NOTES

# The effects of thinning and broadcast burning on sporocarp production of hypogeous fungi

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The objectives of our study were to determine the effects of commercial thinning and broadcast burning on sporocarp production of hypogeous ectomycorrhizal (HEM) fungi. At two sites in northeastern California, Jennie Springs (JS) and Swain Mountain (SM), we compared HEM sporocarp production among units that had been heavily thinned, moderately thinned, and unthinned. At one of those sites, JS, we also compared sporocarp production between units that had been broadcast burned and units left unburned. Sporocarps were sampled in 1992, 10 years after thinning and 9 years after burning occurred at JS, and 17 years after thinning occurred at SM. Total relative frequency and biomass of sporocarps did not differ significantly among thin levels at either site, or between burn levels at JS. There was, however, significant association between thin level and frequencies of the most common genera at JS, suggesting that thinning significantly affected the composition of HEM fungi. The association between burn level and frequencies of the most common genera was also significant, but less pronounced than the association between thin level and the frequencies of common genera.

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Les objectifs de cette étude consistaient à déterminer les effets de l'éclaircie commerciale et du brûlage extensif Sur la production de carpophores par les champignons ectomycorhiziens hypogés. Nous avons comparé la production de carpophores par les champignons ectomycorhiziens hypogés dans des zones qui avaient été fortement éclaircies, modérément éclaircies et non éclaircies dans 2 sites du nord-est de la Californie : Jennie Springs et Swain Mountain. Dans un de ces sites, a Jennie Springs, nous avons aussi comparé la production de carpophores entre des zones qui avaient subi un brûlage extensif et des zones non brûlées. Les carpophores furent échantillonnés en 1992, 10 ans après 1'éclaircie et 9 ans après le brûlage à Jennie Springs, et 17 ans après l'éclaircie à Swain Mountain. La fréquence relative totale et la biomasse de carpophores ne différaient pas significativement entre les niveaux d'éclaircie dans aucun des sites ni entre les niveaux de brûlage à Jennie Springs. Il y avait cependant une relation significative entre 1'intensité de 1'eclaircie et la fréquence des genres de champignons les plus fréquents à Jennie Springs; ce qui suggère que 1'éclaircie affecte significativement la composition des champignons ectomycorhiziens hypogés. La relation entre les niveaux de brûlage et la fréquence des genres de champignons les plus fréquents était aussi significative quoique moins forte que la relation entre l'intensité de 1'éclaircie et la fréquence des genres de champignons les plus fréquents.

[Traduit par la rédaction]

## Introduction

Thousands of species of ectomycorrhizal fungi are associated with trees in North America (Pritchett 1979). The majority of these fruit above ground (epigeous species), but many go through their entire fruiting cycle below the ground surface (hypogeous species). The fruiting ecology of hypogeous ectomycorrhizal (HEM) fungi is poorly understood. Quantitative studies of HEM sporocarp production have primarily documented seasonal and annual variation in sporocarp production (Fogel 1976; Hunt and Trappe 1987; Luoma et al. 1991). Few studies have compared sporocarp production among forest types (see Luoma et al. 1991; Vogt et al. 1981), and we know of no published studies that have evaluated the effects of silvicultural practices on sporocarp production. Although not generally harvested commercially in North America as they are in Europe, sporocarps of HEM fungi are an important food source for numerous species of forest-dwelling small mammals (Fogel and Trappe 1978; Maser et al. 1978, 1986; Ure and Maser 1982; McIntire 1984; Maser and Maser 1987, 1988; Hall 1991).

Most species of ectomycorrhizal fungi rely on photosynthetically produced carbohydrates for carbon (Harley 1971; Last et al. 1979). Levels of ectomycorrhizae and ectomycorrhizal sporocarp production should, thus, be influenced by changes in host density, or any other changes that affect photosynthate production or allocation. Sporocarps of HEM develop in the upper mineral soil and organic layers, so silvicultural practices that alter forest floor conditions also should influence sporocarp production.

