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The Influence of Thinning on Production of Hypogeous Fungus Sporocarps in Douglas-fir Forests in the Northern Oregon Coast Range

Abstract

Sporocarps of hypogeous fungi are an important food resource for many wildlife species. Effects of thinning second-growth (35 to 45 yr-old) Douglas-fir forests on production of hypogeous sporocarps were investigated to test the hypothesis that in the short term thinning would reduce their production and species diversity. We compared sporocarp production among unthinned, moderately thinned, and heavily thinned stands in four locations in the Oregon Coast Range, 1996 and 1997. Distributions of hypogeous sporocarps were clumped. Total biomass of sporocarps was highest in spring 1996 and progressively decreased in subsequent sampling periods. The genera *Alpova*, *Barssia*, *Elaphomyces*, *Truncocolumella*, and *Tuber* appeared to decrease in response to thinning. Thinning significantly reduced total sporocarp frequency among treatments. The mean number of species fruiting was significantly higher in the unthinned than thinned treatments, and more species occurred in the unthinned than thinned treatments in autumn 1996. The array of sporocarp-producing species varied between treatments. Sporocarp distributions were clumped at the plot and grid station levels, and total sporocarp abundance was associated with abundance of coarse woody debris (CWD). These results indicated that commercial thinning influenced hypogeous sporocarp production and sporocarp species diversity at 2 to 3 yr after cutting and that CWD was an important variable for predicting hypogeous sporocarp production. Retention of CWD in commercially thinned sites seems important for sporocarp production of certain hypogeous species and thus to habitat maintenance for many small mammal mycophagists.

Introduction

Hypogeous fungi play important roles in many forest ecosystems. They form mycorrhizae with many trees and shrubs, which depend on them for uptake of nutrients and water; the plant hosts provide photosynthates to the fungi (Read et al. 1992). The sporocarps are an important food source for many small mammal species in the Pacific Northwest, including California red-backed voles (*Clethrionomys californicus*) (Maser et al. 1978, Ure and Maser 1982), northern flying squirrels (*Glaucomys sabrinus*) (Maser and Trappe 1984, Maser et al. 1985, Carey et al. 2002), and wood rats (*Neotoma* spp.) (Parks 1919, Maser et al. 1978). Small mammal mycophagy in turn acts as the primary means of spore dispersal for these fungi (Fogel and Trappe 1978).

Hypogeous sporocarp formation differs in productivity and species diversity in forests of different ages and habitats. Sporocarp production

can be higher in mature conifer stands than in young stands and species composition can differ between the stands (Vogt et al. 1981). This may relate to photosynthetic potential, which is positively correlated with abundance of ectomycorrhizal fungal sporocarps in forests (Termorshuizen and Schaffers 1987). Luoma et al. (1991) compared hypogeous fungal production along moisture and age gradients in Douglas-fir forests in the Oregon Cascades. Biomass was highest in the mesic mature habitats, followed by mesic old-growth, mesic young, wet old-growth, and dry old-growth habitats.

Other researchers have evaluated effects of silvicultural practices on species diversity and sporocarp production. More hypogeous sporocarps occurred in mature stands than in adjacent, regenerated clearcuts, and sporocarp abundance was associated with the presence of coarse woody debris (CWD) in the studies of Amaranthus et al. (1994) and Clarkson and Mills (1994). Colgan et al. (1999) sampled hypogeous sporocarp production at 6-wk intervals over 34 mo after a variable density thinning of Douglas-fir (*Pseudotsuga*

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menziesii) in lowland western Washington. Overall standing crop biomass was significantly lower in the thinned stands compared with unthinned. Some taxa of hypogeous fungi fruited less abundantly in thinned than unthinned stands, and others were more abundant in thinned stands. Waters et al. (1994) evaluated sporocarp standing crop biomass 9 and 10 yr after two levels of commercial thinning and 17 yr after broadcast burning. Thinning did not significantly affect hypogeous sporocarp biomass or frequency, but the fungal community composition differed between levels of thinning. Sporocarp standing crop also varies seasonally and is affected by climate (Fogel 1981, Eveling et al. 1990) and sporocarp moisture content (Johnson 1994), so assessing the overall impact of thinning can be difficult.

The positive association of sporocarp abundance with the presence of CWD can affect the presence of mycophagists in an area, because they are attracted to the sporocarps as a food source. California red-backed voles represent fungal specialists strongly associated with CWD (Maser et al. 1978, Ure and Maser 1982, Maser 1998). Small mammal mycophagists rely on a diversity of fungal species in their diets (Maser et al. 1978, 1985, Carey et al. 2002). This diversity may be a nutritional imperative, as suggested in feeding trials with northern flying squirrels and California red-backed voles, where neither species maintained their body weight on a single species of fungi (Claridge et al. 1999).

Because hypogeous fungal sporocarps are important as food for small mammals in Pacific Northwest forests, management of habitat for those mammals and their predators requires knowledge of how forest management practices affect sporocarp production. Accordingly, we compared sporocarp production of hypogeous fungi among moderately and heavily thinned and unthinned stands in blocks at four locations in second-growth forests in the Oregon Coast Range. We hypothesized that thinning would negatively affect sporocarp production and diversity of sporocarp-producing fungi in the short run, because ectomycorrhizal fungi depend on hosts plants for photosynthates (Molina et al. 1992, Read et al. 1992), and mycorrhizae tend to be concentrated in the upper mineral and organic layers most susceptible to disturbance during timber harvest (Waters et al. 1994).

