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Decay Fungi and Wounding in Advance Grand and White Fir Regeneration

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ABSTRACT. A total of 464 living white and grand fir tree stems in 24 stands in Oregon and Washington were dissected to detect infections of hymenomycetes (decay fungi) and other microorganisms in woody tissue. Of 21.249 attempted isolations from dissected trunks, 43.2% yielded bacteria or yeasts. 38.6% were sterile. 11% were nonhymenomycetes. 3.1% were hymenomycetes, and 4.1% were contaminated or mixed cultures. Hymenomycetes most frequently isolated were *Echinodontium tinctorium* and *Heterobasidion annosum,* both of which caused the most discoloration and decay. Nearly 20%. of all hymenomycetous isolations. particularly *Hericium abietis* and *E. tinctorium,* were from clear tissue not associated with discolored or decayed wood.

More than 300 trunk wounds on 248 dissected trees were classified by size, location, age, and hymenomycetous associations. At least 45% of all trees with wounds had hy - menomycetes present. of which *E. tinctorium* and *Pholiota limonella* were isolated most frequently. Discoloration caused by *E. tinctorium* was associated with wounds as recent as a year or as small as 56 cm^2. All *E. tinctorium* infections that caused discoloration or decay were within 30 cm of a wound, whereas all infections within clear tissue were beyond 30 cm. These data support a hypothesis that *E. tinctorium* enters hosts via minute branchlet stubs, becomes dormant after the branchlet stubs occlude, and is activated by wounds in the vicinity of dormant infections. FOR. SCI. 33(2):347-355.

ADDITIONAL KEY WORDS. ***Echinodontium tinctorium, Abies concolor, Abies grandis.***

WHITE FIR *(Abies concolor* [Gord. & Glend.] Hildebr.) and grand fir *(A. grandis* [Dougl.:Don] Lindl.) are major species in many forests of the western United States. These species are favored for timber management in many areas because of their wide ecological amplitude, excellent growth potential, and ease of natural regeneration. Losses from decay caused by hymenomycetous fungi, however, often are very severe in grand fir (Aho 1977, Hobbs and Partridge 1979) and white fir (Kimmey and Bynum 1961, Aho and Simonski 1975, Aho et al. 1983). Most decay in mature stands has been attributed to .*Echinodontium tinctorium* (Ell. et Ev.), the Indian paint fungus. *Heterobasidion annosum* (Fr.) Bref., *Pholiota limonella* (Pk.) Sacc., *Hericium abietis* (Weir: Huber) K. Harrison, and *Stereum sanguinolentum* (Alb. et Schw.:Fr.) Fr. more commonly are associated with decay in younger firs (Maloy and Gross 1963, Aho 1977, Filip et al. 1983).

Etheridge and Craig (1976) demonstrated that basidiospores of *E. tinctorium* infect western hemlock *(Tsuga heterophylla* [Raf.] Sarg.) primarily

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through recently formed and shade-killed branchlet stubs (1 mm diam.). After spore germination and mycelial development within the branch, *E. tinctorium* growth continues until branchlet stubs are overgrown. When branchlet stubs occlude, *E. tinctorium* forms chlamydospores that can remain dormant for 50 years or more without causing decay. Dormant fungi are activated by mechanical injuries, frost cracks, or formation of large branch stubs that allow air to enter near dormant fungi. A similar mode of infection and decay initiation by *E. tinctorium is* postulated for white fir or grand fir (Hudson 1972, Aho 1977, Aho and Hutchins 1977, Aho and Filip 1982). Parallel mechanisms for other hymenomycetes have not been reported except for *Phellinus pini* (Brot.:Fr.) A. Ames in eastern white pine *(Pinus strobus* L.) (Haddow 1938). In this paper we (1) report on the incidence of hymenomycetes and other microorganisms in living white and grand fir stems and (2) test the hypothesis that *E. tinctorium* (and possibly other hymenomycetes) enters hosts via minute branchlet stubs, becomes dormant after the branchlet stubs occlude, and is activated by wounds in the vicinity of dormant infections in white and grand fir.

