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Truffle production in old-growth and mature fir stands in northeastern California

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Abstract

Few studies have examined fruiting patterns of hypogeous fungi, and relationships between sporocarp production of hypogeous fungi and forest habitat components such as organic soil depth and amounts of decayed wood are poorly understood. We sampled sporocarps of hypogeous fungi (truffles) in four old-growth (> 200 years) and four paired, mature (ca 100 years) fir (*Abies* spp.) stands during four sample periods in 1993 and three sample periods in 1994 in the Lassen National Forest in northeastern California. Truffles were collected from 4-m^2 circular plots systematically located at 36 grid points per stand during each sample period. Habitat characteristics were measured in 50.3-m^2 circles centered at each grid point in 1993. We found a total of 46 truffle species in 30.4% of the 2016 total plots, and the total standing dry weight of truffles was equivalent to 2.43 kg ha^{-1}. Total frequency and biomass of truffles and number of truffle species did not differ significantly between stand types in 1993 or 1994, but species composition did. We found no significant associations between measures of total truffle abundance and measures of habitat structure and composition at the 0.25-ha grid scale or at the 50.3-m^2 habitat plot scale. At the scale of the 4-m^2 truffle plot, plots with decayed wood were more likely to have truffles than plots without decayed wood during the final sample period of each year, but the association was significant only in 1993. Mean organic soil depth was greater in plots with truffles than plots without truffles in each sample period in both years, but ranked values were only marginally significant in one sample period. Goodness-of-fit tests to the Poisson distribution indicated that individual truffles had clumped distributions, but we could not reject the null hypothesis of random distribution of truffle collections. Our results indicate that total truffle production had recovered from stand-replacement wildfire in the mature stands, and that total truffle abundance was not strongly associated with habitat characteristics within the range of habitat variation exhibited in these stands. Individual species, however, were associated with old-growth stands and others with mature stands. © 1997 Elsevier Science B.V.

Keywords: *Abies*; Hypogeous fungi; Sporocarps

1. Introduction

Most species of fungi that produce macroscopic, hypogeous (fruit below ground) sporocarps are ectomycorrhizal basidiomycetes and ascomycetes (Trappe, 1962, 1971, Miller, 1983) and are commonly referred to as 'truffles.' Some of the sporocarpic species within the class zygomycetes form ectomycorrhizae (*Endogone* spp.), and others form vesicular-arbuscular mycorrhizae (*Glomus* spp. and *Sclerocystis* spp.) (Maser et al., 1978, Janos et al.,

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1995). Mycophagy (fungus consumption) is considered the primary method of spore dispersal for fungi that produce hypogeous sporocarps (Fogel and Trappe, 1978). Hypogeous sporocarps are common in the diets of small mammals in temperate forests dominated by ectomycorrhizal fungi throughout the world (e.g. Tevis, 1953, Fogel and Trappe, 1978, Maser et al., 1978, Ure and Maser, 1982, Taylor, 1992, Johnson, 1994), as well as tropical forests dominated by vesicular-arbuscular mycorrhizal fungi (Janos et al., 1995).

Total sporocarp production and species composition of mycorrhizal fungi are expected to change as forest stands age following disturbance (Dighton and Mason, 1985, Termorshuizen, 1991, Vogt et al., 1992). Most species of ectomycorrhizal fungi are considered obligately dependent on their host plants for carbon (Harley, 1971, Hacskaylo, 1973, Last et al., 1979), so stand-replacement disturbance is expected to negatively affect truffle production for some period of time, at least until ectomycorrhizal hosts become reestablished. Disturbance of the organic soil is also expected to affect truffle production because both ectomycorrhizae (Harvey et al., 1978, 1979) and truffles (Waters, J.R., Luoma, D.L., personal observation) are primarily located in organic soil layers and the upper mineral soil. Previous studies have shown that total truffle production was low in young stands. Vogt et al. (1981) found that truffle production was significantly less in a 23-year-old stand of *Abies amabilis* than in a 180-year-old stand, and that truffle composition differed between the two stands. Two studies found that truffle frequency and biomass were significantly less in Douglas-fir (*Psuedotsuga menziesii*) plantations < 30 years old than in nearby, late-seral stands (Clarkson and Mills, 1994, Amaranthus et al., 1994).

Two studies have shown, however, that total truffle production in stands > 70 years old either was greater than or did not differ significantly from truffle production in late-seral stands. Luoma et al. (1991) found that standing crop biomass was greatest in mesic mature (80–199 years) (2.2 kg ha^{-1}) Douglas-fir stands in the Cascade Range of Oregon, followed by mesic old-growth (≥ 200 years) (1.6 kg ha^{-1}), mesic young (< 80 years) (1.2 kg ha^{-1}), wet old-growth (0.9 kg ha^{-1}), and dry old-growth stands (0.7 kg ha^{-1}). North et al. (1997) found no significant difference in standing crop biomass of truffles between natural 70-year-old (4.51 kg ha^{-1}) and old-growth (4.02 kg ha^{-1}) stands located in Washington, but that truffle biomass was significantly less in 60-year-old stands that originated following clearcutting and burning (0.78 kg ha^{-1}). Other studies of truffle production have focused on seasonal and annual variation in sporocarp production (Fogel, 1976, Fogel and Hunt, 1979, States, 1985, Hunt and Trappe, 1987, Luoma, 1991).