Methods

Study Area

The study was located in the northern Oregon Coast Range ~14 km WNW of Forest Grove on Tillamook State Forest and adjacent Stimson Lumber Company lands, Tillamook and Washington Counties, Oregon. The area was chosen for its large acreage of even-aged, closed-canopy, fire-replacement forest. In addition, most of the landscape is dominated by contiguous forest habitat, thus reducing potential confounding influences of forest fragmentation on stand-level phenomena. Douglas-fir was the dominant tree species; red alder (*Alnus rubra*) occupied riparian and recently disturbed areas. Less common trees included western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), and noble fir (*Abies procera*). Vine maple (*Acer circinatum*) and red huckleberry (*Vaccinium parvifolium*) were dominant deciduous shrubs, and salal (*Gaultheria shallon*) and Oregon grape (*Berberis nervosa*) were the most common evergreen shrubs. This area has a maritime climate, with mild, wet winters and cool, dry summers (Brown and Curtis 1985).

Sampling Design

We established four replicate blocks, each initially consisting of three 35- to 45 yr-old unthinned 26-40 ha stands. Stands within blocks were <0.5 km apart, with the exception of one in the Deer Diamond block, which was ca. 1.5 km from the other stands. Blocks were selected to minimize differences among stands within blocks with respect to tree density, stand age, and proportion of hardwoods. One of three treatments was randomly assigned to each of the three stands in each block: 1) no thinning (455-680 trees/ha), 2) moderate thinning (240-330 trees/ha) and, 3) heavy thinning (165-240 trees/ha). Stands were thinned in summer and autumn 1994 following one season of pre-treatment sampling.

Grids with 40 m between sampling stations were established in each stand. Grid arrays varied from 17 X 6 to 10 X 10 with 96-100 stations, depending on size and shape of the stand. Each grid had at least 20 m between its perimeter and the edge of the stand.

Habitat and Fungal Sampling

Habitat characteristics, measured in 10-m radius plots centered at every fourth grid station, included live trees, snags, stumps, CWD, and slash. Species, diameter at breast height (dbh) and height were recorded for all live trees ≥ 2 -m tall and ≥ 10 cm dbh. Stumps ≥ 20 -cm diameter and < 2 -m tall were tallied, CWD ≥ 1 -m long and ≥ 10 -cm in diameter were recorded by size class, and the dimensions of each slash pile (width, length, and height) were estimated. Plots of 20-m radius were established to record dbh, height, and decay class (Maser and Trappe 1984) of each snag ≥ 2 -m high and ≥ 10 cm dbh.

Hypogeous fungal sporocarps were sampled in late April–early June and October–early November of 1996 and again in late April–June of 1997 on 4-m² circular plots located at a random distance between 1 and 20 m from every fourth station on each grid. In autumn 1996 and spring 1997 we located a new sample point 180° from the point originally sampled. Litter was removed and topsoil raked to a depth of 5–10 cm as described by Luoma et al. (1991). All sporocarps were collected, dried, weighed, and identified to genus and, when mature enough, species. Voucher specimens were deposited in the Mycological Herbarium at Oregon State University, Corvallis, Oregon (OSC).

Statistical Analyses

Hypogeous species of the same genus were combined for analysis of standing crop biomass because sample sizes were small for several species and some juvenile specimens were identifiable only to genus. Individual species were used for testing relationships of measured variables to diversity of sporocarp producers: immature specimens could be separated by species in the absences of mature spores through combinations of other characters, even though a species name could not be applied. Differences among treatments were tested for habitat variables, standing crop biomass (dry weight) and percent frequency of sporocarps among treatments and blocks for the five most common genera of hypogeous fungi by ANOVA for a randomized block design. By the same approach total biomass, total frequency, and number of genera were compared among treatments within sample periods. Repeated measures analysis was used to compare total biomass, fre-

quency (percentage of plots where hypogeous sporocarps were found), and number of genera among treatments, with sample period used as the repeated factor. Variables were $\log_{10}(x+1)$ or square-root transformed to adjust for non-normality or lack of homogeneity of variances. Differences in fungal sporocarp associations among treatments were compared by Chi-square goodness-of-fit tests. Number of sporocarps per plot and collections per grid station were compared to numbers expected based on the Poisson distribution (Steele and Torre 1980) by Chi-square analysis. We tested each season by treatment separately at the plot level, because Chi-square tests indicated significant association between treatment and number of sporocarps per plot. Each site was tested separately at the grid station level, because of significant association between site and number of sporocarp collections per grid station. We also conducted pooled analysis across season, site, and treatment.

Associations of sporocarps to habitat characteristics were tested with multiple linear regression (separate analysis by genus was possible only for the most abundant genera). We present the best model chosen from the top ten given by Mallows C_p selection criteria (Mallows 1973) based on the biological significance of the independent variables and the amount of explained variability in the model. The level of significance for all statistical tests was set at $P=0.05$.

Results

Habitat Characteristics

Canopy cover of small conifers ($P<0.001$), total tree cover ($P<0.001$), and abundance of small snags ($P<0.02$) and all snags ($P<0.03$) were significantly higher in unthinned stands than in thinned stands (Table 1). Stump abundance was significantly greater in thinned stands than unthinned ($P<0.001$), and slash was greater in the thinned stands than unthinned ($P=0.001$ for heavy thinning, $P=0.002$ for moderate thinning).