Methods

In 1979, 24 stands on 8 National Forests in Oregon and Washington east of the Cascade Range were sampled. Stands that had previous thinning or harvest entries were selected to ensure that advance regeneration would have wounds of various ages. Only stands with advance regeneration dominated by white or grand fir were examined. No attempt was made to separate data on white fir from data on grand fir because these species are similar and often hybridize where their ranges overlap (Fowells 1965). Three or four parallel transects, 60 to 100 m apart, were used to sample each stand. One potential crop tree, distinguished by superior height and form but not necessarily absence of wounds, was selected nearest sample points located every 100 m along transects. Only potential crop trees were sampled because it was assumed that noncrop trees would be destroyed during stand improvement.

A total of 464 trees averaging 15.0 cm (range 9.1-19.8) in dbh, 77 years (range 43- 115) of age, and 9.4 m (range 1.8-23.9) in height were sampled as follows: Twenty trees were examined in each stand except for one stand where only four trees were sampled. Diameter at 1.4 m above the ground (dbh) and cause (mechanical, fire, animal, or insect) and condition (open or closed) of stem wounds were recorded for each tree. Each tree was then cut at the groundline. total and merchantable height were measured, and tree age was determined by counting annual rings with a dissecting microscope. The cubic volume of each tree greater than 10-cm dbh and of discoloration and decay was determined by the Smalian formula. Volumes were calculated to a 10-cm (merchantable) top. Each tree was dissected into 15- to 30-cm-long bolts to just above the lowest whorl of live branches. Branches and tops were not sampled. All bolts were labeled, placed in plastic bags, taken to the laboratory, and refrigerated at 2°C before further sampling within one week.

A total of 21,249 isolations from 464 trees were attempted as follows: Each bolt was split longitudinally with a flamed chisel to expose wounds and stem and twig piths (occluded branch stubs). Height to base from groundline, size (length × width × 0.75—to compensate for elliptical wound shape), and age were noted for each wound. Six wood chips (5 ×5 × 15 mm) were removed aseptically from each freshly exposed section and

placed in culture tubes containing 2% malt agar. Isolations were attempted from stem and twig piths, heartwood, sapwood, wetwood, ingrown tissue. fir engraver *(Scolytus ventralis* LeConte) galleries, discolored wood, and decayed wood. The location of each isolation in relation to any wounds was recorded. After cultures were incubated for 6 weeks at room temperature, the incidence of bacteria or yeasts, nonhymenomycetes. and hymenomycetes was recorded. Genus and species of hymenomycetes were identified when possible by colony morphology and growth on selective media.

Analysis of variance was used to detect significant differences in wound age, size, or distance from the ground with respect to (1) presence or absence of hymenomycetes and (2) species of hymenomycetes.

Results

General Hymenomycete Frequencies

Because the relation between tree diameter, age, height, and other stand and site characteristics and the incidence of infection and decay were reported earlier (Filip et al. 1983), only the results pertaining to wounds and recovery of hymenomycetes and other microorganisms are reported here. Of 21,249 isolations attempted (mean of 46/tree), 43.2% yielded bacteria or yeasts, 38.6% were sterile, 11.0% yielded nonhymenomycetes, 3.1% yielded hymenomycetes, and 4.1% yielded either mixed cultures or contaminants. More than half (53.2%) of the trees sampled had at least one species of hymenomycetes present.

Of 655 hymenomycetous fungi isolated from 247 of 464 trees. *E. tinctorium* was recovered most frequently, followed by *H. annosum,* and *P. limonella* (Table 1). No *E. tinctoriun* sporophores occurred in trees yielding isolates of this fungus. Other hymenomycetes accounted for 43.6% of the isolations, most of which were unidentified but did include *H. abietis, S. sanguinolentum, Perenniporia subacida* (Pk.) Donk, *Amylostereum chail-*

TABLE 1. Frequency of hymenomycete species from 655 of 21,249 isolation attempts from 247 of 464 white or grand fir trees.