In a previous study designed to evaluate associations between northern flying squirrel (*Glaucomys sabrinus*) density and forest structure, we found that mean truffle frequency did not differ significantly between old-growth and 75–95-year-old fir (*Abies* spp.) stands, but that both were significantly greater than in shelterwood-logged fir stands; mean truffle frequency was greatest in old-growth stands and intermediate in the 75–95-year-old stands (Waters and Zabel, 1995). To better understand the relationships between truffle production and stand age and structure, we designed a study specifically to compare truffle production between old-growth and mature fir stands. Our primary objectives were to (1) compare total frequency and biomass, number of species, and species composition of truffles between old-growth and mature fir stands and (2) evaluate associations between total truffle abundance and measures of habitat structure and composition.

2. Methods

2.1. Study area

Stands were located within the Swain Mountain Experimental Forest, which is located at the southern end of the Cascade Range within the Lassen National Forest in northeastern California. We used a paired study design to help control for site differences other than stand age. We located four areas where an old-growth stand was located in close proximity to a mature stand. Old-growth and mature stands were separated by < 0.4 km for three pairs and by 0.7 km for the fourth pair. Old-growth and mature stands within each pair were similar in elevation, slope, aspect, and tree species composition (Table 1). Soils were well drained and derived from

Table 1
Stand information for old-growth and paired, mature stands. Percent red fir was the percentage of total basal area

Pair	Stand type	Elevation (m)	Aspect	Slope (%)	Percent red fir
1	Old-growth	1988	NW	9	90
	Mature	2003	NW	11	99
2	Old-growth	1796	SE	16	41
	Mature	1811	NE	18	10
3	Old-growth	1799	SE	19	60
	Mature	1823	SE	19	19
4	Old-growth	1945	NE	16	87
	Mature	1954	NE	14	100

mafic andesite. Stands were dominated by red fir (*A. magnifica*) and white fir (*A. concolor*). All stands were unmanaged.

Old-growth stands were multi-layered and contained large amounts of coarse woody debris (logs, stumps, and snags). Other than small firs, only scattered herbaceous plants (e.g. *Pyrola picta*, *Viola purpurea*, and *Corallorhiza maculata*) and occasional shrubs (primarily *Chrysolepis sempervirens*) were present in the understory. The median age estimate from counting rings on 30 large cut stumps (basal diameter > 100 cm) located near the four old-growth stands was 250 years (range: 186–383 years).

Mature stands originated after stand-replacement wildfire and were dense and homogeneous in structure. Few residual logs, snags, or trees were present. Because mature stands had closed canopies, virtually no herbaceous plants or shrubs occurred in the understory. Old shrub stems indicated that mature stands were dominated by brushfields for some period of time after wildfire occurred. We estimate that these stands ranged from 80 to 110 years old. The median age estimate from coring 20 randomly selected dominant and codominant trees was 84 years (range: 64–108 years).

We obtained weather data from a station located in Chester, California, ca 16 km southwest of the study area. Total precipitation was 86 cm in 1992, 105 cm in 1993, and 70 cm in 1994. Average (1947–1989) annual precipitation at the Chester weather station was 84 cm. Most ($\geq 80\%$) of the precipitation at Swain Mountain Experimental Forest typically falls as snow.

2.2. Sampling procedures

Within each of the eight stands we established a 6×6 grid with 10-m spacing (0.25 ha). In 1993 we measured habitat characteristics in 50.3-m^2 circular plots (4-m radius) centered at each grid point. Within each of these habitat plots we measured the diameter at breast height (DBH) of all trees ≥ 12 cm DBH and tallied trees 1–5 cm DBH and 6–11 cm DBH. We also measured the length, mid-point diameter, and decay class (Maser et al., 1979) of portions of logs within the habitat plot with a mid-point diameter ≥ 10 cm.

Truffles were collected within 4-m^2 circular plots (1.13-m radius) positioned systematically near each of the 36 grid points. In 1993 truffles were collected during four sample periods, and the four plots were clustered around each grid point. In 1994 truffles were collected during three sample periods, and the three plots were clustered around each of 36 points offset from the 1993 points. Plots were never located on previously sampled areas. We sampled at monthly intervals with the first sample occurring 6–7 weeks after snowmelt. The two upper elevation pairs were sampled 2–3 weeks later than the two lower elevation pairs because of delayed snowmelt. In 1993, Sample Period 1 began on July 7, Period 2 on August 3, Period 3 on September 8, and Period 4 on October 13. In 1994 Sample Period 1 began on June 21, Period 2 on July 26, and Period 3 on August 19.

After establishing the 4-m^2 truffle plot, we measured the length and diameter of portions of decayed logs (classes 4–5; Maser et al., 1979) within the truffle plot. (Decayed logs were soft and elliptical to flat in cross-sectional shape.) Next we dug a shallow soil pit ca 30 cm wide and measured the depth of the organic soil layer (litter and humus layers combined) at three systematically positioned points. Decayed logs and organic soil depth were measured within truffle plots in all sample periods except the first sample period of 1993. We then used four-tined rakes to carefully rake through the litter, humus, and upper 5–10 cm of mineral soil. Truffle collections (all truffles of the same species found in a plot) were sent to Corvallis, Oregon to be identified, air-dried, and weighed.

To compare soil moisture between stand types, we collected soil samples three times during the

study: October of 1993 and July and October of 1994. We used a small can (5 cm diameter × 8.5 cm length) to collect mineral soil subsamples from a depth of 5–10 cm. Thirty-six systematically located subsamples were combined into one composite sample for each grid. Soil samples were oven-dried at 105°C for 48 h, and soil moisture was determined gravimetrically for each composite sample.

