Occurrence of *Piloderma fallax* in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A.

J.E. Smith, R. Molina, M.M.P. Huso, and M.J. Larsen

Abstract: Yellow mycelia and cords of *Piloderma fallax* (Lib.) Stalp. were more frequently observed in old-growth stands than in younger managed stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Piloderma fallax* frequency and percent cover data were collected from 900 plots in three replicate stands in each of three forest age classes over 2 years in both spring and fall. *Piloderma fallax* is strongly associated with stand age; it occurred in 57% of plots in old-growth, 6% of rotation-age, and 1% of young stands. Presence of *Piloderma fallax* was related to the percent cover of coarse woody debris (CWD) in decay class 5. *Piloderma fallax* was approximately 2.5 times more likely to occur in a plot with CWD decay class 5 present than in plots without. The probability that it would occur in a plot increased by approximately 20% for every 10% increase in percent cover of CWD decay class 5. However, the percent cover of *Piloderma fallax* was not strongly related to the percent cover of CWD in decay class 5. Frequency of occurrence did not differ among sampling times. Occurrence of *Piloderma fallax* may indicate suitable substrate for ectomycorrhizal fungi associated with CWD and may be important in forest management for the maintenance of biodiversity and old-growth components in young managed stands.

Key words: *Piloderma fallax*, coarse woody debris, *Pseudotsuga menziesii*, forest management, ectomycorrhizal fungi, biodiversity.

Résumé : On observe le mycélium et les cordons jaunes du *Piloderma fallax* (Lib.) Stalp. plus fréquemment dans les vieilles forêts que dans les jeunes boisés aménagés du sapin Douglas (*Pseudotsuga menziesii* (Mirb. Franco)). Les auteurs ont récolté des données sur la fréquence et le pourcentage de couverture du *Piloderma fallax* dans 900 parcelles, répliquées dans trois stations, pour chacune des classes d'âge au cours de 2 années, au printemps et á l'automne. La *Piloderma fallax* est fortement associé á l'âge du peuplement; on l'observe dans 57 % des parcelles en forêt âgée, dans 6 % des parcelles en âge de rotation et 1 % dans les jeunes peuplements. La présence du *Piloderma fallax* est reliée au pourcentage de couverture par de gros débris ligneux (CDW) au stade 5 de décomposition. Il y a 2.5 fois plus de chances de rencontrer le *Piloderma fallax* dans une parcelle avec du CDW en classe 5 de décomposition, que dans les parcelles qui n'en ont pas. La probabilité qu'on puisse le retrouver dans une parcelle augmente d'environ 20 % pour chaque augmentation de 10 % dans le pourcentage de couverture par du CDW, en classe 5 de décomposition. Cependant, le pourcentage de couverture par le *Piloderma fallax* n'est pas fortement relié au pourcentage de couverture par le CDW en classe 5 de décomposition. La fréquence de présence ne diffère pas entre les échantillons selon le temps. La présence du *Piloderma fallax* peut indiquer l'existence de substrat favorable aux champignons ectomycorhiziens associés au CDW et pourrait être importante en aménagement forestier pour maintenir la biodiversité et les constituants des forêts âgées, dans les jeunes peuplements sous aménagement.

Mots clés : *Piloderma fallax*, débris ligneux grossiers, *Pseudotsuga menziesii*, aménagement forestier, champignons ectomycorhiziens, biodiversité.

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Introduction

Piloderma fallax (Lib.) Stalp. is a well-known ectomycorrhizal (EM) species with worldwide distribution (Melin 1936; Froidevaux 1975; Zak 1976; Froidevaux and Jaquenoud-Steinlin 1978; Eriksson et al. 1981; Kropp 1982; Harley and Smith 1983; Goodman and Trofymow 1996, 1998*a*, 1998*b*; Larsen et al. 1997). It forms distinctive yellow mycelial and mycelial cord networks within forest soils and litter layers (Mikola 1962; Goodman and Trofymow 1996, 1998*b*). It frequently occurs in stands of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in plots with brown

Table 1. Description of the experimental sites in and bordering the H.J. Andrews Experimental Forest, Oregon.

