

Effects of a native forest pathogen, *Phellinus weirii*, on Douglas-fir forest composition in western Oregon

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The fungal pathogen *Phellinus weirii* (Murrill) Gilbertson (Family: Hymenochaetaceae) causes extensive rot in the roots and bole of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and true firs, eventually leading to tree mortality. The native pathogen spreads slowly via root grafts and root contacts between conifers, leaving behind areas of tree mortality commonly called infection centers. This study determines (i) whether the slow, systematic removal of the Douglas-fir overstory by *P. weirii* changes the community composition of old-growth and mature forests, (ii) if composition is significantly affected, to what degree *P. weirii* influences the composition, (iii) what effects the disease has on individual populations, and (iv) whether vascular plant diversity is affected by disease presence. The herb, shrub, and tree strata were randomly sampled within and adjacent to six *P. weirii* infection centers located in the low-elevation Cascade and Coast ranges of western Oregon. Statistically significant ($P \leq 0.05$) differences in species composition between infected and adjacent noninfected forest were found across all sites. Ordination techniques showed that the distance of vegetation to the infection center edge was a major factor underlying the forest community's structure. The average cover of all herbaceous species was higher inside infection centers as compared with outside, for all locations, though statistically significant at only two sites. In general, species differed in their responses to disease presence. Changes in diversity due to the presence of the root rot were statistically significant in three of the six cases ($P \leq 0.05$) but the patterns of change differed from site to site. The removal of Douglas-fir overstory has strong effects on the plant community, but the specific patterns depend on the species and site involved.

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Le champignon pathogène *Phellinus weirii* (Murrill) Gilbertson (Famille : Hymenochaetaceae) cause une carie de racines et de tronc chez le sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et les vrais sapins qui entraîne éventuellement la mort des arbres. C'est un champignon pathogène indigène qui s'étend lentement via les greffes de racines et les contacts entre les racines des conifères, provoquant des zones de mortalité appelées centres d'infection. Cette étude vise à déterminer (i) si l'élimination lente et systématique de l'étage dominant de sapin de Douglas par *P. weirii* change la composition des vieilles forêts et des forêts matures, (ii) dans quelle mesure *P. weirii* influence la composition dans le cas où celle-ci est significativement affectée, (iii) quels sont les effets de la maladie sur les populations individuelles et (iv) si la diversité des plantes vasculaires est affectée par la présence de la maladie. Les strates herbacée, arbustive et arborescente ont été échantillonnées aléatoirement à l'intérieur et à proximité de six centres d'infection de *P. weirii* situés à basse altitude dans les Cascades et les montagnes côtières de l'ouest de l'Oregon. La composition en espèces différait significativement ($P \leq 0,05$) entre la forêt infectée et la forêt adjacente non infectée pour l'ensemble des sites. Les techniques d'ordination ont montré que la distance de la végétation de la marge du centre d'infection était le principal facteur contrôlant la structure de la communauté forestière. La couverture moyenne de toutes les espèces herbacées était plus élevée dans les centres d'infection qu'à l'extérieur, pour tous les endroits, même si la différence était statistiquement significative seulement dans deux sites. Les espèces différaient généralement dans leur réaction à la présence de la maladie. Les différences dans la diversité dues à la présence de la carie de racines étaient statistiquement significatives ($P \leq 0,05$) dans trois des six cas mais la nature des différences variait d'un site à l'autre. L'élimination de l'étage dominant de sapin de Douglas a d'importants effets sur la communauté végétale mais l'impact spécifique dépend de l'espèce et du site affectés.

[Traduit par la rédaction]

Introduction

Few studies recognize the importance of disease or the full spectrum of biotic agents that may play a role in disturbance, especially in forested communities (Menges and Loucks 1984; Worrall and Harrington 1988). Plant disease has traditionally been viewed as rare in natural systems and a sign that the system is "out of balance" (Dinoor and Eshed 1984; Harlan 1976; Harper 1977). Fungal diseases, however, can be as severe in natural populations as in crop situations (Kranz 1990), can limit host population distributions (Alexander and Burdon 1984; Burdon and Shattock 1980; Rochow 1970) especially in cases with introduced pathogens (Smith 1986), influence host population fitness (Alexander 1988; Burdon and Shattock 1980), and change the competitive interactions

between populations (Alexander 1988; Burdon and Chilvers 1974).

These population effects can have impacts on a community level, although our understanding of the role of pathogens in plant communities is comparatively poor (Burdon 1982). In one of the few studies done on the causal nature of disturbance regimes across a broad landscape, Worrall and Harrington (1988) showed that root rot in combination with windthrow was the primary mortality factor causing forest gaps in high-elevation spruce-fir forest of New Hampshire. Most of the work on the role of native diseases in natural populations, however, has dealt with herbaceous perennial species, not with tree species (see Burdon and Shattock 1980), and with air-borne fungal pathogens (Sewall 1981).

