Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (*Pseudotsuga menziesii*) in the Cascade Range of Oregon, U.S.A.

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Abstract: Knowledge of the community structure of ectomycorrhizal fungi among successional forest age-classes is critical for conserving fungal species diversity. Hypogeous and epigeous sporocarps were collected from three replicate stands in each of three forest age-classes (young, rotation-age, and old-growth) of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated stands with mesic plant association groups. Over four fall and three spring seasons, 48 hypogeous and 215 epigeous species or species groups were collected from sample areas of 6300 and 43 700 m^2, respectively. Cumulative richness of hypogeous and epigeous species was similar among age-classes but differed between seasons. Thirty-six percent of the species were unique to an age-class: 50 species to old-growth, 19 to rotation-age, and 25 to young stands. Seventeen species (eight hypogeous and nine epigeous) accounted for 79% of the total sporocarp biomass; two hypogeous species, *Gautieria monticola* Harkn., and *Hysterangium crassirhachis* Zeller and Dodge, accounted for 41%. Average sporocarp biomass in young and rotation-age stands compared with old-growth stands was about three times greater for hypogeous sporocarps and six times greater for epigeous sporocarps. Average hypogeous sporocarp biomass was about 2.4 times greater in spring compared with fall and for epigeous sporocarps about 146 times greater in fall compared with spring. Results demonstrated differences in ectomycorrhizal fungal sporocarp abundance and species composition among successional forest age-classes.

Key words: ectomycorrhizal fungi, sporocarp production, forest succession, *Pseudotsuga menziesii*, *Tsuga heterophylla* zone, biodiversity.

Résumé : La connaissance de la structure des communautés de champignons ectomycorhiziens au sein des classes d'âge dans la succession forestière est critique pour la conservation de la diversité des espèces. Les auteurs ont récolté les sporocarpes hypogés et épigés dans trois répliques de peuplements pour chacune de trois classes d'âge (jeune, âge de rotation et surannée), dominés par le Douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco), avec des groupes d'associations végétales mésiques. Au cours de quatre automnes et trois printemps, les auteurs ont récolté 48 espèces hypogées et 215 espèces épigées (ou groupes d'espèces) à partir de places échantillons ayant des superficies de 6300 m^2 et 43 700 m^2, respectivement. La richesse cumulée en espèces hypogées et épigées est semblable au sein des classes d'âge, mais diffère avec les saisons. Trente-six pour cent des espèces sont liées à une classe d'âge : 50 espèces aux forêts surannées, 19 aux forêts en âge de rotation et 25 aux jeunes forêts. Dix-sept espèces (8 hypogées, 9 épigées) constituent 79% de la biomasse totale en sporocarpes; deux espèces hypogées, le *Gautiera monticola* Harkn. et l'*Hysterangium crassirhachis* Zeller et Dodge, en représentent 41%. Comparativement aux forêts surannées, la biomasse moyenne des sporocarpes dans les peuplements jeunes ou en âge de rotation est environ 3 fois plus grande pour les sporocarpes hypogés et 6 fois plus grande pour les sporocarpes épigés. La biomasse moyenne des sporocarpes hypogés est environ 2.4 fois plus grande au printemps qu'à

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l'automne, et pour les sporocarpes épigés, environ 146 fois plus grande à l'automne qu'au printemps. Les résultats démontrent qu'il y a des différences dans l'abondance en sporocarpes des champignons ectomycorhiziens et dans la composition en espèces, entre les classes d'âges de la succession forestière.

Mots clés : champignons ectomycorhiziens, production de sporocarpes, succession forestière, *Pseudotsuga menziesii*, zone du *Tsuga heterophylla*, biodiversitée.

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Introduction

Knowledge about community structure and dynamics of ectomycorrhizal (EM) fungi in natural environments is limited. Many factors influence EM fungal community structure, including host plant species composition and stand age, habitat conditions, and edaphic factors (Molina and Trappe 1982; Deacon et al. 1983; Molina et al. 1992; Vogt et al. 1992; Visser 1995; States and Gaud 1997; Gehring et al. 1998; Claridge et al. 2000; Smith et al. 2000). Down wood in various stages of decay influences fungal species occurrence and abundance (Harmon et al. 1994; Smith et al. 2000). Changes in plant species composition from forest succession or large-scale disturbances significantly affect EM species composition and total sporocarp production (Cooke 1955; Dighton and Mason 1985; Arnolds 1988, 1991; Termorshuizen 1991; Vogt et al. 1992; Amaranthus et al. 1994; Visser 1995; North et al. 1997; Waters et al. 1997; Baar et al. 1999; Colgan et al. 1999).

EM fungal succession in forest types worldwide typically is measured by repeated observations of sporocarp occurrence as young stands age and by identifying and quantifying sporocarps in stands of different ages (Deacon et al. 1983; Dighton and Mason 1985; Dighton et al. 1986; Arnolds 1991; Luoma et al. 1991; Termorshuizen 1991; O'Dell et al. 1992; Amaranthus et al. 1994; Clarkson and Mills 1994). In the Pacific Northwestern region of North America, efforts to characterize EM fungal communities have been ongoing for only about the last two decades and have focused mostly on sporocarps of hypogeous fungi in forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Fogel 1976; Fogel and Hunt 1979; Hunt and Trappe 1987; Luoma et al. 1991; Amaranthus et al. 1994; Clarkson and Mills 1994; North et al. 1997; Cazares et al. 1999; Colgan et al. 1999) and to a lesser extent by true fir (*Abies* spp.) (Vogt et al. 1981; Waters et al. 1997). Epigeous sporocarps were recorded in the *Pinus ponderosa* (Dougl.), *Pseudotsuga taxifolia* (Mayr.) Shaw, and *Thuja–Tsuga* forest vegetation zones by Cooke (1955), in the *Abies amabilis* Dougl. ex Forbes zone by Ammirati et al. (1994), and in the *Tsuga heterophylla* (Raf.) Sarg. zone by O'Dell et al. (1999). Most studies comparing EM fungal sporocarp communities among successional forest age-classes have lacked replication of forest age-classes (Vogt et al. 1981; Luoma et al. 1991) or sampling years (O'Dell et al. 1992; Amaranthus et al. 1994; Clarkson and Mills 1994). Only a few published studies include both hypogeous and epigeous EM species richness and abundance in successional age-classes of forests (O'Dell et al. 1992; North et al. 1997).

Most field data on EM fungal species ecology are based on occurrence of sporocarps. Sporocarp studies are the primary bases for understanding ecosystem food web functions involving mammals and insects (Maser et al. 1978; Ingham and Molina 1991) and for documenting fungal diversity. Sporocarp studies of EM fungal communities typically underrepresent belowground EM fungal diversity (Gardes and Bruns 1996; Dahlberg et al. 1997; Kårén et al. 1997; Gehring et al. 1998; Jonsson et al. 1999; Horton and Bruns 2001) but are essential for discerning rare species that form obvious sporocarps. Current conservation efforts regarding EM fungi (Arnolds 1989; Castellano et al. 1999; Molina et al. 2001) rely on comparison of current with historic sporocarp data to identify trends in fungal communities and develop conservation strategies.

Most studies on EM fungal succession in forest communities also have used sporocarp presence and production to measure changes and reflect dominance. Studies of old field succession focused on sporocarps observed near parent trees of various ages (Last et al. 1984; Dighton et al. 1986) and explored factors such as soil and tree age responsible for observed patterns (see review by Deacon and Fleming 1992). Fungal community dynamics are less well understood in forest succession where vegetation dynamics shape community recovery. For example, the rapid reestablishment of pioneering EM host plants can maintain late-seral EM fungi (Perry et al. 1989; Molina et al. 1992). Many fungi are present throughout forest stand development, although their abundance and dominance may change with time or disturbance (Visser 1995; Molina et al. 1999). Comprehensive studies of fungal succession are needed in many forest types to improve understanding of fungal community dynamics.

Federal land management agencies in the Pacific Northwestern region of the United States are concerned about the effects of forest management practices on conservation of fungal species, particularly species associated with diminishing old-growth forests. Plant species richness tends to remain constant or increase slowly with forest age-class in some physiographic provinces in the region (Spies 1991). In contrast, the response of fungal communities to forest succession is largely unknown. The accurate comparison of mycological data in harvested and unharvested forests is essential for determining diversity patterns of fungi, making science-based decisions regarding conservation of fungi (O'Dell et al. 1996; Molina et al. 2001), and developing models for predicting fungal species occurrence (Dreisbach et al. 2002).

Table 1. Description of stands in and adjacent to the H.J. Andrews Experimental Forest, Oregon.

Site name	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
Ref. 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, Oreg. 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 (more than 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.