Site	Age class*	Basal area (m^2/ha)	Stem density (No./ha)	Plant associations†	Elevation (m)	Aspect
L104	Y	27‡	688	Tshe/Pomu–Will	550–610	N
L201	Y	40	655	Tshe/Bene–Gash–Will	700–820	NW
L202	Y	37	615	Tshe/Bene–Gash–Will	760–910	NNW
Mill Creek 1	RA	40	573	Tshe/Bene–Gash–Will	490–550	SW
Mill Creek 2	RA	35	527	Tshe/Bene–Gash–Will	730–790	SSE
Mill Creek 3	RA	36‡	550‡	Tshe/Bene–Gash–Will	430–490	SW
Stand 15	OG	120	391	Tshe/Rhma–Bene–Will	730–820	SSW
Shorter Creek	OG	105	354	Tshe/Libo2	730–850	S
Upper Lookout	OG	92‡	332‡	Tshe/Bene–Gash–Will	850–1000	SW

Note: Stand data are from the Blue River Ranger District, Blue River, Oregon, and from the Forest Science Databank at Oregon State University, Corvallis, Oregon. Plant associations follow Logan et al. (1987) and Hemstrom et al. (1987) for the Willamette National Forest.

*Y, young (30–35 years); RA, rotation-age (45–50 years); OG, old-growth (over 400 years).

†Tshe, *Tsuga heterophylla*; Bene, *Berberis nervosa*; Gash, *Gaultheria shallon*; Libo2, *Linnea borealis* L.; Pomu, *Polystichum munitum*; Rhma, *Rhododendron macrophyllum*; Will, Willamette National Forest.

‡Data not available. Estimates are from neighboring stands similar in age, elevation, and aspect.

rotted coarse woody debris (CWD) in advanced stages of decay, a substrate most frequently associated with older forests (Harvey et al. 1979).

Piloderma fallax and some EM fungi that form readily observable mycelial networks commonly have been termed mat-forming fungi (Fisher 1972; Cromack et al. 1979; Griffiths et al. 1990, 1991*a*). Mat-forming fungi increase nutrient availability to host trees, perhaps in part by enzymatic degradation of forest floor and soil organic matter (Griffiths et al. 1991*b*, 1994; Caldwell et al. 1991; Aguilera et al. 1993). Although some EM fungi are restricted in host range (Molina et al. 1992), *Piloderma* species are broad in host range and associate with angiosperms as well as gymnosperms (Zak 1976; Herrmann et al. 1998).

The taxonomic standing of *Piloderma fallax* has long been debated and was most recently reviewed by Larsen et al. (1997). They determined that *Piloderma fallax* is the most appropriate name for what has been called *Piloderma bicolor* (Peck) Jülich and *Piloderma croceum* J. Erikss. et Hjortstam.

Piloderma fallax produces moist white parchment-like effuse basidiomata on decomposing logs, stumps, and buried wood, where they are usually hidden from view. To determine the occurrence of *Piloderma fallax*, it is necessary to rake through the soil and decayed wood to expose the yellow mycelia and cords associated with the basidiomata.

The bright yellow mycelia and cords of *Piloderma fallax* have long attracted the attention of mycologists. Mikola (1962) noted the common occurrence of this fungus in the humus of older spruce (*Picea* spp.) forests and correlated increased occurrence of *Piloderma fallax* with increased stand age and increased conifer density, in mixed conifer and deciduous stands. Eriksson et al. (1981) noted the frequent occurrence of this fungus in acid forest soils with wood in advanced stages of decay.