Disease as a natural disturbance agent affecting community structure has been examined extensively in the mountain

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hemlock (*Tsuga mertensiana* (Bong.) Carr.) forests of the high Cascades in Oregon. *Phellinus weirii* (Murrill) Gilbertson, a native fungal root rot pathogen, is the major determinant of forest community structure in areas where the pathogen is, or was, present (Copsey 1985). Differences in forest community development inside and outside of infected areas are related to species-specific responses to infection by *P. weirii* and may persist for hundreds of years (Cook 1982; Copsey 1985). Some of the observed differences include changes in successional pathways of infected compared with noninfected areas, higher tree species diversity within infection centers (Cook et al. 1989; Copsey 1985; Dickman and Cook 1989; McCauley and Cook 1980), and changes in the microbial flora (Burket 1989) and soil nutrient status (Matson and Boone 1984).

Another tree species highly susceptible to *P. weirii* infection where infection inevitably leads to mortality. The pathogen is quite common in Douglas-fir forests; an estimated 5 to 12% of Douglas-fir plantations are believed to be infected by *P. weirii* (Gedney 1981; Goheen and Hansen 1991). Currently, we do not know whether the disease affects these forests as it does the mountain hemlock old growth.

The purpose of the following research was to

- (1) determine whether the presence of *P. weirii* in the old-growth Douglas-fir communities of the Cascade Mountains and Coast Ranges of Oregon has an effect on forest composition
- (2) assess the importance of this effect, if present, as an underlying factor determining community patterns using ordination techniques
- (3) determine the effect disease has on the herb, shrub, and tree components of the community
- (4) examine whether presence of disease at each site enhances species diversity
- (5) test the hypothesis that changes in canopy cover is the mechanism responsible for changes in the understory inside infection centers.

Study sites

Six sites of *P. weirii* (infection centers) were chosen in the Cascade Mountains and Coast Ranges of western Oregon. Infection centers were chosen on the basis of the following criteria: (i) the major canopy tree species in the area was Douglas-fir, (ii) the canopy tree species were 200 years or older, (iii) the area had never been logged, (iv) the infection center consisted of the death of at least six Douglas-fir, (v) *P. weirii* was the major disturbance agent presently active at the site, i.e., there was no recent evidence of fires, catastrophic storms, or other major disturbances present, and (vi) infection centers were derived from single clones of the fungus. Four of the six sites were located in the lower elevation Cascade Range in Oregon. Three of the four Cascade sites were located in the H.J. Andrews Experimental Forest near Blue River, Oregon, hereafter called sites HJA 1, HJA 2, and HJA 3, at elevations of 1036, 512, and 914 m, respectively. The fourth site was located at the Rooster Rock area of the Menagerie Wilderness in the Cascade Mountains near Cascadia, Oregon, with an elevation of approximately 610 m. Two of the six sites were located in Siuslaw National Forest in the Coast Ranges: one site in the Mary's Peak watershed near Corvallis, Oregon, and the other site in the Deadwood Creek area near Alsea, Oregon, with elevations of 457 and 340 m, respectively.

The five criteria were met at all six study sites chosen except that the Rooster Rock site was a mature stand (approximately 100 years old), naturally regenerated after fire, and two or three large western

red cedars (*Thuja plicata* Donn) at the HJA 2 site were logged probably in the 1950s (A.W. McKee, personal communication).

Sites were established only in areas where a single clone of the fungus appeared to be present. To insure this, isolates from various locations within the infected area were crossplated and tested for vegetative compatibility (Childs 1963). This compatibility test determines whether or not isolates originated from the same clone. Isolates that grow together freely are compatible, or from the same clone, and isolates that develop barrier zones between them are incompatible, or from different clones. All the data collected were from infection centers originating from single fungal clones only.

Materials and methods

Sampling strategy

At each site, the infection center edge was defined as the area half-way between the last Douglas-fir killed by *P. weirii* and the first symptomless Douglas-fir encountered. The edge was marked with flagging at regular intervals. With the exception of site HJA 1, 40 random vegetation plots were taken from each site: 20 random plots from the outside of the marked infection center edge (non-infected forest) and 20 random plots from inside the marked edge (infected forest). Site HJA 1 consisted of a large infection center approximately 150 m in diameter. This site was more intensively sampled than the other sites, with data collected from 199 plots.

The random plots were found by generating random directions and distances with a random number table in the field. At each random plot, distance to the flagged edge was measured. Distances were negative for plots inside the infection center and positive for plots outside the center. This measurement was called the plot location assignment (PLA) for that plot. Locations in or near riparian areas, on rocks, or in an area that had recently experienced a ground fire were not sampled.

