Effects of Photochemical Oxidant Injury of Ponderosa and Jeffrey Pines on Susceptibility of Sapwood and Freshly Cut Stumps to *Fomes annosus*

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ABSTRACT

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Ponderosa and Jeffrey pine sapwood samples and freshly cut stumps from trees with different amounts of oxidant injury were inoculated with *Fomes annosus*. With stumps, percentage of surface cross-section area infected and extent of vertical colonization were determined 1 mo and 6–10 mo after inoculation, respectively. Increase in surface area infection with increased oxidant injury, expressed as upper-crown needle retention, was statistically significant for ponderosa pine ($P = 0.01$), but was not for Jeffrey pine. Also, the rate of vertical colonization was greater in stumps from severely oxidant-injured trees than in those from slightly injured trees. The relationship between injury and colonization was significant for Jeffrey pine ($P = 0.05$) and for ponderosa pine at one site ($P = 0.03$), but nonsignificant ($P = 0.18$) for ponderosa pine at a second site. Increased susceptibility of stumps to *F. annosus* appeared to be associated with decreased oleoresin exudation and decreased colonization by other fungi (especially *Trichoderma* spp. and blue stain fungi). Laboratory tests indicated that decay susceptibility of excised sapwood to *F. annosus* apparently was not affected by oxidant injury with Jeffrey pine, but weight loss of ponderosa pine sapwood was correlated with decreased injury (greater needle retention). On the other hand, weight losses of Jeffrey pine caused by *Polyporus versicolor* and of ponderosa pine caused by *Poria monticola* were correlated with increased injury (increased needle chlorosis).

Additional key words: root disease, air pollution, epidemiology, decay susceptibility.

Photochemical air pollutants cause chlorotic decline of ponderosa (*Pinus ponderosa* Laws.) and Jeffrey (*Pinus jeffreyi* Grev. and Balf.) pines in the San Bernardino Mountains of southern California (20). Severely affected trees are usually killed by biotic agents such as bark beetles (6) and possibly root pathogens such as *Fomes annosus* (Fr.) Cke.

Fomes annosus, an important root pathogen in California forests (3,10), is widely distributed throughout the state including parts of the San Bernardino Mountains. The pathogen usually colonizes freshly-cut stumps (11,24) and infects surrounding trees through root contacts and grafts. Thus, any influence of oxidant air pollution injury on susceptibility of freshly cut stumps or on the rate at which *F. annosus* colonizes stumps and roots could substantially affect disease epidemiology.

Wood decay is characteristic of *F. annosus* pathogenesis, and decay tests have been used to evaluate the susceptibility of host wood to the fungus (2,7,12). Hence, studies were designed to determine the effects of oxidant injury on the decay susceptibility of sapwood under laboratory conditions and on the susceptibility of freshly-cut stumps and stump colonization in the field.

MATERIALS AND METHODS

For both the decay and the stump susceptibility studies, ponderosa pine was selected at two sites, Barton Flats and Camp Paivika, and Jeffrey pine at one site, Amphitheatre. All sites were located in the San Bernardino Mountains at 1,800 to 1,900 m elevation, all were exposed to relatively moderate levels of photochemical oxidants (19), and the trees exhibited a wide range of oxidant injury. Trees for study were selected so that there were 10 dominant or codominant trees at each site in each of two categories: very severe to moderate injury and slight to no injury. A scoring system (18) which included both upper- and lower- crown needle retention, needle color, needle length, and branch mortality was used to rate the injury to each tree. Selected ponderosa pines averaged 20 cm in diameter at 1.5 m above ground and 9.6 m in height; Jeffrey pines averaged 23 cm diameter and 11.8 m high.