Hypogeous sporocarp diversity and abundance

In all, 3576 m² were sampled. Hypogeous sporocarps were found in 68 (17%) of the 894 plots. The 566 sporocarps collected totaled 106.2 g dry weight and 0.3 kg/ha standing crop biomass. The

TABLE 1. Mean stand characteristics of 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, Spring 1996 and 1997 and Autumn 1996. Means computed from mean of subsamples within each stand (n = 22-34). Variables were $\log_{10}(x + 1)$ transformed.

Variable	Unthinned (n=4)	Treatment Moderate Thinning (n=4)	Heavy Thinning (n=4)	P Value
Deciduous trees 10-49 cm dbh: no./ha.	33.4 ± 12.1	29.9 ± 14.3	37.9 ± 7.3	0.884
Deciduous trees ≥ 50 cm dbh: no./ha.	0.6 ± 0.3	1.6 ± 1.6	0.3 ± 0.3	0.601
Conifer trees 10-49 cm dbh: no./ha.	506.1 ± 54.4	229.2 ± 22.9	145.1 ± 7.0	0.001
Conifer trees ≥ 50 cm dbh: no./ha.	36.3 ± 2.9	24.5 ± 9.2	20.1 ± 7.6	0.530
Total trees: no./ha.	576.8 ± 45.8	285.2 ± 16.2	203.1 ± 10.8	0.001
Small snags 10-49 cm dbh: no./ha.	54.6 ± 11.9	20.9 ± 4.8	13.7 ± 3.2	0.011
Large snags ≥ 50 cm dbh: no./ha.	9.0 ± 4.0	3.5 ± 1.4	4.7 ± 1.5	0.223
Total snags: no./ha.	63.7 ± 15.5	24.4 ± 5.9	18.4 ± 4.6	0.026
Stumps ≥ 20 cm diam < 2m ht: no./ha.	81.2 ± 11.5	316.7 ± 15.6	338.7 ± 35.0	0.001
Small logs 10-49 cm diam: no./ha.	131.1 ± 12.7	169.7 ± 35.6	195.4 ± 36.9	0.321
Large logs ≥ 50 cm diam: no./ha.	135.3 ± 19.4	137.5 ± 4.5	154.7 ± 20.4	0.469
Total logs: no./ha.	266.4 ± 25.5	306.8 ± 32.5	346.9 ± 35.6	0.367
Slash: m ³ /ha.	6.7 ± 5.4	331.0 ± 106.9	648.4 ± 378.8	0.001

20 genera and 34 species included 4 undescribed species (Table 2). Fourteen species were Ascomycetes, 17 Basidiomycetes, 1 Glomeromycetes, and 2 Zygomycetes. *Hysterangium* (33%) and *Rhizopogon* (23%) spp. together accounted for ca. 56% of the total sporocarp biomass (Tables 3 and 4). *Rhizopogon* and *Alpova* spp. produced their highest standing crop biomass in autumn 1996 and *Hysterangium* and *Gautieria* spp. in spring 1997 (Table 4). *Hysterangium* spp. occurred on 24% of the plots with sporocarps, and *Rhizopogon* and *Tuber* each on 18% (Table 3). *Tuber* spp. were collected in more of the stands (92%) than any other genus, followed by *Rhizopogon* (75%) and *Hysterangium* (67%). Total biomass of sporocarps was highest in spring 1996 and progressively decreased in subsequent sampling periods (Table 4). Sporocarps biomass of *Hysterangium*, *Barssia*, and *Endogone* spp. was higher in spring than autumn. *Gautieria* and *Leucangium* occurred exclusively in spring, whereas *Alpova*, *Truncocolumella*, and *Geopora* fruited only in autumn (Table 4).

Fruiting of several genera appeared to decrease in response to thinning, including *Alpova*, *Barssia*, *Elaphomyces*, *Truncocolumella*, and *Tuber* (Figure 1A); however, species in these genera were of low abundance, so the power of statistical tests was minimal. Mean hypogeous sporocarp biomass did not differ significantly among treatments

for any of the five more common genera (Table 5). Mean total standing crop biomass did not differ significantly among treatments (Figure 1B) or sample periods. Thinning did not significantly affect total sporocarp frequency among treatments or sample periods (Figure 1C).

The mean number of sporocarp-producing species was significantly higher in the unthinned than thinned treatments ($P < 0.05$, Figure 2), and more species fruited in the unthinned than thinned treatments in autumn 1996 ($P < 0.04$). The overall mean of fruiting species did not differ significantly among sample periods.

The array of taxa fruiting varied between treatments (Figure 3), but number of collections of sporocarps was not significantly associated with level of thinning. This analysis could only be completed for *Hysterangium*, *Rhizopogon*, and *Tuber*, because the small sample sizes for the other species produced expected cell frequencies < 5 in the analysis.

Hypogeous sporocarp distribution

More hypogeous sporocarps occurred per plot in unthinned than thinned stands ($P = 0.04$, Figure 4A), and more sporocarps were found per grid station (n=3 sample plots or periods per station or grid point) in unthinned than thinned stands (Figure 4B). Sporocarps were not randomly dis-

TABLE 2. Taxa of hypogeous fungi collected in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, Spring 1996 and 1997 (S) and Autumn 1996 (A). Numbers after each species name refer to collections deposited in the Mycological Herbarium of Oregon State University, Corvallis (OSC).