Our study was designed to examine changes in species richness, abundance, and composition of both hypogeous and epigeous EM sporocarps among successional forest age-classes of Douglas-fir in mesic stands of the *Tsuga heterophylla* zone. Our primary study objectives were to determine (*i*) if EM fungal species richness increases with stand age, (*ii*) whether EM fungal species composition and dominance shift as forest stands age, and (*iii*) whether some EM fungal species are closely associated with old-growth stands. Seasonal dichotomy in fruiting patterns, typical of the Pacific Northwest (Fogel 1976; Hunt and Trappe 1987; Luoma 1991; Luoma et al. 1991), influences interpretation of species composition and dominance. Consequently, we examine seasonal variation in hypogeous and epigeous sporocarp occurrence. We present data concerning the influence of forest age on fungal sporocarp production in nine forest stands that range in age from 30 to more than 400 years.

Methods

Study area

The study area was located in and adjacent to the H.J. Andrews Experimental Forest, 80 km east of Eugene, Oregon, in the Willamette National Forest (Lane and Linn counties) along the west slope of the Cascade Range of Oregon. The climate is maritime with mild, wet winters and warm, dry summers. Temperatures range from –2°C (mean January minima) to 28°C (mean July maxima). Annual precipitation is about 230 cm, with about 90% falling between October and April (McKee and Bierlmaier 1987). Winter snowpacks above 900 m elevation 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). Soils are mainly Inceptisols (Brown and Parsons 1973; Franklin and Dyrness 1984). Parent materials are basalt and andesite (Franklin and Dyrness 1984).

Nine 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 selected stands encompassed a range of mesic plant association groups for the *Tsuga heterophylla* zone (Franklin and Dyrness 1984) and were dominated by Douglas-fir with western hemlock (*Tsuga heterophylla*) and Oregon grape (*Berberis nervosa* Pursh) in the understory. Stand data and plant association groups are presented in 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 shows a dominance of swordfern (*Polystichum munitum* (Kaulf.) Presl) and Oregon oxalis (*Oxalis oregana* Nutt.), mesic sites by Oregon grape and Pacific rhododendron (*Rhododendron macrophyllum* G. Don.), and dry sites by salal (*Gaultheria shallon* Pursh) and ocean spray (*Holodiscus discolor* (Pursh) Maxim.) (Franklin and Dyrness 1984). Elevations of our stands ranged from 430 to 1000 m (Table 1). Slope gradients ranged from 0 to 35°.

The study examined three age-classes: young with closed canopy (30–35 years), rotation-age (ready for harvest, 45–50 years), and old-growth (more than 400 years) (Table 1). The most rapid growth period in forest development is the first 50 years. Thus, even though a relatively small number of years separate the age-classes defined as rotation-age and young, differences in stand development, stem density, and tree size are evident (Table 1). Mean annual increment is approaching or at its peak in the young age-class whereas it is steady or declining in the rotation-age. The rotation-age stands have reached maturity from a forest economic definition (steady or decreasing mean annual increment) but do not meet the ecological criteria of mature stands in age or structure (Spies and Franklin 1991). The young and rotation-age stands 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.

Experimental design and sampling procedures

The study design is a completely randomized design with three replications (stands) of each of the three treat-

Table 2. Total and average cumulative number of species or species groups by habit, season, and age-class (95% CI in parentheses).

Habit and season	No. of taxa	Cumulative no. of taxa by age-class		
		Old-growth	Rotation-age	Young
Hypogeous total (over all seven seasons)	48	17.0 (11.7, 22.3)	17.3 (12.1, 22.6)	17.3 (12.1, 22.6)
Epigeous total (over all seven seasons)	215	62.7 (54.9, 70.4)	57.7 (49.9, 65.4)	57.7 (49.9, 65.4)
Epigeous permanent strip plots	125	29.7 (19.0, 40.3)	38.0 (27.3, 48.7)	41.3 (30.7, 52.0)
Epigeous temporary strip plots	104	26.0 (19.2, 32.8)	33.7 (26.9, 40.5)	27.3 (20.5, 34.1)
Hypogeous, fall	26	10.7 (7.7, 13.6)	10.3 (7.4, 13.3)	7.7 (4.7, 10.6)
Hypogeous, spring	34	12.0 (9.0, 15.0)	11.3 (8.3, 14.3)	13.0 (10.0, 16.0)
Epigeous, fall	212	61.3 (55.0, 67.6)	54.3 (48.0, 60.6)	55.0 (48.7, 61.3)
Epigeous, spring	21	2.0 (–4.3, 8.3)	8.7 (2.4, 15.0)	5.0 (0.0, 11.6)
Total	263			

ments (young, rotation-age, and old-growth). All stands were sampled for hypogeous and epigeous sporocarps seven times (fall 1991, spring 1992, fall 1992, spring 1993, fall 1993, spring 1994, and fall 1994). Sampling was terminated due to the partial harvest of rotation-age stands in 1995. Each measurement period occurred within 3 weeks for all stands and constituted a "stand sample". A stand sample refers to the total collection area for a given stand at a given seasonal harvest in a given year (Luoma et al. 1991). Sporocarp sampling coincided with the peak of seasonal fruiting as determined from weather reports, reports of field cooperators, and known sporocarp phenology (Smith 1975; Fogel 1976). Sampling was conducted in both spring and fall to capture the seasonal dichotomy in fruiting patterns. Sporocarp production and diversity vary annually, so stands were sampled over a period of several years to detect fluctuations. Volunteers worked in teams led by professional mycologists.

For each sample period, hypogeous and epigeous sporocarps were collected from each of 25 circular plots (4 m^2) within each stand. A sporocarp collection comprised one to several sporocarps of the same species within about a 20-cm radius on a single circular plot. In each stand, plots were distributed along three systematically placed transects of eight, nine, and eight plots each (modified from Luoma et al. 1991). Transects were stratified by upper, middle, and lower slope position. Plots were placed cross-slope at 25-m intervals along each transect. Circular plots were raked with hand tools to a depth of at least 5 cm into mineral soil to expose hypogeous sporocarps. Raking also exposed not yet emergent epigeous sporocarps, which also were collected. All plots were marked to avoid repeat sampling of the same area in subsequent seasons. Raked substrate was replaced. Hypogeous sporocarps were collected from a total area of 6300 m^2.

Epigeous sporocarps were also collected from a total area of 700 m^2 per stand per collecting season from six strip plots (2 × 50 m) and from the circular plots (described above). Strip plots for epigeous sporocarps were narrow in width to avoid trampling in the plot when collections were made. Three permanent strip plots were randomly placed within each stand. Collections from permanent strip plots comprised one to several epigeous sporocarps of the same species from each 1 m^2 of the permanent plots. Three temporary strip plots were positioned in the upper, middle, and lower slopes of each stand and were placed cross-slope. Temporary strip plots were stratified by slope position and moved each sampling season. Temporary strip plots provided increased sample area coverage throughout each stand. Collections from temporary strip plots comprised one to several epigeous sporocarps of the same species within about a 20-cm radius from along each temporary plot. In fall 1994, snow prevented sampling of four strip plots (two temporary and one permanent strip plot in a rotation-age stand and one permanent strip plot in a young stand). Epigeous sporocarps were collected from a total area of 43 700 m^2.

Specimen identification and processing

At the end of each field day, notes about fresh characters were recorded and collections identified to the taxonomic level possible without the use of a compound microscope. Collections were dried in portable or on-site dehydrators for between 12 and 24 h and later weighed in the laboratory to the nearest 0.01 g.

Further identification of collections, typically to species level, was accomplished in the laboratory. Collections belonging to genera not adequately monographed for the western United States were placed into species complexes or groups. Representative voucher collections of each identified species were accessioned into the Oregon State University Herbarium.

Genera that were problematic because of a lack of regional taxonomic materials and abundant fruiting included *Cortinarius*, *Inocybe*, and *Russula*. Fresh collections of these genera were placed in broad subgenera or species groups according to Arora (1986). Dried collections of *Cortinarius* (about 20%) and *Inocybe* (about 10%) were examined with compound microscopy to estimate the number of species within each group. *Cortinarius* collections were identified by use of Ammirati (1983) and *Inocybe* collections by use of Stuntz (1965), Moser (1983), and Kuyper (1986). Nearly all dried collections of *Russula* were examined with compound microscopy and identified using the keys of Woo (1993) and Thiers (1994, 1997*a*, 1997*b*) (see Smith and Lebel 2001).

Analysis

β *diversity between stands*

The Sorenson index, designed to equal 1 in cases of complete similarity and 0 if the sites are dissimilar and have no

species in common, was used to measure β diversity (Magurran 1988). Similarity coefficients for species between all pairs of stands were assessed to examine the effects of aspect or environmental conditions compared with stand age.