Data collection

Data on the herb, shrub, and tree species present in each plot were taken. The cover and species of each vascular plant present in a 1 × 1 m area were recorded. Shrub or tree species present below a 1 m height over the plot were included in this measurement. The diameter at breast height (DBH) of all live tree and shrub species with diameters greater than 1 cm within a 6 m radius (4 m at the Mary's Peak site) of the plot center was recorded. Over each plot, canopy cover was measured with a spherical convex densiometer (Lemmon 1956).

Data reductions

Diameters for all trees and shrubs greater than 1 cm within the 6 m (or 4 m) radii for each plot were converted to basal areas. For further analysis, the basal area data were then standardized to be compatible with the data taken for the smaller 1 × 1 m plots. This conversion was done by dividing the basal area of a species per hectare by the greatest possible basal area found per hectare for species of that group, according to which level in the canopy they were usually found. For Douglas-fir, this maximum was 352 m²/ha. For the replacement species, *Tsuga heterophylla* (Raf.) Sarg. (western hemlock), *Thuja plicata* (western red cedar), *Taxus brevifolia* Nutt. (Pacific yew), and *Acer macrophyllum* Pursh (big leaf maple), this value was 143 m²/ha. The last group consisted of species that would never obtain canopy status; these shrubby species included *Rhododendron macrophyllum* D. Don ex G. Don (rhododendron), *Acer circinatum* Pursh (vine maple), *Corylus cornuta* Marsh. (western hazel), and *Holodiscus discolor* (Pursh) Maxim. (ocean spray). The maximum for this group was set at 8 m²/ha.

The only direct effect of the pathogen on the communities sampled was the removal of the Douglas-fir canopy. Because the purpose of this study was not to assess this known direct effect of the disease, but if and how the removal of the dominant canopy species by *P. weirii* affected other components of the forest community, the Douglas-fir data were not included in the species × plots data matrices.

Statistical analyses

A multi-response permutation procedure (MRPP) was used to determine whether the presence of the disease had a statistically significant effect on the community (McCune 1987; Mielke et al. 1981; Zimmerman et al. 1985). MRPP is similar to a multivariate analysis of variance but with relaxed requirements on the data structure. The test statistic, δ , is based on the within-group average of pairwise distance measures, groups defined a priori, of data points in euclidean space.

Ordination techniques were used to determine the strength of this effect, if significant, for each site. Ordination techniques organize multivariate data in a pattern of "relatedness" of plots by species or vice versa. By relating this pattern to a known variable, one can assess the relative importance of the variable to the underlying structure of the community, population, etc. Detrended correspondence analysis (DCA, Hill and Gauch 1980) ordination scores of the vegetation data for each site were correlated using Spearman's rank correlation coefficient against the PLAs for that site. A plot's PLA, or location relative to the leading edge of the infection, was a criterion defined solely by disease presence. Disease presence was interpreted to be the major, or a major, factor underlying community composition patterns if the PLAs were significantly correlated with the main ordination axes.

Mann-Whitney rank tests (Conover 1980) were used to examine which populations had significantly different ($P \leq 0.05$) cover values between infected and noninfected areas of each site. Because most species were absent or uncommon at several sites, eight of the most common and ubiquitous species were analyzed.

To explore the mechanisms by which disease was influencing vegetation, Mann-Whitney tests were also used to determine whether total canopy cover differed between infected and noninfected forest.

For each plot of each site, diversity of the herb, shrub, and tree species present (with the exception of Douglas-fir) was calculated using Hill's diversity index (Hill 1973), $e^{H'}$, where H' is Shannon's diversity index. An unpaired t -test was used to determine whether diversity was significantly different between infected and noninfected areas.

Results and discussion

Thirty-two species were encountered in at least two of the six sites. Average basal area for *Acer circinatum*, *Pseudotsuga menziesii*, *Taxus brevifolia*, and *Thuja plicata* peaked in site HJA 3; *Tsuga heterophylla* peaked in HJA 2. Cover for herb and shrub species peaked at 18% *Berberis nervosa* Pursh (Oregon grape) at the Rooster Rock site (Table 1).

Does the disease have an effect on the forest community?

The composition of infected areas was compared with the community found in adjacent noninfected areas for each site in order to address this question, utilizing the multivariate, nonparametric analysis of variance test MRPP. The composition of the forest community inside the infection center was significantly different from that found outside the infection center for each site (MRPP analysis, $P \leq 0.05$). Since Douglas-fir was excluded from these analyses, results show that the presence of the root rot can have an indirect effect on forest community composition, through the selective removal of this major canopy species.

To what degree does *P. weirii* influence community composition?

Ordination scores for the first DCA axis for each site were significantly correlated ($P < 0.02$) with the PLAs for four of the six sites and with the second axis DCA axis at a fifth site (Table 2). Thus the presence of the disease is likely to be a primary factor determining community composition.