The objectives of our study were to determine the effects of commercial thinning and broadcast burning, two common silvicultural practices, on sporocarp production of HEM fungi. At two sites we compared sporocatp production among units that had been heavily thinned, moderately thinned,

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and unthinned. At one of these sites we also compared sporocarp production between units that had been broadcast burned and units left unburned. We predicted that total sporocarp production of HEM fungi would differ significantly among thin levels and between burn levels. We also predicted that composition of HEM sporocarps would differ significantly among thin levels and between burn levels.

## Study area and experimental design

*Jennie Springs*

The Jennie Springs site (JS) (40°24'N, 121°5'W) is located in Plumas County on the Lassen National Forest in northeastern California. The site has an elevation of 1860 m, a gentle slope of approximately 2%, and a southeasterly aspect. Soils are deep (1.0-2.4 m), well drained, and derived from mafic andesite. The long-term (1958-1991) average annual precipitation at a nearby (4.5 km away) precipitation gauge was 1165 mm. Most (≥80%) of the precipitation at this elevation typically falls as snow. Total precipitation during the 1992 hydrologic year (September 1991-October 1992) was 660 mm, 57% of the long-term average. Total precipitation ranged from 53-80% of the long-term average during the previous 5 years.

Prior to thinning, the site was covered by a homogeneous stand of white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) that originated following a stand-replacing wildfire. No trees, snags, or logs from the previous stand were present. Average age at breast height in 1992 -was 70 years (Oliver et al. 1981). Essentially no understory vegetation was present at the time of sporocarp sampling.

Because of its homogeneity, the stand was selected as the site for an experimental study on the effects of thinning intensity and broadcast burning on various tree and stand parameters (Oliver et al. 1981). Square units, 0.39 ha in size, were logged in 1982. Cut trees ≥30 cm diameter breast height (DBH) were removed by horse or cable. Units were burned during the spring and fall of 1983. Burn intensities were light to moderate with flame heights averaging approximately 0.5-1.0 m.

We sampled sporocarps of HEM fungi in 21 units, a subset of the units originally treated. Seven were heavily thinned (approximately 70% of basal area removed), seven were moderately thinned (approximately 35% of basal area removed), and seven were not thinned. Within each thin level, four units were broadcast burned and three were not burned. Burned units were distributed evenly between two spatial blocks (two replicates from each thin level in each block), and unburned units were distributed evenly among three spatial blocks (one unit from each thin level in each block).

Within each thin level, two of the burned units were burned in the spring of 1983 and two were burned in the fall of 1983. Using analysis of variance (ANOVA), we tested four variables for treatment effects between spring and fall burn levels: surface area of all logs (see below for description of variables), organic soil depth (combined depth of litter and humus), soil pH, and the soil carbon/nitrogen ratio. Each test was nonsignificant except soil pH ($F = 6.4$; df = 1, 10; $P = 0.0299$), which was slightly higher in the fall burn units ($\bar{x} = 5.93$, SE = 0.04) than the spring burn units ($\bar{x} = 5.80$, SE = 0.03). Therefore, we pooled spring and fall burn units for all analyses, creating a two-factor experimental design: three levels of thinning (heavily thinned, moderately thinned, and unthinned), and two levels of burning (burned and unburned).

*Swain Mountain*

The Swain Mountain site (SM) (40°26'N, 121°7'W) is located within the Swain Mountain Experimental Forest, 4.2 km northwest of JS. The site has an elevation of 1950 m, a gradual slope of 2-3%, and a northwest aspect. Soil and weather conditions are similar to those at JS. The current stand is a mix of white and red fir (*Abies magnifica* A. Murr.) that also originated following a stand-replacing wildfire. Average age at breast height in 1992 was 99 years (Oliver 1988).

This stand had also been used for a study on the effect of thinning intensity on tree and stand growth (Oliver 1988). In the summer of 1975, twelve 0.40-ha units were thinned to six basal area stand densities. Each level of thinning was replicated twice in a fully randomized design. After felling, cut trees ≥30-cm DBH were removed by rubber-tired skidder. Cut trees <30-cm DBH were piled as slash and burned during the fall of 1975.