Hymenomycete species	Percentage of isolations yielding hymenomycetes[a]	Percentage of total decay[b]	Percentage of wounds with hymenomycetes
Echinodontium tinctorium	36.6 (83)	21.5 (46)	30.1 (71)
Heterobasidion annosum	14.2 (29)	21.5 (17)	5.8 (21)
Pholiota limonella	5.0 (42)	10.8 (21)	12.8 (33)
Stereum sanguinolentum	2.9 (13)	1.1 (4)	0
Hericium abietis	2.7 (29)	1.1 (4)	2.6 (17)
Perenniporia subacida	3.2 (4)	4.3 (4)	0
Amylostereum chailletii	0.9 (4)	1.1 (4)	1.9 (4)
Phlebia rufa	0.2 (4)	0	0
Poria tsugina	0.2 (4)	0	0
Mixtures	0.8 (4)	14.0 (21)	7.1 (21)
Unidentified	33.3 (21)	24.7 (58)	39.7 (67)
Total	100.0	100.0	100.0

[a] Number in parentheses is percentage of stands with that species either present, causing decay, or associated with wounds.

[b] Percentage of total decay volume (0.26 m^3) caused by fungi identified as hymenomycetes.

letii (Pers. :Fr.) Boid., *Poria tsugina* (Murr.) Sacc. et Trott., and *Phlebia rufa* (Pers.:Fr.) M. P. Chris.

Hymenomycetes Causing Decay

Discoloration and decay accounted for 0.98 m^3 or 2.2% of the total merchantable stand volume. Hymenomycetes causing 0.26 m^3 of this decay volume were identified. Most (53.8%) was caused by *E. tinctorium, H. annosum,* and *P. limonella* (Table 1). Mixtures of two or more hymenomycetes were isolated from 14.0% of the decay volume. Common mixtures included *E. tinctorium-H. abietis, E. tinctorium-P. limonella,* and *H. abietis-P. limonella.*

Hymenomycetes in Wounded Trees

A total of 334 external wounds on 248 trees were classified and dissected. Wounds averaged 576 cm^2 (range 7-5936) in size and 16.9 years (range 0-108) in age. Most wounds were mechanically caused, completely closed, and located below dbh but not in contact with the soil. At least 45% of all trees with wounds had hymenomycetes present. Hymenomycetes most frequently recovered from wounded trees were *E. tinctorium, P. limonella,* and *H. annosum* (Table 1). Mixtures of two or more hymenomycetes frequently were isolated from wounded trees and included *E, tinctorium-H. abietis, E. tinctorium-S. sanguinolentum,* and *H. abietis-P. limonella.* Nearly 40% of the wounds were associated with hymenomycetes that could not be identified. Presence or species of hymenomycetes were not related ($P = 0.05$) to wound age, size, or distance from the ground (Table 2).

Hymenomycetes by Tissue Type

Most of the isolation attempts (43.4%) were from clear stem piths, and the fewest (1.0%) were from advanced decay (Table 3). These percentages reflect the relative presence of tissue types; clear stem piths and wetwood were most common, ingrown tissue and advanced decay were least common. The greatest number of hymenomycetous isolations were from clear stem piths. This tissue was sampled more frequently, however. so numbers are disproportionately high. On a percentage basis. more hymeno-

TABLE 2. Frequency of hymenomycetes by wound age, size, and height above ground for white or grand fir trees in 24 stands.

Hymenomycete species	Wound age (yr)			Wound size (cm^2)			Wound height (m)		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Echinodontium tinctorium	16.1a[a]	10.5	17	908.2a	1020.0	17	1.3a	1.7	17
Heterobasidion annosum	15.0a	1.8	4	1179.8a	1580.9	4	1.7a	2.4	4
Hericium abietis	23.8a	18.0	6	752.5a	861.7	4	0.2a	0.2	6
Pholiota limonella	12.8a	6.1	6	1008.9a	766.1	7	0.5a	0.3	7
Any hymenomycete	15.5a	7.3	24	935.3a	775.8	24	1.3a	0.8	23
No hymenomycete	17.6a	6.8	23	629.7a	548.5	23	1.3a	1.2	23

[a] Means followed by the same letter are not significantly ($P = 0.05$) different according to analysis of variance. Means are the average for each stand (i.e., $n = 17$ stands).

TABLE 3. Number of hymenomycetes from 464 living white and grand firs, by sources.

