Chemistry and ectomycorrhizal communities of coarse wood in young and old-growth forests in the Cascade Range of Oregon

J.C. Elliott, J.E. Smith, K. Cromack Jr., H. Chen, and D. McKay

Abstract: Coarse wood provides important ecosystem structure and function such as water and nutrient storage and critical habitat for the conservation of a variety of organisms, including ectomycorrhizal (EM) fungi. The chemistry and EM communities were compared in coarse wood samples collected from two advanced decay stages of logs in 12 paired young and old-growth stands in the Oregon Cascade Range. Average total C and nonpolar extractives were higher in young stands (15–55 years) (mean = 53.38%, 95% CI of 52.48–54.27 and mean = 8.54%, 95% CI of 6.92–10.16, respectively) compared with old-growth stands (200–500 years) (mean = 51.22%, 95% CI of 49.67–52.77 and mean = 6.75%, 95% CI of 5.88–7.62, respectively). Averages for total and extractable P were higher in old-growth stands (mean = 0.03%, 95% CI of 0.02–0.04 and mean = 82.91, 95% CI of 52.24–113.57, respectively) compared with young stands (mean = 0.02%, 95% CI of 0.02–0.02 and mean = 56.17, 95% CI of 45.84–66.50, respectively). Average pH and total N were highest in logs in the most advanced decay stage (mean = 4.17, 95% CI of 3.97–4.38 and mean = 0.35%, 95% CI of 0.29–0.40, respectively). No differences between log decay class or stand age were detected for water-soluble extractives, hemicellulose plus cellulose (or acid-hydrolyzable fraction), or acid-unhydrolyzable residue. Observed differences in average wood property values between decay stages and between young and old-growth stands were small and, although statistically significant, may not reflect an important difference in EM fungal habitat. EM communities were similar between young and old-growth stands and between logs in decay classes 4 and 5. Results suggest that down wood in advanced decay stages provides similar habitat for EM fungi in both old-growth and young, managed stands.

Résumé : Les débris ligneux grossiers fournissent d'importantes structures et fonctions dans les écosystèmes telles que l'emmagasinage d'eau et de nutriments ainsi qu'un habitat crucial pour la conservation d'une variété d'organismes, incluant les champignons ectomycorhiziens (EM). Les caractéristiques chimiques et les communautés de champignons EM ont été comparées dans des échantillons de débris ligneux grossiers prélevés sur des billes à deux stades de décomposition avancée dans 12 paires de jeunes et de vieux peuplements situés dans la chaîne des Cascades en Oregon. Les quantités totales de C et de substances extractibles non polaires étaient en moyenne plus élevées dans les jeunes peuplements (15–55 ans) (moyenne 53,38 %, IC 95 % de 52,48 à 54,27 et moyenne 8,54 %, IC 95 % de 6,92 à 10,16, respectivement) que dans les vieux peuplements (200–500 ans) (moyenne 51,22 %, IC 95 % de 49,67 à 52,77 et moyenne 6,75 %, IC 95 % de 5,88 à 7,62, respectivement). Les moyennes pour les quantités de P total et extractible étaient plus élevées dans les vieux peuplements (moyenne 0,03 %, IC 95 % de 0,02 à 0,04 et moyenne 82,91, IC 95 % de 52,24 à 113,57, respectivement) comparativement aux jeunes peuplements (moyenne 0,02 %, IC 95 % de 0,02 à 0,02 et moyenne 56,17, IC 95 % de 45,84 à 66,50, respectivement). Le pH et la quantité totale de N étaient en moyenne les plus élevés dans les billes au stade de décomposition le plus avancé (moyenne 4,17, IC 95 % de 3,97 à 4,38 et moyenne 0,35 %, IC 95 % de 0,29 à 0,40, respectivement). Aucune différence entre les classes de décomposition des billes ou l'âge des peuplements n'a été détectée dans le cas des substances extractibles en solution aqueuse, des hémicelluloses et de la cellulose (ou fraction hydrolysable dans l'acide) ou des résidus non hydrolysables dans l'acide. Les différences observées dans la valeur moyenne des propriétés du bois entre les stades de décomposition et entre les jeunes et les vieux peuplements étaient faibles et, bien que statistiquement significatives, pourraient ne pas refléter une différence importante dans l'habitat des champignons EM. Les communautés de champignons EM étaient semblables dans les jeunes et les vieux peuplements ainsi que dans les billes dans les classes de décomposition 4 et 5. Les résultats indiquent que les débris ligneux à un stade de décomposition avancée fournissent des habitats similaires pour les champignons EM dans les peuplements aménagés, qu'ils soient vieux ou jeunes.

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Introduction

Down coarse wood is an important component of coniferous forest ecosystems that provides wildlife habitat (Maser et al. 1979), seedling microsites (Harmon and Franklin 1989), C, nutrient, and water reserves (Harmon et al. 1986; Sollins et al. 1987; Laiho and Prescott 2004), and substrate for saprobic and mycorrhizal fungi (Kropp 1982; Harmon et al. 1994; Smith et al. 2000). Coarse wood has been identified as a key feature for the survival of rare fungal species in boreal (Berg et al. 1994) and temperate forests (T.A. Dreisbach and J.E. Smith, unpublished data). Coarse wood decay patterns have been examined primarily in old-growth and mature stands (Sollins et al. 1987; Means et al. 1992; Goodman and Trofymow 1998*a*) or in large roots taken from trees cut within the last 50 years (Chen et al. 2001). Little is known about whether the decay patterns and physical and chemical properties of down coarse wood in young, managed stands are similar to those in old-growth stands. Forest management strategies in North America and Europe currently emphasize protecting biodiversity while sustaining site productivity by maintaining old-growth components, including coarse wood, in managed stands (Berg et al. 1994; Molina et al. 2006).