Live Douglas-fir inside the infection center at HJA 3 produced conditions similar to those found in adjacent non-

infected forest. The presence of Douglas-fir, used as a surrogate for disease presence, was significantly correlated with the first DCA axis at HJA 3 ($r = -0.45$, $P = 0.005$).

Because other unexamined environmental factors, such as water relations or soil nutrient gradients, play a role in community patterns, the conclusion cannot be drawn that disease presence was the only factor underlying the forest structure. However, because of the close association found between PLA (a criterion defined solely by disease presence) and the major DCA ordination axes for each site, there is a strong indication that *P. weirii* is a major determinant underlying community composition patterns.

Which plant populations are affected by disease presence?

Eight species from the tree, shrub, and herb and strata that occurred most commonly across all sites were chosen for this analysis.

Tree species

Douglas-fir, the canopy species for all six sites, had significantly different cover values ($P \leq 0.05$) for all sites except HJA 3 ($P = 0.15$) (Table 3). This last site was different because of the live large Douglas-fir present directly inside the infection center; these trees were more resistant to the root rot, were infected by still symptomless, or had been isolated in some way such that their roots were not exposed to the fungus.

Though not statistically significant, *Tsuga heterophylla* and *Thuja plicata*, both late-successional species in these forests, generally had higher percent cover on plots located inside the infection center at the Cascade sites (Table 3). The exception to this was HJA 3, a site that had significantly higher *Tsuga heterophylla* cover outside the infection center. *Tsuga heterophylla* in this area was not as common as in the other old-growth Cascade sites and was not the major replacement canopy tree for Douglas-fir at the site. *Taxus brevifolia* and *Thuja plicata* both had a higher average basal area (14.4 and 19.6% cover/ha, respectively) for inside areas than *Tsuga heterophylla* at this site. The unusually high cover of *Taxus brevifolia* may have been due to a suppression of *Tsuga heterophylla* dominance in the area by two other native diseases at the site: a mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones), stunting seedlings and young trees, and white heart rot of *Tsuga heterophylla* (*Phellinus hartigii* (Alesch. & Schnabl) Pat.), killing mature canopy trees (Boyce 1961).

The Coast Ranges sites had no significant differences in *Tsuga heterophylla* cover inside and outside *P. weirii* infection centers. *Tsuga heterophylla*, the only replacement tree at these sites, generally had a lower relative basal area than what was found in the old-growth Cascade sites. Coastal forests tend to develop dense shrub communities, especially with disturbance (Franklin and Dyrness 1984). Increased competition with shrubs in infection centers may have hindered *Tsuga heterophylla* establishment and growth in the Coast sites examined, as compared with the Cascade sites. Competition below ground can be an important factor controlling *Tsuga heterophylla*'s growth to canopy status (Christy 1986).

Thuja plicata had greater cover inside infected areas for the two sites in which it was present, significantly higher at HJA 2 (Table 3). The mature site, Rooster Rock, did not have any potential canopy tree species present to replace Douglas-fir.

TABLE 1. Average basal area of common trees and shrub species for each site and average cover for herb and shrub species occurring in 1 × 1 m plots