We sampled sporocarps in three thin levels that were similar to thin levels at JS: heavily thinned (approximately 62% of basal area removed), moderately thinned (approximately 37% of basal area removed), and unthinned. Thus, for the Swain Mountain site, we had a single-factor experimental design with three levels and two replicates per level.

## Methods

*Field and laboratory methods*

Within each unit we established a 5 X 6 grid with 8-m spacing. At each grid point we established a 4-$m^2$ circular sample plot (1.13-m radius). We used four-tined rakes to carefully rake through the litter, humus, and upper 5-10 cm of mineral soil within each sample plot. We sampled each grid point (30/unit) once in early summer (June 22 - July 2 at JS; July 13-15 at SM) and midway between adjacent grid points (15/unit) once in early fall (September 24-29 at JS; September 29-30 at SM) of 1992. Sporocarp collections were placed in labeled wax bags and stored in a refrigerator until identified to genus. A collection was defined as any group of one or more sporocarps of the same genus found within a sample plot. Sporocarps were then air-dried and weighed on a Sartorius top-loading balance to the nearest 0.01 g.

We sampled log and tree variables in four 0.02-ha circular plots (8-m radius) systematically located within each unit. Within each plot we measured DBH for all trees and snags ≥8-cm DBH, measured the length and midpoint diameter for logs ≥12-cm diameter at the midpoint, and obtained three systematically located estimates of canopy cover using a spherical densiometer (Lemmon 1956). Logs were classified by decay class (Maser et al. 1979).

At 12 systematically located points within each unit, we dug small soil pits using narrow-bladed shovels to measure the depths of the litter and humus layers. At JS we also obtained small samples from the litter and humus layers and the upper mineral soil (5 cm below the humus-mineral soil interface). The 12 subsamples were combined into one composite sample for each unit, and soil moisture was determined gravimetrically for each composite sample. Litter and humus samples were oven-dried at 72°C for 72 h, and mineral soil samples were oven-dried at 105°C for 48 h.

To perform certain chemical analyses, we also obtained a separate systematically located composite sample (six subsamples were combined) from each unit at JS; subsamples were taken from a depth of 1-5 cm in the mineral soil. Composite samples were sieved to <2 mm, oven-dried at 105°C overnight, and ground to a fine powder with mortar and pestle. Percent total nitrogen and percent total carbon were determined by flash combustion using a Carlo-Erba NA 1500 Analyzer. Soil pH was measured with a standard pH meter and electrode using a one part soil to five parts water ratio. Chemical analyses were performed at the Oregon State University soils laboratory.

*Analyses*

As a measure of relative log abundance, we calculated log surface area using the area formula for a rectangle. We classified logs in decay classes 1-3 (Maser et al. 1979) as undecayed, and logs in decay classes 4-5 as decayed.

At JS we used two-way ANOVA to test for thin and burn effects in environmental and sporocarp variables. To determine

TABLE 1. Means and standard errors of variables measured at Jennie Springs by thinning level (pooled across burn level) and burn level (pooled across thin level), and *P*-values from *F*-tests from two-way ANOVA