Total and average cumulative species richness

The numbers of hypogeous and epigeous species or species groups found were tallied separately for the four fall and three spring collecting seasons to provide a measure of the cumulative seasonal richness in a stand. Because some species fruit in both spring and fall, a separate assessment was made of the total number of species or species groups found on a stand throughout the seven seasons of sampling.

Average cumulative richness was analyzed separately for hypogeous and epigeous fungi in a one-way analysis of variance, with age-class (young, rotation-age, and old-growth) as the single factor. No transformations of the data were necessary to meet model assumptions. Analysis was conducted by using the SAS v. 7.0 MIXED procedure (SAS Institute Inc. 1996).

Average seasonal cumulative richness was analyzed separately for hypogeous and epigeous fungi in a weighted (4 years for fall and 3 years for spring) two-way analysis of variance, with season (fall and spring) and age (young, rotation-age, and old-growth) as the two factors. No transformations of the data were necessary to meet model assumptions. Analysis was conducted using the SAS v. 7.0 MIXED procedure (SAS Institute Inc. 1996).

Chi-square tests were used to compare numbers of species or species groups unique to the different age-classes and found in more than one stand.

Sporocarp biomass and frequency

Sporocarp production for each stand sample was calculated by summing hypogeous and epigeous sporocarp biomass for each visit and standardizing the values to kilograms per hectare for reporting habitat and seasonal results. The masses of all hypogeous and epigeous sporocarps found in fall were averaged over the four fall collecting seasons. Similarly, the masses of all hypogeous and epigeous sporocarps found in spring were averaged over the three spring collecting seasons. Average seasonal sporocarp biomass was analyzed separately for hypogeous and epigeous sporocarps in a weighted two-way analysis of variance, with season (fall and spring) and age-class (young, rotation-age, and old-growth) as the two factors. The number of seasons over which sporocarp production measurements were taken were the weights (4 years for fall and 3 years for spring). Data were log transformed to stabilize variance. Analysis was conducted using the SAS v. 7.0 MIXED procedure (SAS Institute Inc. 1996).

The total sporocarp biomass for a species in a season or age-class category was divided by the appropriate fraction of a hectare sampled in that category to obtain equivalent sporocarp biomass on a grams dry mass per hectare basis. Relative species importance was measured by sporocarp biomass. Following Luoma et al. (1991), dominant species or genera that are ≥5% of the total sporocarp biomass are considered "major" species or genera and those that are ≥1% of the total are considered "important".

Frequency of occurrence for the dominant species was determined as a percentage of the total number of stand samples (9 stands × 7 seasons = 63). Similarly, frequency of occurrence within age-classes was determined as a percentage of the total number of stand samples within an age-class (3 stands × 7 seasons = 21).

Results

Species richness

Overall patterns

During the course of the study, 263 species or species groups (48 hypogeous and 215 epigeous) within 51 genera (26 hypogeous and 25 epigeous) were recorded from 4590 collections (1069 hypogeous and 3521 epigeous) (Tables 2, 3, and 4). Forty-one of the genera belonged to the Basidiomycotina, nine to the Ascomycotina, and one to the Zygomycotina. One hypogeous genus and one species each of *Russula* and *Rhizopogon* were new to science.

The greatest number of collections belonged to the genera *Cortinarius*, *Inocybe*, and *Russula* (508, 1022, and 739, respectively) and accounted for 49% of the total collections and about 52% of the total species. Eight subgenera of *Cortinarius* were separated into 21 macroscopic subgroups and 81 species, eight broad species groups of *Inocybe* were separated into 12 subgroups and 31 species, and the genus *Russula* was separated into 25 species or species groups (Table 3).

Cumulative species richness increased more rapidly during the course of the study for epigeous compared with hypogeous species or species groups (Fig. 1). In Fig. 1, epigeous species groups were counted once for each sampling period in which they were found, resulting in a conservative estimate that is slightly less than the total number of species or species groups identified in the study. Curves for epigeous species or species group richness appeared to approach an asymptote in spring 1994 and then increased in fall 1994. The curve for hypogeous species richness began to level out in fall 1993 at 3600 m^2 with 39 species total.

β diversity between stands

Stand age had a greater effect than aspect or environmental conditions on species similarity. Stand richness ranged from 12 to 22 for hypogeous species and from 54 to 72 for epigeous species or species groups. β diversity between pairs of stands within age-classes (0.56–0.68) and between pairs of young and rotation-age stands (0.58–0.68) was higher than comparisons between pairs of young and old-growth stands (0.41–0.48) and pairs of rotation-age and old-growth stands (0.43–0.54) (Fig. 2). The rotation-age stand most similar to the old-growth stands in environmental conditions (Table 1) did not differ from the other rotation-age stands (0.68) (Fig. 2).

Age-class and seasonal comparisons

Hypogeous species richness totaled 28 each in the old-growth and rotation-age-classes; 27 species were found in the young age-class. In old-growth stands, 105 epigeous species or species groups were found compared with 83 in rotation-age and 86 in young stands.

Table 3. List of species or species groups, percent biomass within each age-class, and occurrence by season.

	Age-class*			Season†	
Species	OG	RA	Y	Fall	Spring
Epigeous taxa					
Amanita aspera			+	1‡	
Amanita muscaria, yellow	+	+			2
Amanita pantherina		+	+	1	1
Amanita porphyria		+			1‡
Amanita silvicola	+			1‡	
Boletus chrysenteron gp.		+			1‡
Boletus mirabilis	+		+	2	
Boletus piperatus	+		+	4	
Boletus subtomentosus		+		2	
Boletus zelleri	+	+	+	1	
Camarophyllus borealis			+	1‡	
Cantharellus formosus	2	2	4	4	
Cantharellus subalbidus	1			2	
Chroogomphus tomentosus	1	+	+	4	
Clavariadelphus ligula	+			2	
Clavariadelphus mucronatus	+			2	
Clavulina sp.	+			1	
Cortinarius subgp. *Bulbopodium* (4 species)	+§	+§	+§	3	1
Cortinarius calyptratus	+	+	+	2	
Cortinarius subgp. *Bulbopodium*-1	+			1	
Cortinarius subgp. *Cortinarius*: *C. violaceus*	+			2	
Cortinarius subgp. *Dermocybe* (5 species)	+§	+§	+§	3	
Dermocybe cinnamomeus gp.		+		1	
Dermocybe sanguinea	+	+	+	2	
Dermocybe semisanguinea			+	1‡	
Cortinarius subgp. *Leprocybe* (9 species)	+§	+§	+§	2	
Cortinarius cotoneus	+		+	2	
Cortinarius subgp. *Leprocybe*-1	+			1	
Cortinarius subgp. *Leprocybe*-2	+	+	+	3	
Cortinarius subgp. *Myxacium* (4 species)	+§	+§	+§	2	
Cortinarius* subgp. *Phlegmacium (17 species)	3§	2§	+§	4	2
Cortinarius latus var. *brevisporus*	+			1	
***Cortinarius* cf. *multiformis* gp.**	3	+	+	3	
Cortinarius subgp. *Phlegmacium*-1	+	+		3	
Cortinarius subgp. *Phlegmacium*-2		+	+	2	
Cortinarius subgp. *Phlegmacium*-3		+		2	
Cortinarius subgp. *Phlegmacium*-4			+	1‡	
Cortinarius subgp. *Sericeocybe* (8 species)	+§	+§	+§	4	
Cortinarius cf. *alboviolaceus* gp.	+		+	1	
Cortinarius cf. *anomalus*	+	+		2	
Cortinarius subgp. *Sericeocybe*-3	+§	+§	+§	2	
Cortinarius traganus		+		1‡	
Cortinarius* subgp. *Telamonia (33 species)	2§	+§	+§	3	2
Cortinarius cf. *langier*	+			1‡	
Cortinarius subgp. *Telamonia*-1		+		1	
Cortinarius subgp. *Telamonia*-2	+	+	+	1	
Gomphidius glutinosus		+		1‡	
Gomphidius subroseus	+	2	2	3	
Gomphus clavatus	+			1‡	
Gomphus floccosus	+			1‡	
Hebeloma crustuliniforme	+	+	1	4	1
Hebeloma mesophaeum gp.		+	+	2	
Hebeloma cf. *sacchariolens*	+	+	+	2	

Table 3 (*continued*).

