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Response of ectomycorrhizal fungus sporocarp production to varying levels and patterns of green-tree retention

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Abstract

Forest management activities can reduce ectomycorrhizal fungus diversity and forest regeneration success. We examine contrasts in structural retention as they affect sporocarp production of ectomycorrhizal fungi (EMF)—a functional guild of organisms well suited as indicators of disturbance effects on below-ground ecosystems. Our results are from an experiment that tests the biodiversity assumptions behind current guidelines for ecosystem management. Ours is the first study complete with pre-treatment data that examines the effects of silvicultural manipulations on both epigeous (mushroom) and hypogeous (truffle) sporocarp production by EMF.

We tested the effects of two patterns (aggregated [A], dispersed [D]) and four levels (100, 75, 40, and 15%) of green-tree retention on standing-crop sporocarp biomass for spring and fall fruiting seasons. This study employed a randomized block design that replicated six retention treatments in three locations (blocks).

A total of 150 mushroom taxa and 58 truffle taxa were identified from the sample plots. Before treatment, the total number of mushroom taxa for each treatment ranged from 58 to 72 while the total number of truffle taxa ranged from 22 to 29. The pre-treatment condition was characterized by mushroom and truffle total fall biomass exceeding total spring biomass in two of three blocks. Although experimental units within blocks were selected for apparent similarity, our results show that uniformity of EMF populations in forests cannot be inferred from stand structure alone.

During the post-treatment sample period, the number of mushroom taxa detected in the 100% retention decreased by 34% while the number of truffle taxa increased by 20%. The number of taxa was reduced most in the 15%D treatment followed by the 15%A treatment. The 75%A retention treatment showed the least reduction in number of fruiting taxa.

After treatment, sporocarp production declined in all treatments, but these effects varied by season and treatment. Sporocarp production was nearly eliminated from the 15%A retention treatment. Mushroom and truffle production were significantly reduced in the 15%D treatment, though spring truffle biomass was maintained at 33% of the pre-treatment value. No treatment effect was detected on the fall mushroom or truffle standing crop in the 40%D treatment. Our results lend support to the use of

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dispersed green-tree retention in combination with aggregated retention when maintaining sporocarp production is a goal. Such a mix would ameliorate the effects of clearcutting as demonstrated in this study and may maintain higher levels of sporocarp production in the aggregates by reducing edge effects.

Keywords: Fungi; Mushroom; Truffle; Biomass; Mycophagy; Diversity

1. Introduction

Historically, clearcutting has been used as an economically viable way of harvesting timber from the predominately Douglas-fir forests of the Pacific Northwest (Tappeiner et al., 1997; Aubry et al., 1999). However, the complete removal of mature trees from large tracts of land and the use of heavy logging machinery can severely impact a forest ecosystem by drastically altering moisture and temperature regimes, stand structure, and soil microsite conditions (Franklin and DeBell, 1973; Rogerson, 1976; Stark, 1982). In reviewing the cumulative evidence from the Pacific Northwest, Franklin et al. (2002) note that the ecosystem effects of natural disturbances and processes differ dramatically from those engendered by clearcutting and other even-aged management practices that emphasize commodity production.

Concerns about timber management practices and the loss of habitat for certain species led to the creation of the Northwest Forest Plan which set specific guidelines for the management of federally-owned late-successional and old-growth forests within the range of the northern spotted owl (USDA and USDI, 1994). The plan also set a minimum standard of 15% green-tree retention in ''matrix'' lands that are open to timber harvest. In response to the plan, new silvicultural practices that attempt to balance ecosystem and commodity values of forests are being implemented across the region, but the need to test the assumptions behind the guidelines remains (Halpern et al., in press).

The ecosystem science approach to forest management pursues multiple objectives including the maintenance of biodiversity and the essential functions of a diverse biota in healthy, resilient ecosystems (e.g. Maser et al., 1978; Kohm and Franklin, 1997). Ectomycorrhizal fungi (EMF) are among the more critically important soil biotic components of forests in the Pacific Northwest. The symbiotic root fungus facilitates uptake of nitrogen, phosphorus, other minerals, and water to the plant (Marks and Kozlowski, 1973; Allen, 1991; Smith and Read, 1997). Mycorrhizal associations are vital to the existence of most vascular plants (Trappe, 1987; Trappe and Luoma, 1992; Smith and Read, 1997).