In natural ecosystems of the Pacific Northwest, old-growth stands (>200 years old) typically have the greatest coarse wood accumulation (Spies and Cline 1988; Janisch and Harmon 2002). Most coarse wood in young natural stands is residual coarse wood from the previous old-growth stand left after disturbances, such as fire, windthrow, and disease outbreak. A young, managed stand may have significantly less coarse wood than a natural, young stand (Spies and Cline 1988). Coarse wood is one of the slowest ecosystem components to recover after disturbance, taking up to 400 years (Spies et al. 1988). Coarse wood has higher C concentration, is less nutrient rich, holds larger amounts of water, and tends to have a lower pH than other forms of organic matter. Since coarse wood releases nutrients much more slowly than fine litter, nutrients can be retained in the ecosystem until tree production recovers following stand-replacing events (Harmon and Chen 1991).

Down coarse wood in various stages of decay influences fungal species occurrence and abundance (Harmon et al. 1994; Smith et al. 2000; Trappe 2004). Fungi perform critical functions in forest ecosystems including nutrient cycling, maintaining soil structure, and providing food for mammals and insects. While the role of decomposers has been extensively studied, the physical and chemical properties of coarse wood and their influence on the distribution of fungal species, particularly ectomycorrhizal (EM) species, are poorly understood. Some EM fungal species are found in close association with coarse wood in advanced decay stages or with late-successional stands, suggesting that specific habitat conditions may be critical to maintaining EM fungal diversity (Harvey et al. 1979; Goodman and Trofymow 1998*a*; Smith et al. 2000; Tedersoo et al. 2003). EM fungal diversity appears to be important to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) ecosystem resilience and function (Smith et al. 2002; Horton et al. 2005). The formation of active EM associations is dependent on the presence of inoculum as well as the physical and chemical properties of the substrate, whether it is wood or soil (Harvey et al. 1987). However, the content and type of organic matter are considered the most important properties influencing EM occurrence (Harvey et al. 1979; Tedersoo et al. 2003).

Most temperate forest tree species form a mutualistic, symbiotic relationship with EM fungi and depend on EM formation for normal function and survival (Smith and Read 1997). Ectomycorrhizas are best known for their ability to enhance P and water uptake by the host plant and also to aid in the uptake of other nutrients and to protect against root pathogens (Smith and Read 1997). Some EM species use complex organic N sources, including proteins (Abuzinadah and Read 1986; Finlay et al. 1992) and chitin (Leake and Read 1990). Numerous studies have shown the potential role of EM fungi in the degradation of complex detrital C sources (Entry et al. 1991; Durall et al. 1994; Bending and Read 1997); however, the mechanisms remain unclear (Cairney and Burke 1998).

Coarse wood is thought to be critical to the recruitment and retention of mature and old-growth associated EM species in young, managed stands (Harvey et al. 1976; Smith et al. 2000). Coarse wood may function as a moisture-retaining substrate, supporting plant roots and active EM in times of seasonal dryness (Harvey et al. 1987; Amaranthus et al. 1994). We hypothesized that EM species composition in logs in old-growth and young stands may differ because of differences in canopy cover that may influence temperature and log moisture content. The objectives of our study were to (*i*) determine if properties of logs in advanced decay stages differ between young and old-growth stands and between two stages of advanced decay and (*ii*) assess whether coarse wood in advanced decay stages in younger, managed stands supports an EM fungi community similar to that found in comparably decayed coarse wood in old-growth stands.

Methods

Study area

The study area, located along the west slope of the Cascade Range in the Willamette National Forest, extended about 65 km along a north-to-south transect from 80 km east of Albany, Oregon, on State Highway 20 to 90 km southeast of Eugene, Oregon. The area was divided into four regions, each with three sets of paired stands (12 paired stands, 24 stands total). Each pair consisted of one old-growth stand (200–500 years) and one young, managed stand (15–55 years). Paired stands were randomly selected from a list of 20 paired old-growth and young, managed stands. The stands in a pair were not more than 700 m apart. Most of the stands are within the *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) Zone (Franklin and Dyrness 1984) and are mesic to moist sites containing a mix of western hemlock and Douglas-fir (Table 1). Moist sites are typified by an understory that includes *Polystichum munitum* (Kaulf.) Presl and *Oxalis oregana* Nutt., mesic sites by *Berberis nervosa* Pursh and *Rhododendron macrophyllum* G. Don., and dry sites by *Gaultheria shallon* Pursh (Franklin and Dyrness 1984). Site elevations range from 600 to 1350 m; slope gradients range from 0% to 90%. Soils are mainly In-

Table 1. Location and characteristics of stands.