2.3. Analyses

We compared means of habitat variables between old-growth and mature grids using analysis of variance (ANOVA). We used a randomized complete-blocks ANOVA design for this and each subsequent ANOVA test; each pair of old-growth and mature grids was a block. Logs in decay classes 1–3 were classified as undecayed and logs in decay classes 4–5 were classified as decayed.

We used repeated-measures ANOVA (sample period was the repeated factor) to test whether total truffle frequency (percentage of 36 plots in which one or more truffle collection was found), total truffle biomass (dry weight), and number of truffle species varied between old-growth and mature grids. ANOVAs were performed separately for 1993 (four sample periods) and 1994 (three sample periods). Biomass values were log transformed to reduce skewness. To compare truffle composition between stand types, we used a contingency table to test whether there was significant association between stand type and truffle species. Numbers of truffle collections were pooled across sample periods and years for this test. We included ten species in this analysis that met the following conditions: present in three or more of the four grids and one or more of the two stand types, and comprised $\geq 2\%$ of the total number of collections found during the study. Expected frequency was > 5 for each cell within this 2×10 table.

We evaluated associations between truffle presence or abundance and measures of decayed wood and organic soil depth at three spatial scales, and between total truffle abundance and other measures of habitat structure and composition at two spatial scales. At the scale of the 0.25-ha grids, we computed Spearman rank correlations among the eight grids between total frequency and biomass of truffles (pooled across sample periods and years) and eight measures of habitat structure and composition: white fir basal area, red fir basal area, snag basal area, number of 1–5-cm-DBH stems, number of 6–11-cm-DBH stems, surface area of undecayed logs, surface area of decayed logs, and organic soil depth. Values were the means from the 36 habitat plots sampled in each grid.

At the scale of the 50.3-m^2 habitat plots, we evaluated associations between two measures of total truffle abundance and habitat characteristics using the 1993 data. The first measure of truffle abundance was the number of plots at each grid point in which one or more truffle collections were found during 1993; values ranged from 0 to 4 because four plots were sampled at each grid point in 1993. (In 1994 truffle plots fell outside of the 50.3-m^2 habitat plots.) The second measure of truffle abundance was the sum dry weight of truffle collections found in the four plots at each grid point. We pooled across stand type ($n = 288$ grid points) and performed a stepwise multiple regression for each measure of truffle abundance. Independent variables were the same eight variables used in the previous analysis, except they were not averaged across habitat plots. The significance level for entry and removal to the multiple regression model was 0.15.

At the scale of the 4-m^2 truffle plot, we also evaluated associations between truffle presence and (1) presence of decayed wood and (2) organic soil depth. We used a 2×2 contingency table to test for association between truffle presence (plots with truffles and plots without truffles) and presence of decayed wood (plots with no decayed wood and plots with at least some decayed wood). We used the Wilcoxon rank-sum test (SAS Institute Inc., 1989, p. 1196) to compare organic soil depth values between plots with truffles and plots without truffles. Tests were performed separately for Sample Periods 2–4 in 1993 and 1–3 in 1994.

We also used the frequency distributions of individual truffles and truffle collections to characterize their spatial distributions. We used goodness-of-fit tests to the Poisson distribution (Zar, 1984, p. 409) to test the null hypotheses that individual truffles and truffle collections were randomly distributed. For the first hypothesis, we compared numbers of truffles found per truffle plot with numbers expected based

on the Poisson distribution. We tested each year-by-sample period combination separately ($n = 288$ plots for each of the seven tests). For the second hypothesis, we compared numbers of truffle collections found per grid point to numbers expected based on the Poisson distribution (four plots per grid point were sampled in 1993 and three plots per grid point were sampled in 1994). We tested each year separately ($n = 288$ grid points for each of the two tests). We pooled across stand type for both sets of tests because contingency tables indicated no significant association between stand type and numbers of truffles/plot ($\chi^2 = 1.51$, d.f. = 3, $P = 0.679$) or between stand type and numbers of truffle collections per grid point ($\chi^2 = 2.27$, d.f. = 6, $P = 0.894$). We pooled frequency classes so that no class had an expected frequency < 1.0.

3. Results

3.1. Stand characteristics

Of the 1236 live trees ≥ 12 cm DBH counted within the 288 habitat plots, 530 were red fir, 704 were white fir, one was lodgepole pine (*Pinus contorta*), and one was Jeffrey pine (*P. jeffreyi*). Old-growth grids had much greater mean values for trees 1–5 cm DBH, trees > 90 cm, snags > 52 cm, and percent ground cover of undecayed and decayed logs > 25 cm (Table 2). Mature grids had much greater mean values for trees 12–27 cm, trees 28–52 cm, and snags 12–52 cm. Soil moisture in October of 1993 was slightly, but significantly, greater in mature grids. Organic soil depth did not differ significantly between old-growth and mature grids.

3.2. Truffle frequency and biomass, species richness, and composition

We sampled 8064 m^2 over 2 years and found truffles in 30.4% of the 2016 plots; total standing dry biomass was equivalent to 2.43 kg ha^{-1}. Neither mean total frequency (Fig. 1) or mean total biomass (Fig. 2) of truffles differed significantly between old-growth and mature grids in 1993 or 1994. In 1993 mean total frequency and biomass were lowest in July 1, but in 1994 declined from June 1 through August 3.