Ectomycorrhizal fungus species are highly diverse with over 2000 species symbiotic with Douglas-fir (Trappe, 1962, 1977). They vary in their response to seasonal or environmental change, their benefits to hosts (Trappe, 1987; Arnolds, 1992) or in the nutritional value of their sporocarps to mycophagists (Fogel and Trappe, 1978; Claridge and Cork, 1994; Luoma et al., 2003). Ectomycorrhizal fungus functional diversity provides buffering capacity and resilience to forest systems (Perry et al., 1989): different species enhance fitness and growth of host trees at different seasons, in different niches in the soil, or in response to different perturbations. Thus, high levels of EMF diversity may be linked to the ability of Douglas-fir to grow well over a wide range of habitats and over long periods of time.

Ectomycorrhizal fungi are, with few exceptions, asco- and basidiomycetes and most species produce macroscopic sporocarps in the form of mushrooms and truffles (epigeous or above-ground fruiting bodies and hypogeous or below-ground fruiting bodies, respectively). Sporocarps produce spores that contribute to dissemination of the species and provide for genetic recombination within and among populations. Many EMF species, especially those that produce truffles, are also important dietary items for vertebrates and invertebrates: some small mammal species rely on them for over 90% of their diet (Maser et al., 1978, 1985; Hayes et al., 1986; Claridge et al., 1996; Carey et al., 1999; Jacobs, 2002). Truffle species diversity provides necessary nutritional diversity to the diet of mammal mycophagists (see review by Luoma et al., 2003). Small mammals, in turn, form important links in the trophic

structure of forest ecosystems as prey for raptors (e.g. owls and goshawks) and mammalian carnivores (e.g. martens and fishers) (Fogel and Trappe, 1978; McIntire, 1984; Hayes et al., 1986; Carey, 1991). The potential for indirect consumption of truffles by predators of small mammals has been recognized, but there is also evidence that fishers consume truffles directly (Grenfell and Fasenfest, 1979; Zielinski et al., 1999).

Several studies in the Pacific Northwest and other northern temperate forests have examined the effects of silvicultural practices, particularly clearcutting, on the EMF community (see review by Jones et al., 2003). Most studies focused on effects of disturbance on residual fungus inoculum and on the amount and diversity of ectomycorrhiza (EM) types on seedlings planted in situ or in greenhouse experiments (Perry et al., 1982; Parke et al., 1983b, 1984; Pilz and Perry, 1984; Dahlberg and Stenström, 1991; Harvey et al., 1996; Jones et al., 1997, 2002). Some studies have also examined EM diversity on seedlings planted near forest edges or aggregates of retained live trees (Kranabetter and Wylie, 1998; Kranabetter, 1999; Kranabetter et al., 1999; Kranabetter and Friesen, 2002). A universal finding emerges from this work: the EMF community as seen on root tips changes significantly in disturbed sites compared to undisturbed, nearby forests (Jones et al., 2003). These changes might be due as much to environmental and biotic factors as to loss of host trees (Jones et al., 2003).

Fewer studies have examined silvicultural effects on EMF sporocarp production (Waters et al., 1994; Colgan et al., 1999). Although EMF sporocarps do not reveal as complete a picture of the below-ground EMF community as root tip studies (Gardes and Bruns, 1996; Dahlberg et al., 1997; Yamada and Katsuya, 2001; Horton and Bruns, 2002), silvicultural effects on sporocarp production mirror the effects found in root-tip studies: species diversity and community composition can change dramatically. For example, initial effects of thinning include reduced truffle biomass, reduced frequency of sporocarps, and shifts in species dominance (Colgan et al., 1999). However, total truffle biomass and frequency of sporocarps may recover 10–17 years after thinning, while shifts in species dominance persist longer (Waters et al., 1994).