Hymenomycete species	Trees (no.)	Total isolations	Source of isolates							
			Clear wood							
			Stem pith	Twig pith	Other wood	Wet wood	Ingrown tissue	Fir engraver	Incipient decay	Advanced decay
			no. of isolates							
Echinodontium tinctorium	87	240	112	13	13	24	9	3	45	21
Heterobasidion annosum	11	93	10	4	3	3	5	1	34	33
Pholiota limonella	17	33	10	2	2	2	4	2	9	2
Stereum sanguinolentum	6	19	3	0	1	1	0	0	11	3
Hericium abietis	11	18	10	2	0	3	0	0	2	1
Perenniporia subacida	1	21	2	1	0	2	0	1	15	0
Amylostereum chailletii	2	6	1	0	3	0	0	0	2	0
Phlebia rufa	1	1	0	0	1	0	0	0	0	0
Poria tsugina	1	1	1	0	0	0	0	0	0	0
Mixtures	5	5	3	0	0	1	0	0	1	0
Unidentified	105	218	108	8	29	38	5	5	22	3
No hymenomycetes	217	20594	8955	1278	2209	4466	601	674	2257	154
Total	464	21249	9215	1308	2259	4540	624	686	2398	217
Percent of tissue type		100.0	43.4	6.2	10.6	21.4	2.9	3.2	11.3	1.0
Percent with hymenomycetes		3.1	2.8	2.3	2.3	1.6	3.7	1.7	5.9	29.0

mycetes were isolated from advanced decay and incipient decay than from other tissue types.

Many isolations of hymenomycetes were from clear tissue; however, some of this tissue was adjacent to discolored or decayed wood that may have been an active margin of infection. More than 19% of all hymenomycetous isolations were farther than 90 cm from discolored or decayed tissue (Table 4). A high proportion of isolations of *H. abietis* and *E. tinctorium* were farther than 90 cm from discolored or decayed tissue, whereas most (97.8%) of the *H. annosum* isolations were either from visibly altered tissue or within 90 cm of discoloration or decay.

External Wound Characteristics

From 14 trees with external wounds, 20 of 644 isolates were *E. tinctorium* from clear wood that was located 90 cm (range 90-900) beyond discolored or decayed wood. Associated wounds averaged 323 cm^2 (range 21-1724) in size, 19.1 years (range 0-161) of age, and were located 2.2 m (range 0-8.6) from the *E. tinctorium* isolations (Figure 1). All wounds within 30 cm of *E. tinctorium* isolations from clear tissue were less than 1 year old.

From another 16 trees with external wounds, 16 of 736 isolations were of *E. tinctorium* from discolored or decayed tissue. Associated wounds averaged 1567 cm^2 (range 56-7525) in size, 16.1 years (range 1–61) in age, and were located 0.8 m (range 0-4.5) from the *E. tinctorium* isolations. All *E. tinctorium* isolations from discolored or decayed tissue farther than 30 cm from a wound actually were within 30 cm of a column of advanced and unidentified decay that was within 30 cm of a wound. Most wounds associated with discoloration or decay were mechanically caused and located below 1.4 m but not in contact with the soil. Almost half of these wounds had closed completely.

Infections of other hymenomycetes, *H. abietis, S. sanguinolentum, P. subacida, P. limonella,* and *A. chailletii,* that caused discoloration or decay were all within 2 cm of external wounds or columns of decay. Infections of

TABLE 4. Frequency by source of hymenomycetes isolated from 137 living white or grand fir trees.

Hymenomycete species	Isolations (no.)	Source of isolates		
		Discolored or decayed wood[a]	Clear wood	
			Within 90 cm[b]	Beyond 90 cm[c]
		..... % of isolations		
Echinodontium tinctorium	240	27.9 (42)	44.6 (63)	27.5 (79)
Heterobasidion annosum	93	72.0 (21)	25.8 (17)	2.2 (4)
Pholiota limonella	33	36.4 (17)	48.4 (29)	15.2 (17)
Stereum sanguinolentum	19	73.7 (4)	15.8 (4)	10.5 (8)
Hericium abietis	18	5.6 (4)	44.4 (21)	50.0 (17)
Perenniporia subacida	21	81.0 (4)	19.0 (4)	0
Amylostereum chailletii	6	50.0 (4)	50.0 (4)	0
Poria tsugina	1	0	100.0 (4)	0
Phlebia rufa	1	0	0	100.0 (4)
Total or average	432	41.8	38.6	19.6

[a] Number in parentheses is percentage of stands with that infection type (i.e., 42% of the sampled stands had active infections of *E. tinctorium*).