	HJA 1 (199 plots)	HJA 2 (40 plots)	HJA 3 (40 plots)	Rooster Rock (39 plots)	Mary's Peak (40 plots)	Alesea (40 plots)
Trees and shrubs (m ² /ha)						
<i>Acer circinatum</i>	0.7 (103)	0.2 (27)	1.3 (37)	0.2 (17)	0.8 (31)	0.8 (19)
<i>Holodiscus discolor</i>	tr ^a (2)	—	—	—	0.3 (25)	—
<i>Pseudotsuga menziesii</i>	45.8 (77)	45.8 (14)	63.4 (17)	49.3 (36)	21.1 (31)	52.8 (30)
<i>Rhododendron</i>						
<i>macrophyllum</i>	tr ^b (1)	0.1 (17)	5 ^b (8)	0.2 (20)	—	—
<i>Taxus brevifolia</i>	1.4 (16)	0.4 (19)	10.0 (36)	—	—	—
<i>Thuja plicata</i>	tr (2)	2.9 (19)	11.4 (22)	—	—	—
<i>Tsuga heterophylla</i>	30.0 (188)	27.2 (39)	7.2 (34)	—	2.9 (22)	11.4 (34)
Herbs and shrubs (% cover/m ²)						
<i>Achlys triphylla</i>	tr ^c (3)	tr (2)	—	0.3 (3)	—	—
<i>Adenocaulon bicolor</i>	—	—	—	0.3 (5)	0.1 (1)	—
<i>Anemone oregana</i>	0.1 (12)	—	0.1 (2)	0.6 (16)	—	—
<i>Berberis nervosa</i>	11 (128)	3 (14)	6 (24)	18 (21)	15 (37)	2 (7)
<i>Castanopsis</i>						
<i>chrysophylla</i>	—	—	0.2 (1)	—	0.1 (2)	—
<i>Chimaphila menziesii</i>	tr (2)	—	—	tr (1)	—	—
<i>Cornus canadensis</i>	0.2 (5)	—	3 (23)	—	—	—
<i>Coptis laciniata</i>	8 (133)	3 (24)	—	—	—	—
<i>Galium triflorum</i>	—	0.1 (3)	—	1 (18)	tr (3)	tr (1)
<i>Gaultheria shallon</i>	—	1 (6)	8 (21)	6 (12)	15 (23)	10 (31)
<i>Goodyera oblongifolia</i>	0.1 (11)	tr (1)	0.4 (8)	—	—	—
<i>Linnaea borealis</i>	1 (53)	4 (32)	8 (31)	0.1 (1)	0.1 (2)	—
<i>Oxalis oregana</i>	—	13 (29)	—	—	—	0.8 (6)
<i>Pachystima myrsinites</i>	tr (2)	—	0.1 (1)	—	—	—
<i>Polystichum munitum</i>	0.8 (18)	15 (22)	2 (6)	13 (14)	6 (17)	13 (18)
<i>Rosa gymnocarpa</i>	0.1 (4)	—	—	—	0.6 (6)	0.1 (1)
<i>Rubus</i> sp. ^d	0.6 (57)	0.8 (12)	1 (13)	0.5 (11)	—	1 (15)
<i>Symphoricarpus mollis</i>	0.2 (1)	—	—	—	0.1 (1)	—
<i>Tiarella unifoliata</i>	0.3 (30)	0.6 (15)	—	—	—	—
<i>Trientalis latifolia</i>	tr (4)	0.1 (2)	tr (2)	0.3 (7)	tr (2)	tr (1)
<i>Trillium ovatum</i>	tr (5)	0.1 (2)	tr (1)	—	tr (1)	0.1 (4)
<i>Vaccinium</i>						
<i>membranaceum</i>	tr (4)	—	—	—	tr (1)	—
<i>Vaccinium parvifolium</i>	0.1 (12)	1 (7)	0.1 (2)	0.2 (2)	—	1 (7)
<i>Vancouveria</i>						
<i>hexandra</i>	0.1 (6)	0.2 (4)	—	0.1 (2)	—	—
<i>Viola orbiculata</i>	1 (74)	0.4 (18)	0.1 (1)	3 (26)	—	—

NOTE: Species listed occurred at two or more sites. Frequency of each species for each site is in parentheses. tr, trace.

^aBasal area < 0.1 m²/ha.^b% cover/m².^cCover < 0.1%/m².^dEither *R. nivalis* or *R. ursinus*.

TABLE 2. Spearman rank correlation coefficients (with their associated probability values in parentheses) for the plot location assignments (PLAs) and the first two DCA ordination axes for each site two DCA ordination axes for each site

	PLA vs. DCA	
	Axis 1	Axis 2
Cascade sites		
HJA 1	-0.17 (0.02)	-0.07 (0.35)
HJA 2	-0.53 (0.00)	0.38 (0.02)
HJA 3	0.004 (0.98)	-0.04 (0.79)
Rooster Rock	-0.59 (0.00)	-0.09 (0.56)
Coast sites		
Mary's Peak	0.24 (0.14)	0.50 (0.00)
Alesea	-0.37 (0.02)	0.10 (0.51)

Shrub species

For all of the Cascade sites, there was a general trend of lower average percent cover of *A. circinatum* inside infection centers (Table 3). The Coast Ranges sites had a much higher percent cover of *A. circinatum* inside infection centers, statistically significant at the Alesea site. The different responses of *A. circinatum* to disease presence at these two types of sites may be because replacement trees with dense canopies, such as *Tsuga heterophylla* were not as common at the Coast sites examined. The increased light made available by Douglas-fir removal at the Coast sites could promote an increase in *A. circinatum*, whereas replacement canopy species eventually suppress *A. circinatum* inside the infection centers at old-growth Cascade sites.

With the exception of the Mary's Peak site, all sites had a higher average percent cover of *B. nervosa* outside infection centers (Table 3). *Gaultheria shallon* Pursh (salal) exhibited

TABLE 3. A comparison of the average cover \pm SE of tree species (% cover/ha), arborescent shrub species (% cover/m²), and all shrub species (% cover/m²) inside and outside *Phellinus weirii* infection centers, and the associated Mann-Whitney test statistic and probability values for these differences