Green-tree retention, the practice of leaving live, structurally-sound, large trees in a stand after extracting timber, is an alternative forest management method designed to accelerate the development of late-successional forest characteristics in young, managed stands (Franklin et al., 1997). The demonstration of ecosystem management options (DEMO) experiment is a long-term study designed to examine the effects of strongly contrasting levels and patterns of green-tree retention on multiple forest attributes (see Aubry et al., 1999). Research results are needed by forest managers seeking to incorporate basic ecological knowledge into forest management policies and practices.

The DEMO experiment allows us to test some of the assumptions behind the current guidelines for ecosystem management as they affect a functional guild (Root, 1967) of organisms (EMF) that can be used as indicators of the below-ground ecosystem response. For example, we expect that complete removal of trees from one ha patch cuts would eliminate production of EMF sporocarps due to removal of the photobiont and alteration of temperature and moisture regimes. Conversely, retention of intact forest aggregates should preserve near pre-treatment levels of sporocarp production in those areas; resulting in experimental unit sporocarp standing crops that are proportional to the green-tree retention level. Also, we would expect epigeous sporocarp production to be more sensitive to variation in the level and spatial pattern of retention than hypogeous sporocarp production due to more equable environmental conditions in the hypogeous environment than above ground. Overall, we hypothesize that EMF sporocarp production is positively related to basal-area retention due to the reliance of EMF on autotrophic hosts for their carbon supply.

In this paper we assess the initial responses of EMF sporocarp production to green-tree retention treatments and lay the foundation for the long-term monitoring of these responses. Ours is the first study in the context of a manipulative experiment that is complete with pre-treatment data and considers both epigeous and hypogeous sporocarp production.

Our objective was to compare pre- and post-treatment standing-crop biomass of EMF sporocarps within no harvest, 75, 40% (dispersed and aggregated), and 15% (dispersed and aggregated) retention

treatments. We tested the null hypothesis of no significant among treatment differences in sporocarp standing-crop biomass over time; e.g. from the pre-treatment condition to the post-treatment condition. As part of our discussion of changes in sporocarp production, we examined changes in EMF fruiting species richness as it varied by treatment.

2. Methods

The DEMO study replicated six green-tree retention treatments in six geographic locations (blocks). These experimental treatments are described in detail by Aubry et al. (1999). The treatments consisted of four levels of live-tree retention (15, 40, 75, and 100% of existing live-tree basal area), with two patterns of retention (aggregated and dispersed) applied to the 15 and 40% retention treatments (Fig. 1). The aggregated pattern consisted of residual trees retained in clumps of about 1 ha and the dispersed pattern left residual trees homogeneously dispersed throughout the unit. For the 75% retention treatment, basal area was cut from three 1-ha gaps that were systematically located in the unit. The 100% retention represents the control. Within each 13 ha (32 acre) treatment unit, grid points were established for sampling wildlife populations and vegetation. The most common grid pattern was 8 × 8 points spaced 40 m apart (Fig. 2), though 7 × 9 grids were used in some units. Fungal sporocarp sampling was limited to three blocks. The blocks were named for local geographic features: Butte, Dog Prairie, and Watson Falls.

2.1. Study areas

General environmental characteristics of the sites are described by Halpern et al. (1999) and Halpern et al. (in press). The Butte block is located on the Gifford Pinchot National Forest in southwestern Washington. The Dog Prairie and Watson Falls blocks are located on the Umpqua National Forest in southwestern Oregon. Principle site characteristics are presented in Table 1. Prior to harvest, all blocks were dominated by Douglas-fir. The importance of other tree species varied by block (Halpern et al., 1999). Harvesting was completed on the Butte block in 1997 and on the Umpqua National Forest blocks in 1998.