[b] Isolates obtained from clear tissue within 90 cm of discolored or decayed wood.

[c] Isolates obtained from clear tissue farther than 90 cm from discolored or decayed wood.

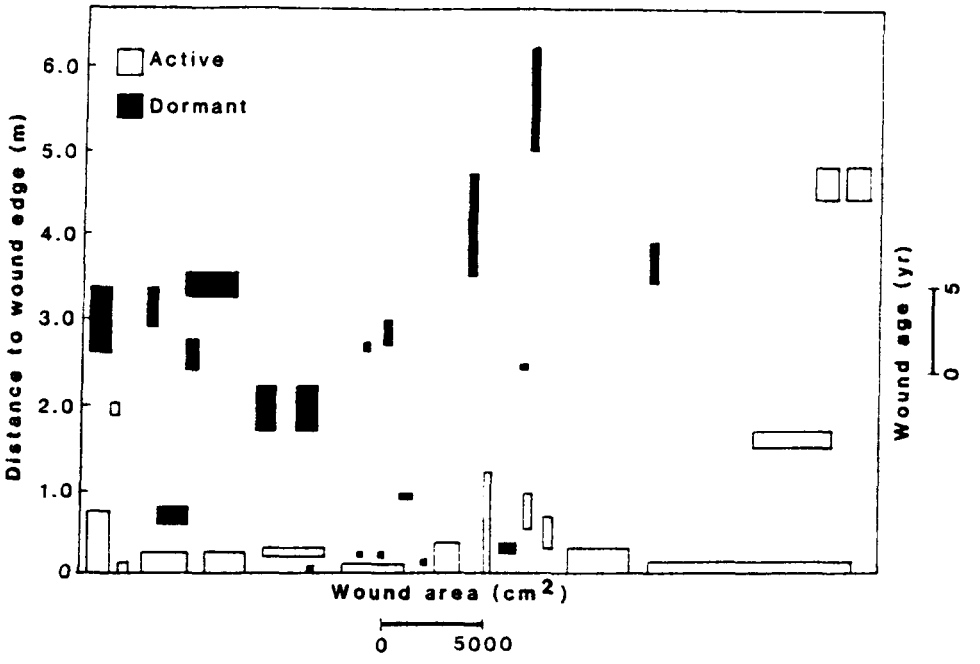

FIGURE 1. Wound area, wound age, and distance to wound edge for 35 infections of *Echinodontium tinctorium* classified as either (1) active from discolored or decayed tissue or (2) apparently dormant from clear tissue beyond 90 cm of discolored or decayed tissue.

H. annosum that caused discoloration or decay were within 2 cm of wounds in four trees, but in three trees active infections were not associated with any external wound. In all cases, however, these decay columns originated from the root collar, which suggested that infection was through the root systems. External wounds associated with infections of hymenomycetes other than *E. tinctorium* in clear wood averaged 314 cm^2 (range 42-1722) in size, 30.5 years (range 5-48) in age, and were located 1.8 m (range 0.5-3.9) from isolations.

INTERNAL WOUND CHARACTERISTICS

A total of 603 internal wounds on 234 trees were discovered after the trees were dissected. Most of these wounds were very small (2-5 cm long), apparently caused by fir engraver beetles, and associated with little or no discoloration. Twenty-four trees without external wounds had 45 infections of *E. tinctorium* in clear wood; 8 of these trees had minute wounds that had become encased in wood and were within 30 cm of the infections. Many of the wounds appeared to be caused by fir engravers. Either these wounds were too small to activate fungi or they were created before infection. Seven trees had *E. tinctorium* infections in visibly altered wood that was not associated with an external wound. After the trees were dissected, however, buried wounds adjacent to discolored or decayed tissue were found in two trees. Two other trees had extensive decay columns that may have obscured possible buried wounds. Three trees had no apparent injury associated with small but active *E. tinctorium* infections.