Location	Site name	Age class[a]	Canopy closure (%)	Elevation (m)	Aspect	Slope (%)	Plant association[b]
Sweet Home	BC	OG	85	1050	SSE	70	TSHE/BENE
		Y	60	1050	SSE	25	TSHE/BENE
	GLT	OG	70	850	N	10	TSHE/POMU
		Y	75	850	ENE	10	TSHE/POMU
	SODA	OG	50	650	E	90	TSHE/POMU
		Y	50	650	SE	90	TSHE/POMU
McKenzie	CR	OG	75	600	SE	35	TSHE/GASH
		Y	60	650	NE	20	TSHE/BENE–OXOR
	FP	OG	60	600		0	TSHE/BENE–GASH
		Y	90	600	NE	40	TSHE/BENE
	HL	OG	80	1050		0	TSHE/RHMA3/XETE
		Y	75	950	SE	<1	TSHE/RHMA3–BENE
H.J. Andrews	HJA	OG	75	800	SSE	10	TSHE/BENE
		Y	75	800	S	5	TSHE/LIBO3
	SC	OG	95	800	SE	15	TSHE/LIBO3
		Y	80	800	S	10	TSHE/LIBO3
	ULO	OG	90	850	S	30	TSHE/BENE
		Y	85	850	SW	15	TSHE/LIBO3
Middle Fork	GC	OG	75	1250	NE	10	ABAM–ABGR/MAST
		Y	75	1350	E	5	ABAM–ABGR/MAST
	SR	OG	90	900	W	<1	TSHE/ACTR
		Y	80	900	SW	3	TSHE/ACTR
	TM	OG	90	1050	W	25	TSHE/BENE
		Y	90	1050	N	40	TSHE/POMU

[a]Y, young (15–55 years); OG, old-growth (200–500 years).

[b]TSHE, *Tsuga heterophylla*; BENE, *Berberis nervosa*; GASH, *Gaultheria shallon*; PSME, *Pseudotsuga menziesii*; LIBO3, *Linnea borealis*; POMU, *Polystichum munitum*; ACTR, *Achlys triphylla*; RHMA3, *Rhododendron macrophyllum*; XETE, *Xerophyllum tenax*; OXOR, *Oxalis oregano*; ABAM, *Abies amabilis*; ABGR, *Abies grandis*; MAST, *Maianthemum stellatum* (McCain and Diaz 2002).

ceptisols with some areas of Alfisols (Franklin and Dyrness 1984). The climate is maritime with mild, wet winters, when most precipitation falls. Annual average precipitation ranges from 2300 mm at the lower elevations to 3550 mm at the higher elevations. Mean monthly temperatures range from 1 °C in January to 18 °C in July (430 m) (McKee and Bierlmaier 1987).

Experimental design and sampling procedures

A split-plot experimental design consisting of 12 sites (blocks) with paired young and old-growth stands was employed (Steel et al. 1997). The whole plots were the paired stands within a site in which wood chemistry, log moisture content, and canopy closure measurements were taken. Percent canopy closure, because of its influence on log moisture content, was estimated visually at each stand. The split-plots were the coarse wood samples collected from logs in two advanced decay stages. Two coarse wood samples, one each from decay class 4 or 5 logs, were collected from each stand in June 2002. Log decay class was based on visual criteria as described by Spies and Cline (1988), adapted from Maser et al. (1979).

Logs in decay classes 4 and 5 are entirely on, or sunken into, the ground and have no bark or limbs. Decay class 4 logs are round or oval and composed of small, soft, blocky pieces of light brown to reddish-brown wood, whereas decay class 5 logs are oval with softer wood and less structural integrity and are darker in color. Logs meeting the decay class criteria of >1 m in length and >30 cm in diameter and at least 50 m from the edge of the stand were randomly selected for sampling. A sliding hammer soil corer was used to obtain two adjacent coarse wood samples (5 cm diameter × 15 cm length) from each sampled log. These samples were collected in small plastic bags and stored at 4 °C for 2–3 weeks until analysis. One coarse wood sample was analyzed for physical and chemical properties and one for EM species composition.

Wood chemistry analysis

Coarse wood samples were weighed before and after oven-drying at 55 °C to calculate moisture content. Dried coarse wood samples were ground in a Wiley Mill to pass a No. 40 (0.4 mm) mesh screen for analysis of ash content, pH, total N, total P, total C, and major C fractions, including hemicellulose plus cellulose (acid-unhydrolyzable fraction (AHF)) and recalcitrant C (acid-unhydrolyzable residue (AUR)). This AUR previously was called "Klason lignin" (Valachovic et al. 2004). Ash content was determined by loss on ignition of 1 g samples at 550 °C for 5 h. Organic constituents are reported on an ash-free basis. Analysis of pH, total P, extractable P, total C, and total N was conducted by the Central Analytical Laboratory at Oregon State University. A 1:10 (sample–water) dilution was used for pH analysis, total P was determined by microwave digestion with ICP (inductive coupled plasma) determination, extractable P was determined by the Bray-1 P method using ammonium fluoride and hydrochloric acid, and total C and total N were determined by combustion using a LECO CNS-2000 (Sparks et al. 1996).

Carbon fractionation was accomplished by determination of (*i*) nonpolar extractives (NPE): fats and waxes, (*ii*) hot water soluble extractives (WSE): simple sugars, (*iii*) AHF, and (*iv*) AUR using forest products methods adapted from TAPPI (1975*a*, 1975*b*) and Chen et al. (2001). The C fractionation terminology follows the scheme presented in fig. 1 of Valachovic et al. (2004).

For determination of NPE, 1 g of sample and 30 mL of dichloromethane were added to a Gooch crucible and placed in a 100 mL beaker in a sonicating bath for 30 min, dichloromethane was removed by vacuum-filtration, and the sample was rinsed (10 mL of dichloromethane) and vacuum-filtered. This procedure was repeated a total of three times. The residual material was oven-dried overnight and weighed. For the WSE extraction, 500 mg of the remaining sample was placed in a BD-40 digestion tube with 35 mL of deionized water, boiled gently at approximately 100 °C for 3 h in a digestion block, vacuum-filtered through preashed and weighed Gooch crucibles, rinsed with deionized water several times, oven-dried overnight, and weighed. For determination of acid-soluble components, 200 mg of the previous sample and 2 mL of 72% sulfuric acid were placed in a 15 mL test tube and frequently stirred in a 30 °C water bath for 1 h, at which time incubation was ended with the addition of 6 mL of deionized water. The sample then was transferred to a 250 mL Erlenmeyer flask with 50 mL of water, covered with foil, autoclaved at 120 °C for 1 h for secondary hydrolysis, and vacuum-filtered through a preashed and weighed Gooch crucible. The remaining AUR was washed several times with deionized water, oven-dried overnight, and weighed.