This study was designed to quantify and explore the underlying causes for the difference in the frequency of occurrence of *Piloderma fallax* in old-growth stands compared with that in younger managed stands of Douglas-fir. Study objectives were to determine (*i*) if *Piloderma fallax* is differentially associated with old-growth versus younger managed stands and (*ii*) whether or not there was a correlation between the amount and level of decay of brown rotted CWD and the occurrence of *Piloderma fallax*. Secondarily, we wanted to determine whether our survey method for determining the frequency of occurrence of *Piloderma fallax*, i.e., a one time survey versus surveys in different seasons and years, yield different results. Sampling was done at different times over a 2-year period to determine whether or not there was variation in detection.

Study area

Our study was conducted in nine stands within the Western Hemlock (*Tsuga heterophylla* (Raf.) Sarg.) Zone (Franklin and Dyrness 1984) located in and near the H.J. Andrews Experimental Forest, Willamette National Forest, along the west side of the Cascade Range of Oregon. Stand data and plant associations are presented in Table 1. Most of our stands are mesic sites with *Berberis nervosa* Pursh and *Gaultheria shallon* Pursh in the understory (Table 1). Forest communities within the *Tsuga heterophylla* Zone are arranged along moisture gradients (Zobel et al. 1976). Moist sites are typified by an understory that includes *Polystichum munitum* (Kaulf.) Presl and *Oxalis oregana* Nutt., mesic sites by *Berberis nervosa* and *Rhododendron macrophyllum* G. Don., and dry sites by *Gaultheria shallon* (Franklin and Dyrness 1984). Elevations of our stands range from 430 to 1000 m (Table 1). Slope gradients range from 0 to 35°. Soils are mainly Inceptisols (Brown and Parsons 1973; Franklin and Dyrness 1984). Parent materials are basalt and andesite (Franklin and Dyrness 1984).

The climate is maritime with mild, wet winters, and warm, dry summers. Mean monthly temperatures range from 1°C in January to 18°C in July. Annual precipitation is about 230 cm, with about 90% falling between October and April (McKee and Bierlmaier 1987). Winter snowpacks above an elevation of 900 m accumulate to a depth of 1 m or more and may persist into June; snowpack melts quickly below 900 m (Franklin and Dyrness 1984; Bierlmaier and McKee 1989).

The study is comprised of three forest age classes dominated by Douglas-fir with western hemlock in the understory: young with closed canopy (30–35 years), rotation-age (ready for harvest, 45–50 years), and old-growth (over 400 years) (Table 1). The rotation-age stands have reached matu-

Table 2. Number of plots out of 25 per stand with *Piloderma fallax* and coarse woody debris (CWD) decay class 5 for each of three stands in each age class.

Sampling period	*Piloderma fallax*			CWD decay class 5		
	OG	RA	Y	OG	RA	Y
Spring 1993	8,18,15	1,2,0	0,0,0	15,20,22	21,16,21	10,11,12
Fall 1993	9,17,14	1,2,7	0,1,0	19,20,20	16,10,17	15,14,15
Spring 1994	13,17,15	0,1,2	0,1,2	20,18,20	11,10,12	7,13,13
Fall 1994	11,18,17	0,0,2	0,0,0	18,19,18	13,10,12	8,5,9
Total	41,70,61	2,5,11	0,2,2	72,77,80	61,46,62	40,43,49

Note: Y, young (30–35 years); RA, rotation-age (45–50 years); OG, old-growth (over 400 years).

rity from a forest economic definition but do not meet the ecological criteria of mature in age or structure (Spies and Franklin 1991). Stands were subjectively chosen to represent a range of age classes and meet the criteria of study objectives from a list of possible sites suggested by the H.J. Andrews site manager. The two younger age classes are plantations that were previously clearcut, broadcast burned soon afterward, and allowed 2–4 years to regenerate naturally before being replanted with Douglas-fir. The old-growth stands were naturally established after catastrophic wildfire.