Sapwood decay study. Bole sections approximately 0.5 m in length were taken from each tree beginning about 40 cm above ground level (stump height). Wood samples were cut from sapwood adjacent to the cambium, and annual growth ring counts (number of rings per 2.5 cm) were taken. Procedures outlined by the American Society for Testing and Materials (1) were used to evaluate decay susceptibility. Wood was kiln dried about 14 days until weight equilibrium was reached. Test blocks of standard size ($2.5 \times 2.5 \times 0.9$ cm) were cut, the edges were smoothed with fine sandpaper, labeled with India ink, and conditioned at constant temperature (27 C) and relative humidity (70%) for 9 days. This conditioning brought test blocks to a constant, reproducible moisture content. Conditioned test blocks were weighed to the nearest 0.001 g, autoclaved for 15 min at 121 C, and placed in specially prepared soil bottles. Equal numbers of blocks were prepared from each tree. Soil bottles $12.5 \times 5.5 \times 5.5$ cm were prepared by placing within them 200 g of fine soil, enough distilled water to bring the soil moisture content up to the testing standard, and a thin (0.5 g) piece of alder sapwood (*Alnus* sp.) feeder strip upon the soil. Bottles were loosely capped, autoclaved at 121 C for 30 min and cooled. Feeder strips were inoculated with mycelium of the test fungus taken from 14-day-old cultures grown on potato dextrose agar. Bottles were placed in incubators until feeder strips were completely covered with mycelium. Sterile test blocks were then aseptically placed on feeder strips.

Three fungi were used in the ponderosa pine decay test: *F.*

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annosus (isolate SV); *Poria monticola* Murr., a standard brown-rot organism; and *Polyporus versicolor* (L.) Fr., a standard white-rot organism. The Jeffrey pine test included a second *F. annosus* isolate (JL) in addition to the three fungi above. Both *F. annosus* isolates were obtained from infected Jeffrey pine stumps in the San Bernardino Mountains. White fir reference blocks were included in each test to follow decay rate over the duration of the study. Reference blocks were analyzed for weight loss at weekly intervals starting at 9 wk. Maximum decay occurred just prior to 12 wk incubation. Controls consisted of ponderosa and Jeffrey pine test blocks in non-inoculated soil bottles. They provided a comparison of weight differences due to moisture content before and after each decay test.

Blocks were removed from soil bottles at completion of the test and carefully brushed to remove superficial mycelium. Blocks again were conditioned and weighed. Weight loss caused by decay was computed by subtracting the weight of the decayed block from its initial weight with adjustment for controls.

Initially, a full-screen regression analysis was performed which compared mean weight loss percent (dependent variable) to all possible linear combinations of independent variables to find the most reasonable, significant set of variables for further analysis. The independent variables were: study site and isolate, tree height, diameter, crown class, and eight components of the oxidant injury score. Regression analysis was then used to determine the coefficients for the best set of independent variables. When appropriate, an arcsine-square root conversion of percentage values was used to remove dependence of variances to means. Weight loss of decay blocks versus that of controls was compared with one-way analyses of variance.

Stump susceptibility. The trees at the Barton Flats, Amphitheatre, and Camp Paivika sites were cut and the stumps inoculated in September 1974, March 1975, and September 1975, respectively. Stumps approximately 40 cm high were inoculated with conidial suspensions of *F. annosus* within 24 hr after being cut. Conidia were harvested from 14-day-old cultures grown on potato dextrose agar slants by adding 5 ml of sterile water to each slant and removing spores with a fine, camel hair brush. Suspensions were then filtered through sterilized cheesecloth to remove large mycelial fragments. Spore concentrations were determined with a standard haemacytometer (Levy-Hausser counting chamber) and adjusted to about 40,000 conidia per milliliter. Each stump surface was uniformly inoculated with 5 ml of suspension (~ 200,000 conidia) by using a fine-mist atomizer. Samples of the spore suspensions were tested for viability, and all had approximately 90% germination after 24 hr. *Fomes annosus* isolate SV was used for inoculations at the Barton Flats and Amphitheatre sites, and isolate JL was used at Camp Paivika.