Sorting and processing of ectomycorrhizas

Coarse wood samples were soaked in water to soften and facilitate breaking apart and picking through the core to obtain root tips embedded in the wood. A stereo dissecting microscope was used to sort ectomycorrhizas into morphological types (morphotypes) based primarily on color, mantle surface texture, rhizomorph presence or absence, and mycorrhizal branching pattern. Viability assessment of the root tips was based on color and turgidity (Harvey et al. 1976). Two root tips from each morphotype within a core sample were placed directly in cetyltrimethyl ammonium bromide (CTAB) buffer and stored at 4 °C.

Fungi and plants from ectomycorrhizas were identified by comparing restriction fragment length polymorphism (RFLP) patterns with those from voucher specimens of sporocarps or plant leaves. DNA extraction, polymerase chain reaction (PCR) amplifications, and RFLP protocols followed Gardes and Bruns (1993). DNA was extracted individually from at least two root tips from each morphotype within a core sample. About 90% of the 554 ectomycorrhizas yielded PCR product.

Identification of the plant symbiont was based on amplification of the 28S gene in the nuclear rRNA repeat using the plant-specific primer pair 28KJ and TW14 (Cullings 1992). Dominant tree species in the western hemlock zone, namely western hemlock and Douglas-fir, can be unambiguously differentiated with RFLP patterns generated when this gene region is digested with the restriction enzyme *Hinf* I (Horton et al. 2005). Fungal symbiont identification was based on amplification of the internal transcribed spacer (ITS) region of the nuclear rDNA using the fungal-specific primer pair

ITS-1f and ITS-4 (Gardes and Bruns 1993). Two restriction enzymes (*Dpn* II and *Hinf* I) in single-enzyme digests were used initially to characterize and match fungal ITS-RFLP patterns. Restriction fragments subsequently were separated on agarose gels (3% agarose) and visualized with ethidium bromide under ultraviolet light. All RFLPs were recorded using AlphaImager™. After visual assessment of the RFLP patterns and comparisons of morphotype descriptions and scores of the two restriction enzymes from all photographed images, potentially matching samples were run in adjacent lanes of the same agarose gel with three restriction enzymes (*Alu* I, *Dpn* II, and *Hinf* I) in single-enzyme digests. Identical RFLP matches with digests for all three endonucleases determined species-level identification. There is general correspondence between ITS-RFLP types and species (Gardes and Bruns 1996; Kårén et al. 1997).

Taxonomic identification was attempted for the majority of our RFLP types by sequencing both spacers of the ITS region of the nuclear ribosomal repeat and the intercalated 5.8S rRNA gene using primer pair ITS-1f and ITS-4 for amplification. The PCR products were cleaned using Qbiogene Geneclean®. Samples were sent to the Center for Gene Research and Biotechnology at Oregon State University for sequencing on an ABI 377 automated sequencer. The resulting sequences were edited in SeqEd (PE Biosystems) and aligned manually using PAUP 3.1 (Swofford 1993) and PAUP* (Swofford 1999) and a color font. A sequence similarity search of the National Center for Biotechnology Information (NCBI) database, GenBank, was conducted using the Basic Local Alignment Search Tool (BLAST) 2.0 algorithm.

Statistical analysis

The mean responses for 12 measured wood chemistry attributes (Table 2) were compared between old-growth and young stands and between logs of decay classes 4 and 5. The mean response for percent canopy closure was compared between old-growth and young stands using ANOVA. The ANOVA structure accounted for variation due to site and variation due to stand age for comparisons between decay classes. Two replicates of hemicellulose plus cellulose content were deleted from the data set because samples were destroyed in the laboratory procedures. Because AUR content is calculated using hemicellulose plus cellulose content, two measurements were likewise deleted from the two analyses for AUR. The final degrees of freedom for the hemicellulose plus cellulose and AUR analyses therefore are lower by 2 df compared with the other analyses. Results were considered significant at $p < 0.05$ and considered a statistical trend at $p < 0.1$. The variability inherent in field studies with smaller sample numbers affords practical value for using statistical trends at $p < 0.1$ (Steel et al. 1997). All computations were carried out with S-Plus version 2000 software (MathSoft 1988–2000).

Results

Canopy closure, log moisture content, and pH

Canopy closure did not differ between stand ages (Table 2). The average moisture content for logs in decay class 4 in young stands (mean = 326.50, SE = 12.65, n = 12) was greater than all other combinations of stand age and log decay class (mean = 260.26, SE = 14.06, n = 36) (Table 2). Average log moisture content (percent dry mass) varied from 248% for decay class 4 in old-growth stands to 326% for decay class 4 in young stands.

Average pH of logs differed between decay classes but not between stand ages (Table 2). There was no evidence of an interaction for pH between log decay class and stand age (Table 2). On average, over the two age classes, pH was slightly higher in logs in decay class 5 (mean = 4.17, 95% CI of 3.97–4.38) compared with logs in decay class 4 (mean = 3.91, 95% CI of 3.79–4.03) (Table 2).