Materials and methods

Experimental design and sampling procedures

The study design is a completely randomized design with three replications (stands) of each of the three treatments (old-growth, rotation-age, and young). All stands were measured for *Piloderma fallax* four times (spring 1993; fall 1993; spring 1994; and fall 1994), and each measurement period occurred within 3 weeks for all stands. At each measurement period, the presence of *Piloderma fallax* was recorded for each of 25 circular plots (4 m^2) within each stand (Table 2). In each stand, plots were distributed along three randomly placed transects of 8, 9, and 8 plots each (modified from Luoma et al. 1991). Plots were placed cross-slope at 25-m intervals along each transect. Transect placement was stratified by upper, middle, and lower slope position. Natural gaps were sampled when they fell within the random placement of the plots. No attempt was made to analyze gap data separately.

In each plot, *Piloderma fallax* and CWD by decay class was measured as percent cover (Mueller-Dombois and Ellenberg 1974). CWD was classified following Spies and Cline (1988) as adapted from Maser et al. (1979), inclusive of five decay classes where continuum extremes are characterized by recent down wood with bark and twigs (class 1) and soft and powdery brown rot pieces (class 5).

Plots were raked with garden cultivators to expose *Piloderma fallax* mycelia and cords and marked with a flag to avoid repeat sampling of the same area in subsequent seasons. Data collected for *Piloderma fallax* frequency and percent cover were based on the observed occurrence of bright yellow mycelia and cords. The yellow pigmentation of mycelial cords is a reliable field character for detecting *Piloderma fallax* (Larsen et al. 1997). Occasionally *Piloderma* basidioma were found and collected. These were confirmed by microscopic examination to be *Piloderma fallax* (Larsen et al. 1997).

Statistical analysis

To assess whether the presence of *Piloderma fallax* in a plot was a function of stand age and whether this effect varied with time (season), the data were modeled using a general mixed model (Table 3). The 25 plots within a stand were grouped and a logit transformation was found to be appropriate to stabilize the variance. Computations were carried out using the SAS Institute version 6.12 statistical procedure MIXED (SAS Institute Inc. 1997). A simple covariance structure (0 off-diagonal elements and equal diagonal elements) for the repeated measures was selected based on maximizing the akaike information criterion.

To assess whether the presence of *Piloderma fallax* in a 4-m^2 plot was associated with the presence of CWD of different decay classes and the abundance of CWD of different decay classes, the data were modeled using a generalized linear model for a binary response with a canonical link. The data could not be grouped since each plot had a unique combination of presence or absence of CWD in the different decay classes. To allow for nonindependence of plots coming from the same stand, a stand effect was included in all models. Since binary data cannot be overdispersed, no dispersion parameter was estimated. Computations were carried out using the SAS Institute version 6.12 statistical procedure GENMOD (SAS Institute Inc. 1997).

A regression analysis was used to assess whether the percent cover of *Piloderma fallax* was related to the percent cover of CWD in decay class 5. This analysis was carried out only on the subset of the plots (194 of 900) on which *Piloderma fallax* occurred. A ln transformation of the percent cover of *Piloderma fallax* was imposed to stabilize the variance. Again, a stand effect was included in the model to account for the nonindependence of plots from the same stand. Computations were carried out using the SAS Institute version 6.12 statistical procedure GLM (SAS Institute Inc. 1996). Analysis of the other decay classes was not possible because they were poorly represented in the plots on which *Piloderma fallax* was found.

To assess whether the presence of CWD in decay class 5 in a plot was a function of age, the data were modeled using a generalized linear model for grouped binomial data. Although *Piloderma fallax* presence might be expected to vary with time, CWD in decay class 5 is a static measure whose value in a plot would not be expected to change noticeably over the short duration of this study. Thus, the 100 plots within a stand were grouped and assumed to be binomially distributed with binomial $m = 100$. The effect of stand age on the probability of CWD in decay class 5 being present in a plot was evaluated using a generalized linear model for binomial response with the canonical link. A scale parameter was estimated to allow for extra-binomial variation and lack of independence. Computations were carried out using the SAS Institute version 6.12 statistical procedure GENMOD (SAS Institute Inc. 1997).