Approximately 1 mo after inoculation, a chain saw with bar and chain sprayed with 95% ethanol before each cut was used to remove a 3-cm-thick disk from the top of each stump. Sections were immediately wrapped in moist newspaper, placed in polyethylene bags, incubated for 7 – 10 days at room temperature (20–24 C) and examined with a dissecting microscope for characteristic *F. annosus* conidiophores. Portions of each section with conidiophores were outlined with a felt pen and percentage surface area colonized was determined by using a dot grid overlay. At the time of cutting, oleoresin exudation at the surface of each stump was visually classified as either light, moderate, or heavy.

Stumps were dissected to determine rate of vertical colonization 6 mo (Barton Flats and Amphitheatre) and 10 mo (Camp Paivika) after inoculation. At Barton Flats, stumps were cut off at ground level and split longitudinally into four sections. At Amphitheatre and Camp Paivika stumps were cut into several disks 3–5 cm thick successively from top to ground level. The chain saw blade and wedge were sprayed with 95% ethanol before each cut. Individual sections were wrapped in moistened newspaper and incubated in polyethylene bags for 7 – 10 days. The dot grid overlay system was used to estimate extent of colonization by *F. annosus* and associated fungi (*Trichoderma* spp. and the blue stain fungus) based on location of reproductive structures.

With the same set of independent variables that was used in the statistical analysis of sapwood decay, a full-screen analysis was made with percent surface colonization and colonization rate as dependent variables. Again, regressions were made to determine coefficients for the best set of independent variables.

RESULTS

Sapwood decay. All fungi caused significant weight losses ($P = 0.01$) compared to the uninoculated controls (Table 1). When the weight loss data was lumped into two overall oxidant score categories, there was only one significant difference between high and low injury categories, that for *P. monticola* on ponderosa pine. The full-screen analysis and regression provided more detailed analyses of oxidant injury by individual oxidant score components. One analysis showed a significant ($P = 0.016$) correlation ($r = 0.56$) between first-year needle condition (normal vs. chlorotic) in the lower crown and percent weight loss caused by *P. monticola* on ponderosa pine. Greater weight loss correlated with increased oxidant injury as indicated by needle chlorosis. For *P. versicolor* on Jeffrey pine a similar correlation with lower crown and first-year needle chlorosis was detected ($r = 0.51$). However, there were no variables significantly related to weight loss caused by *P. monticola* on Jeffrey pine and *P. versicolor* on ponderosa pine. Likewise, there were no significant relationships with two *F. annosus* isolates on Jeffrey pine. On the other hand, for the SV isolate on ponderosa pine higher percent weight loss showed a significant correlation ($r = 0.56$) with decreasing injury indicated by years of needle retention in the lower crown.

P. monticola caused about the same amount of decay of both Jeffrey and ponderosa pine sapwood, as did the SV isolate of *F. annosus,* but *P. versicolor* caused more decay of Jeffrey pine than of ponderosa pine. *Fomes annosus* SV isolate caused relatively little weight loss in either tree species, whereas isolate JL caused substantial weight loss in Jeffrey pine, the only species that was tested with that isolate.

Sapwood blocks from ponderosa pines with severe oxidant injury had an average of 19 growth rings per 2.5 cm versus 14 rings per 2.5 cm in trees with slight to no visible injury. Severely injured Jeffrey pines had an average of 23 rings per 2.5 cm versus 16 rings per 2.5 cm in less injured trees of that species.

Stump susceptibility. All inoculated stumps became infected with *F. annosus* (Table 2), but the levels of infection among "treatments" were different. The full-screen regression indicated that the most significant independent variables were site and needle retention in the upper crown (NRU), defined as the number of years of needle growth retained on the majority of branches. Tree size and all other components of the injury score were insignificant when NRU was included in the regression equation. Thus, the trees

TABLE 1. Decay caused by *Poria monticola, Polyporus versicolor,* and two isolates of *Fomes annosus* in Jeffrey and ponderosa pine sapwood from trees with different levels of oxidant injury