Species	Age-class*			Season†	
	OG	RA	Y	Fall	Spring
Hydnum umbilicatum	+		+	2	1
Hygrocybe flavescens			+	1‡	
Hygrocybe laeta	+				1‡
Hygrocybe miniata	+			1‡	
Hygrophorus agathosmus			+	1‡	
Hygrophorus bakerensis	+			2	
Hygrophorus cf. *calyptraeformis*		+			1‡
Hygrophorus cf. *camarophyllus*	+			1‡	
Hygrophorus chrysodon			+	1‡	
Hygrophorus eburneus		+		1	
Inocybe cf. *lanuginosa* (7 species)	+§	+§	+§	3	2
Inocybe cf. *lanuginosa*-1	+	+	+	3	2
Inocybe cf. *lanuginosa*-2	+	+	+	3	
Inocybe cf. *lanuginosa*-3	+	+	+	3	
***Inocybe geophylla* gp.** (3 species)	+	2	1	3	1
Inocybe maculata gp.: *I.* cf. *lanatodisca*			+	1‡	
***Inocybe mixtilis* gp.** (3 species)		2	1	3	3
Inocybe pudica gp. (3 species)	+	+	+	3	
Inocybe pyriodora gp. (1 species)		+		1‡	
Inocybe sororia gp. (22 species)	+§	+§	+§	3	3
Inocybe sororia-1		+	+	3	2
Inocybe suaveolens gp. (1 species)			+		2
Laccaria amethysteo-occidentalis gp.	+	+	+	2	
Laccaria bicolor			+	1‡	
Laccaria laccata	+	+	+	2	
Lactarius alnicola gp.	+		+	1	
Lactarius deliciosus		+	+	1	1
Lactarius fallax			+	1‡	
Lactarius pallescens	+			2	
Lactarius pseudodeceptivus	+			1‡	
Lactarius pseudomucidus	+	+	+	2	
Lactarius rubrilacteus	+	3	**6**	3	1
Lactarius scrobiculatus gp.	+	+	+	2	
Lactarius subflammeus			+	1‡	
Lactarius vinaceorufescens	+	+	+	2	
Paxillus atrotomentosus		+		1‡	
Paxillus involutus	+			1‡	
Phaeocollybia sp.	+	+		1	
Phylloporus rhodoxanthus	+	+	+	1	1
Ramaria acrisiccesscens	+			1‡	
Ramaria celerivirescens	+			2	
Ramaria claviramulata	+			1‡	
Ramaria cystidiophora v. *fabiolens*	+			1‡	
Ramaria fennica	+			1	
Ramaria formosa	+			2	
Ramaria sandaracina v. *sandaracina*	+			1‡	
Ramaria gp. 1	+			1	
***Ramaria* gp. 2**	4	+		3	
***Ramaria* gp. 3A**	2			2	
Ramaria gp. 3B	+			1	
Ramaria gp. 3C	+			1	
***Ramaria* gp. 4**	2			2	
Ramaria stuntzii	+			1‡	
Ramaria subbotrytis	+			1	
Russula aeruginea	+	+	+	3	

Table 3 (*continued*).

Species	Age-class*			Season†	
	OG	RA	Y	Fall	Spring
Russula albidula	+		+	2	
Russula albonigra	**5**	+	+	4	
***Russula alutacea* gp.**	+	2	3	3	
Russula amoenolens		+	+	1	
Russula brevipes	3	1		3	
Russula cascadensis	+	+		2	
Russula cerolens gp.	+	+	+	2	
***Russula cessans* gp.**	+	1	2	3	
Russula cf. *cyanoxantha*	+	+	+	2	
Russula cremoricolor			+	1	
Russula crenulata	3	+	+	1	
Russula decolorans	+	+		2	
Russula densifolia	2	+	+	1	
Russula dissimulans	+	+		1	
Russula ellenae	+	+	+	1	
Russula fragilis	+	+	+	3	
Russula fragrantissima	4		+	2	
Russula gracilis			+	1‡	
Russula integra gp.	+	+	+	3	
Russula laurocerai	+			1	
Russula pectinatoides			+	1‡	
Russula placita			+	1‡	
Russula sanguinea	+			2	
Russula sp.nov. "B"		+	+	1	
Suillus lakei	+	2	**8**	3	
Suillus ponderosus	+		1	2	
Thelephora terrestris gp.		+	+	2	
Tricholoma cf. *aestuans*	+			1‡	
Tricholoma flavovirens		+		1	
Tricholoma pardinum	+			1‡	
Tricholoma saponaceum	+			1	
Tricholoma sulphureum	+	+		2	
Tricholoma terreum gp.		+	+	2	
Tricholoma virgatum gp.	+			1‡	
Hypogeous species					
Alpova trappei			+		2
Balsamia magnata			+		1‡
Barssia oregonensis			+		2
Cortinomyces sublilacinus	+				1‡
Elaphomyces granulatus	**12**	+	+	3	2
Elaphomyces muricatus	+	+		2	1
Endogone lactiflua	+	+	+		2
Gautieria caudata		+		1‡	
Gautieria monticola	2	**23**	**15**	3	3
gen.nov.		+		1‡	
Genabea cerebriformis		+	+		2
Genea intermedia		+			1‡
Geopora cooperi var. *cooperi*			+	3	
Hydnoplicata gautierioides			+		1
Hydnotrya variiformis	+		+		2
Hymenogaster F2514			+		1
Hysterangium aureum			+		1‡
Hysterangium coriaceum	3	4	4	1	3
Hysterangium crassirhachis	1	**26**	**32**	4	3
Hysterangium setchellii	3	**6**	1	4	3

Table 3 (*concluded*).

Species	Age-class*			Season†	
	OG	RA	Y	Fall	Spring
Leucogaster rubescens	2	+	+	2	3
Leucophleps levispora	+	+			2
Leucophleps magnata	2	+			2
Martellia ellipsospora	+				1‡
Martellia subochracea		+			1
Melanogaster tuberiformis			+		2
Pyrenogaster atrogleba		+	+		3
Radiigera fuscogleba		+	+		3
Radiigera taylori	+	+	1	1	3
Rhizopogon cf. *exiquus*			+	1‡	
Rhizpopgon gilkeyae	+				1
Rhizopogon hawkerae	+	+	+	1	
Rhizopogon parksii	4	2	3	4	
Rhizopogon sp.nov.	+				1
Rhizopogon subcaerulescens	1	+		2	1
Rhizopogon subclavitisporus	+			1	2
Rhizopogon villescens	+			1	1
Rhizopogon villosulus	1	+		2	
Rhizopogon vinicolor	**10**	4	3	3	3
Scleroderma fuscum		+		1‡	
Truncocolumella citrina	2	1	2	4	
Tuber californicum	+				1
Tuber gibbosum		+	+	2	
Tuber monticola	+			1‡	
Tuber shearii	+			1‡	
Tuber sp. nov.		+		1‡	
Tuber sphaerosporum	+				1‡
Zelleromyces gilkeyae		+	+	3	

Note: Estimated number of species for *Cortinarius* and *Inocybe* groups are listed in parentheses. Dominant species or species groups within an age-class are shown in bold.

*Percentage of biomass for species is calculated by the total biomass for each age-class (biomass ≥5% shown in bold; + represents occurrence of <1%). OG, old-growth; RA, rotation-age; Y, young.

†Number of seasons species occurred; maximum four falls and three springs.

‡Single collection.

§Biomass of all collections in this subgenus category.

Average cumulative richness, measured over seven seasons, did not differ among age-classes for hypogeous species ($F_{[2,6]}$ = 0.01, p = 0.99) or epigeous species or species groups ($F_{[2,6]}$ = 0.83, p = 0.48) (Table 2). The average cumulative richness of epigeous species or species groups also did not differ among age-classes when collected only from permanent strip plots ($F_{[2,6]}$ = 1.90, p = 0.23) or only from temporary strip plots ($F_{[2,6]}$ = 2.17, p = 0.20) (Table 2).

Average seasonal cumulative richness of hypogeous species in stands was found to differ among age-classes ($F_{[2,6]}$ = 14.27, p = 0.005). Seasonal richness of hypogeous species was similar in old-growth and rotation-age stands (Table 2). Seasonal richness of hypogeous species in young stands was lower in fall and higher in spring than richness in the other two age-classes (Table 2). In young stands, there were, on average, five species more in spring compared with fall (Table 2).

Average seasonal cumulative richness of epigeous species or species groups in a stand differed between seasons ($F_{[1,6]}$ = 539.59, p < 0.0001) but not among age-classes ($F_{[2,6]}$ = 0.18, p = 0.84). There was no evidence of an interaction between season and age-class ($F_{[2,6]}$ = 3.34, p = 0.11). Within any age-class, about 50 more epigeous species or species groups were found in the fall compared with spring (95% confidence interval (CI) = 46.1–57.0) (Table 2).

Sporocarp production

Hypogeous sporocarp production

Hypogeous sporocarps yielded 2.44 kg/ha over all stand samples: 1.43 kg/ha in fall and 3.8 kg/ha in spring. The maximum single stand sample for hypogeous sporocarps was 10.9 kg/ha from a young stand in spring.