2.2. Data collection

Eighteen treatment units (six in each of three blocks) were sampled for EMF sporocarps during the peak spring and fall fruiting seasons. Data was collected from 1993 to 2001. Spring pre-treatment data were collected during three different years in each block except for the Butte block which was sampled in two different years. Fall pre-treatment data were collected from three different years for all blocks. Spring and fall post-treatment data were collected during three different years in all blocks. Data collection during a particular season was termed the ‘‘sample period’’. Due to logistical constraints, the calendar years in which the blocks were sampled sometimes did not coincide. The treatments (harvests) were implemented in the Butte block during the spring and summer of 1997 while the Dog Prairie and Watson

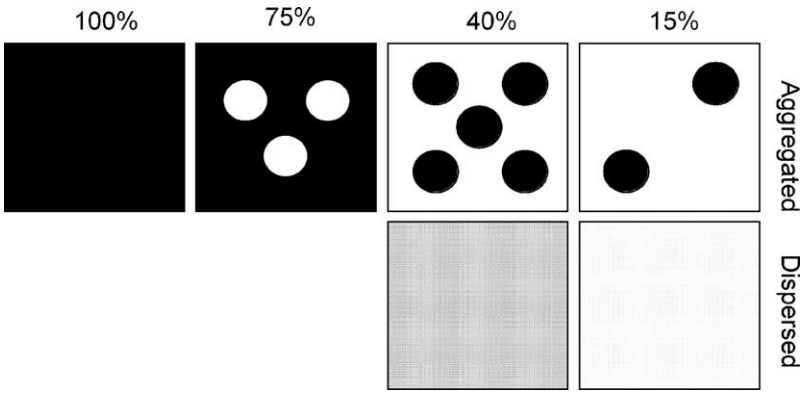

Fig. 1. Schematic representation of the six levels of green-tree retention, percent basal area in 13 ha treatment units, and pattern of retention.

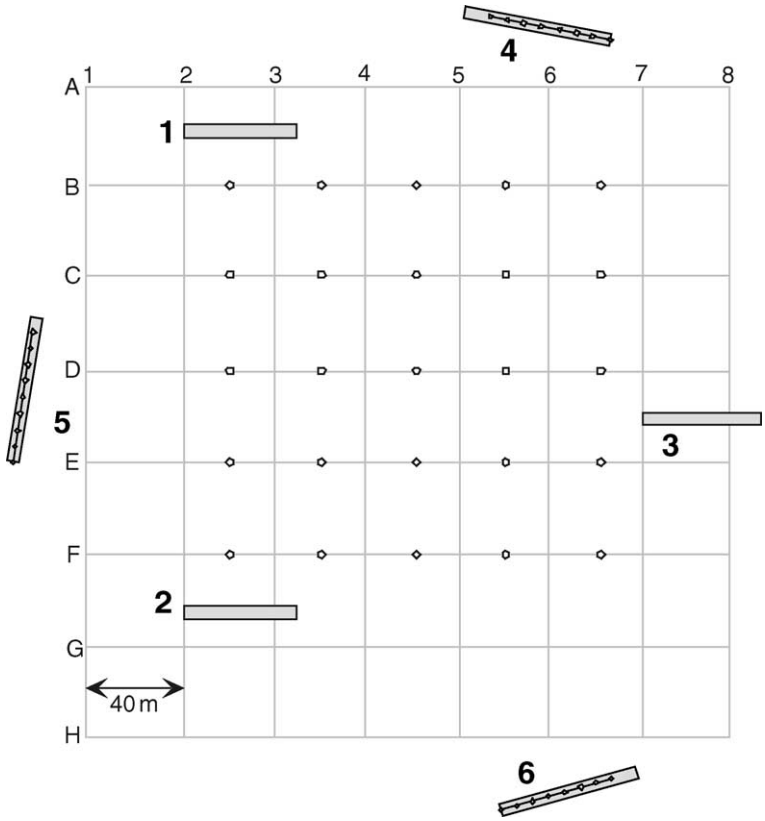

Fig. 2. Schematic of sample plot layout for fungi. Plots were dispersed throughout each experimental unit. Three, permanent, 2 m × 50 m mushroom sample plots (numbered 1–3) were located within the primary sampling grid (8 × 8 at 40-m spacing). Three transient, 2 m × 50 m mushroom plots (numbered 4–6) were established at different locations around the grid and were replaced each sample season. Transects located down the center of the non-permanent mushroom plots contained, respectively, 8, 9, and 8, circular 4-m^2 truffle plots totaling 100 m^2 each sample period. Small circles between grid points indicate approximate locations of dispersed truffle plots. See Section 2 for further details.