Species	Oxidant injury	Test blocks per fungus[a] (no.)	Avg. % weight loss (Decay)[b] F.a. SV	F.a. JL	P.m.	P.v.
Jeffrey pine	Very severe to moderate	50	1.1	27.0	64.3	56.9
	Slight to no injury	50	1.2	26.4	63.8	55.4
Ponderosa pine	Very severe to severe	45	1.3	···	67.7[c]	46.7
	Slight to very slight	45	2.1	···	66.0[c]	45.2

[a] Blocks taken from 10 Jeffrey pines and nine ponderosa pines in each injury category (five blocks per tree for each fungus).

[b] F.a. SV = *F. annosus* isolate SV; F.a. JL = *F. annosus* isolate JL; P.m. = *Poria monticola*, standard brown rot fungus; and P.v. = *Polyporus versicolor,* standard white rot fungus.

[c] The difference between these values is significant, $P = 0.01$. The levels of probability for all other comparisons were $> P = 0.05$.

were grouped on the basis of needle retention (Table 2) rather than the initial injury categories.

Stumps from trees with NRU $\leqslant$ 2 yr (severely injured) had about twice the surface area infected than did stumps from trees with NRU $\geqslant$ 3 yr (slight or no injury). Infection levels for Jeffrey pine at Amphitheatre and for ponderosa pine at Barton Flats both inoculated with the SV isolate, were similar. More than twice the surface infection occurred in ponderosa pine at Camp Paivika where the JL isolate was used.

Regression lines comparing NRU with percentage of surface area infected by *F. annosus* (Fig. 1) show that stump surface infection increased as the NRU for both ponderosa and Jeffrey pines decreased. This relationship was statistically significant for ponderosa pine at both sites (Barton Flats, $P = 0.007$ and Camp Paivika, $P = 0.001$). For Jeffrey pine at Amphitheatre, the regression was significant only at $P = 0.12$. The regressions for ponderosa pine at Barton Flats and Jeffrey pine did not show significant differences in slope or intercept. However, the regression for ponderosa pine at Camp Paivika was significantly greater than that for the other two sites in both slope and intercept.

Rate of vertical colonization by *F. annosus* was greater in stumps of trees severely injured by oxidants than in the stumps of trees with slight or no injury (Table 2). The rate in Jeffrey pine was about 49% greater in stumps of injured trees, while those in ponderosa pine at Camp Paivika and Barton Flats were about 23 and 17%, respectively. The mean colonization rate at Barton Flats was substantially less than at the other two sites, probably because the inoculation was in the fall as temperatures were about to drop and the apparently less virulent SV isolate was used.

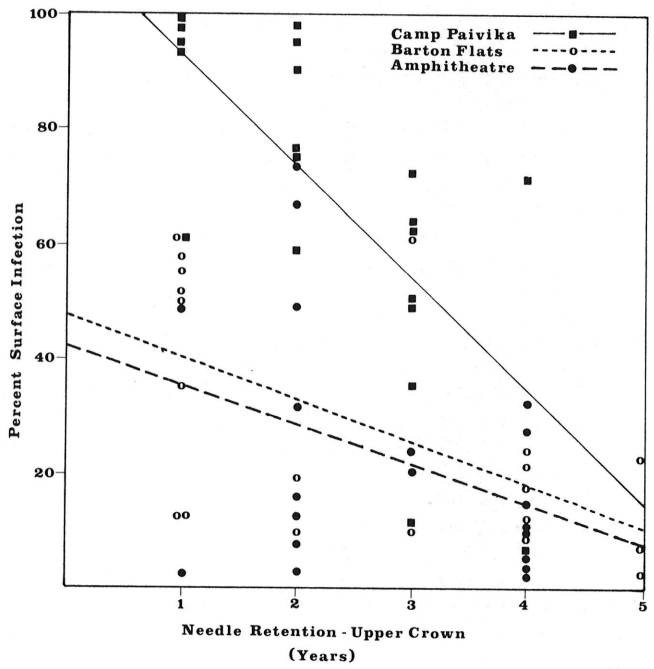

Fig. 1. Relationships between upper crown needle retention and percent surface infection of inoculated pine stumps by *Fomes annosus*. Data are for ponderosa pine at Camp Paivika and Barton Flats and Jeffrey pine at Amphitheatre in the San Bernardino Mountains of California. Stumps at Amphitheatre and Barton Flats were inoculated with isolate SV, and stumps at Camp Paivika were inoculated with isolate JL.