Table 2
Means (x), standard errors (SE), and P values from ANOVA tests comparing habitat variables between four old-growth and four mature fir stands

	Old-growth		Mature		Stand type, P [a]
	x	SE	x	SE	
Trees 1–5 cm DBH ha^{-1}	355.1	158.3	33.2	20.6	0.148
Trees 6–11 cm DBH ha^{-1}	353.7	117.9	182.4	48.9	0.299
Trees 12–27 cm DBH ha^{-1}	349.5	100.0	708.7	46.3	0.030
Trees 28–52 cm DBH ha^{-1}	172.7	35.6	530.5	45.3	0.001
Trees 53–90 cm DBH ha^{-1}	92.6	27.6	69.1	11.2	0.319
Trees > 90 cm DBH ha^{-1}	23.5	4.7	0.0	0.0	
Snags 12–52 cm DBH ha^{-1}	45.6	6.5	193.4	58.9	0.085
Snags > 52 cm DBH ha^{-1}	5.5	2.3	0.0	0.0	
% Ground cover undecayed logs 10–25 cm diam.	0.88	0.22	2.37	0.54	0.084
% Ground cover undecayed logs > 25 cm diam.	1.33	0.45	0.38	0.20	0.046
% Ground cover decayed logs 10–25 cm diam.	0.73	0.17	1.32	0.38	0.251
% Ground cover decayed logs > 25 cm diam.	5.35	1.51	0.62	0.12	0.052
Organic soil depth (cm)	5.18	0.17	4.65	0.29	0.176
% Soil moisture					
October 1993	28.4	0.8	31.7	0.5	0.024
July 1994	19.2	0.6	20.7	0.8	0.287
September 1994	16.4	0.8	17.0	0.8	0.576

[a] Degrees of freedom for each test were 1 for the numerator and 3 for the denominator.

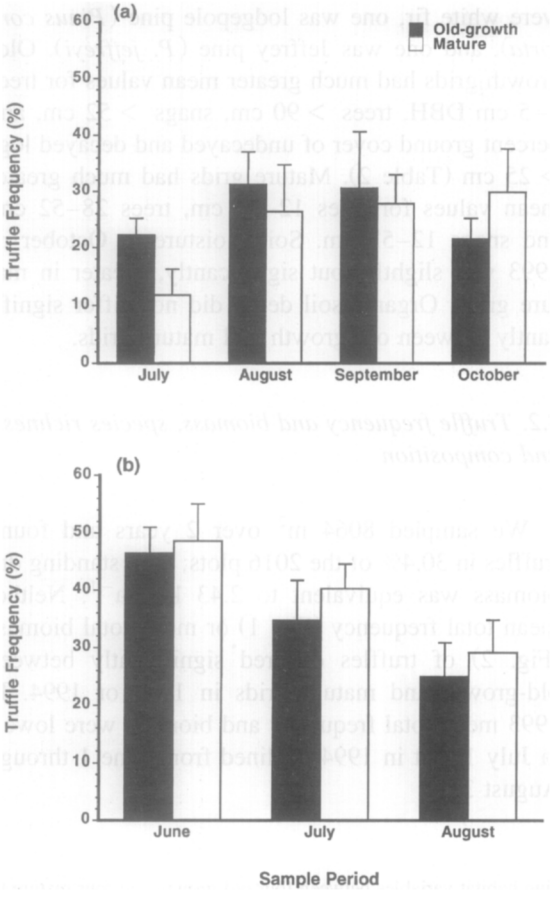

Fig. 1. Means and standard errors of total truffle frequency in four old-growth and four mature fir stands during (a) four sample periods in 1993 and (b) three sample periods in 1994. Stand type effect from repeated measures ANOVA was not significant in 1993 ($F_{1,3} = 0.10$, $P = 0.775$) or 1994 ($F_{1,3} = 0.62$, $P = 0.488$); sample period effect was nearly significant in 1993 ($F_{3,9} = 3.32$, $P = 0.071$) and significant in 1994 ($F_{2,6} = 13.39$, $P = 0.006$).

We found a total of 46 species of truffles (Table 3). Four of these species were secotioid fungi (Table 3), which are considered evolutionary intermediates between gilled mushrooms and truffles. We grouped secotioid species with truffles because they were ecologically similar in being mycorrhizal and primarily hypogeous in fruiting habit. Only three species individually contributed $> 4\%$ of the total number of collections found and ten species contributed $\geq 2\%$. *Gautieria monticola* was the most abundant species; it comprised 30.1% of the total number of truffle collections and 56.5% of total biomass. The next two most common species were *Alpova trappei*, which comprised 8.4% of total collections and 6.6% of total biomass and *Gymnomyces abietis*, which comprised 8.8% of total collections and 4.0% of total biomass.

Thirty-eight species were found in both old-growth and mature grids. Mean number of truffle species did not differ significantly between stand types in 1993 ($F_{1,3} = 0.74$, $P = 0.452$) or 1994 ($F_{1,3} = 0.16$, $P = 0718$).

