beetle populations provided that these trees are adequately adapted to the physiographic factors of the growing site. At Camino, many of the nonsusceptible exotic provenances had grown fully as tall as the best-growing local provenances, indicating that they were thus far as well adapted to the growing site.

Another important implication of the Camino results is that maintenance of genetic diversity in conifer populations may be an important safeguard in protecting conifer stands against bark beetles. The much greater mortality experienced in the elevational transect plantations containing only four provenances may be an expression of this, although it was evidently also influenced by the local origin of all four of these provenances.

Results from the geographic range plantations suggest that planting well-adapted exotic and local provenances in mixture may be a useful strategy for avoiding problems from bark beetles and their fungal symbionts. Any use of exotic provenances should probably be limited to high-value trees, particularly those grown on stressful sites, because more widespread planting could lead to loss of resistance through local pest populations becoming adapted to them.

SUMMARY

During a drought-associated fir engraver outbreak in California, local white fir provenances were more susceptible than exotic provenances, and, doubtless partly in consequence, less genetically diverse plantations were more susceptible than plantations with greater genetic diversity.

Mechanisms underlying the observed differential susceptibility remain unknown but are the subject of continuing investigations.

Results suggest that planting a mixture of well-adapted exotic, as well as local, provenances for maintenance of high genetic diversity may be an important strategy for protecting conifer hosts against bark beetles and their symbiotic fungi.

ACKNOWLEDGMENTS

We thank Dr. Tom Conkle and staff of the Pacific Southwest Research Station's Institute of Forest Genetics and Prof. Bill Libby of the cooperating University of California College of Environmental Science, Berkeley, for access to plantations and for encouragement.

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