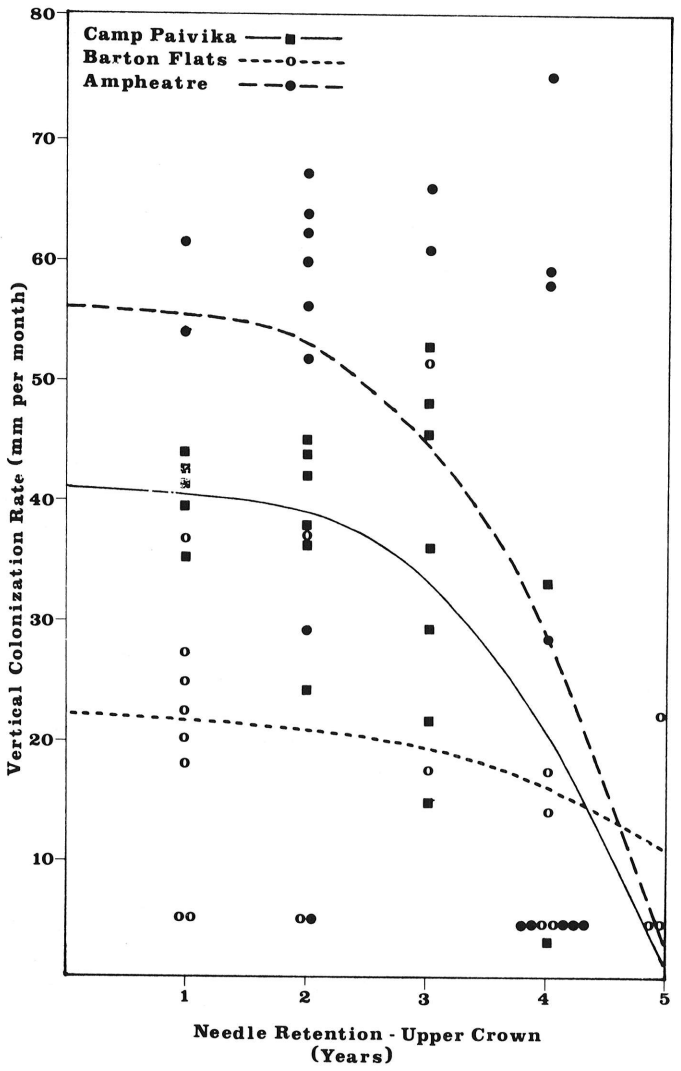

Fig. 2. Relationships between upper crown needle retention and vertical colonization rate of *Fomes annosus* in inoculated pine stumps. Data are for ponderosa pine at Camp Paivika and Barton Flats and Jeffrey pine at Amphitheatre in the San Bernardino Mountains of California. Stumps at Amphitheatre and Barton Flats were inoculated with isolate SV and stumps at Camp Paivika were inoculated with isolate JL.