Carbon constituents

Average total C content of logs differed between stand ages (Table 2). On average, over the log decay classes, average total C of logs was slightly higher in young stands (mean = 53.38%, 95% CI of 52.48–54.27) compared with old-growth stands (mean = 51.22%, 95% CI of 49.67–52.77) (Table 2). Average total C of logs did not differ between decay classes, and there was no evidence of an interaction between stand age and decay class (Table 2).

Average NPE content differed between stand ages (Table 2). On average, over the log decay classes, average NPE was slightly higher in young stands (mean = 8.54%, 95% CI of 6.92–10.16) compared with old-growth stands (mean = 6.75%, 95% CI of 5.88–7.62) (Table 2). Average NPE of logs did not differ between decay classes, and there was no evidence of an interaction between stand age and decay class (Table 2).

No differences were detected for WSE constituents, hemicellulose plus cellulose (AHF), or AUR content between stand ages or log decay classes (Table 2).

Nutrient content

On average, over the log decay classes, average total P was slightly higher in old-growth stands (mean = 0.03%, 95% CI of 0.02–0.04) compared with young stands (mean = 0.02%, 95% CI of 0.02–0.02) (Table 2). Although not significantly different, average total P tended to be greater in logs of decay class 5 than in logs of decay class 4 (Table 2). There was no evidence of an interaction between stand age and decay class (Table 2).

Average available P did not significantly differ between stand ages or decay classes, and there was no evidence of an interaction between stand age and decay class (Table 2).

On average, over stand age, average total N in logs was higher in decay class 5 (mean = 0.35%, 95% CI of 0.29–0.40) compared with decay class 4 (mean = 0.27%, 95% CI of 0.22–0.31) (Table 2). Average total N in logs did not significantly differ between stand ages, and there was no evidence of an interaction between stand age and decay class (Table 2).

The average N/P ratio in logs did not differ between decay classes or stand ages, and there was no evidence of an interaction between stand age and decay class (Table 2).

Average C/N ratio in logs was higher for decay class 4 (mean = 228, 95% CI of 192–265) compared with decay class 5 (mean = 174, 95% CI of 141–208) (Table 2). There was suggestive evidence of a stand age effect. The mean C/N ratio for logs in young stands (mean = 213, 95% CI of 179–247) was higher than that for logs in old-growth

Table 2. Physical and chemical characteristics of heavily decayed logs in the Willamette National Forest.

Stand age[a]	Decay class[b]	Water (% dry mass)	pH[c]	NPE (%)[d]	WSE (%)[d]	AHF (%)[d]	AUR (%)[d]
Old	4 and 5	258 (20)	4.00 (0.1)	6.75 (0.42)	8.12 (0.65)	25.4 (2.8)	59.4 (3.4)
Young	4 and 5	295 (12)	4.08 (0.06)	8.54 (0.78)	7.24 (0.33)	20.7 (1.9)	63.6 (2.2)
Old and young	4	287 (17)	3.91 (0.06)	8.06 (0.82)	7.44 (0.36)	24.6 (2.4)	59.8 (2.4)
Old and young	5	266 (16)	4.17 (0.10)	7.23 (0.42)	7.92 (0.64)	21.3 (2.4)	63.4 (3.1)
Old	4	248 (27)	3.88 (0.09)	6.93 (0.77)	7.64 (0.5)	27.1 (4.1)	58.0 (4.2)
Young	4	327 (13)	3.94 (0.07)	9.20 (1.4)	7.23 (0.52)	22.2 (2.8)	61.4 (2.7)
Old	5	268 (30)	4.12 (0.18)	6.57 (0.38)	8.59 (1.2)	23.7 (4.1)	60.9 (5.4)
Young	5	264 (15)	4.22 (0.09)	7.89 (0.73)	7.25 (0.41)	19.1 (2.7)	65.8 (3.4)
p (df = 1)							
Stand age		0.15	0.45	0.02	0.25	0.36	0.55
Decay class		0.18	0.02	0.38	0.51	0.13	0.19
Stand age × decay class		0.01	0.86	0.62	0.52	0.93	0.79

Note: Means are listed with standard errors in parentheses.

[a]Stand age: old, 200–500 years; young, 15–55 years.
[b]Decay class is assigned by visual criteria based on Spies and Cline (1988), as adapted from Maser et al. (1979).
[c]pH is for a 1:10 (sample–water) dilution.
[d]NPE (nonpolar extractives), WSE (water-soluble extractives), AHF (cellulose and hemicellulose), and AUR (lignin) are reported on an ash-free basis.
[e]AUR (acid-unhydrolyzable residue)/N.

stands (mean = 190, 95% CI of 151–229). There was no evidence of an interaction between stand age and decay class for the C/N ratio (Table 2).

The average ratio of recalcitrant C (AUR)/N in logs did not differ between decay class or stand age, and there was no evidence of an interaction between stand age and decay class (Table 2).