| Variable | Thin level | | | Thin effect | Burn level | | Burn effect | Interaction |
|---|---|---|---|---|---|---|---|---|
| | Heavy | Moderate | Unthinned | *P* | Burned | Unburned | *P* | *P* |
| Environmental variables | | | | | | | | |
| Trees/ha | 101.2±6.3 | 248.7±24.1 | 749.6±74.0 | 0.0001 | 350.2±71.2 | 388.2±128.9 | 0.481 | 0.019 |
| % canopy cover | 41.7±2.7 | 66.5±3.1 | 85.2±1.0 | 0.0001 | 61.8±5.9 | 68.0±6.1 | 0.022 | 0.818 |
| Undecayed logs ($m^2$/ha) | 417.5±57.4 | 435.0±61.2 | 160.0±36.7 | 0.004 | 295.9±57.7 | 393.0±52.1 | 0.143 | 0.996 |
| Decayed logs ($m^2$/ha) | 59.9±13.0 | 91.4±23.9 | 79.0±17.3 | 0.424 | 64.1±13.6 | 93.6±16.0 | 0.191 | 0.482 |
| Litter depth (cm) | 1.9±0.3 | 2.5±0.3 | 2.8±0.2 | 0.0003 | 1.8±0.1 | 3.1±0.1 | 0.0001 | 0.600 |
| Humus depth (cm) | 1.0±0.3 | 1.2±0.2 | 2.0±0.2 | 0.015 | 1.1±0.2 | 1.9±0.2 | 0.007 | 0.903 |
| % moisture litter* | 4.9±0.7 | 8.5±1.1 | 15.2±1.7 | 0.0002 | 8.5±1.4 | 11.5±2.5 | 0.059 | 0.869 |
| % moisture humus* | 14.3±2.3 | 17.6±2.8 | 26.2±3.0 | 0.006 | 16.2±1.7 | 25.6±3.5 | 0.003 | 0.839 |
| % moisture mineral soil* | 22.7±1.7 | 25.0±1.2 | 24.4±0.6 | 0.771 | 23.5±1.0 | 25.1±0.8 | 0.297 | 0.211 |
| % total carbon | 12.25±0.57 | 13.75±1.33 | 12.14±1.19 | 0.575 | 12.99±0.79 | 12.35±1.02 | 0.642 | 0.766 |
| % total nitrogen | 0.59±0.04 | 0.62±0.06 | 0.58±0.07 | 0.920 | 0.61±0.04 | 0.58±0.05 | 0.738 | 0.687 |
| Soil pH | 5.79±0.06 | 5.82±0.07 | 5.80±0.03 | 0.904 | 5.87±0.03 | 5.72±0.05 | 0.032 | 0.861 |
| Sporocarp variables | | | | | | | | |
| Total biomass (kg/ha) | 1.99±0.68 | 1.27±0.34 | 1.41±0.37 | 0.897 | 1.40±0.35 | 1.76±0.45 | 0.601 | 0.756 |
| Total relative frequency | 0.34±0.07 | 0.31±0.04 | 0.33±0.04 | 0.963 | 0.32±0.04 | 0.34±0.05 | 0.804 | 0.884 |
| ALPO relative frequency | 0.02±0.01 | 0.03±0.02 | 0.05±0.02 | 0.422 | 0.05±0.02 | 0.01±0.01 | 0.099 | 0.465 |
| GAUT relative frequency | 0.00±0.00 | 0.01±0.01 | 0.05±0.02 | 0.022 | 0.02±0.01 | 0.03±0.02 | 0.603 | 0.932 |
| HYST relative frequency | 0.01±0.01 | 0.02±0.01 | 0.12±0.05 | 0.009 | 0.05±0.02 | 0.06±0.03 | 0.464 | 0.534 |
| GYMN relative frequency | 0.26±0.06 | 0.18±0.06 | 0.06±0.01 | 0.019 | 0.15±0.04 | 0.19±0.05 | 0.486 | 0.497 |
| BALS relative frequency | 0.02±0.01 | 0.02±0.01 | 0.02±0.01 | 0.607 | 0.03±0.01 | 0.02±0.01 | 0.521 | 0.080 |

NOTE: Data are untransformed means. ALPO, *Alpova;* GAUT, *Gautieria;* HYST, *Hysterangium;* GYMN, *Gymnomyces;* BALS, *Balsamia.* $n = 7$ for each thin level; $n = 12$ for the burned level; $n = 9$ for the unburned level.

*$n = 6$ for each thin level; $n = 12$ for burned level; $n = 6$ for unburned level.

treatment effects on composition of HEM sporocarps, we computed separate two-way contingency tables: thin level (pooled across burn level) X frequencies of the five most common genera, and burn level (pooled across thin level) X frequencies of the five most common genera. We used the *G*-test (log-likelihood ratio test) (Sokal and Rohlf 1981, p. 735) to test for significant association. Expected frequencies were too small for too many cells to test for interaction between thin level and burn level using a three-way contingency table; however, we did test for significant interaction for each of the five most common genera individually using two-way ANOVA. None of these five tests was significant.