	PSME	TSHE	THPL	ACCI	BENE	GASH	Total shrub cover
Cascade sites							
HJA 1							
Inside	37.7 \pm 3.1	32.5 \pm 3.0	—	6.1 \pm 1.3	8.3 \pm 1.7	—	11.4 \pm 2.2
Outside	56.7 \pm 2.1	26.9 \pm 2.3	—	10.8 \pm 1.4	12.4 \pm 1.7	—	16.7 \pm 2.4
<i>t</i> (<i>P</i> -value)	3.90 (0.048)	2.70 (0.10)	—	4.27 (0.04)	1.82 (0.18)	—	1.11 (0.29)
HJA 2							
Inside	1.9 \pm 1.9	37.2 \pm 7.4	6.7 \pm 3.2	0.7 \pm 0.3	1.7 \pm 0.7	0 \pm 0	5.2 \pm 1.5
Outside	88.5 \pm 4.9	15.9 \pm 2.5	0.3 \pm 0.3	5.1 \pm 1.2	4.5 \pm 1.8	1.7 \pm 1.7	8.3 \pm 2.3
<i>t</i> (<i>P</i> -value)	16.14 (0.00)	2.81 (0.09)	15.78 (0.00)	11.94 (0.00)	1.74 (0.19)	8.18 (0.00)	0.50 (0.48)
HJA 3							
Inside	32.4 \pm 4.4	1.7 \pm 0.9	19.6 \pm 9.5	15.7 \pm 3.5	4.3 \pm 1.4	11.5 \pm 4.4	26.1 \pm 5.6
Outside	93.3 \pm 7.3	12.9 \pm 2.6	4.3 \pm 2.4	16.5 \pm 3.3	8.1 \pm 2.2	4.5 \pm 1.5	17.2 \pm 4.3
<i>t</i> (<i>P</i> -value)	2.08 (0.15)	17.08 (0.00)	4.39 (0.12)	0.04 (0.85)	2.08 (0.15)	0.07 (0.80)	1.06 (0.30)
Rooster Rock							
Inside	29.0 \pm 1.7	—	—	1.2 \pm 0.8	2.7 \pm 1.1	5.6 \pm 3.5	10.9 \pm 3.4
Outside	69.1 \pm 1.6	—	—	3.1 \pm 1.1	34.1 \pm 8.2	6.6 \pm 3.1	43.5 \pm 8.1
<i>t</i> (<i>P</i> -value)	14.8 (0.00)	—	—	3.07 (0.08)	11.09 (0.00)	0.43 (0.51)	6.72 (0.01)
Coast sites							
Mary's Peak							
Inside	2.6 \pm 0.5	2.4 \pm 0.9	—	14.6 \pm 3.2	16.6 \pm 2.8	22.8 \pm 7.3	42.2 \pm 8.5
Outside	38.9 \pm 3.8	3.9 \pm 0.9	—	5.3 \pm 1.3	13.5 \pm 3.9	8.0 \pm 4.9	24.0 \pm 7.1
<i>t</i> (<i>P</i> -value)	8.72 (0.00)	3.05 (0.08)	—	3.13 (0.08)	1.69 (0.19)	9.00 (0.00)	5.94 (0.01)
Alsea							
Inside	22.0 \pm 1.9	12.0 \pm 3.5	—	17.1 \pm 4.8	0.5 \pm 0.5	7.4 \pm 2.3	10.4 \pm 2.5
Outside	84.9 \pm 1.9	11.2 \pm 2.5	—	3.0 \pm 1.4	3.3 \pm 1.4	12.2 \pm 4.2	17.2 \pm 4.8
<i>t</i> (<i>P</i> -value)	20.49 (0.00)	0.46 (0.50)	—	6.78 (0.01)	4.17 (0.04)	0.05 (0.82)	0.36 (0.55)

NOTE: Only sites in which the tree species occurred are listed. Sample sizes for each site are as follows: 20 plots inside and outside the infection center for HJA 2, HJA 3, Mary's Peak, and the Alsea site; 19 plots inside and 20 plots outside for the Rooster Rock site; and 73 plots inside and 126 plots outside for HJA 1. Species codes: ACCI, *Acer circinatum*; BENE, *Berberis nervosa*; GASH, *Gaultheria shallon*; PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*.

a more variable pattern, with cover being significantly higher ($P \leq 0.05$) outside the infection center at HJA 2 and lower at the Mary's Peak site (Table 3).

Differences in total shrub cover inside and outside diseased areas across all sites were not statistically significant except at Mary's Peak, where shrub cover was significantly higher inside the infection center (42 vs. 24%, $P = 0.02$) and at the Rooster Rock site, where cover was significantly lower inside the infection center (11 vs. 44%, $P = 0.01$).

Results indicate that response to disease presence is highly species specific and dependent on site characteristics, thus making it difficult for generalizations to be made. Some species, such as *A. circinatum*, were quite sensitive to the disturbance induced by the disease; cover increased with disease in the Coast sites and generally decreased inside infection centers of the old-growth Cascade sites. Other species, such as *G. shallon*, generally did not exhibit cover differences in response to disease.