Ascomycota	
<i>Barssia oregonensis</i> (S, A): Trappe 22765	
<i>Elaphomyces granulatus</i> (S): Trappe 22724	
<i>Genea intermedia</i> (S): Trappe 22757	
<i>Geopora cooperi</i> var. <i>cooperi</i> (A): Trappe 22766	
<i>Hydnotrya cubispora</i> (S, A): Trappe 22726, 22773	
<i>Hydnotrya variiformis</i> (S): Trappe 22755	
<i>Leucangium carthusianum</i> (S): Trappe 22769	
<i>Leucangium</i> sp. nov. (S) ¹ : Trappe 22763, 22764, 22767	
<i>Tuber gardneri</i> (S, A): Trappe 22731	
<i>Tuber gibbosum</i> (S): Trappe 22727, 22768	
<i>Tuber monticola</i> (A): No collection retained	
<i>Tuber oregonense</i> sp. nov. (A) ¹ : Trappe 22753	
<i>Tuber shearii</i> (A): Trappe 22729	
<i>Tuber</i> sp. nov. (S) ¹ : Trappe 22768	
Basidiomycota	
<i>Alpova diplophloeus</i> (A): Trappe 22761	
<i>Gautieria monticola</i> (S): Trappe 22745	
<i>Gymnomyces</i> sp. nov. (A) ¹ : Trappe 22756	
<i>Hymenogaster gilkeyae</i> (S): Trappe 22728, 22749	
<i>Hymenogaster subalpinus</i> (A): Trappe 22750, 22752	
<i>Hymenogaster subtilacinus</i> (S): Trappe 22751	
<i>Hysterangium coriaceum</i> (S, A): No collections retained	
<i>Hysterangium crassirhachis</i> (S): Trappe 22746	
<i>Leucogaster citrinus</i> (S): No collection retained	
<i>Leucophleps magnata</i> (S): Trappe 22754	
<i>Melanogaster tuberiformis</i> (S): Trappe 22747	
<i>Rhizopogon ater</i> (A) ¹ : Trappe 22770	
<i>Rhizopogon hawkeri</i> (A): Trappe 22771	
<i>Rhizopogon parksii</i> (A): Trappe 22760, 22772	
<i>Rhizopogon villosulus</i> (A): Trappe 22759	
<i>Rhizopogon vinicolor</i> (S): Trappe 22762	
<i>Truncocolumella citrina</i> (A): Trappe 22725	
Glomeromycota	
<i>Glomus macrocarpum</i> (S): Trappe 22758	
Zygomycota	
<i>Endogone flammicorona</i> (S): No specimen retained	
<i>Endogone lactiflua</i> (S, A): Trappe 22748	

¹New species are given provisional names and will be described in separate papers.

TABLE 3. Sporocarp biomass and percent frequencies of hypogeous fungal genera in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands (3576-m² total sample area), Oregon Coast Range, 1996 and 1997.

Genera	Number of Sporocarps	Dry weight (g)	% frequency of stands ¹	% frequency of plots ²
<i>Alpova</i>	24	6.8	3.8	42
<i>Barssia</i>	26	3.0	3.8	33
<i>Elaphomyces</i>	5	5.2	1.5	17
<i>Endogone</i>	16	1.0	6.8	58
<i>Gautieria</i>	12	7.7	2.3	17
<i>Genea</i>	15	0.9	1.5	17
<i>Geopora</i>	2	0.4	0.8	8
<i>Glomus</i>	3	0.1	2.3	25
<i>Hydnotrya</i>	21	1.1	6.8	42
<i>Hymenogaster</i>	10	1.9	5.3	25
<i>Hysterangium</i>	231	34.9	24.8	67
<i>Leucangium</i>	2	3.4	6.0	33
<i>Leucophleps</i>	29	0.1	0.8	8
<i>Gymnomyces</i>	1	0.7	0.8	8
<i>Melanogaster</i>	11	2.7	0.8	8
<i>Rhizopogon</i>	85	24.8	18.0	75
<i>Truncocolumella</i>	16	4.7	7.5	42
<i>Tuber</i>	54	6.8	18.8	92
TOTAL	566	106.2		

¹Percentage of total number of plots with truffles.

²Percentage of total number of stands.

TABLE 4. Sporocarp biomass by fungal genera (g/ha) from 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands during 3 seasons. Oregon Coast Range.

Genera	Spring 1996	Autumn 1996	Spring 1997	Total
<i>Alpova</i>	0	689	0	689
<i>Barssia</i>	88	13	206	307
<i>Elaphomyces</i>	517	0	0	517
<i>Endogone</i>	86	1	13	100
<i>Gautieria</i>	209	0	560	769
<i>Genea</i>	0	0	93	93
<i>Geopora</i>	0	38	0	38
<i>Glomus</i>	0	0	11	11
<i>Hydnotrya</i>	88	10	12	110
<i>Hymenogaster</i>	107	67	15	189
<i>Hysterangium</i>	2523	234	743	3500
<i>Leucangium</i>	221	0	119	340
<i>Leucophleps</i>	0	0	14	14
<i>Gymnomyces</i>	0	60	0	60
<i>Melanogaster</i>	0	0	271	271
<i>Rhizopogon</i>	1231	1170	86	2487
<i>Truncocolumella</i>	0	470	0	470
<i>Tuber</i>	273	268	146	687
TOTAL	5343	3020	2289	10652