Because there were only two replicates for each thin level at SM, we analyzed the SM data primarily to determine whether patterns were consistent with those from JS. We used ANOVA to test for an effect of thinning on total relative frequency and total biomass of sporocarps.

All variables that had a significant non-normal distribution were either log or arc sine transformed prior to analysis. We used the Shapiro-Wilks statistic (W) to test variables for normality (SAS Institute Inc. 1988). The SAS Institute Inc. (1988) statistics package was used for all analyses.

## Results

### *Jennie Springs*

#### *Environmental variables*

Of the 1081 trees sampled, 55% were white fir, 2% were red fir, and 43% were fir snags. Total tree density in the unthinned units was 3.0 times greater than in the moderately thinned units and 7.4 times greater than in the heavily thinned units (Table 1). Tree density did not differ significantly between burned and unburned units (Table 1). Although the surface area of decayed logs did not differ significantly among thin levels or between burn levels, the surface area of undecayed logs was significantly greater in the thinned units than in the unthinned units. This was a result of logging slash in the thinned units. Litter and humus depths were significantly less in thinned and burned units.

Percent moisture was significantly different among thin levels for litter and humus samples, but not for mineral soil samples (Table 1). Lower moisture levels in the organic layers of the thinned units were probably a result of increased evaporation rates resulting from increased solar radiation. There was a significant positive correlation between canopy cover and percent moisture for both litter ($r = 0.846$, df = 16, $P = 0.0001$) and humus ($r = 0.671$, df = 16, $P = 0.0023$) layers. The effects of thinning on percent moisture in the litter and humus were no longer significant after using canopy cover as a covariate in an analysis of covariance (ANCOVA) (litter: $F = 2.5$, df = 2, 15, $P = 0.1180$; humus: $F = 0.73$, df = 2, 15, $P = 0.5015$). Percent moisture in the humus was significantly less in burned than in unburned units, but this was probably primarily a result of the thinner litter and humus layers (increased evaporation rates) in the burned units. When we used thickness of the organic layer as a covariate, the ANCOVA test on the effect of burning on percent moisture in the humus was not significant ($F = 0.04$; df = 1, 16; $P = 0.8368$).

Percent total carbon and nitrogen did not differ significantly among thin levels or between burn levels (Table 1). The carbon/nitrogen ratio ranged from 19 to 25 and averaged 21.5 across all 21 units. Soil pH did not differ significantly among thin levels, and was slightly but significantly greater in burned than in unburned units.

#### *Sporocarp variables*

We found sporocarps of 14 hypogeous ectomycorrhizal genera, representing 10 families from the Basidiomycotina,

TABLE 2. Frequencies of sporocarp collections by genus and study site

| Taxonomic group | Jennie Springs | | Swain Mountain | |
|---|---|---|---|---|
| | Frequency | Percent | Frequency | Percent |
| Basidiomycotina | | | | |
| Boletaceae | | | | |
| *Rhizopogon* | 6 | 2.6 | 4 | 3.0 |
| *Alpova* | 21 | 9.2 | 6 | 4.5 |
| Melanogastraceae | | | | |
| *Melanogaster* | 1 | 0.4 | 0 | 0.0 |
| Russulaceae | | | | |
| *Martellia** | | | | |
| *Gymnomyces** | 105 | 45.9 | 64 | 48.5 |
| *Zelleromyces* | 1 | 0.4 | 2 | 1.5 |
| *Arcangeliella* | 1 | 0.4 | 0 | 0.0 |
| Strobilomycetaceae | | | | |
| *Gautieria* | 14 | 6.1 | 7 | 5.3 |
| Astraeaceae | | | | |
| *Radiigera* | 2 | 0.9 | 1 | 0.8 |
| Hysterangiaceae | | | | |
| *Hysterangium* | 34 | 14.8 | 1 | 0.8 |
| Ascomycotina | | | | |
| Balsamiaceae | | | | |
| *Balsamia* | 14 | 6.1 | 6 | 4.5 |
| Pyronemataceae | | | | |
| *Geopora* | 1 | 0.4 | 0 | 0.0 |
| Terfeziaceae | | | | |
| *Choiromyces* | 1 | 0.4 | 20 | 15.2 |
| Zygomycotina | | | | |
| Endogonaceae | | | | |
| *Endogone* | 5 | 2.2 | 2 | 1.5 |
| Unknown immature sporocarps | 23 | 10.0 | 17 | 12.9 |