Average seasonal biomass of hypogeous sporocarps in a stand differed among age-classes ($F_{[2,6]}$ = 5.33, p = 0.047) and between seasons ($F_{[2,6]}$ = 9.37, p = 0.022). There was no strong evidence of an interaction among these factors ($F_{[2,6]}$ = 2.90, p = 0.131). Within a season, young and rotation-age stands had similar average biomass (Table 5). These yields were about three times greater (t_6 = 3.13, p = 0.020, 95% CI = 1.28–7.61) than that of old-growth stands in the same season (Table 5). Within any age-class, average biomass of hypogeous sporocarps in spring was about 2.4 times greater (t_6 = 3.06, p = 0.022, 95% CI = 1.19–4.72) compared with fall (Table 5).

Table 4. Total percent biomass and percent biomass within each age-class by genus.

Genus	% of total	% of age-class biomass OG	RA	Y
Epigeous				
Amanita	+	+	+	+
Boletus	+	1	+	+
Camarophyllus	+			+
Cantharellus	3	3	2	4
Chroogomphus	+	1	+	+
Clavariadelphus	+	+		
Clavulina	+	+		
Cortinarius	3	**6**	3	2
Gomphidius	2	+	2	2
Gomphus	+	+		
Hebeloma	1	+	1	1
Hydnum	+	+		+
Hygrocybe	+	+		+
Hygrophorus	+	+	+	+
Inocybe	4	+	**5**	3
Laccaria	+	+	+	+
Lactarius	**5**	1	4	**7**
Paxillus	+	+	+	
Phaeocollybia	+	+	+	
Phylloporus	+	+	+	+
Ramaria	2	**11**	+	
Russula	**11**	**23**	**10**	7
Suillus	**5**	+	2	**9**
Thelephora	+		+	+
Tricholoma	+	+	1	+
Hypogeous				
Alpova	+			+
Balsamia	+			+
Barssia	+			+
Cortinomyces	+	+		
Elaphomyces	2	**13**	+	+
Endogone	+	+	+	+
Gautieria	**16**	2	**23**	**15**
gen.nov	+		+	
Genabea	+		+	+
Genea	+		+	
Geopora	+			+
Hydnoplicata	+			+
Hydnotrya	+	+		+
Hymenogaster	+			+
Hysterangium	**32**	**7**	**36**	**37**
Leucogaster	+	2	+	+
Leucophleps	+	2	+	
Martellia	+	+	+	
Melanogaster	+			+
Pyrenogaster	+		+	+
Radiigera	+	+	+	1
Rhizopogon	**9**	**21**	**7**	**6**
Scleroderma	+		+	
Truncolumella	2	2	1	2
Tuber	+	+	+	2
Zelleromyces	+		+	+

Note: Dominant genera within an age-class are shown in bold. Percentage of biomass for genera is calculated by the total biomass for each age-class (biomass ≥5% shown in bold; + represents occurrence of <1%). OG, old-growth; RA, rotation age; Y, young.

Overall, hypogeous sporocarps were found in 37% of the 1575 circular plots. Hypogeous sporocarps were found in 27% of the plots in old-growth stands compared with 44% in rotation-age and 42% in young stands. Hypogeous sporocarps were found in 52% of the plots in spring compared with 26% in fall.

Epigeous sporocarp production

Epigeous sporocarps yielded 1.6 kg/ha over all stand samples: 2.8 kg/ha in fall and 0.04 kg/ha in spring. The maximum single stand sample for epigeous sporocarps was 14.7 kg/ha from a young stand in fall.

Average seasonal biomass of epigeous sporocarps in a stand differed among age-classes ($F_{[2,6]} = 6.82$, $p = 0.029$) and between seasons ($F_{[2,6]} = 120.55$, $p < 0.0001$). There was a weak interaction between age-class and season ($F_{[2,6]} = 3.41$, $p = 0.102$). Within a season, young and rotation-age stands had similar average biomass (Table 5). These yields were about six times greater ($t_6 = 3.68$, $p = 0.010$, 95% CI = 1.81–19.14) than that of old-growth stands (Table 5). Within any age-class, average biomass of epigeous sporocarps was about 146 times greater in fall ($t_6 = 10.96$, $p < 0.0001$, 95% CI = 48.0–444.0) compared with spring (Table 5).

Seasonal comparison of total sporocarp production

The majority of species in our study showed strong seasonal variation in relative sporocarp biomass. Similar sporocarp biomass was produced in fall (53%) and spring (47%) for combined hypogeous and epigeous sporocarps. Sporocarp biomass in fall was about twice as great for epigeous compared with hypogeous sporocarps and in spring about 84 times greater for hypogeous compared with epigeous sporocarps.

Dominant genera and species

Four major genera (*Gautieria*, *Hysterangium*, *Rhizopogon*, and *Russula*) comprised 68% of the total biomass; *Hysterangium*, *Rhizopogon*, and *Russula* were dominant in all age-classes (Table 4). Most of the dominant genera differed in relative percentage of biomass among the stand age-classes (Table 4). *Cortinarius*, *Elaphomyces*, *Ramaria*, *Rhizopogon*, and *Russula* all had a higher percentage of the biomass in the old-growth stands than in the young and rotation-age stands. In contrast, *Gautieria* and *Inocybe* had a higher percentage of the biomass in the rotation-age and, to a lesser extent, the young stands compared with the old-growth stands. *Hysterangium* had a higher percentage of the biomass in both the young and rotation-age stands compared with the old-growth stands. *Lactarius* and *Suillus* both had a higher percentage of the biomass in the young and, to a lesser extent, rotation-age stands compared with old-growth stands.

Seventeen important species (nine epigeous and eight hypogeous) within 11 genera accounted for 79% of the total sporocarp biomass; two major species (*Gautieria monticola* Harkn. and *Hysterangium crassirhachis* Zeller and Dodge) accounted for 41% (Table 6). Summaries are provided separately for the important epigeous and hypogeous species (Appendix A) to facilitate comparison of results from this study with study results where only epigeous or hypogeous sporocarps were reported.

Fig. 1. Cumulative number of species or species groups by plot type. Epigeous species groups with multiple species were counted once each sample time that they occurred. Cumulative number of species or species groups is largely a function of time on permanent strip plots and a function of both time and area on temporary strip plots and circular plots. Epigeous species or species groups were collected from a total area of 18 700 m^2 each on temporary and permanent strip plots. Hypogeous species were collected from a total area of 6300 m^2 on circular plots.

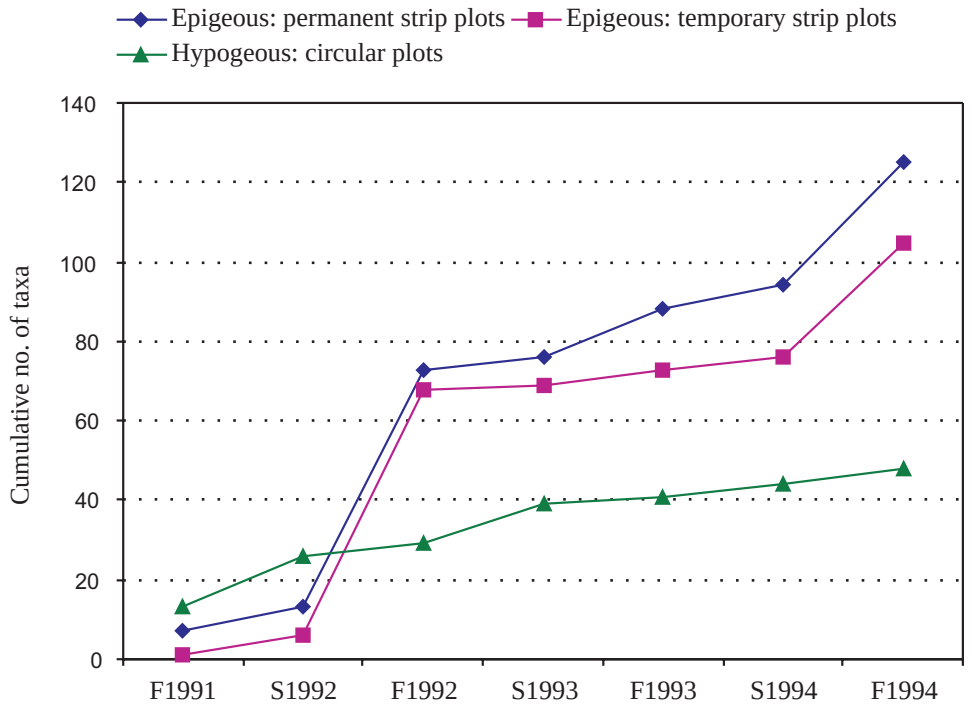

Fig. 2. Matrix showing β diversity between pairs of stands. Unshaded, similarity coefficients from the Sorenson index; shaded, number of species in common; Y, young; RA, rotation-age; OG, old-growth.