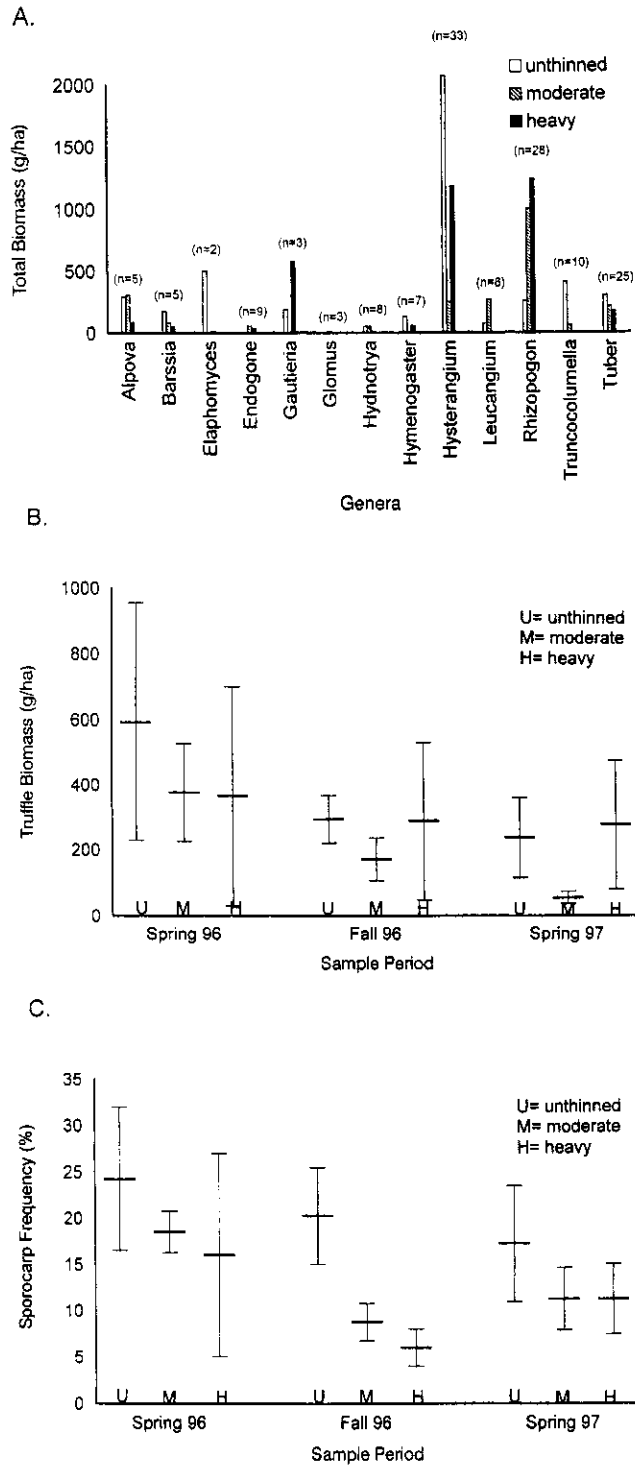


Figure 1. a) Total hypogeous sporocarp biomass of common genera by treatment; b) total sporocarp biomass and c) total frequency, in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

TABLE 5. Mean standing crop biomass (g/ha) of hypogeous fungal sporocarps by genus in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997. Means computed from mean of subsamples within each stand (n = 23-28).

Genus	Unthinned	Moderate thinning	Heavy thinning	P value
<i>Endogone</i>	1.3 ± 1.3	14.2 ± 7.8	9.5 ± 8.8	0.20 ¹
<i>Hydnomya</i>	12.6 ± 7.6	12.3 ± 12.3	2.5 ± 2.5	0.44 ¹
<i>Hysterangium</i>	517.0 ± 408.9	62.6 ± 39.6	295.2 ± 271.8	0.46 ¹
<i>Rhizopogon</i>	64.4 ± 28.2	248.4 ± 137.7	308 ± 209.5	0.35 ¹
<i>Tuber</i>	75.5 ± 19.4	56.5 ± 26.2	43.6 ± 24.2	0.37 ²
Total biomass	1124.9 ± 417.0	603.7 ± 177.6	934.5 ± 512.0	0.38

¹Variable was $\text{Log}_{10}(X + 1)$ transformed.

²Variable was square-root transformed.

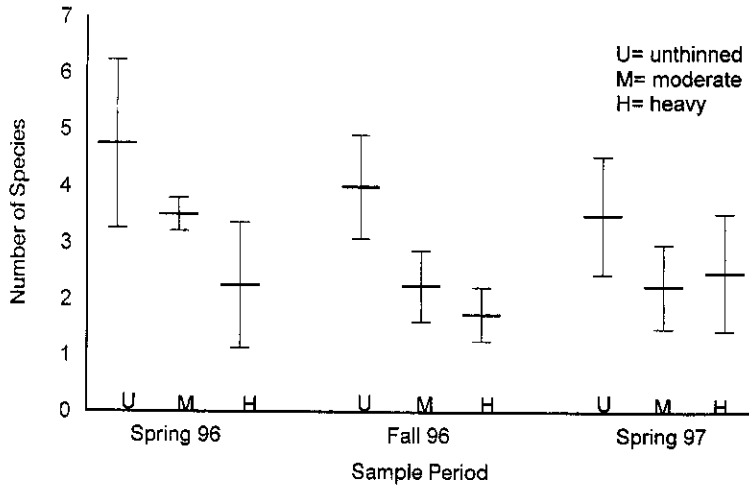


Figure 2. Mean number of hypogeous fungal species in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