Understory responses to canopy gaps have been found to be species specific (Collins and Pickett 1988), with changes in species composition often associated with increased site availability due to tip-up mounds or some sort of soil disturbance (Beatty 1984), both of which are common in infection centers. Community response to *P. weirii* disturbance was largely a reorganization of populations already present on the site, rather than the establishment of new species. This "reorganization" response also occurs in openings caused by gypsy moths in eastern mature oak forests (Ehrenfeld 1980).

Herb species

In 9 of 11 comparisons, *Polystichum munitum* (Kaulfuss) K. Presl (sword fern), *Linnaea borealis* L. (twinline), and *Coptis laciniata* Gray (golden thread) exhibited a trend of higher average cover inside infected areas than outside (Table 4). Only three of these differences were statistically significant at $P = 0.05$. Likewise, the total cover of all the herb species was higher inside infection centers at each site (Table 4), although significantly higher ($P < 0.01$) only at the Rooster Rock site.

In general, the herbaceous populations examined did exhibit a consistent pattern of being more abundant within infection centers, though this pattern can be attributed, for the most part, to the response of *Polystichum munitum* to disease presence.

Does the diversity of plant species differ between infected and noninfected areas?

The old-growth Cascade sites, HJA 2 and 3, exhibited a trend toward decreased species diversity in the infected forest (Table 5), with diversity significantly lower at HJA 2 ($P = 0.04$) and nearly significant at HJA 3 ($P = 0.097$). In contrast, the mature stand at Rooster Rock and the Mary's Peak site both had significantly higher diversity in the infected area of the forest ($P < 0.01$). HJA 1 and the Alsea site had no significant differences in vascular plant diversity inside and outside infection centers ($P > 0.25$).

These results exemplify how the population responses depend on site conditions. Similar species occurred across all

TABLE 4. A comparison of the average cover \pm SE ($\%/m^2$) for *Coptis laciniata* (COLA), *Linnaea borealis* (LIBO), *Polystichum minutum* (POMU), and total herbaceous species inside and outside *Phellinus weirii* infection centers using the Mann-Whitney tests and the associated probability values for these differences

	COLA	LIBO	POMU	Total herb cover
Cascade sites				
HJA 1				
Inside	8.9 \pm 1.6	1.5 \pm 0.3	1.0 \pm 0.4	14.0 \pm 1.8
Outside	8.0 \pm 1.2	0.7 \pm 0.2	0.6 \pm 0.3	11.7 \pm 1.4
<i>t</i> (<i>P</i> -value)	0.04 (0.84)	20.21 (0.00)	1.58 (0.21)	2.27 (0.13)
HJA 2				
Inside	1.2 \pm 0.5	2.0 \pm 0.4	24.8 \pm 6.1	41.3 \pm 6.9
Outside	4.2 \pm 1.3	5.1 \pm 2.0	4.6 \pm 2.8	29.7 \pm 5.7
<i>t</i> (<i>P</i> -value)	6.45 (0.01)	0.02 (0.88)	11.60 (0.00)	1.42 (0.23)
HJA 3				
Inside	—	10.5 \pm 5.2	2.9 \pm 2.1	17.4 \pm 5.9
Outside	—	6.3 \pm 1.7	1.4 \pm 1.0	10.7 \pm 2.0
<i>t</i> (<i>P</i> -value)	—	0.04 (0.84)	0.76 (0.38)	0.06 (0.81)
Rooster Rock				
Inside	—	0.7 \pm 0.4	—	35.7 \pm 6.5
Outside	—	0.1 \pm 0.1	—	8.5 \pm 3.3
<i>t</i> (<i>P</i> -value)	—	2.40 (0.12)	—	17.00 (0.00)
Coast sites				
Mary's Peak				
Inside	—	—	6.4 \pm 2.7	7.7 \pm 2.8
Outside	—	—	5.0 \pm 2.6	5.6 \pm 2.6
<i>t</i> (<i>P</i> -value)	—	—	0.59 (0.44)	1.09 (0.30)
Alsea				
Inside	—	—	15.6 \pm 5.4	17.1 \pm 5.4
Outside	—	—	10.3 \pm 5.5	11.1 \pm 5.5
<i>t</i> (<i>P</i> -value)	—	—	1.82 (0.18)	3.67 (0.06)

NOTE: Broken lines indicate that the species was either very rare or not present at that site. Sample sizes for each site are as follows: 20 plots inside and outside the infection center for HJA 2, HJA 3, Mary's Peak, and the Alsea site; 19 plots inside and 20 plots outside for the Rooster Rock site; and 73 plots inside and 126 plots outside for HJA 1.