	Y: L104	**Y:** L201	**Y:** L202	**RA:** MC1	**RA:** MC2	**RA:** MC3	**OG:** SC	**OG:** ST15	**OG:** ULO
Y: L104	1.00	54	43	50	48	44	35	38	34
Y: L201	0.66	1.00	46	52	52	45	36	40	35
Y: L202	0.59	0.67	1.00	41	45	42	29	34	32
RA: MC1	0.60	0.66	0.59	1.00	53	45	40	40	32
RA: MC2	0.59	0.68	0.66	0.68	1.00	48	36	40	39
RA: MC3	0.58	0.63	0.67	0.68	0.68	1.00	34	34	39
OG: SC	0.43	0.46	0.42	0.51	0.47	0.47	1.00	49	44
OG: ST15	0.43	0.48	0.45	0.47	0.48	0.43	0.58	1.00	50
OG: ULO	0.41	0.45	0.46	0.46	0.50	0.54	0.56	0.59	1.00

The 17 important species comprised 86 and 82% of the biomass in young and rotation-age stands, respectively, compared with only 46% in old-growth stands (Table 6). *Elaphomyces granulatus* Fr. and *Rhizopogon vinicolor* Smith were major biomass dominants in old-growth stands, *Gautieria monticola*, *Hysterangium crassirhachis*, and *Hysterangium setchellii* Fischer were major biomass dominants in rotation-age stands, and *Gautieria monticola*, *Hysterangium crassirhachis*, *Lactarius rubrilacteus* Smith and Hesler, and *Suillus lakei* (Murr.) Smith and Thiers were major biomass dominants in young stands (Tables 3 and 6). Eight of the 17 species (*Cantharellus formosus*, *Gautieria monticola*, *Hysterangium coriaceum*, *Hysterangium crassirhachis*, *Hysterangium setchellii*, *Rhizopogon parksii* Smith, *Rhizopogon vinicolor*, and *Truncocolumella citrina* Zeller) each comprised ≥1% of the biomass within each of the age-classes (Table 6). These eight species comprised 68 and 63% of the biomass in rotation-age and young stands, respectively, compared with 26% in old-growth stands.

Table 5. Average standing crop (kg/ha) by age-class, habit, and season (95% CI in parentheses).

	Age-class		
Habit and season	Old-growth	Rotation-age	Young
Hypogeous, fall	0.80 (0.33, 1.93)	0.90 (0.37, 2.17)	2.00 (0.83, 4.85)
Hypogeous, spring	0.82 (0.31, 2.23)	4.87 (1.80, 13.16)	4.77 (1.76, 12.81)
Epigeous, fall	1.81 (0.51, 6.38)	2.53 (0.72, 8.92)	3.74 (1.06, 13.16)
Epigeous, spring	0.002 (0, 0.01)	0.05 (0.01, 0.21)	0.05 (0.01, 0.20)

Frequency provides another means of measuring importance of a species. On a stand sample basis, *Hysterangium crassirhachis* was the most frequently collected (68%) and the only species found in more than 50% of the stand samples (Table 6). *Hysterangium crassirhachis* was most often collected in young and rotation-age stands; *Elaphomyces granulatus* was collected almost exclusively in old-growth stands (Table 6). *Inocybe* species were infrequent in old-growth stands but common in rotation-age and young stands (Table 6).

Hysterangium crassirhachis and *Hysterangium setchellii* were the only species found in all collecting seasons (Table 3). Other important species frequently collected included *Rhizopogon parksii* and *Rhizopogon vinicolor.* Both were collected with similar frequency in each of the age-classes (Table 6).

All of the 17 important species predominantly occurred in either fall or spring; 13 species produced more than 95% of their biomass in one of the two seasons (Table 7). In fall, 17 species or species groups comprised 65% of the total fall biomass compared with spring where 10 species or species groups comprised 94% of the total spring biomass. Biomass dominance in fall and spring was distributed among five species (Table 7). However, only *Hysterangium crassirhachis* dominated in both seasons, being 14% of the fall biomass and 37% of the spring biomass (Table 7). Together, *Hysterangium crassirhachis* and *Gautieria monticola* comprised 70% of the spring biomass (Table 7).

Species or species groups unique to an age-class

Fifteen of 51 genera (Table 4) and 94 of 263 species or species groups (Table 3) were unique to a particular age-class. Four genera (one hypogeous and three epigeous) were collected only from old-growth stands, three (hypogeous) only from rotation-age stands, and eight (seven hypogeous and one epigeous) only from young stands (Table 4). None of the genera unique to an age-class comprised ≥1% of the biomass within the age-class (Table 4). Fifty species or species groups (10 hypogeous and 40 epigeous) were collected only from old-growth stands, 19 (six hypogeous and 13 epigeous) only from rotation-age stands, and 25 (nine hypogeous and 16 epigeous) only from young stands (Table 3). Three species or species groups, *Cantharellus subalbidus* Smith and Morse, *Ramaria* gp. 3A, and *Ramaria* gp. 4, were unique to old-growth stands and each comprised ≥1% of the biomass in old-growth stands (Table 3).

Most (72) of the species or species groups unique to an age-class were collected from a single stand sample; 52 represented single collections (Table 3). Twenty-two species or species groups unique to an age-class were found in two or more stands. Species or species groups unique to the young and rotation-age stands were combined for the analysis. Probability of occurrence of these unique species or species groups differed between old-growth stands and the combined young and rotation-age stands ($p < 0.003$). Seventy-three percent of the unique species or species groups (95% CI = 54–91%) were found in old-growth stands.

Discussion

Species richness of EM fungi in mesic Douglas-fir associations in the *Tsuga heterophylla* zone in the Cascade Range of Oregon is relatively stable from canopy closure through late succession. Working in Douglas-fir stands similar to ours in age, plant association, and location, Spies (1991) found that richness of plant species also did not differ in relation to age-class. Furthermore, differences in species abundance and occurrence were detected among forest age-classes for EM sporocarps in our study as well as for plants in the study by Spies (1991). Most understory species in these plant associations are not EM symbionts but belong to plant families that characteristically form arbuscular and ericoid mycorrhizas (Trappe 1987; Molina et al. 1992). The degree to which edaphic factors and understory plant species abundance and occurrence influence sporocarp production of EM fungi among stands with similar plant associations is poorly known.

In our old-growth, rotation-age, and young stands, we found average cumulative richness values of 27, 28, and 28 hypogeous species, respectively. In Douglas-fir stands, North et al. (1997) sampled an area nearly four times the size of that sampled in our study yet found hypogeous species richness values similar to ours, i.e., 34, 29, and 27 in natural old-growth stands, mature stands, and managed young stands, respectively. Our finding of 48 total hypogeous species is similar to total species richness values found in other hypogeous sporocarp censuses in Douglas-fir-dominated stands (Luoma et al. 1991; North et al. 1997; Colgan et al. 1999). Luoma et al. (1991) sampled from a total area similar in size to that sampled in our study, and Colgan et al. (1999) sampled from a total area about twice the size of that sampled in our study. Only about 50% of the hypogeous species found by Luoma (1989) and Colgan et al. (1999) were common to our study, suggesting that differences among the studies in microhabitat conditions influence the composition of hypogeous species.

Our epigeous richness value of 215 species or species groups is higher than those from similar sporocarp censuses in spruce (*Picea* spp.) and hardwood forests with sample areas about two times (Bills et al. 1986) and seven times (Villeneuve et al. 1989) larger than was sampled in our

Table 6. Sporocarp habit, biomass, percentage of total biomass, percentage of each species biomass distributed across age-class, percentage of age-class biomass for each species, total frequency, and relative proportion by age-class for the 17 important species.