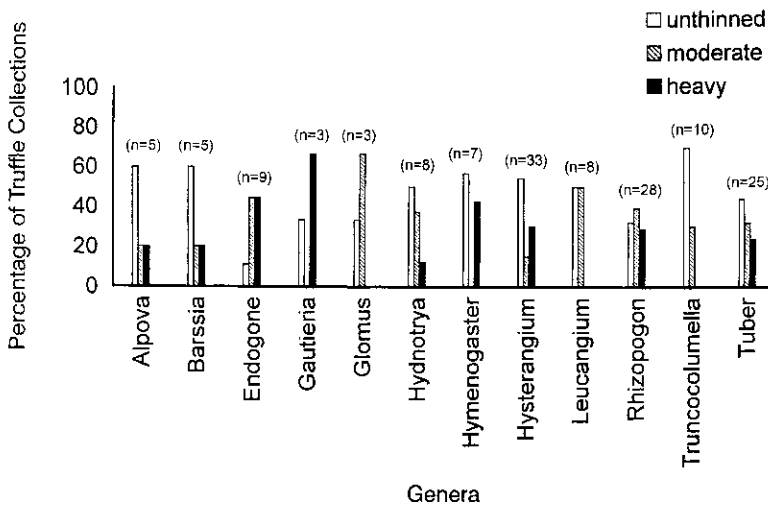


Figure 3. Percentage of hypogeous sporocarp collections of genera found in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997.

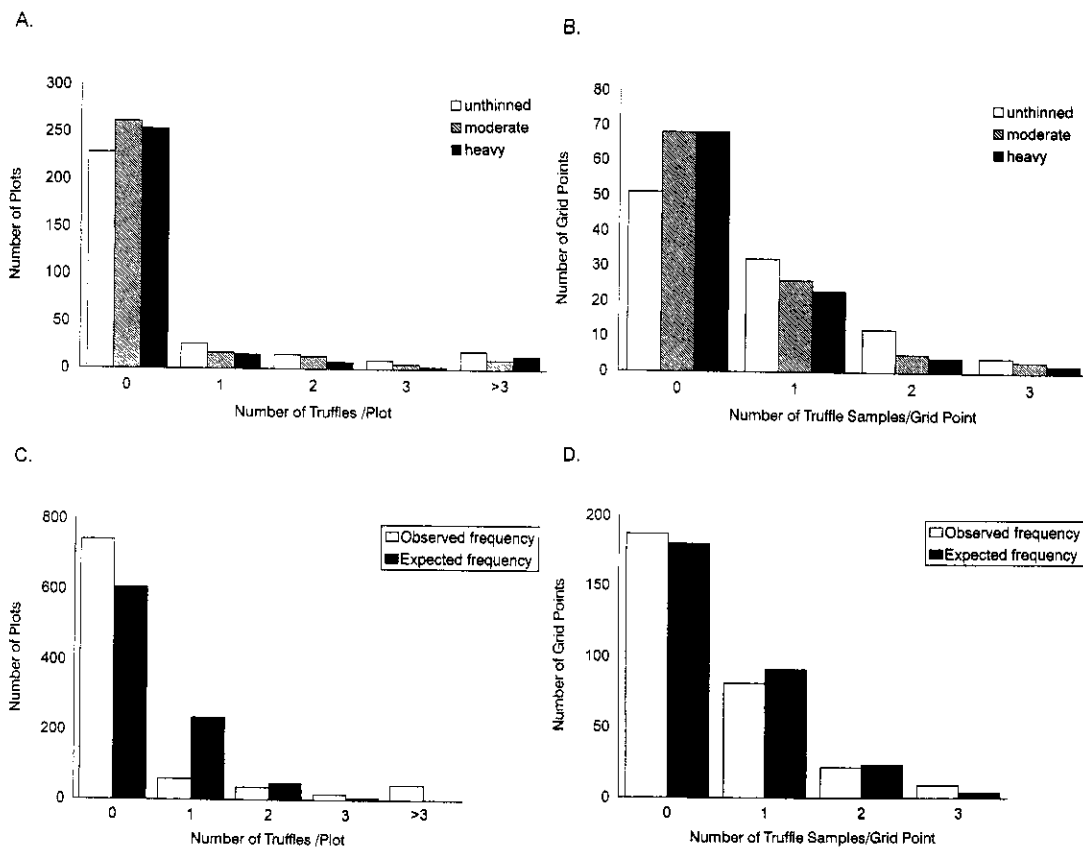


Figure 4. A) Frequency of hypogeous sporocarp plots with different numbers of sporocarps found per plot (n=894 total plots) in 4 unthinned, 4 moderately thinned, and 4 heavily thinned Douglas-fir stands, Oregon Coast Range, 1996 and 1997; B) frequency of grid points with different numbers of sporocarp samples per grid point (n=298 total grid points) by treatment; C) observed vs expected frequencies (based on Poisson distributions) of numbers of sporocarps found per plot (n=894 total plots); and D) observed vs expected frequencies (based on Poisson distributions) of numbers of sporocarp samples per grid point (n=298 total grid points) in Oregon Coast Range, 1996 and 1997.

tributed on the 4-m² plot scale for any of the nine season-by-treatment combinations ($P < 0.001$ for each test) or when seasons and treatments were combined ($P < 0.001$, Figure 4C). Sporocarps were randomly distributed among grid points for all study sites for all locations. When the data for locations were combined, however, the sporocarps were significantly clumped at grid points ($P < 0.05$, Figure 4D).