**Martellia* and *Gymnomyces* were pooled for all analyses.

Ascomycotina, and Zygomycotina (Table 2). We pooled sporocarps from the genera *Gymnomyces* and *Martellia* (hereafter, referred to as *Gymnomyces*) because we believed we could not reliably separate these two closely related genera.

During the summer sample period, we found sporocarp collections in 206 of the 630 plots sampled (total relative frequency = 0.327). Most were found in the humus or in the upper mineral soil near the mineral soil - humus interface. Total biomass of all HEM collections was 1.56 kg/ha. Total relative frequency and total biomass did not differ significantly among thin levels or between burn levels (Table 1).

The test for association between thin level and frequencies of the five most frequently found genera was highly significant ($G$ = 72.58, df = 8, $P$ = 0.0001). *Gautieria* and *Hysterangium,* and to a lesser extent *Alpova,* were found more frequently in unthinned units than in thinned units (Fig. l*a*). *Balsamia* was found in similar numbers in all thin levels. *Gymnomyces* was the only taxonomic group found more frequently in thinned units than in unthinned units, but it was the most frequently found taxonomic group. Two-way ANOVA results for individual genera were consistent with contingency table results: relative frequencies of *Gautieria, Hysterangium,* and *Gymnomyces* differed significantly among thin levels (Table 1).

The test for association between burn level and frequencies of the five most common genera was significant ($G$ = 10.99, df = 4, $P$ = 0.027), but relative frequencies of the five individual genera did not differ significantly between burn levels (Table 1). *Alpova* was found more frequently in burned units (Fig. lb).

During the fall sample period, we found sporocarp collections of HEM fungi in only 13 of the 315 plots sampled (total relative frequency = 0.041). Pooled across burn levels, 10 of these plots were in unthinned units, two were in moderately thinned units, and one was in a heavily thinned unit. Pooled across thin levels, six were in burned units and seven were in unburned units. Only one of the collections was fresh, the other 12 were dry or rotting (several were infested with insect larvae).

*Swain Mountain*

*Environmental variables*

Of 222 trees sampled at SM, 47% were white fir, 31% were red fir, and 22% were fir snags. Mean tree density in the two unthinned units was 2.2 times greater than in the two moderately thinned units, and 5.6 times greater than in the two heavily thinned units (Table 3). Average canopy cover in the two unthinned units, however, was only 1.1 times greater than in the two moderately thinned units, and 1.4 times greater than in the two heavily thinned units. Average surface areas of undecayed and decayed logs were greatest in unthinned units and least in heavily thinned units. Average litter and humus depths were lowest in the heavily thinned units.

*Sporocarp variables*

During the summer sample period, we found sporocarp collections of HEM fungi in 109 of the 176 plots sampled

TABLE 3. Means and standard errors of variables measured at Swain Mountain

| Variable | Thin level | | |
|---|---|---|---|
| | Heavy | Moderate | Unthinned |
| Environmental variables | | | |
| Trees/ha | 118.2±18.7 | 304.6±6.2 | 659.0±62.2 |
| % canopy cover | 64.8±0.1 | 78.2±3.8 | 88.1±0.8 |
| Undecayed logs ($m^2$/ha) | 199.5±53.1 | 310.6±67.8 | 369.9±82.2 |
| Decayed logs ($m^2$/ha) | 147.2±48.3 | 231.2±41.2 | 550.2±38.0 |
| Litter depth (cm) | 1.4±0.4 | 2.9±0.2 | 3.5±0.4 |
| Humus depth (cm) | 1.2±0.6 | 2.5±0.3 | 2.2±0.2 |
| Sporocarp variables | | | |
| Total relative frequency | 0.52±0.15 | 0.68±0.15 | 0.62±0.05 |
| Total biomass (kg/ha) | 5.16±2.03 | 3.28±0.59 | 1.21±0.38 |

NOTE: Data are untransformed means. $n = 2$ for each thin level.