EM species richness and community patterns

Seventy-five RFLP taxa were distinguished on the roots. Of these, 50 were identified to genus or family (Table 3) and one matched a sporocarp collection of *Lactarius pseudomucidus* Hesler and Smith (JS4948) based on RFLP patterns and DNA sequences. RFLP species belonged to the Russulaceae (13 species), Atheliaceae (11 species), Cortinariaceae (eight species), Thelephoraceae (seven species), Corticiaceae (five species), Cantharellaceae (two species), *Cenococcum* (two species), and Boletaceae and Tricholomataceae (each with one species). *Piloderma* (10 species) and *Russula* (eight species) were the most species-rich genera detected. A similar number of RFLP species occurred in young and old-growth stands (42 and 43, respectively) (Table 3). Only 10 RFLP species were common to both young and old-growth stands; however, most genera comprised species equally distributed between young and old-growth stands (Table 3). Even though most (51) RFLP species were detected in only one paired-stand site, 10 species showed a broader geographic range, occurring in at least three of the four regions and in 25% or more of the paired-stand sites. *Cenococcum* species (RFLP 23), *Lactarius pseudomucidus* (RFLP 79), and *Piloderma* species (RFLP 3) each occurred in more than half of the 12 paired-stand sites, and Corticiaceae (RFLP 47), *Craterellus* species (RFLP 67), and *Russula* species (RFLP 8) each were detected in five of the paired-stand sites. With our sampling effort, a similar number of species were detected per region (range 25–34), with, on average, 11 species (SE = 0.27) per paired-stand site. One third more of the RFLP species were detected in logs in decay class 5 compared with logs in decay class 4 (55 and 36, respectively) and about twice as many of the RFLP species were detected on western hemlock roots compared with Douglas-fir roots (55 and 26, respectively).

Discussion

We found that coarse wood in advanced decay stages has similar physical and chemical properties in both old-growth and young, managed stands in the western Cascade Range of Oregon. These results suggest that coarse wood in advanced decay stages provides suitable habitat for organisms associated with such old-growth legacy, regardless of whether it is in old-growth or young, managed stands. Most physical and chemical properties also did not differ between logs in decay classes 4 and 5. Although analyses detected statistically significant differences for some coarse wood properties between young and old-growth stands and between logs in decay classes 4 and 5, the differences were slight and likely do not represent biological differences that would influence fungal species occurrence.

The interception of precipitation by tree canopies is known to influence log moisture content (Berg et al. 2000). Canopy closure did not differ between young and old-growth stands in our study. However, the average moisture content for logs in decay class 4 in young stands was about 20% greater than for all other combinations of stand age and log decay class. This difference in log moisture may be an artifact of our one-time sampling effort. Means et al. (1992) reported that log moisture content varies throughout the year and that logs in advanced decay stages hold more water at dry times of the year than less decayed logs. Similar to our findings in most combinations of stand age and log decay class, Sollins et al. (1987) found no difference in the water content of logs between decay classes 4 and 5. Values for average moisture content of logs in our study are similar to those reported by Sollins et al. (1987) and Means et al. (1992) for logs in advanced decay stages in old-growth

Bray P (μg/g)	Total P (%)	Total C (%)	Total N (%)	C/N	N/P	AUR/N[e]	Canopy closure (%)
82.9 (14.3)	0.03 (0.00)	51.2 (0.8)	0.33 (0.03)	190 (19)	13 (0.8)	244 (32)	78 (4)
56.2 (5.0)	0.02 (0.00)	53.4 (0.4)	0.28 (0.02)	213 (17)	14 (0.3)	254 (21)	75 (4)
57.6 (8.3)	0.02 (0.00)	52.6 (0.5)	0.27 (0.02)	228 (18)	13 (0.5)	272 (27)	
81.5 (13.4)	0.03 (0.00)	52.0 (0.8)	0.35 (0.03)	174 (16)	13 (0.7)	227 (27)	
67.3 (15)	0.03 (0.00)	51.7 (0.5)	0.30 (0.03)	197 (22)	13 (0.9)	243 (34)	
47.8 (7.5)	0.02 (0.00)	53.4 (0.7)	0.23 (0.03)	260 (25)	14 (0.4)	301 (34)	
98.5 (25.7)	0.03 (0.01)	50.8 (1.4)	0.36 (0.05)	182 (31)	13 (1.3)	246 (51)	
64.5 (6.0)	0.02 (0.00)	53.2 (0.5)	0.33 (0.02)	166 (10)	14 (0.4)	208 (19)	
0.09	0.04	0.05	0.07	0.06	0.36	0.89	0.41
0.14	0.06	0.38	0.03	0.03	0.90	0.51	
0.65	0.96	0.73	0.53	0.10	0.91	0.58	

stands along the west slope of Oregon's Cascade Range. Decayed logs provide ideal substrate for EM formations across various site conditions, in part due to the large water-holding capacity of decayed wood (Harvey et al. 1979).

Average pH values for logs (about pH 4) in our study are more basic, by about 1 unit, than those reported by Goodman and Trofymow (1998*a*) for logs in mature and old-growth Douglas-fir-dominated stands on southeastern Vancouver Island and more acidic, by about 1 unit, than those reported by Harvey et al. (1979) for logs in Douglas-fir, western hemlock, and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests in northwestern Montana. High relative moisture and low relative pH values found in decayed wood compared with fine litter, humus, and mineral soil enhance EM formation and activity, emphasizing the importance of down wood to ecosystem function (Harvey et al. 1979).

Obtaining accurate values for nutrient concentrations is important for understanding decay processes of organic matter and mycorrhizal colonization of decomposing wood. Average total C concentrations of logs in our study (about 50%) are comparable to values reported in previous studies for logs in advanced decay stages in mature and old-growth forests (Sollins et al. 1987; Means et al. 1992; Goodman and Trofymow 1998*a*). Nitrogen concentration in logs levels off above decay class 4, suggesting that there is a net N accumulation in logs undergoing advanced decay by various ecosystem processes (Sollins et al. 1987). Nitrogen concentrations for logs in decay classes 4 and 5 in our study are similar to those reported by Sollins et al. (1987). Average total N concentrations for logs in our project were nearly 50% higher, and consequently the C/N ratios were considerably lower, than values reported by Means et al. (1992). Reasons for these differences may include the use of different total N analysis methods, the study area's location, and the research design. Another source of variation is the wide range in time of decay for logs in advanced decay stages.