TABLE 5. Hill's diversity index inside and outside infection centers for all sites and the results of an unpaired *t*-test used to test whether the diversity between these two areas is significantly different from random

	Hill's diversity index		<i>t</i> -statistic (<i>P</i> -value)
	Inside	Outside	
Cascade sites			
HJA 1	3.1	2.9	1.1 (0.26)
HJA 2	3.5	4.5	2.1 (0.04)
HJA 3	3.7	4.5	1.7 (0.10)
Rooster Rock	4.1	2.4	3.6 (0.00)
Coast sites			
Mary's Peak	3.9	2.7	3.1 (0.00)
Alsea	2.6	2.5	0.3 (0.78)

sites and yet diversity is enhanced within centers at some sites and decreased at other sites. Late-successional tree species were not common in the Coast Ranges stands, allowing understory shrubs and herbs to grow. Late-successional tree species generally increased with disease presence in the old-growth Cascade sites, decreasing understory growth and diversity.

Although host-specific diseases and predators may sometimes act similarly to diversity community structure (Harper

1977), this does not seem to be the case for *P. weirii* in the Cascade sites. Diversity here did not consistently increase with disease presence. Effective generalizations about the effect of disease on diversity must consider the interactions between specific disturbance regimes and species life histories.

What are the possible mechanisms by which disease presence induces species compositional changes?

The only direct effect *P. weirii* has on the forest community is to slowly kill Douglas-fir. The results presented here, however, show that this effect has far-reaching consequences throughout the plant community. The initial hypothesis was that a change in canopy cover induced the compositional changes. Canopy cover was expected to be higher inside infection centers because of the late-successional species that would replace Douglas-fir would have denser, lower canopies (Grier and Logan 1977). However, only the Rooster Rock site had statistically significant differences in canopy cover ($P = 0.02$), and this difference was slight, with 76% cover inside the infection center and 81% outside. This mature stand did not have any potential replacement canopy tree species present, such as *Tsuga heterophylla* or *Thuja plicata*, thus canopy cover was not expected to be higher inside this infection center.

An infection center is composed of a somewhat orderly series of single, sometimes multiple, tree gaps that have occurred over a long period of time. Single-tree gaps have been found to have very little effect on the understory light

regime of old-growth forests in the Pacific Northwest. This is because of the high ratio of canopy height to gap diameter (Canham et al. 1990) and the high degree of crown overlap (15–30%) of dominant Douglas-fir with the subdominant canopy species (Spies et al. 1990). Only the simultaneous death of 5 to 10 trees, rare in most *P. weirii* infection centers, would create a gap large enough for high light intensities at ground level (Spies et al. 1990). Methods used may also be suspect because densimeters tend to overestimate percent cover in canopies that have many gaps (Bunnell and Vales 1990).

Pure canopies of late-successional species such as *Tsuga heterophylla* and *Thuja plicata* transmit less direct and diffuse radiation to the forest floor than do pure Douglas-fir canopies (Stewart 1988). A decreased understory diversity and development of herbs, shrubs, and regenerating tree species found under *Tsuga heterophylla* canopies have been attributed to a poor lighting regime associated with such canopies (Stewart 1986, 1988). Thus changes in the quality of light due to disease presence, rather than simply changes in the quantity of canopy cover, may be the underlying mechanism for the observed differences in plant communities experiencing the disease.

Alternative hypotheses can also explain patterns of community response. Because tree species vary in root uptake and exudation, the nutrients and microbial communities beneath different canopy species can vary significantly (Collins and Good 1986; Turner and Franz 1985). Old-growth hemlock-cedar forests of northern Idaho show a strong differentiation between *Thuja plicata* and *Tsuga heterophylla* microsites (Turner and Franz 1985). Turner and Franz (1986) attributed a less diverse understory beneath *Tsuga heterophylla* as compared with *Thuja plicata* to lower pH, fewer nitrifying bacteria, and less available calcium, rather than differences in the light regime.

Conclusions

Although the initial distribution of infection centers across a landscape may be random, subsequent spread of the disease through the forest is not random. In general, mortality due to root rots, beetle-vectored diseases, and diseases with steep spore dispersal gradients are probably not stochastic, though this will depend on one's spatial scale. Thus, small forest disturbances that on first appearance seem to be random and abiotically caused may have been wholly or partially biotically caused and their occurrence may have been predictable given some knowledge of the biotic interactions involved.

Disturbance caused by biotic agents has important ramifications if one is using disturbance to help predict forest composition changes through time. Incorporating disturbance into forest composition models can be used to explore future, as well as past, successional patterns, to predict timber volume over time for management practices, and to test hypotheses on how varying disturbance characteristics affect composition through time. If biotic influences, such as root disease, play a role in the forested ecosystem, the size, frequency, and intensity of the disturbance variable(s) could be realistically estimated. Models would then gain in their accuracy and predicting power, and we would have a better understanding of the mechanics behind forest ecosystems.

This study has shown that the long-term presence of laminated root rot caused by *P. weirii* in old-growth and mature Douglas-fir stands of the Pacific Northwest can significantly

impact community composition. Although specific changes differed from site to site and were often species specific, a disease that affected one species had a cascading effect throughout various populations in these multistratum forests.

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