Association between stand type and truffle species was significant (Fig. 3), indicating that composition

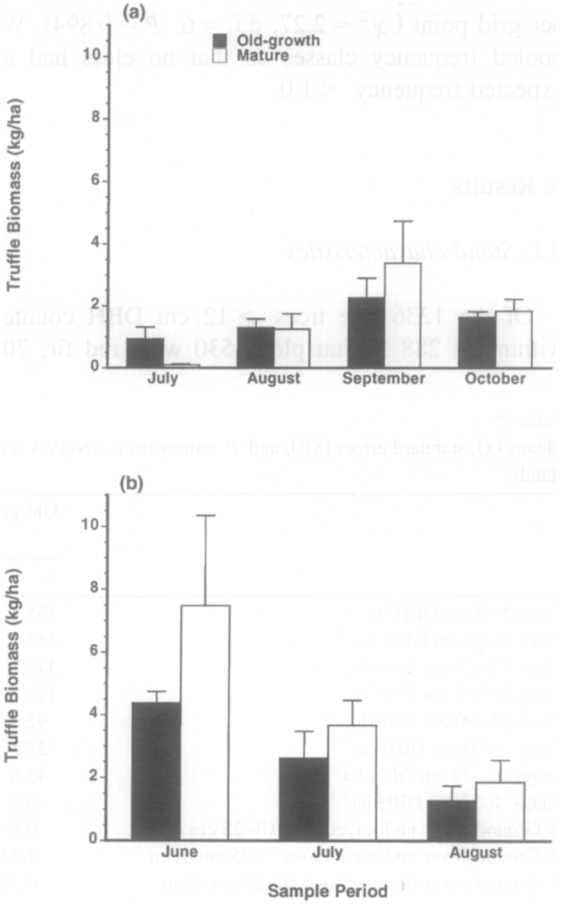

Fig. 2. Means and standard errors of total truffle biomass in four old-growth and four mature fir stands during (a) four sample periods in 1993 and (b) three sample periods in 1994. Stand type effect from repeated measures ANOVA was not significant in 1993 ($F_{1,3} = 3.38$, $P = 0.163$) or 1994 ($F_{1,3} = 0.68$, $P = 0.470$); sample period effect was significant in 1993 ($F_{3,9} = 23.17$ $P < 0.001$) and 1994 ($F_{2,6} = 8.14$, $P = 0.020$).

Table 3
Frequencies (%) and dry weights (g ha^{-1}) of truffle collections (pooled across sample period) found in four old-growth and four mature fir stands in the Lassen National Forest in northeastern California. Within each stand type, 576 4-m^2 plots were sampled in 1993 (four sample periods) and 432 in 1994 (three sample periods)

Species	1993				1994			
	Old-growth		Mature		Old-growth		Mature	
	Frequency	Dry weight	Frequency	Dry weight	Frequency	Dry weight	Frequency	Dry weight
Alpova trappei	3.3	85.59	2.3	138.72	4.4	242.94	2.5	211.57
Arcangeliella lactarioides [a]	0.7	37.20	1.0	57.34	0.2	32.93	0.2	5.67
Balsamia magnata	0.0	0.00	0.2	3.86	0.0	0.00	0.0	0.00
Brauniellula albipes	0.2	2.17	0.0	0.00	0.0	0.00	0.0	0.00
Choiromyces alveolatus	0.2	3.47	0.7	105.17	0.5	17.82	0.2	5.61
Cortinarius velatus [a]	0.9	7.94	0.2	2.82	0.0	0.00	0.0	0.00
Cortinarius verrucisporus [a]	0.3	18.58	0.0	0.00	0.0	0.00	0.0	0.00
Elaphomyces decipiens	0.2	0.69	0.0	0.00	0.0	0.00	0.0	0.00
Elaphomyces granulatus	0.0	0.00	0.2	59.03	0.0	0.00	0.0	0.00
Elaphomyces muricatus	0.9	192.32	0.0	0.00	0.0	0.00	0.0	0.00
Endogone flamicorona	0.0	0.00	0.2	0.61	0.0	0.00	0.0	0.00
Endogone lactiflua	0.2	0.30	0.3	0.65	0.0	0.00	0.7	1.85
Gautieria crispa	0.0	0.00	0.3	11.07	0.0	0.00	0.2	20.25
Gautieria monticola	8.5	651.87	6.1	715.67	15.3	1625.64	16.4	2960.76
Gautieria pterosperma	0.2	12.98	0.0	0.00	0.2	13.83	0.0	0.00
Genabea cerebriformis	0.0	0.00	0.0	0.00	0.0	0.00	0.2	0.41
Geopora cooperi	0.7	65.97	0.2	13.02	0.7	19.68	0.0	0.00
Gymnomyces abietis	2.8	49.91	3.6	99.44	3.5	73.73	3.0	182.52
Gymnomyces sp.	0.2	1.74	0.5	86.37	0.0	0.00	0.0	0.00
Hydnotrya cerebriformis	0.3	10.85	0.7	37.54	0.2	1.04	1.4	60.07
Hydnotrya cubispora	0.0	0.00	0.2	1.30	0.0	0.00	0.0	0.00
Hydnotrya variiformis	0.2	3.60	0.0	0.00	0.0	0.00	0.2	7.41
Hydnotrya sp.	0.2	0.78	0.0	0.00	0.0	0.00	0.0	0.00
Hymenogaster sublilacinus	0.5	6.51	0.3	1.26	1.6	48.21	0.7	11.05
Hysterangium coriaceum	0.0	0.00	0.0	0.00	0.9	18.40	3.5	209.66
Hysterangium crassirhachis	1.4	12.24	2.4	49.96	0.5	3.94	0.9	21.76
Leucogaster rubescens	0.9	21.92	0.5	14.63	0.2	8.22	0.2	3.41
Leucophleps magnata	0.0	0.00	0.0	0.00	0.9	15.74	0.5	30.79
Leucophleps spinispora	1.4	32.08	1.6	174.96	0.5	16.38	0.5	9.49
Macowanites setchellianus	0.0	0.00	0.0	0.00	0.5	32.41	0.2	23.38
Macowanites sp.	0.0	0.00	0.0	0.00	0.0	0.00	0.5	12.21
Martellia californica	0.0	0.00	0.0	0.00	0.2	2.20	0.5	32.29
Martellia fragrans	0.0	0.00	0.2	0.74	0.2	4.22	0.5	38.48
Martellia fulvispora	1.0	23.05	0.5	9.07	0.2	2.31	0.9	33.91
Martellia reticulosa	0.0	0.00	0.0	0.00	0.2	4.05	0.2	1.27
Martellia subochracea	0.7	28.65	0.0	0.00	0.2	1.22	0.0	0.00
Martellia subfulva	0.0	0.00	0.0	0.00	0.5	6.48	2.1	102.03
Martellia vesiculosa	0.0	0.00	0.0	0.00	0.0	0.00	0.2	10.19
Martellia sp.	0.2	0.26	0.3	0.65	0.7	6.31	2.3	92.65
Melanogaster tuberiformis	0.0	0.00	0.0	0.00	1.4	43.40	1.6	30.61
Melanogaster varigatus	0.2	20.83	0.2	2.17	2.1	123.84	1.2	29.51
Pyrenogaster atrogleba	0.2	15.06	0.2	2.52	0.2	9.90	0.2	5.50
Rhizopogon evadens	2.3	90.63	0.0	0.00	1.2	171.01	0.0	0.00
Rhizopogon subcaerulescens	0.7	67.10	0.3	6.94	0.2	2.95	0.0	0.00
Rhizopogon vulgaris	0.2	3.34	0.2	24.31	0.7	106.71	0.5	36.11
Rhizopogon sp.	0.0	0.00	0.0	0.00	2.1	67.42	0.5	11.05
Sedecula pulvinata	0.2	27.78	0.0	0.00	0.0	0.00	0.2	15.45
Thaxterogaster pingue [a]	1.0	25.09	0.5	13.28	1.9	27.55	2.3	107.00