Relationship between habitat variables and hypogeous sporocarp abundance

Hypogeous sporocarp frequency was negatively associated with stump density ($Y = 0.59 - 0.0009X$, $R^2 = 0.42$, $P = 0.02$, Figure 5). Snag density (X_1),

stump density (X_2), and large log density (≥ 50 -cm diam, X_3) explained much of the variability in the regression model with sporocarp biomass (Y): $Y = 487.4 - 7.21X_1 - 1.86X_2 + 3.66X_3$, $R^2 = 0.64$, $P = 0.04$. Sporocarp biomass was negatively related to stump density ($r = -0.40$) and positively associated with large log density ($r = 0.38$) in this model. Density of large snags (≥ 50 -cm dbh, X_1), density of small logs (10-49-cm diam, X_2), density of large logs (X_3), and density of slash (X_4) explained a significant amount of the variability in the data set with sporocarp frequency (Y): $Y = 0.03 - 0.13X_1 - 0.02X_2 + 0.17X_3 - 0.73X_4$, $R^2 = 0.96$, $P = 0.001$. Sporocarp frequency was positively related to large log density ($r = 0.37$) and negatively

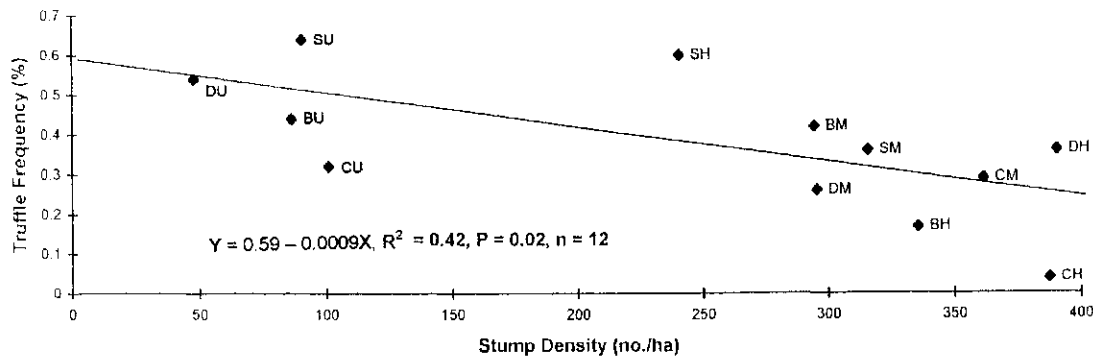


Figure 5. Relation between truffle percent frequency and stump density (no./ha), Oregon Coast Range, 1996 and 1997. Point labels designate stands (SU=Stimson unthinned, SM=Stimson moderate, SH=Stimson heavy, CU= C-line unthinned, CM= C-line moderate, CH= C-line heavy, DU=Deer Diamond unthinned, DM=Deer Diamond moderate, DH= Deer Diamond heavy, BU=Bensmith unthinned, BM=Bensmith moderate, BH=Bensmith heavy).

related to slash ($r=-0.48$) in this model. Large snags (X_1), stumps (X_2), and small logs (X_3) explained much of the variability in the regression model with *Hysterangium* standing crop biomass (Y): ($Y=1.23-0.47X_1-0.08X_2+0.04X_3$, $R^2=0.60$, $P=0.05$). *Hysterangium* biomass was negatively related to large snag density ($r=-0.55$) in this model. Large deciduous tree density (≥ 50 -cm diam, X_1) small snag density (10-49-cm diam, X_2), large snag density (X_3), and slash density (X_4) explained much of the variability in the regression model with *Tuber* biomass (Y): ($Y=0.25+1.67X_1+0.05X_2-0.26X_3-0.003X_4$, $R^2=0.73$, $P=0.04$). *Tuber* standing crop biomass was positively related to large deciduous tree density ($r=0.45$).

Discussion

The number of sporocarp-producing species (Table 2, Figure 2) and large proportion of sporocarp standing crop biomass produced by a relatively few of those species (Table 3) in our study agree with results of others in the Pacific Northwest, as reviewed by Carey et al. (2002). We hypothesized that sporocarp production and diversity would decrease with commercial thinning, because hypogeous fungi depend on their mycorrhizal host plants for photosynthates and their thalli tend to be concentrated in the upper mineral and organic soil, layers, which are disturbed during timber harvesting. Our data showed that commercial thinning reduced hypogeous sporocarp frequency and mean number of species fruiting at 2-3 yr after cutting (Figure 2). Colgan et al. (1999) drew similar conclusions from sampling within 3 yr since thin-

ning. Photosynthetic potential is positively correlated with abundance of ectomycorrhizal fungal sporocarps in forests (Termorshuizen and Schaffers 1987). Our results may in part result from differences in photosynthetic potential of the host tree canopy between the thinned and unthinned stands together with loss of the fungus-supporting root systems of the cut trees, as also evidenced by the negative correlation of hypogeous sporocarp frequency and stump density (Figure 5).