Falls blocks were harvested in spring and summer of 1998. For analysis, data from the fall immediately following harvest were not included.

All epigeous sporocarps (mushrooms) of EM species were collected from six strip plots (2 m × 50 m each) in each of the 6 treatment units in each block for a total sample area of 600 m^2 pre–treatment unit per sample period (hereafter referred to as a treatment sample). Each sample period had a total of 3600 m^2 sampled for each block. Each treatment unit was stratified into upper, mid-, and lower slope portions. One strip plot was permanently located in each slope position category. The other three mushroom plots were systematically repositioned each sampling period. This approach provided a large total sample area as recommended by Arnolds (1991) but also dispersed the sampling in order to include within-treatment variation in species distributions (Luoma et al., 1991). The Watson Falls block had little slope, therefore the plots were placed systematically in a manner consistent with that used in the blocks with steep slopes (Fig. 2). Post-treatment sampling in the aggregate retention treatments provided distribution of plots between the harvested areas and the aggregates in proportion to the treatment, i.e. for the 40%A treatment, 40% of the total sample plot area was in aggregates and 60% was in harvested areas.

Hypogeous sporocarps (truffles) were sampled by use of twenty-five 4-m^2 plots per experimental unit for a total area of 100 m^2 per treatment sample and a total of 600 m^2 for each block per sample period. The truffle plots were placed within the three shifting mushroom plots in transects of eight or nine plots. One transect was located in each slope position category

Table 1
Environmental and forest structural characteristics of each study block. Where ranges are presented, minimum and maximum values represent treatment-unit means (modified from Halpern et al., in press)

	Block		
	Watson Falls	Dog Prairie	Butte
Environmental characteristics			
Elevation (m)	945–1310	1460–1710	975–1280
Slope (%)	4–7	34–62	40–53
Aspect	Flat	SW	E–SE
Precipitation (mm)[a]	1443	1683	1860
Forest structural characteristics prior to harvest			
Stand age (year)	110–130	165	70–80
Tree basal area (m^2 ha^{-1})	36–52	72–106	48–65
Forest zone[b]	Tshe	Abco	Tshe
Overstory cover (%)[c]	51–70	68–78	72–82

[a] Estimated mean annual precipitation, derived from DAYMET (Thornton et al., 1997), a set of 1-km GIS raster coverages that were generated from meteorological records (1980–1997) and digital elevation data.
[b] Defined by potential climax tree species: Abco, *Abies concolor*, Tshe, *Tsuga heterophylla* (Franklin and Dyrness, 1973).
[c] Estimated using a moosehorn densiometer.

(as above). Truffle plots were centered every 6 m along each transect. During most sample periods, transects were located within the treatment area but outside the grid established for vegetation and other data collection (Fig. 2). For one pre-treatment and one post-treatment spring and fall sample period, truffle plots were systematically dispersed throughout each experimental unit along the grid lines but 20 m from the gridline intersections (Fig. 2). This was done to ensure dispersed sampling of within-treatment variation while limiting disturbance to the area within the interdisciplinary sampling grid. Post-treatment sampling in the aggregate retention treatments was further modified as necessary to ensure proportional distribution of plots between the harvested areas and the aggregates (as noted for mushrooms above). In each truffle plot, the forest floor was raked to a 5–10-cm depth, thereby exposing sporocarps in the upper soil layers. Sporocarps were bagged and labeled by block, treatment, plot number, and date.

At the end of each collection day, specimens were identified to the lowest taxonomic level possible using stereo microscopy. Notes on fresh characters including color, order, taste, and reaction to standard reagents (Smith et al., 1979) were entered on the collection note sheet, and the specimens were dried for 8–18 h at 63 °C in a portable dehydrator until crisp-dry. Upon return to the laboratory, specimens were identified to genus and, when possible, species. Many specimens could not be identified to species, either because they were immature or because they belonged to genera not adequately monographed for the western United States (especially *Cortinarius*, *Gymnomyces*, *Inocybe*, *Russula*, and *Tricholoma*). All collections were weighed to the nearest 0.01 g. Weight data for unidentified species were included in the total weights for each stand sample. Representative voucher collections of each identified species were deposited in the Mycological Herbarium of Oregon State University. Unidentified collections were saved in the laboratory herbarium of D. Luoma for eventual taxonomic study by specialists as available.