Table 3 (continued)

Species	1993				1994			
	Old-growth		Mature		Old-growth		Mature	
	Frequency	Dry weight	Frequency	Dry weight	Frequency	Dry weight	Frequency	Dry weight
Trappea darkeri	1.2	14.84	0.7	3.95	0.0	0.00	0.2	2.72
Trappea phillipsii	0.0	0.00	0.0	0.00	0.2	6.37	0.0	0.00
Unidentified truffle	0.9	0.17	0.9	0.43	1.4	1.68	2.8	14.29
Zelleromyces sp.	0.0	0.00	0.3	6.51	0.0	0.00	0.0	0.00

[a] Secotioid fungal species.

differed between old-growth and mature stand types. Percentages of *Gautieria monticola*, *Gymnomyces abietis*, *Thaxterogaster pingue*, and *Leucophelps spinispora* collections were similar between stand types. Percentages of *Hysterangium crassirhachis* and *Hysterangium coriaceum* collections were greater in mature grids, and percentages of *Alpova trappei*, *Rhizopogon evadens*, *Melanogaster varigatus*, and *Hymenogaster sublilacinus* collections were greater in old-growth grids.

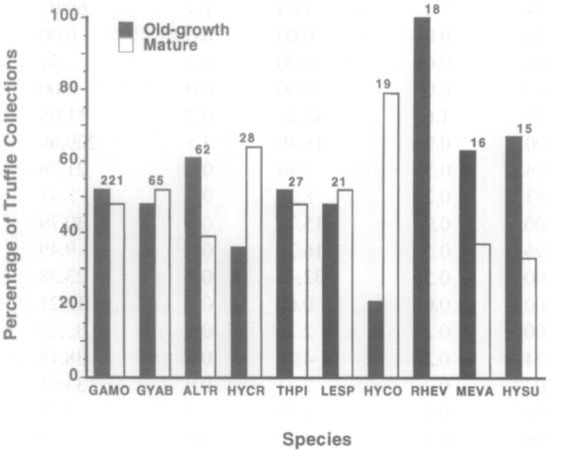

Fig. 3. Percentages of truffle collections found in four old-growth and four mature fir stands in the Lassen National Forest. Total number of collections found for each species (pooled between 1993 and 1994) is listed above columns. Contingency table analysis indicated significant association between stand age and numbers of collections of ten most common truffle species ($\chi^2 = 31.58$, d.f. = 9, $P < 0.001$). Species were *Gautieria monticola* (GAMO), *Gymnomyces abietis* (GYAB), *Alpova trappei* (ALTR), *Hysterangium crassirhachis* (HYCR), *Thaxterogaster pingue* (THPI), *Leucophelps spinispora* (LESP), *Hysterangium coriaceum* (HYCO), *Rhizopogon evadens* (RHEV), *Melanogaster varigatus* (MEVA), and *Hymenogaster sublilacinus* (HYSU).