Results

The repeated measures analysis indicated that the probability of *Piloderma fallax* occurring in a stand was strongly correlated with stand age ($F_{[2,6]} = 53.9$, $p = 0.0001$) and, with no difference between ages, with season ($F_{[6,18]} = 1.6$, $p = 0.21$) (Table 3). *Piloderma fallax* was about 49 times more likely to occur in a plot in an old-growth stand than in

Table 3. General mixed model results for likelihood ratio tests of whether the presence of *Piloderma fallax* in a plot was a function of stand age and whether this effect varied with season.

Source	Numerator df	Denominator df	*F* value	*p* > *F*
Age	2	6	53.91	<0.001
Time	3	18	1.54	0.237
Age × time	6	18	1.60	0.205

a plot in a young stand (95% confidence interval (CI) = 18.6–130.3) and 23 times more likely to occur in a plot in an old-growth stand than in a plot in a rotation-age stand (95% CI = 8.6–60.3). On average, *Piloderma fallax* was present in 57% of the plots in old-growth stands, but in only 6 and 1% of the plots in rotation-age and young stands, respectively (Table 2). Additionally, the probability of occurrence of *Piloderma fallax* within a stand of a particular age remained constant through all four measurement periods ($F_{[3,18]}$ = 1.54, p = 0.24) (Table 3).

The presence of CWD in decay class 5 was related to the presence of *Piloderma fallax* (χ_1^2 = 13.5, p = 0.0002) (Table 4). *Piloderma fallax* was approximately 2.5 times more likely to occur in a plot with CWD decay class 5 present than in one without (95% CI = 1.5–4.0). In addition, the presence of *Piloderma fallax* was related to the percent cover of CWD in decay class 5 (χ_1^2 = 10.32, p = 0.001) (Table 4). The probability that *Piloderma fallax* would occur in a plot increased by approximately 20% for every 10% increase in percent cover of CWD decay class 5 (95% CI = 7–35%). The presence of *Piloderma fallax* was not related to the presence of CWD in any of the other decay classes (p > 0.45 for all decay classes). Similarly, the presence of *Piloderma fallax* was not related to the percent cover of CWD in any of the other decay classes (p > 0.12 for all decay classes). There was no evidence of confounding of decay class 5 with any of the other decay classes (χ_1^2 < 2.6, p > 0.11 for all classes) among the 900 plots in the study.

Of the 900 plots measured, *Piloderma fallax* occurred in only 194 of them, 172 of these in old-growth stands. In most of these plots (157) CWD in decay class 5 was present, and its percent cover ranged from 1 to 90%; 86 plots had CWD in decay class 5 with percent cover of more than 10%. In contrast, none of the plots had CWD in decay classes 1 and 2 with more than 10% cover, and only 3 and 9 of the plots had CWD in decay classes 3 and 4, respectively, with more than 10% cover. The paucity of data in the lower decay classes made regression analysis of their relationship to *Piloderma fallax* impossible. The percent cover of *Piloderma fallax* was not related to the percent cover of CWD in decay class 5 on plots in which *Piloderma fallax* was found ($F_{[1,181]}$ = 0.74, p = 0.39).

The probability of occurrence of CWD in decay class 5 was strongly related to the age of the stand ($F_{[2,6]}$ = 22.92, p = 0.0016). Coarse woody debris in decay class 5 was approximately 2.4 times more likely to occur in an old-growth plot than in a rotation-age plot (95% CI = 1.6–3.8) and about 3.8 times more likely to occur in an old-growth plot than in a plot in a young stand (95% CI = 2.5–5.6). The overdispersion parameter was calculated as 1.15, giving no indication of extra variation nor that a binomial model was inappropriate for these data. About 75% (95% CI = 69–80) of the old-growth plots had CWD in decay class 5 whereas only 56% (95% CI = 38–51) of the rotation-age plots and 44% (95% CI = 49–62) of the plots in young stands had CWD in decay class 5 present.