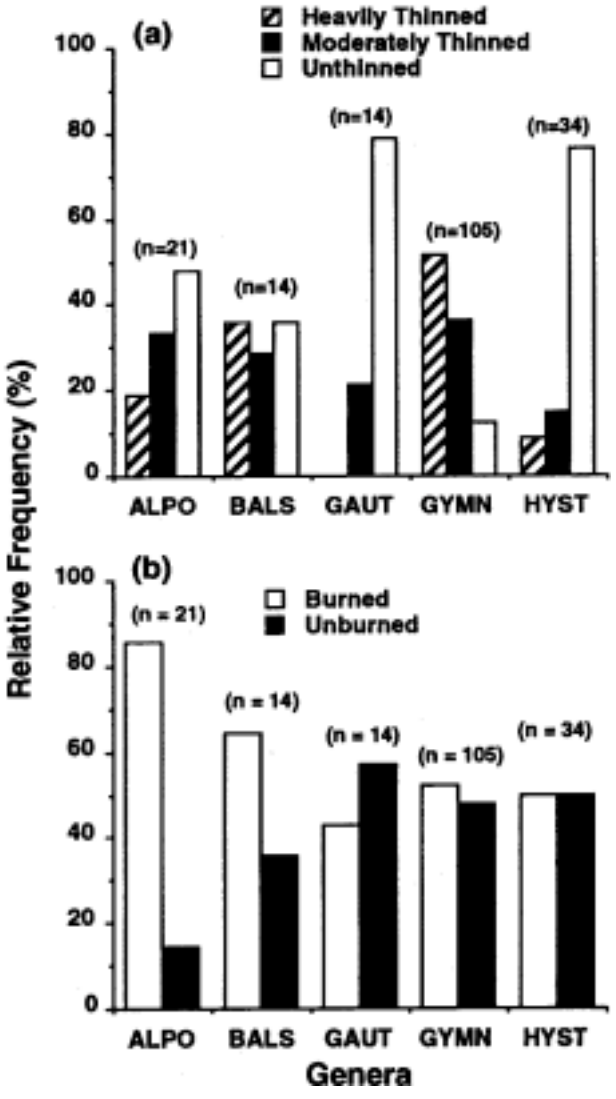


FIG. 1. Percentages of sporocarp collections found at Jennie Springs in (a) different thin levels pooled across burn level and in (b) different burn levels pooled across thin level for the five most common genera. ALPO, *Alpova;* BALS, *Balsamia;* GAUT, *Gautieria;* GYMN, *Gymnomyces;* HYST, *Hysterangium.*

(total relative frequency = 0.619). Total biomass of all HEM collections was 3.29 kg/ha. Similar to JS, we found no significant differences among thin levels for total relative frequency ($F = 0.25$; df = 2, 3; $P = 0.7920$) or total biomass ($F = 2.54$; df = 2, 3; $P = 0.2264$). Average total biomass was greatest in the heavily thinned units and least in the unthinned units (Table 3).

Relative frequencies of genera found at SM were similar to those at JS except for two genera (Table 2). The relative frequency of *Hysterangium* was much greater at JS, and the relative frequency of *Choiromyces* was much greater at SM. Only *Gymnomyces* and *Choiromyces* were found frequently enough to assess their association with thin level. This 3 X 2 contingency table was not significant ($G = 1.292$, df = 2, $P = 0.524$).

During the fall sample period, we found 28 sporocarp collections of HEM fungi in 27 of 88 plots sampled (total relative frequency = 0.307). Fifteen of these sample plots were in unthinned units, eight were in moderately thinned units, and four were in heavily thinned units. Four of the 28 collections were fresh, the others were dry or rotting (many were infested with insect larvae).