Discussion

Most isolation attempts from stems of live grand and white firs yielded bacteria, yeasts, or nothing, as reported by others (Hudson 1972. Aho 1976,

Aho and Hutchins 1977). Some bacteria associated with decay in living trees fix nitrogen (Aho et al. 1979b) or utilize calcium oxalate produced by hymenomycetes such as *E. tinctorium* (Aho et al. 1979a). Some of our isolations yielded nonhymenomycetes which, with bacteria and yeasts, may precede hymenomycetes in wounded tissue (Shigo 1967, Hudson 1972) or inhibit infection by hymenomycetes (Etheridge 1968, Hudson 1972. Etheridge and Craig 1976).

E. tinctorium was isolated most frequently in our study as was noted by others (Hudson 1972, Aho 1977, Aho and Filip 1982). Although *E. tinctorium* occurred in more than 20% of the 464 trees sampled. this percentage probably is conservative because branches that likely contained the fungus were not sampled. Other hymenomycetes *(H. annosum, H. abietis, P. limonella, S. sanguinolentum,* and *P. subacida)* were recovered occasionally as reported by others (Maloy 1968, Hudson 1972, Chacko and Partridge 1976, Aho 1977, Hobbs and Partridge 1979, Aho and Filip 1982). Mixtures of *E. tinctorium-S. sanguinolentum, E. tinctorium-H. abietis, E. tinctorium-P. limonella,* and *H. abietis-P. limonella* were isolated from firs in our study as they were in studies by Hudson (1972) in Washington and Aho (1977) in Oregon. Mixed infections by two or more hymenomycetes have caused more decay than have single infections, which may explain how extensive decay columns develop so rapidly in grand fir and white fir (Aho 1976, 1977).

Nearly 20% of all hymenomycetous isolations were from clear tissue farther than 90 cm from discolored or decayed wood. Boyce (1961) states that with *E. tinctorium* "wood from one to several feet in advance of discoloration is invaded by hyphae." Presumably, isolations from clear wood beyond 90 cm would be from apparently dormant infections. *H. abietis* was isolated in high frequency from clear wood. The possibility that infections of *E. tinctorium* and *H. abietis* are recent and have not had time to cause decay is unlikely because associated wounds were very old, and many had healed completely. Also, most isolations were from trunk-encased twig and stem piths that had occluded decades before. In addition to *E. tinctorium, P. pini, H. annosum, P. rufa, Fomitopsis pinicola* (Swartz:Fr.) Karst., *Ganoderma applanatum* (Pers.) Pat., and *Coriolus versicolor* (L.:Fr.) Quel. also have been reportedly isolated from clear tissue (Haddow 1938, Etheridge and Craig 1977, Aho and Hutchins 1977).

H. abietis has been classified as a wound-invading hymenomycete (Boyce 1961), but it may infect through branchlet stubs as well and become activated by wounds in a way similar to that reported by Etheridge and Craig (1976) for *E. tinctorium.* In a study of Pacific silver fir *(A. amabilis* Dougl.:Forbes) in western Washington. *H. abietis* was not associated with external wounds, which suggests that infection courts other than mechanical wounds were present (Filip and others 1984). *H. abietis* has been isolated from branches (Aho and Filip 1982). and the high frequency of infections not associated with discoloration or decay in our study suggests that infection mechanisms may be similar to those of *E. tinctorium.*

Our study also strengthens the argument that *E. tinctorium* infects grand and white firs through shade-killed branchlet stubs and that dormant fungi are activated by injuries. Wound age apparently is not as important as other wound attributes because both active and dormant infections were associated with wounds of any age. Wounds as small as 56 cm^2 and as recent as a year apparently can activate dormant *E. tinctorium,* provided they are within 30 cm of such injuries (Figure 1). Larger and deeper trunk wounds

probably would have a greater likelihood of activating dormant fungi because they would be more likely to affect chlamydospores.

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