Species	Habit	Dry mass (g/ha)*	% of total biomass	% of species biomass by age-class			% of age-class biomass for each species			Total frequency†	Relative proportion by age-class (%)‡		
				OG	RA	Y	OG	RA	Y		OG	RA	Y
Cantharellus formosus	E	200	3	10	25	65	2	2	4	38	25	29	46
Elaphomyces granulatus	H	163	2	93	6	1	**12**	<1	<1	14	78	11	11
Gautieria monticola	H	1310	**16**	2	55	43	2	**23**	**15**	38	21	50	29
Gomphidius subroseus	E	124	2	9	40	52	1	2	2	41	31	35	35
Hysterangium coriaceum	H	309	4	12	40	48	3	4	4	35	18	41	41
Hysterangium crassirhachis	H	2017	**25**	1	40	59	1	**26**	**32**	68	12	40	49
Hysterangium setchellii	H	285	4	12	70	19	3	**6**	1	37	26	52	22
Inocybe geophylla gp.	E	107	1	<1	56	44	<1	2	1	32	5	45	50
Inocybe mixtilis gp.	E	91	1	0	54	47	0	2	1	46	0	41	59
Lactarius rubrilacteus	E	317	4	1	34	65	<1	3	**6**	29	22	44	33
Rhizopogon parksii	H	241	3	21	31	48	4	2	3	43	33	30	37
Rhizopogon vinicolor	H	342	4	37	35	29	**10**	4	3	46	31	34	34
Russula albonigra	E	901	1	66	30	4	**5**	1	<1	17	45	36	18
Russula alutacea gp.	E	181	2	4	32	65	1	2	3	27	21	37	42
Russula cessans gp.	E	104	1	9	35	56	1	1	2	25	19	38	44
Suillus lakei	E	343	4	1	15	84	<1	2	**8**	22	14	43	43
Truncocolumella citrina	H	139	2	14	23	63	2	1	2	37	35	22	43
Total		6362	79	9	41	50	46	82	86				

Note: Epigeous species (E) are from a 43 700-m^2 total sample and hypogeous species (H) are from a 6300-m^2 total sample in nine Douglas-fir stands. Sporocarp biomass ≥5% shown in bold. OG, old-growth; RA, rotation-age; Y, young.

*Dry mass sporocarp biomass on an annual basis.

†Frequency determined as a percentage of the total number of stand samples (9 stands × 7 seasons = 63).

‡Relative proportion by age-class determined as a percentage of the number of occurrences in each age-class divided by the total number of occurrences.

study. Species richness values in our managed forest age-classes were higher than those reported in forest types between 55 and 70 years old in the studies by Bills et al. (1986) and Villeneuve et al. (1989), suggesting that Douglas-fir and western hemlock forests are particularly species rich. In old-growth stands, we found a number of epigeous species, after estimating species numbers within subgroups of *Cortinarius*, similar to the number reported by O'Dell et al. (1999) in a 2-year study; total area sampled in the two studies was similar.

Our finding of a greater percentage of the more common unique species in old-growth stands is in keeping with observations for succession of EM fungi with accumulations of recalcitrant plant litter (Last et al. 1984, 1987). The large number of species or species groups found uniquely, but only rarely, in old-growth stands in our study is consistent with that of O'Dell et al. (1999). Results of our study and the study by O'Dell et. al (1999) suggest that old-growth stands contain many species of fungi that infrequently produce sporocarps.

Some genera in our study contained species with notable annual variability. For example, the number of *Russula* species varied from three to 23 per fall season, and 11 were found only in a single fall season. Seven of these were found in the final fall collecting season, strongly contributing to the continued increase in the diversity curve (Fig. 1).

Our study shows that the number of sampling visits and area sampled influence species richness values in dispersed plots. The increase in epigeous species or species groups from permanent strip plots is largely a function of time because the same area was sampled at each sample time. Conversely, the increase in epigeous species or species groups from temporary strip plots and in hypogeous species from circular plots is a function of both time and area sampled; new plots are installed each collecting season. Our slightly higher cumulative epigeous species richness collected from permanent strip plots compared with temporary strip plots suggests that the number of times an area is sampled may be more important to detecting species than sampling new area (Fig. 1). O'Dell et al. (1999) suggested that more species will be detected with the same effort by sampling from noncontiguous plots. We cannot rule out that sampling more dispersed plots or sampling more times per season may have evened out the richness values between plot types.

Our once-per-season sampling coincided with peak biomass and species diversity in the Pacific Northwest (Fogel 1976; Hunt and Trappe 1987; Luoma 1991). It is possible that the temporal peaks of sporocarp production differed among stand ages. However, seasonal fruiting typically commences and terminates within a few weeks, and stands within each age-class were sampled in most weeks. Most EM sporocarp studies in this region sampled once or twice per season (Luoma et al. 1991; North et al. 1997; Colgan et al. 1999; O'Dell et al. 1999). The sporocarp longevity of most species is unknown (Weber 2001). Species richness values decline when sampling

Table 7. Percentage of total sporocarp biomass by season and percent contribution to total seasonal biomass for the 17 important species.

		% total by season		% of season total	
Species	Habitat	Spring	Fall	Spring	Fall
Cantharellus formosus	E		100		**5**
Elaphomyces granulatus	H	24	76	1	3
Gautieria monticola	H	97	3	**33**	1
Gomphidius subroseus	E		100		3
Hysterangium coriaceum	H	97	3	**8**	<1
Hysterangium crassirhachis	H	70	30	**37**	**14**
Hysterangium setchellii	H	78	22	**6**	1
Inocybe geophylla gp.	E	<1	99	<1	2
Inocybe mixtilis gp.	E	26	74	1	2
Lactarius rubrilacteus	E	1	99	<1	**7**
Rhizopogon parksii	H		100		**6**
Rhizopogon vinicolor	H	97	3	**9**	<1
Russula albonigra	E		100		2
Russula alutacea gp.	E		100		4
Russula cessans	E		100		2
Suillus lakei	E	<1	99	<1	**8**
Truncocolumella citrina	H		100		3
Total		44	34	94	65

Note: Epigeous species (E) are from a 43 700-m^2 total sample and hypogeous species (H) are from a 6300-m^2 total sample in nine Douglas-fir stands. Within-season sporocarp biomass ≥5% shown in bold.

occurs at less than weekly intervals (Richardson 1970; Egli et al. 1997). Colgan et al. (1999) reported the same number of hypogeous species as in our study when sampling was conducted at 6-week intervals throughout the year. Sampling more than once per season in our study likely would have detected more epigeous species but not necessarily a significantly greater number of hypogeous species.

Sporocarp production responds to changes in habitat associated with forest succession. In our study, sporocarp production was significantly greater in young and rotation-age stands compared with old-growth stands. In contrast, mean epigeous sporocarp biomass did not differ significantly among stand types in the study by North et al. (1997). Because our study did not examine mature (80–195 years) or very early (1–20 years) stages of forest succession, the entire pattern of changes in EM sporocarp abundance, as well as species richness, in Douglas-fir forests in the Oregon Cascade Range cannot be examined with these data. However, in a study in the H.J. Andrews Experimental Forest, Luoma et al. (1991) reported greater hypogeous sporocarp biomass in mesic stands of mature forest (80–199 years) compared with old-growth (≥200 years) and young (70–80 years). North et al. (1997) reported the highest production of hypogeous sporocarps in natural mature and old-growth and the lowest in managed young (55–60 years) stands in the Olympic and North Cascade ranges of Washington. In a comparison of paired old-growth and mature true fir stands, species richness and biomass of hypogeous sporocarps did not differ, but species composition did (Waters et al. 1997). Other studies showed that after stand replacing disturbance, stand biomass and species richness of hypogeous EM fungi is significantly less in very young stands (4–27 years) compared with adjacent late seral stands of Douglas-fir (Amaranthus et al. 1994; Clarkson and Mills 1994) and of Pacific silver fir (*Abies amabilis*) (Vogt et al. 1981).

The incongruity between hypogeous sporocarp production patterns across age-class gradients in our study, most notably our low sporocarp biomass value for old-growth stands, and studies by Luoma et al. (1991) and North et al. (1997) may be due to the composition of the hypogeous community sampled, the sporadic detection of large clusters of sporocarps, and the small sample size. In our study, the hypogeous sporocarp biomass value in old-growth stands was about three times less than in young stands. In contrast, the sporocarp biomass value was about 1.3 and 5 times greater in old-growth stands compared with young stands in the studies by Luoma et al. (1991) and North et al. (1997), respectively. In our study, five major hypogeous biomass dominants made up a majority of the biomass in old-growth stands compared with only two and one in the studies by Luoma et al. (1991) and North et al. (1997), respectively.

One species, *Elaphomyces granulatus*, accounted for 25% of the biomass in old-growth stands in our study compared with 63 and 95% in old-growth stands in the studies by Luoma et al. (1991) and North et al. (1997), respectively. *Elaphomyces granulatus* sometimes produces large clusters of sporocarps (Vogt et al. 1981; Luoma et al. 1991; North et al. 1997), making interpretation of study results problematic. North et al. (1997) found a greater number of large clusters of *Elaphomyces granulatus* in old-growth compared with younger stands. Luoma et al. (1991), however, found only one large cluster and substituted a lesser value for the data analysis. The adjusted biomass value for *Elaphomyces granulatus* in the study by Luoma et al. (1991) produced hypogeous sporocarp production patterns across age-class

gradients similar to those of our study as well as composition of biomass dominant species and total biomass in mesic old-growth stands similar to those of our study. We found no clusters of *Elaphomyces granulatus* large enough to consider adjusting the biomass.