Discussion

Species of *Piloderma*, including *Piloderma fallax* and *Piloderma byssinum*, are commonly associated with older stands (Danielson 1984; Agerer 1987–1997; Dighton et al. 1986; Chu-Chou and Grace 1988; Bradbury et al. 1998; Goodman and Trofymow 1998*a*, 1998*b*). In this study, *Piloderma fallax* occurred in 57% of the plots in old-growth, compared with only 6% in rotation-age and 1% in young Douglas-fir stands. In a similar study in Finland, *Piloderma fallax* occurred in more than 50% of plots in 80-year-old stands compared with 20–30% in 40- to 60-year-old stands and in less than 5% of plots in 20-year-old spruce stands (Mikola 1962). Bradbury et al. (1998) observed *Piloderma fallax* basidioma or colonized root tips in more than 30% of plots in 90-year-old, less than 5% of plots in 10- and 19-year-old, and none in 6-year-old lodgepole pine (*Pinus contorta* Loud.) stands. Similarly, *Piloderma byssinum* occupied 10% of Jack pine (*Pinus banksiana* Lamb.) root tips in 65- and 122-year-old stands compared with 0.2 and 0% in 41- and 6-year-old stands, respectively (Visser 1995). Kranabetter and Wylie (1998) found no *Piloderma fallax* colonization of western hemlock seedling roots in 4-year-old forest openings compared with 1.5% colonization under canopies of mature (140-year-old) and old-growth (350-year-old) western hemlock dominated stands. Goodman and Trofymow (1998*a*) observed similar mean numbers of *Piloderma fallax* colonized root tips in mature (approximately 90-year-old) and old-growth (288- and 441-year-old) stands of Douglas-fir.

In our study, *Piloderma fallax* was strongly associated with CWD decay class 5, suggesting factors other than tree age influence *Piloderma fallax* occurrence. However, CWD decay class 5 occurred most often in plots in old-growth stands, making it difficult to separate the influence of tree age from that of CWD decay class 5 on *Piloderma fallax* occurrence. Several studies show that soil processes are more important than tree processes to EM root tip development and sporocarp production (Baar and Kuyper 1993; Baar and ter Braak 1996; Baar 1997). In our study, the probability of finding *Piloderma fallax* was about 2.5 times higher in plots with CWD decay class 5 compared with plots without CWD decay class 5. Our data support observations that *Piloderma fallax* commonly occurs in rotten wood (Mikola 1962; Zak 1976; Kropp 1982; Agerer 1987–97; Goodman and Trofymow 1998*b*).

Large-scale disturbances, such as logging, are known to affect EM formation and basidioma and ascoma production in forests (Dighton and Mason 1985; Termorshuizen 1991; Vogt et al. 1992; Amaranthus et al. 1994; North et al. 1997; Waters et al. 1997; Kranabetter and Wylie 1998; Colgan et al. 1999) and likely influence the composition and distribution of *Piloderma fallax*. We found no relation between percent cover of CWD decay class 5 and percent cover of *Piloderma fallax*, implying that *Piloderma fallax* can occupy small or large pieces of habitat. Goodman and Trofymow

Table 4. Results from a generalized linear model to test whether the presence of *Piloderma fallax* was associated with the presence of coarse woody debris (CWD) of different decay classes and with the percent cover of CWD of different decay classes.

Source	χ_1^2	$p > \chi_1^2$
CWD present or absent		
CWD 1	0.222	0.638
CWD 2	0.317	0.574
CWD 3	0.485	0.486
CWD 4	0.058	0.810
CWD 5	13.539	<0.001
CWD % cover		
CWD 1	0.633	0.426
CWD 2	2.361	0.124
CWD 3	0.027	0.871
CWD 4	0.037	0.849
CWD 5	10.322	0.001

(1998*b*) report that they often found *Piloderma fallax* in small pieces of wood or bark. We found, however, that the likelihood of *Piloderma fallax* occurring in a plot increased by approximately 20% for every 10% increase in percent cover of CWD decay class 5.