## Discussion

We found no evidence at either the JS or SM site that commercial thinning resulted in decreased total HEM sporocarp production 10 years (JS) or 17 years (SM) after thinning. At both sites photosynthetic potential was probably less in the heavily thinned units than in the unthinned units (Oliver 1988; W.W. Oliver, unpublished data). Our results, therefore, provide no evidence of a strong association between photosynthetic potential and total sporocarp production of HEM fungi. Termorshuizen and Schaffers (1987) found a significant positive correlation between an index of photosynthetic potential and sporocarp production of epigeous ectomycorrhizal fungi. Last et al. (1979) showed that sporocarp production of epigeous ectomycorrhizal fungi was closely associated with leaf production of *Betula* spp.; they also found that when all leaves were experimentally removed, sporocarp production ceased almost immediately.

We also found no evidence that light to moderate broadcast burns at JS resulted in differential total sporocarp production of HEM fungi 9 years after burning. Studies by Harvey et al. (1980a, 1980b) suggest that broadcast burning has negative short-term effects on numbers of ectomycorrhizal root tips. Harvey et al. (1980b) compared numbers of active ectomycorrhizal root tips among an area that had been partially harvested (50% of basal area removed) 3 years before sampling, an area that had been partially harvested

3 years before sampling and broadcast burned 2 years before sampling, and an undisturbed area. The mean number of active ectomycorrhizal root tips in the partially harvested area was 27% as great as the mean number in the undisturbed area, and the mean number in the partially harvested and broadcast burned area was only 5% as great as the mean number in the undisturbed area. They concluded that the low number of ectomycorrhizal root tips in the broadcast burned area was due to physical and chemical changes in the forest soil as a result of burning.

Our data do suggest, however, that commercial thinning and, to a lesser extent, broadcast burning influenced composition of HEM sporocarps. Relative frequencies of *Gautieria* and *Hysterangium* were significantly greater in unthinned units, whereas the relative frequency of *Gymnomyces* was significantly greater in the thinned units at JS. Because *Gymnomyces* was the most commonly found taxonomic group, these different association patterns canceled each other and resulted in no significant difference among thin levels in total relative frequency or total biomass. Moisture levels in the organic layers differed significantly among thin and burn levels, and soil temperatures undoubtedly differed substantially among thin levels. Luoma et al. (1991) found that relative abundances of HEM species varied substantially along both moisture and stand age gradients.

Our study is limited because our data are primarily from one sample period (sampling intensity for the fall sample was low) during 1 year. The summer sample, however, was timed to coincide with the period of greatest fruiting of HEM sporocarps. Timing of the summer sample was determined by the following criteria: time since snowmelt, knowledge of HEM fruiting period from the previous year at a nearby site, and the frequency of diggings left by small mammals foraging for HEM sporocarps. Snow did not melt from the JS site until about the 2$^{nd}$ week in May, and our fall sample shows that sporocarp production had declined substantially by mid-September.

Estimates of HEM sporocarp biomass from our study sites were comparable with estimates from other published studies. Our biomass estimates ranged from 0.10-4.30 kg/ha and averaged 1.56 kg/ha at JS, and ranged from 0.83-7.18 kg/ha and averaged 3.29 kg/ha at SM. Luoma et al. (1991), who sampled across a range of Douglas-fir *(Pseudotsuga menziesii* (Mirb.) Franco) stands over a 4-year period, found a maximum sample estimate of 9.9 kg/ha and an overall total biomass of 1.3 kg/ha. Fogel (1976) studied sporocarp phenology in a young Douglas-fir stand over a 3-year period; he found a maximum sample estimate of 9.6 kg/ha and an annual standing crop that ranged from 2.3-5.4 kg/ha. Hunt and Trappe (1987), who also studied sporocarp phenology in a young Douglas-fir stand, found a maximum sample estimate of 17.5 kg/ha, but their estimates of annual production ranged from 2.0-3.2 kg/ha.

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