TABLE 2. Percentage infection of stump surfaces by *Fomes annosus* and vertical colonization rate of inoculated ponderosa and Jeffrey pine stumps in the San Bernardino Mountains of southern California

Site and tree species	Inoculation (isolate/time)	Needle retention upper crown (yrs)	Stumps inoculated[a] (no.)	Surface infection[b] (mean %)	Mean vertical colonization rate[c] (mm/mo)
Amphitheatre (Jeffrey pine)	SV/Spring	1–2	10	31.8 ± 18.6	51.2 ± 13.6
		3–4	10	16.2 ± 7.6	34.4 ± 22.0
Barton Flats (ponderosa pine)	SV/Fall	1–2	10	36.8 ± 14.5	20.3 ± 8.7
		3–5	10	19.2 ± 11.6	17.4 ± 11.6
Camp Paivika (ponderosa pine)	JL/Fall	1–2	11	85.6 ± 10.2	39.2 ± 3.8
		3–4	9	47.2 ± 17.9	31.9 ± 12.5

[a] All inoculated stumps became infected.
[b] Measured 1 mo after inoculation. Range indicates confidence interval, $P = 0.05$.
[c] Measured 6 mo after inoculation at Amphitheatre and Barton Flats and 10 mo after inoculation at Camp Paivika. Range indicates confidence interval, $P = 0.05$.

Regression analyses indicated that vertical colonization rate (VCR) was inversely related to the cube of upper crown needle retention, NRU^3, a nonlinear relationship (Fig. 2). The relationship ($VCR = 22.5 - 0.930\ NRU^3$) was not statistically significant ($P = 0.18$) for ponderosa pine at Barton Flat, apparently because of the lower VCR and greater variability. However, the relationships for ponderosa pine at Camp Paivika ($VCR = 41.8 - 0.316\ NRU^3$) and for Jeffrey pine ($VCR = 56.5 - 0.435\ NRU^3$) were significant ($P = 0.03$ and 0.05, respectively). The regressions indicate a sharply lower rate of colonization in stumps of trees with slight or no oxidant injury than in those of more severely injured trees.

Both stump surface oleoresin exudation and colonization by *Trichoderma* spp. and the blue stain fungi were less in trees with low needle retention than in those with 3- to 5-year needle retention (Table 3). Oleoresin exudation was recorded 1 mo after the trees were cut and colonization by other fungi was recorded after 6 – 10 mo.

DISCUSSION

Susceptibility of ponderosa and Jeffrey pine sapwood to decay by *Poria monticola* and *Polyporus versicolor* apparently was unaffected by prior oxidant injury in two of four cases studied. In the other two cases, *P. monticola* on ponderosa pine and *P. versicolor* on Jeffrey pine, weight loss was correlated with increasing oxidant injury (increasing needle chlorosis), but the analyses explained only 26 – 31% of total variation in weight loss. Since the differences were small, we must conclude that such increases in decay susceptibility, if indeed real, would have no practical impact.

Prior injury appeared to have no effect upon susceptibility of sapwood of Jeffrey pine to decay by two isolates of *Fomes annosus*. However, for one of the isolates on ponderosa pine, weight loss percentage was correlated with decreasing oxidant injury (higher needle retention); again, only 31% of the variation was explained in the analysis. The low, explained variation for this case and the lack of apparent effects for the two isolates on Jeffrey pine may be due to the nature of soil-block decay tests which preclude study of live host tissue. Wood samples were removed from trees and treated so that host defense mechanisms, such as resin exudation, were not involved in decay resistance. The major determinant of wood decay susceptibility was probably the nutritional value of wood. If a wood is a good nutritive substrate, more decay usually will occur (22). Wood extracted from trees severely injured by air pollutants apparently provided as good a substrate for *F. annosus* as did wood from trees with slight or no damage. Nor did growth rate of the tree appear to influence sapwood decay by *F. annosus*; there were substantially more annual growth rings per 2.5 cm in trees with severe injury than in trees with slight or no injury.

When freshly-cut stumps of living pines were inoculated with *F. annosus*, differences in both the amount of stump surface infection and the rate of vertical colonization of sapwood were observed. Surface infection was about 100% greater and colonization was up to 50% greater in stumps from severely injured trees than in those of trees with little or no injury. Hence, there is a substantial increase in stump susceptibility with increased oxidant injury that appears to be due to effects upon the living host rather than upon nutritive value of the sapwood substrate.