It is unclear why we found less sporocarp biomass in old-growth stands compared with younger managed stands. Possible explanations include (*i*) a decrease in net primary production or differences in belowground carbon allocation with stand age (Waring and Schlesinger 1985; Waring and Running 1998), (*ii*) differences among forest age-classes that influence microhabitat conditions contributing to the development of sporocarps, (*iii*) a larger number of EM species not producing conspicuous sporocarps in old-growth stands compared with younger stands, (*iv*) an artifact of the single-interval sampling method, and (*v*) a high level of small mammal mycophagy in our old-growth stands. Small mammal population densities and small mammal mycophagy are highly variable across stands and landscapes (Cazares et al. 1999). However, mycophagy likely did not have a significant effect on biomass because we sampled at times of sporocarp abundance (North et al. 1997).

The most dominant genera appeared in all age-classes. However, about 25% of the genera in our study appeared exclusively in either young or old-growth stands (Table 4), suggesting genus-level patterns of EM sporocarp succession as forests age. Fox (1986) noted a EM genus-level distinction between young and aging birch (*Betula* spp.) forests. However, many of the genera characterized as early stage or late stage in the study by Fox (1986) were multistage in our study. Differences seen in age-class association of genera in our study compared with those in the study by Fox (1986) suggest that it is difficult to (*i*) to generalize patterns of EM succession between different forest types and (*ii*) define ecological traits common to all species within a genus. Nevertheless, sporocarp production occurring exclusively and repeatedly in a single age-class by some genera suggests similar habitat requirements for species within those genera. Defining distribution patterns associated with taxa at levels higher than species would be helpful for landscape-scale models of fungi occurrence (Dreisbach et al. 2002).

Each forest age-class, as well as our study overall, was characterized by a few biomass dominant species of both hypogeous and epigeous sporocarps and a larger number of less abundant species. This pattern of biomass dominance by a few species is common to many groups of organisms and has been documented in EM sporocarp communities, especially among hypogeous fungi (Luoma et al. 1991; North et al. 1997; Waters et al. 1997; Colgan et al. 1999). Many species appeared in greater abundance in a particular age-class (Table 6). Repeatedly detected species provide a framework for exploring microhabitat variables contributing to their occurrence and abundance. Such knowledge may provide insight into the habitat requirements of more rare species and is essential to species conservation efforts.

Other studies in Douglas-fir in our region also have reported higher biomass of hypogeous sporocarps in spring compared with fall (Fogel 1976; Luoma et al. 1991; North et al. 1997; Cazares et al. 1999). Epigeous sporocarps show relative rarity in seasons other than fall in our region (Fogel and Hunt 1979; North et al. 1997; O'Dell et al. 1999). The more even production of hypogeous sporocarps in spring and fall makes them a more reliable food supply for mycophagists (North et al. 1997; Cazares et al. 1999). Colgan et al. (1999) reported that some species of hypogeous fungi produce sporocarps throughout the winter when many food resources are scarce.

Species richness and patterns of EM community structure reported in this study are based on the sporadic production of ephemeral fungal sporocarps and our ability to detect them. Describing EM communities by sampling sporocarps provides data essential for predicting impacts of disturbance and management on sporocarp diversity and production but not total EM diversity. Species richness, composition, and relative abundance likely would have differed if we had sampled EM roots (Gardes and Bruns 1996). To further increase knowledge of the community dynamics of EM fungi, both sporocarp and root tip approaches should be considered for determining EM species diversity and dominance in future studies.

Knowledge of EM fungal communities improves our ability to maintain biological diversity in old-growth, managed rotation-age, and young stands. In summary, we found (*i*) high EM species richness in forests in the *Tsuga heterophylla* zone in the Cascade Range in Oregon, (*ii*) a similar number of EM fungal species among forest age-classes with similar plant association groups, (*iii*) a change in abundance of some dominant species or species groups as forest stands age, and (*iv*) a greater likelihood for species or species groups unique to an age-class to occur in old-growth stands. Our results suggest that all age-classes of forests are important for maintaining the biological diversity of EM fungi and the organisms they support.

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Appendix A

Table A1. Sporocarp biomass, percentage of total biomass, percentage of each species biomass distributed across age-class, percentage of age-class biomass for each species, total frequency, and relative proportion by age-class for the 20 important epigeous species that are ≥1% of the total epigeous sporocarp biomass from a 43 700-m^2 total sample in nine Douglas-fir stands.

			% of species biomass by age-class			% of age-class biomass for each species				Relative proportion by age-class (%)[‡]		
Species	Dry mass (g/ha)*	% of total biomass	OG	RA	Y	OG	RA	Y	Total frequency[†]	OG	RA	Y
Cantharellus formosus	200	**7**	10	25	65	3	**5**	**10**	38	25	29	46
Cortinarius cf. *multiformis* gp.	50	2	69	31	<1	**6**	2	<1	21	61	31	8
Gomphidius subroseus	124	4	9	40	52	2	**5**	5	41	31	35	35
Hebeloma crustuliniforme	73	3	3	41	56	<1	3	3	38	25	46	29
Inocybe geophylla gp.	107	4	<1	56	44	<1	**6**	4	32	5	45	50
Inocybe mixtilis gp.	91	3	0	54	47	0	**5**	3	46	0	41	59
Inocybe sororia gp.	41	1	3	68	29	<1	3	1	54	18	38	44
Lactarius rubrilacteus	317	**11**	1	34	65	1	**11**	**16**	29	22	44	33
Lactarius scrobiculatus gp.	30	1	12	36	52	1	1	1	10	17	17	66
Ramaria gp. 2	47	2	97	3	0	**8**	<1	0	13	88	12	0
Russula albonigra	91	3	66	30	4	**10**	3	<1	17	45	36	18
Russula alutacea gp.	181	**6**	4	32	65	1	**6**	**9**	27	21	37	42
Russula brevipes	71	3	48	52	0	**6**	4	0	13	63	37	0
Russula cessans gp.	104	4	9	35	56	1	4	4	25	19	38	44
Russula crenulata	41	1	88	7	2	**6**	<1	<1	13	50	17	33
Russula densifolia	45	2	48	51	<1	4	3	<1	10	50	33	17
Russula fragrantissima	45	2	98	0	2	**7**	0	<1	11	86	0	14
Russula integra gp.	35	1	12	55	33	1	2	1	24	20	45	35
Suillus lakei	343	**12**	1	15	84	1	**6**	**22**	22	14	43	43
Suillus ponderosus	49	2	9	0	91	1	0	3	6	25	0	75
Total	2084	73	17	31	52	56	70	83				

Note: Sporocarp biomass ≥5% shown in bold. OG, old growth; RA, rotation age; Y, young.
*Dry mass sporocarp biomass on an annual basis.
[†]Frequency determined as a percentage of the total number of stand samples (9 stands × 7 seasons = 63).
[‡]Relative proportion by age-class determined as a percentage of the number of occurrences in each age-class divided by the total number of occurrences.

Appendix continued on following page.

Table A2. Sporocarp biomass, percentage of total biomass, percentage of each species biomass distributed across age-class, percentage of age-class biomass for each species, total frequency, and relative proportion by age-class for the nine hypogeous species that are ≥1% of the total hypogeous sporocarp biomass from a 6300-m^2 total sample in nine Douglas-fir stands.

			% of species biomass by age-class			% of age-class biomass for each species				Relative proportion by age-class (%)‡		
Species	Dry mass (g/ha)*	% of total biomass	OG	RA	Y	OG	RA	Y	Total frequency†	OG	RA	Y
Elaphomyces granulatus	1623	3	93	6	1	**25**	1	<1	14	78	11	11
Gautieria monticola	1310	**25**	2	55	43	3	**33**	**23**	38	21	50	29
Hysterangium coriaceum	309	**6**	12	40	48	**6**	**6**	**6**	35	18	41	41
Hysterangium crassirhachis	2017	**39**	1	40	59	3	**37**	**49**	68	12	40	49
Hysterangium setchellii	285	**6**	12	70	19	**5**	**9**	2	37	26	52	22
Radiigera taylori	77	2	11	29	59	1	1	2	35	14	36	50
Rhizopogon parksii	241	5	21	31	48	**8**	4	5	43	33	30	37
Rhizopogon vinicolor	342	**7**	37	35	29	**21**	**5**	4	46	31	34	34
Truncocolumella citrina	139	3	14	23	63	3	1	4	37	35	22	43
Total	4882	94	9	44	47	76	97	95				

Note: Sporocarp biomass ≥5% shown in bold. OG, old-growth; RA, rotation-age; Y, young.
*Dry mass sporocarp biomass on an annual basis.
†Frequency determined as a percentage of the total number of stand samples (9stands x 7seasons = 63)
‡Relative proportion by age-class determined as a percentage of the number of occurrences in each age-class divided total number of occurrences.