Total N affects C/N, availability and quality of N, and the presence of some species of ectomycorrhizas. Sollins et al. (1987) and Means et al. (1992) used the Kjeldahl method for total N determination, while we used combustion. Prietzel et al. (1997) showed that combustion resulted in a 5% increase in total N measured when compared with the Kjeldahl method for forest floor material. Given that Sollins et al. (1987) used Kjeldahl and still reported N values similar to ours may be a result of an increased digestion time during the Kjeldahl procedure. Holub et al. (2001) addressed another source of error in determining nutrient concentrations by correcting for mass lost during decomposition and also recommended the use of isotopic or conservative element tracers. For elements such as N, much could be learned about EM fungal use of this element through ^{15}N labeling during advanced log decay stages.

The AUR/N ratio is considered a better predictor of litter decomposition than the C/N ratio (Preston et al. 2000; Trofymow et al. 2002). Our average AUR/N values for logs in advanced decay stages are about one and one-half times higher than those reported by Chen et al. (2001) for large (5–10 cm) woody roots of western hemlock excavated from stumps with ages of up to 46 years. Conversely, our values for average AHF concentration and the C/N ratio in coarse wood were lower than those reported by Chen et al. (2001) for roots. Our values for AUR and AHF concentrations are similar to those reported by Means et al. (1992). Values for C concentration, NPE%, and WSE% are similar to those reported for large woody roots (Chen et al. 2001).

Results of our study suggest that coarse wood in advanced decay stages in young, managed stands provides habitat suitable for EM species associated with coarse wood in old-growth stands. A similar number of EM RFLP species were detected in logs in advanced decay stages in young and old-growth stands, and about one third more EM RFLP species were detected in logs in decay class 5 compared with decay class 4. Our sampling of the EM communities showed an overall similarity between young and old-growth stands and between logs in decay classes 4 and 5 for most taxa groups (Corticiaceae, *Lactarius*, *Piloderma*, *Russula*, and Thelephor-

Table 3. Occurrence within stands (n = 12) by age class and by log decay class of ectomycorrhizal RFLP species.

	Stand age class		Log decay	
Taxonomic identification	Old-growth	Young	Class 4	Class 5
Atheliaceae (RFLP 40)[a]	0	1	0	1
Cenococcum (RFLP 23)[a]	3	6	3	6
Cenococcum (RFLP 34)[a]	0	2	0	2
Corticiaceae (RFLP 13)[a]	0	1	1	0
Corticiaceae (RFLP 46)[a]	1	0	0	1
Corticiaceae (RFLP 47)[a]	4	2	5	3
Corticiaceae (RFLP 58)[a]	1	0	1	0
Corticiaceae (RFLP 59)[a]	1	0	1	0
Cortinarius sp. (RFLP 12)[a]	1	0	0	1
Cortinarius sp. (RFLP 61)[a]	0	1	0	1
Craterellus sp. (RFLP 38)[a]	0	2	2	0
Craterellus sp. (RFLP 67)[a]	1	1	2	3
Dermocybe sp. (RFLP 32)[a]	1	0	1	0
Dermocybe sp. (RFLP 50)[a]	0	1	0	1
Inocybe sp. (RFLP 49)[a]	1	0	1	0
Inocybe sp. (RFLP 55)[a]	0	1	0	1
Inocybe sp. (RFLP 57)[a]	2	0	1	2
Inocybe sp. (RFLP 81)[a]	0	1	1	0
Lactarius sp. (RFLP 17)[a]	2	0	0	2
Lactarius sp. (RFLP 21)[a]	0	1	1	0
Lactarius sp. (RFLP 28)[a]	1	2	2	1
Lactarius sp. (RFLP 70)[a]	0	1	0	1
Inocybe sp. (RFLP 81)[a]	0	1	1	0
Lactarius sp. (RFLP 17)[a]	2	0	0	2
Lactarius sp. (RFLP 21)[a]	0	1	1	0
Lactarius sp. (RFLP 28)[a]	1	2	2	1
Lactarius sp. (RFLP 70)[a]	0	1	0	1
Lactarius pseudomucidus (RFLP 79)[a,b] No. JS4948	2	6	5	4
Piloderma sp. (RFLP 1)[a]	1	0	1	0
Piloderma sp. (RFLP 3)[a]	4	5	5	5
Piloderma sp. (RFLP 19)[a]	1	0	1	0
Piloderma sp. (RFLP 20)[a]	2	0	0	2
Piloderma sp. (RFLP 33)[a]	0	1	1	0
Piloderma sp. (RFLP 39)[a]	1	0	0	1
Piloderma sp. (RFLP 41)[a]	0	1	0	1
Piloderma sp. (RFLP 66)[a]	1	0	1	0
Piloderma sp. (RFLP 75)[a]	0	1	0	1
Piloderma sp. (RFLP 78)[a]	0	1	1	0
Rhizopogon sp. (RFLP 10)[a]	0	1	0	1
Russula sp. (RFLP 2)[a]	1	0	0	1
Russula sp. (RFLP 8)[a]	5	3	5	4
Russula sp. (RFLP 18)[a]	1	0	0	1
Russula sp. (RFLP 51)[a]	0	1	0	1
Russula sp. (RFLP 69)[a]	1	0	0	1
Russula sp. (RFLP 77)[a]	1	0	0	1
Russula sp. (RFLP 87)[a]	2	0	1	1
Russula sp. (RFLP 88)[a]	2	0	1	1
Thelephora sp. (RFLP 4)[a]	2	1	1	2
Thelephora sp. (RFLP 9)[a]	2	0	0	2
Thelephora sp. (RFLP 14)[a]	2	2	3	0
Thelephoraceae (RFLP 76)[a]	0	1	1	0
Tomentella sp. (RFLP 42)[a]	0	2	2	2
Tomentella sp. (RFLP 62)[a]	0	1	0	1
Tomentella sp. (RFLP 68)[a]	0	2	1	1
Tricholomataceae (RFLP 15)[a]	3	1	1	3
Unknown (RFLP 6)	1	0	0	1

Table 3 (*concluded*).