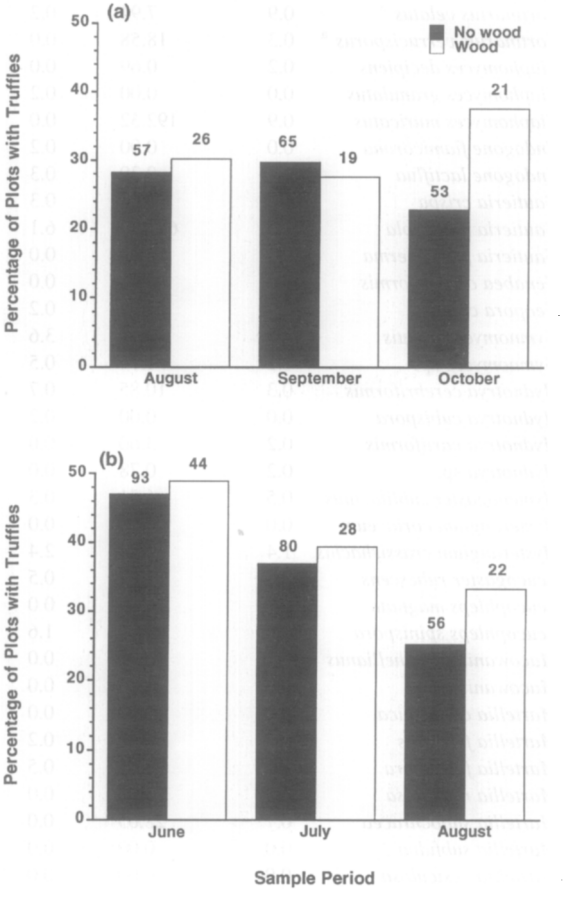

Fig. 4. Percentages of 4-m^2 truffle plots (pooled between old-growth and mature grids) in (a) 1993 and (b) 1994 without decayed wood and with at least some decayed wood that had one or more truffle collection ($n = 288$ plots for each sample period). Numbers of plots with truffles are listed above columns. P values from 2×2 contingency tables (d.f. = 1) testing for association between truffle presence and presence of decayed wood were 0.730 in August of 1993, 0.733 in September of 1993, 0.024 in October of 1993, 0.762 in June of 1994, 0.698 in July of 1994, and 0.193 in August of 1994.

3.3. Associations between truffle abundance and habitat characteristics

At the 0.25-ha grid scale, none of the correlations between mean habitat characteristics and truffle frequency among the eight grids was significant ($P \geq 0.320$), nor were any of the correlations with truffle biomass ($P \geq 0.139$). At the scale of the 50.3-m^2 habitat plots, little of the variation in either measure of truffle abundance was explained by the eight habitat variables. For the stepwise multiple regression using the number of truffle plots at each grid point with one or more truffle collection as the dependent variable ($n = 288$ grid points), red fir basal area and surface area of undecayed logs entered the model, producing an R^2 of 0.063. Using the dry weight of all truffles found in the four plots at each grid point as the dependent variable ($n = 288$ grid points), only red fir basal area entered the model, and R^2 was 0.015.

At the scale of the 4-m^2 truffle plot, only one of

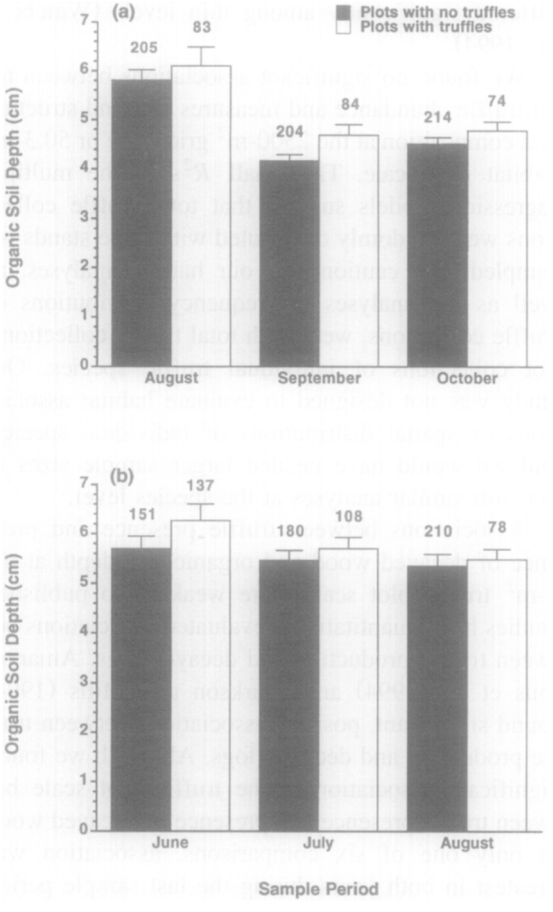

Fig. 5. Means and standard errors for organic soil depth in (a) 1993 and (b) 1994 within 4-m^2 plots with no truffles and plots with one or more truffle collection (pooled between old-growth and mature grids). Number of plots is given above each column. P values from Wilcoxon ranksum tests comparing ranked values between plots without truffles and plots with truffles were 0.447 in August of 1993, 0.057 in September of 1993, 0.330 in October of 1993, 0.351 in June of 1994, 0.494 in July of 1994, and 0.096 in August of 1994.