No differences in sporocarp standing crop biomass could be detected in our data because of large variance. However, number of stumps was significantly greater on thinned than unthinned stands (Table 1) and sporocarp biomass and frequency were negatively related to number of stumps (Figure 5). The correlation analyses thus permit an inference that the larger the number of trees cut, the smaller the standing crop biomass. Colgan et al. (1999) drew similar conclusions, their study and ours both being 3 yr after thinning. In northern California, species composition of hypogeous sporocarps differed between thinned and unthinned stands 10 yr after thinning, but overall sporocarp standing crop biomass did not differ between treatments (Waters et al. 1994). The reduction of standing crop biomass with increasing number of trees cut in the short term thus may be mitigated over time. However, changes in the species of hypogeous fungal sporocarps can persist for a decade or more. We and Colgan et al. (1999) both showed the fruiting of fungal species differed between thinned and unthinned stands

within 3 yr after cutting (Table 5, Figure 1), and Waters et al. (1994) detected similar differences 10 yr after thinning. *Gautieria* and *Hysterangium* were more abundant in the unthinned stands than thinned both within 3 yr and after 10 yr of cutting (Waters et al. 1994, Colgan et al. 1999). This trend was not evident in our study, possibly because the climate and soils differed substantially from those of the other studies cited. The Coast Range of Oregon is characterized by relatively high rainfall and moderate temperatures that likely allow some species to better tolerate disturbance by thinning.

The higher sporocarp species richness in the unthinned than thinned treatment of our study (Figure 2) is noteworthy in light of the fungal species diversity common to the diet of small mammal mycophagists (Maser et al. 1978, 1985, Carey et al. 2002). This diversity may be a nutritional imperative for fungal specialists: Claridge et al. (1999) demonstrated by feeding trials that the northern flying squirrel (*Glaucomys sabrinus*) and California red-backed vole (*Clethrionomys californicus*) did not maintain their body weight on a diet solely of *Rhizopogon vinicolor*. Their chemical analyses of this fungus, which abounded both in our study and that of Colgan et al. (1999), showed a relatively low nutritional value to mammals. They suggested that a diet of diverse fungal species might be required to provide the needed array of dietary constituents. Northern flying squirrels supplement their diet with staminate catkins of conifers (Maser et al. 1985), mast of maples (Carey et al. 2002), and various other materials (Thysell et al. 1997). They are not highly mobile (Martin and Anthony 1999) but can readily visit a variety of habitats within their home range (Carey 2000). Small scale thinnings therefore may not seriously impinge on the amount or diversity of their food supply. Large scale thinnings, in contrast, could reduce quality of their habitat by decreasing the amounts or diversity of hypogeous sporocarps: we documented a positive relation between flying squirrel abundance and sporocarp biomass in a companion study to this one. The California red-backed vole, in contrast, an extreme mycophagist, typically ingests eight or more species of hypogeous fungi in a day (Maser et al. 1978) and has habitat requirements and behaviors that severely restrict its home range (Rosenburg et al. 1994, Maser 1998). Reducing fungal diver-

sity in its habitat by thinning even on a relatively small scale could be seriously detrimental.

Sporocarp standing crop of nine hypogeous genera varied seasonally: total sporocarp standing crop was highest in spring 1996 and lowest in autumn 1997 (Table 4). Fungal species commonly fruit only in one particular season each year, but weather patterns within a season may also produce marked year-to-year variation (Fogel 1981, Eveling et al. 1990). Data must be collected over many years as done by Louma et al. (1991) to address seasonal relationships of any taxon adequately. Other species attributes may also come into play. For example, Johnson (1994) placed species into two groups based on sporocarp moisture content. Fleshy or succulent species with high moisture content fruited in response to rainfall or in cool months of the year, whereas species that form relatively dry sporocarps did not respond to rainfall. In our study only *Elaphomyces granulatus* would be categorized as having dry sporocarps, and its frequency was too low to evaluate effects of thinning.

Distributions of hypogeous sporocarps were clumped at the plot and grid station levels (Figure 4), and total sporocarp abundance was associated with abundance of CWD. Clearly, hypogeous sporocarps were not randomly distributed. Fogel (1976) and Hunt and Trappe (1987) also reported clumped distributions of hypogeous sporocarps. Hypogeous sporocarp production has been associated with CWD elsewhere (Amaranthus et al. 1994, Clarkson and Mills 1994). This association likely results from the ability of decayed CWD to absorb and retain the moisture essential for hypogeous sporocarp production in dry months (Amaranthus et al. 1994). Clarkson and Mills (1994) suggested that the frequency of CWD use by some mycophagists would also increase the incidence of hypogeous sporocarps there, because that is where the spore-bearing feces are likely to be deposited. At the same time, the presence of the sporocarp food resource in and near decayed CWD would attract the animals. Most particularly, the occurrence of the fungal specializing California red-backed vole is strongly tied to CWD (Maser et al. 1978, Ure and Maser 1982, Maser 1998).

Commercial thinning in the Oregon Coast Range influenced hypogeous sporocarp production and species richness at 2-3 yr after cutting,

but the overall impact of thinning is difficult to assess because of seasonal and local fluctuations in hypogeous sporocarp populations. Because CWD was an important variable for predicting hypogeous sporocarp production, the retention of CWD in commercially thinned sites is likely important to sporocarp production of certain hypogeous species and to habitat maintenance for many small mammal mycophagists.

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