Taxonomic identification	Stand age class		Log decay	
	Old-growth	Young	Class 4	Class 5
Unknown (RFLP 7)	0	1	0	1
Unknown (RFLP 24)	1	0	0	1
Unknown (RFLP 26)	0	2	0	2
Unknown (RFLP 27)	1	0	0	1
Unknown (RFLP 29)	1	0	1	0
Unknown (RFLP 30)	0	1	0	1
Unknown (RFLP 31)	0	1	0	1
Unknown (RFLP 35)	1	0	0	1
Unknown (RFLP 44)	0	1	0	1
Unknown (RFLP 45)	0	1	1	0
Unknown (RFLP 48)	2	0	2	0
Unknown (RFLP 54)	1	0	0	1
Unknown (RFLP 60)	2	0	1	1
Unknown (RFLP 64)	0	1	0	1
Unknown (RFLP 65)	0	1	0	1
Unknown (RFLP 71)	1	0	0	1
Unknown (RFLP 72)	1	0	1	0
Unknown (RFLP 73)	3	0	3	0
Unknown (RFLP 80)	0	1	0	1
Unknown (RFLP 82)	0	1	0	1
Unknown (RFLP 83)	1	0	0	1
Unknown (RFLP 84)	0	1	0	1
Unknown (RFLP 85)	1	0	1	0
Unknown (RFLP 86)	0	1	0	1

[a]RFLP species identified by nucleotide sequencing of the ribosomal DNA.
[b]RFLP species identified by RFLP matching of EM and sporocarp.

aceae) containing five or more RFLP species. *Russula* species, however, were most often found in old-growth stands and in logs in decay class 5 (Table 3). The most species-rich EM genera in our study, *Piloderma* and *Russula*, are typically abundant in mature and late-successional stands of temperate forests where large down wood in advanced decay stages is common (Goodman and Trofymow 1998*a*, 1998*b*; Smith et al. 2000, 2002; Bergemann and Miller 2002). Similar to our findings, Tedersoo et al. (2003) showed a strong preference of resupinate thelephoroid and athelioid fungi for coarse wood. Indeed, species of many of the genera detected in our study have been reported to be associated with coarse wood and old-growth forests (Goodman and Trofymow 1998*b*; Smith et al. 2002). As reported in other studies, our sample of the EM community showed high abundance of species of Russulales and Thelephorales (Horton and Bruns 2001; Dickie et al. 2002; Lilleskov et al. 2002).

Coarse wood in advanced decay stages is often more abundant in old-growth forests than in younger, managed stands, making it difficult to separate the influence of tree age from that of coarse wood on EM fungal occurrence (Smith et al. 2000). Trappe (2004), however, found that both stand age and the volume of decay class 4 and 5 coarse wood were significant in determining the probability of *Craterellus tubaeformis* (Fries) Quélet occurrence in stands with western hemlock. Recent studies showed that soil conditions and substrate layers affect EM fungal diversity and fine-scale distribution (Dickie et al. 2002; Rosling et al. 2003; Tedersoo et al. 2003). Given that as much as half of the fungal diversity may be restricted to mineral soil (Rosling et al. 2003) further suggests a specialized EM fungal community in coarse wood. Furthermore, Lilleskov et al. (2002) demonstrated the importance of soil chemistry to EM diversity, showing a change in EM community structure and decline in EM species richness along a gradient of increasing N deposition.

Western hemlock roots were twice as likely as Douglas-fir roots to be detected in the logs. Western hemlock seedlings commonly establish on logs in advanced decay stages, sending their roots down into the coarse wood (Harmon and Franklin 1989). In contrast, Douglas-fir establishes in mineral soil (Franklin and Dyrness 1984), suggesting that roots of Douglas-fir were growing upward into the logs for nutrients or moisture. We may have detected a greater percentage of western hemlock roots compared with Douglas-fir roots because our core samples were taken from the tops of logs.

Overall, we found that only a few variables differed significantly between advanced decay stages (pH, total N, C/N) and between stand age (total C, total P, NPE) and that differences between mean values for these variables were small. Coarse wood in decay class 4 or 5 in young and old stands appears to provide a similar substrate for organisms that associate with it. Large-scale factors (e.g., stand density, understory vegetation, coarse wood abundance) or dispersal mechanisms have been suggested to influence old-growth-associated EM species occurrence in coarse wood more strongly than wood chemistry (Luoma et al. 1991; Goodman and Trofymow 1998*a*). Goodman and Trofymow (1998*a*) reported the absence of a strong correlation between the presence of EM fungi and the chemistry of mineral soil, wood, or fine litter, suggesting that the micro-

habitat of the rhizosphere or soil biota may have a stronger influence on the fungi than the bulk substrate chemistry. Proximity to old-growth legacy is thought to explain the similar EM communities found by Goodman and Trofymow (1998*b*) in adjacent old-growth and mature stands of Douglas-fir. Our results suggest, nevertheless, that forest management strategies that maintain old-growth components (e.g., coarse wood) in young, managed stands have the potential to conserve biodiversity through retention and recruitment of old-growth-associated EM species in young, managed stands.

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