The patchy distribution of *Piloderma fallax* in our study can be explained by a patchy distribution of suitable habitat (Dahlberg 1990; Bradbury et al. 1998). Coarse woody debris is unevenly distributed on the forest floor (Harmon et al. 1985; Spies and Cline 1988; Graham et al. 1994). Goodman and Trofymow (1998*b*) found *Piloderma fallax* absent, or nearly so, from mineral soil. Harvey et al. (1979, 1980*a*, 1980*b*) report a positive correlation between the occurrence of EM with CWD in advanced stages of decay in a study of EM distribution in mixed conifer forests in Idaho, Montana, Oregon, and Wyoming. Similarly, Amaranthus et al. (1994) report higher numbers and biomass of hypogeous fungi in a summer sample in plots with CWD rather than soil in a mature forest. The relation between amounts and patterns of distribution of large CWD and occurrence and dispersal of *Piloderma fallax* and other EM fungi that associate with CWD in advanced stages of decay warrants further investigation in various forest ecosystems to provide land managers with guidelines for leaving CWD necessary for ensuring persistence of EM fungi dependent on it.

It is particularly easy to confidently distinguish the diagnostically colored mycelia of *Piloderma fallax* in situ year-round, making it an attractive EM fungus for assessing soil conditions. It is well known that EM fungi are associated with particular habitat conditions, such as host species, forest age, and soil qualities (Harvey et al. 1979; Deacon et al. 1983; Mason et al. 1983; Luoma et al. 1991; Molina et al. 1992; Vogt et al. 1992; O'Dell et al. 1992; Richter and Bruhn 1993; Visser 1995; Simard et al. 1997; Gehring et al. 1998; Goodman and Trofymow 1998*a*, 1998*b*). However, the use of most species of EM fungi to indicate stand condition or development is problematic. Most EM species are most easily and positively identified by their basidioma or ascoma, and recognition is difficult from mycelia alone. However, molecular techniques such as polymerase chain reaction (PCR) and restriction fragment length polymorphism (RFLP) are facilitating the identification of EM fungi in the absence of basidioma or ascoma (Bruns and Gardes 1993; Gardes and Bruns 1993, 1996; Horton et al. 1998). Basidioma and ascoma production of most EM fungi fluctuates widely with variations in seasonal and annual weather patterns (Fogel 1976; Hunt and Trappe 1987; Luoma 1991; Luoma et al. 1991). The use of basidioma and ascoma as indicators of soil components, therefore requires long-term monitoring to obtain data sufficient to overcome the sporadic nature of basidioma and ascoma production.

No differences in the occurrence of *Piloderma fallax* were found among sampling seasons for any of the age classes in our study. These results suggest that surveys to detect the presence of *Piloderma fallax* may be conducted with similar results throughout the year, and that our sampling method adequately detected the distribution of *Piloderma fallax* in stands of different age classes of Douglas-fir.

The correlation between specific habitat conditions (e.g., decayed wood) and *Piloderma fallax* occurrence is a critical step toward determining the environmental and stand variables that influence the occurrence of *Piloderma fallax* and developing functional hypotheses of *Piloderma fallax* importance in ecosystem dynamics. Our observations suggest that *Piloderma fallax* may be important in assessing soil conditions suitable for functionally similar EM fungi that associate with CWD in advanced stages of decay. Forest management strategies currently emphasize protecting biodiversity while sustaining site productivity by maintaining old-growth components in young managed stands. Indicators of old-growth forest legacy in young managed stands will be useful for evaluating management plans for maintaining biodiversity. Indicator species can provide clues about the way in which community structure is changing (Magurran 1988). In our study and studies by Mikola (1962) and Goodman and Trofymow (1998*b*), *Piloderma fallax* occurred most often in soils with conifer components in advanced stages of decay. The similarity of these results regarding *Piloderma fallax* occurrence in different forest habitats—Douglas-fir in our study and that of Goodman and Trofymow (1998*b*) and spruce in Mikola's (1962) study—suggests the need to explore these trends in other forest habitats and establish frequency of occurrence parameters for *Piloderma fallax* for assessing old-growth habitat and fungal community dynamics. Additionally, studies further distinguishing stand age from CWD effects on *Piloderma fallax* occurrence are needed.

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