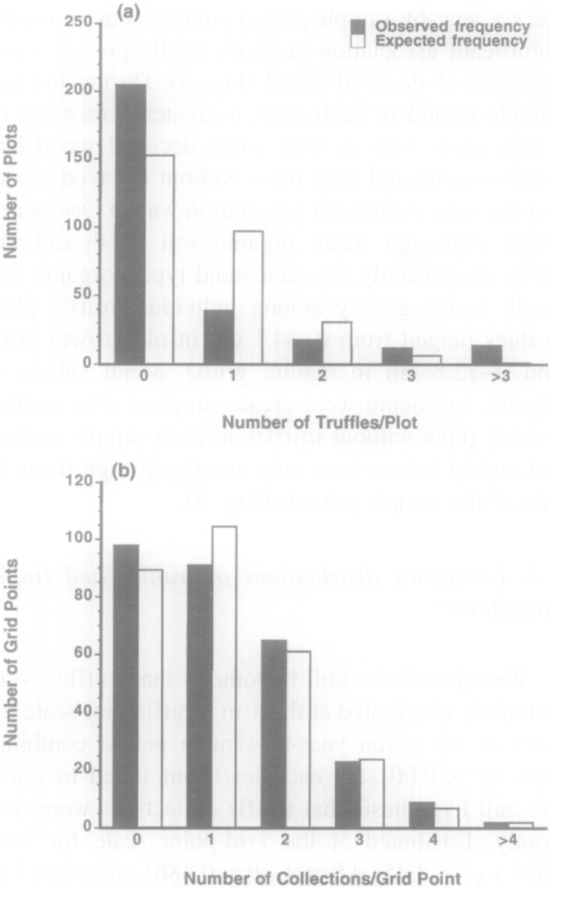

Fig. 6. (a) Observed frequencies of truffle plots with different numbers of truffles found/plot for the 288 truffle plots sampled in August of 1993 and expected frequencies based on Poisson expectations; goodness-of-fit result: $\chi^2 = 201.40$, d.f. = 3, $P < 0.001$. (b) Observed frequencies of grid points with different numbers of truffle collections found/grid point for the 288 grid points sampled in 1993 and expected frequencies based on Poisson expectations.

the six year-by-sample period comparisons showed a significant association between truffle presence and presence of decayed wood (Fig. 4). During the last sample period of each year, a greater percentage of truffle plots with at least some decayed wood had truffles compared with plots without decayed wood, but the only significant association was in October of 1993. Although mean organic soil depth did not differ significantly between stand types, organic soil depth varied greatly among individual truffle plots (values ranged from 0–34.1 cm in old-growth grids and 0–22.8 cm in mature grids). Mean values of organic soil depth were greater in plots with truffles than in plots without truffles in each sample period, but ranked values were only marginally significant in one of the sample periods (Fig. 5).

3.4. Frequency distributions of truffles and truffle collections

We rejected the null hypothesis that truffles were randomly distributed at the 4-m^2 truffle plot scale for each of the seven year-by-sample period combinations ($P < 0.001$ for each test), but failed to reject the null hypothesis that truffle collections were randomly distributed at the grid-point scale for both 1993 ($\chi^2 = 3.45$, d.f. = 4, $P = 0.486$) and 1994 ($\chi^2 = 5.18$, d.f. = 4, $P = 0.270$). Greater numbers of truffle plots had 0 or > 3 truffles/plot (tails of the distribution) than expected based on Poisson expectations (e.g., Fig. 6a), indicating distributions of truffles were clumped (Sokal and Rohlf, 1981, p. 89). We found no evidence, however, of clumped distributions of truffle collections at the grid-point scale (e.g. Fig. 6b).

4. Discussion

Our results are consistent with those of North et al. (1997) in finding no significant difference in total truffle production between mature and old-growth conifer stands. Luoma et al. (1991) did not statistically compare truffle production among stand age classes, but found that standing crop biomass was greater in mesic mature stands than in mesic old-growth stands. Although we found no significant differences in total frequency or biomass of truffles and number of truffle species, species composition did differ significantly between old-growth and mature stands. Of the ten most frequently found species, four were similarly abundant in both stand types, four were found more frequently in old-growth stands, and two were found more frequently in mature stands. In a previous study, we found no significant difference in total frequency or biomass of truffles among units within a large white fir stand that had not been thinned, moderately thinned, and heavily thinned 10 years previously, but composition differed significantly among thin levels (Waters et al., 1994).

We found no significant associations between total truffle abundance and measures of stand structure and composition at the 2500-m^2 grid scale or 50.3-m^2 habitat plot scale. The small R^2s of the multiple regression models suggest that total truffle collections were randomly distributed within the stands we sampled. We caution that our habitat analyses, as well as the analyses of frequency distributions of truffle collections, were with total truffle collections, not collections of individual truffle species. Our study was not designed to evaluate habitat associations or spatial distributions of individual species, and we would have needed larger sample sizes to perform similar analyses at the species level.

Associations between truffle presence and presence of decayed wood and organic soil depth at the 4-m^2 truffle plot scale were weak. Two published studies have quantitatively evaluated associations between truffle production and decayed logs. Amaranthus et al. (1994) and Clarkson and Mills (1994) found significant, positive associations between truffle production and decayed logs. Although we found significant association at the truffle plot scale between truffle presence and presence of decayed wood in only one of six comparisons, association was greatest in both years during the last sample period when soils were dry. Decayed logs retain large amounts of water and may influence truffle production most when soils are driest (Amaranthus et al., 1994).

We found evidence that total truffles were clumped but no evidence that total truffle collections were nonrandomly distributed. The tendency of truffles to be found in clusters has been shown or noted

by several authors (Fogel, 1976, States, 1985, Hunt and Trappe, 1987).

5. Conclusions

We conclude that total truffle production had recovered from stand-replacement wildfire in the mature stands within ca 100 years of stand origin. Weak associations between total truffle abundance and habitat characteristics suggest that total truffle collections were randomly distributed within the stands we sampled. Species composition of truffles, however, did differ significantly between stand types; some species showed no association with stand type, others were associated with old-growth stands, and others with mature stands.

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