Investigation of the mechanisms by which susceptibility was increased was not included in the current study. However, resinosis and oleoresin exudation are considered to be resistance mechanisms in pine (26), and in earlier studies, Cobb et al (8) reported less oleoresin yields from oxidant-injured trees. Our results show that oleoresin exudation on the freshly cut stump surface is less in trees with severe oxidant injury. Thus, there may be less barrier to initial infection by *F. annosus*.

Colonization of stump sapwood of severely injured trees by hyperparasites and competitors of *F. annosus,* specifically *Trichoderma* spp. and blue stain fungi, also was less in injured trees. Whether the lesser colonization was caused by increased initial infection and subsequent exclusion of other fungi by *F. annosus*, or the greater colonization of stumps of less severely injured trees resulted in exclusion of *F. annosus* is unclear. Barriers to initial infection may have greater effects than later colonization by competitors, but the two factors probably interact and influence *F. annosus* root rot epidemiology.

Differences between *F. annosus* isolates and SV and JL were detected both in the laboratory decay study and in the field study. Isolate SV caused relatively little weight loss of sapwood samples during the 12-wk test, whereas isolate JL caused greater weight loss than that reported in other studies of *F. annosus* on pines (2,7,23). Such variability has been reported (7,16,21,23, and others). However, in this study, differences in isolates also are supported by the results of stump inoculations in which both infection and colonization by JL were substantially greater than those by SV. In another study (15) in which tree roots were inoculated, isolate JL apparently was more virulent than was isolate SV. These differences also were confirmed in a seedling inoculation study (14) under controlled conditions.

Infection and colonization of freshly-cut stumps and their roots is a crucial phase in the epidemiology of root rot caused by *F. annosus* in pine stands. Subsequent spread of *F. annosus* to nearby trees has been correlated with stump surface infection (17), and evidence (4,13,25,27) indicates that the fungus tends to colonize the sapwood in somewhat restricted, vertical columns. Thus, an increase in horizontal distribution of the fungus within stump sapwood, associated with oxidant injury, increases the probability that roots will become colonized and that spread to adjacent trees will occur. Also, by increasing the rate of colonization, oxidant injury reduces the generation time for *F. annosus*. Over the rotation period of a forest stand (approximately 50 yr), these changes could lead to dramatic increases in annosus root rot.

Furthermore, *F. annosus* may have little chance to become established in some forest stands without oxidant injury or other debilitating factor. The data indicate a sharp decrease in colonization rate at two of the sites in trees with needle retention ≥ 3 years. If all trees on these sites were in optimum condition (ie, with 4 to 5-yr needle retention), the hazard of live-tree infection by *F. annosus* would probably be quite low.

That all inoculated stumps in this study became infected may, in itself, be significant. Reports of other studies (5,9,10,24) with similar inoculation procedures show infection levels of 60-95%. Thus, the general level of stump susceptibility in those areas of the San Bernardino Mountains where the plots were located may be

TABLE 3. Pine stump surface oleoresin exudation and percent stump colonization by *Trichoderma* spp. and blue stain fungi in the San Bernardino Mountains of southern California

Site	Needle retention in upper crown (yr)	Mean oleoresin exudation[a]	Colonization by *Trichoderma* spp.[b] (mean %)	Colonization by blue stain fungi[b] (mean %)
Amphitheatre	1–2	1.8	5.3	18.2
	3–4	2.9	25.2	20.3
Barton Flats	1–2	1.4	7.1	9.5
	3–5	2.9	9.6	20.1
Camp Paivika	1–2	1.3	2.9	2.7
	3–4	2.6	8.0	11.5

[a] Ratings of oleoresin exudation on the stump surface were light = 1, moderate = 2, or heavy = 3.
[b] Measured 6 mo (Amphitheatre and Barton Flats) or 10 mo (Camp Paivika) after inoculation.

unusually high. Whether this apparent difference is real and whether it is due to oxidant air pollution exposure or to other factors should be determined by further study.

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