2.3. Statistical analysis

We analyzed total epigeous and total hypogeous, EMF sporocarp mean standing-crop biomass (g/ha dry weight). For each spring or fall sample, total epigeous and hypogeous sporocarp biomass was calculated for each experimental unit. A mean pre-treatment total standing-crop biomass (epigeous or hypogeous) value was then calculated for each experimental unit for the spring and fall samples. Similarly, mean post-treatment total biomass values were calculated from the 3 years post-treatment period. To more closely meet the assumptions of normal distribution and constant variance, the biomass values were transformed (Sabin and Stafford, 1990). We used the hyperbolic arcsine

Table 2
Mean total mushroom and truffle standing-crop biomass (g/ha dry weight) by season and block during pre-treatment sampling of the DEMO experiment

	Butte				Dog Prairie				Watson Falls			
	Spring (n = 12)	S.E.	Fall (n = 18)	S.E.	Spring (n = 18)	S.E.	Fall (n = 18)	S.E.	Spring (n = 18)	S.E.	Fall (n = 18)	S.E.
Epigeous	145	51	2018	559	580	215	4068	1230	529	263	2934	595
Hypogeous	217	63	2435	470	407	99	1415	198	3253	921	2307	442

N, the number of treatment unit samples that form the basis of the mean; S.E., standard error of the mean.

transformation $[\ln(x + \sqrt{x^2 + 1})]$ (SAS Institute, 1998). We used MANOVA repeated measures for a randomized block design to test the overall significance of the time (pre-/post-harvest) × treatment interaction. When the time × treatment interaction was found to be significant, MANOVA repeated measures contrasts of the time × treatment interaction tested the null hypothesis of no difference between treatments

Contrasts between treatments tested the null hypotheses that the change in EM sporocarp biomass did not differ over time (from pre- to post-treatment). For those contrasts with significant differences in the change in biomass (the time × treatment interaction), the post-treatment biomass of a treatment was calculated as a percentage of the pre-treatment biomass. The difference in those changes (Δ treatment $a\%$ − Δ treatment $b\%$) was then determined for each significant contrast. These comparisons were made separately for the spring and fall fruiting seasons. Because this type of data is highly variable, we increased the alpha level in order to increase our ability to detect a difference if the difference is there (power). We choose an alpha level of 0.1 as appropriate to discuss statistically significant differences prior to beginning the data analysis with the attendant risk of type I error. Analyses were performed with JMP® 5 (SAS Institute, 2002). Test of treatment effects on taxa diversity at the genus or species level will be reported in a subsequent paper.

3. Results

The pre-treatment baseline condition was characterized by total fall standing-crop biomass exceeding total spring biomass for both EM mushrooms and truffles except in the Watson Falls block where spring truffle biomass was greater (Table 2). A total of 150 epigeous fruiting taxa and 58 hypogeous fruiting taxa were identified from the sample plots. Before treatment, the total number of mushroom taxa for each treatment ranged from 58 to 72 while the total number of truffle taxa ranged from 22 to 29 (Table 3). During the post-treatment sample period, the number of mushroom taxa detected in the 100% retention decreased by 34% while the number of truffle taxa increased by 20% (Table 3). The number of sporocarp producing species was reduced most in the 15%D treatment followed by the 15%A treatment. The 75%A retention treatment showed the least reduction in number of fruiting taxa as compared to the control (Table 3).

Within each season, the time × treatment interaction (change in biomass from pre- to post-treatment) was significant for both mushroom and truffle total biomass (Table 4). After treatment, total spring mushroom biomass declined significantly in the 15%D basal area retention treatment as compared to all other treatments (Fig. 3). Total spring truffle biomass was significantly decreased by all green-tree

Table 3
Total number of identified mushroom or truffle taxa pre- and post-treatment with percent change (Δ%) from the pre-treatment condition

	Treatment																	
	100%			75%A			40%D			40%A			15%D			15%A		
	Pre	Post	Δ%	Pre	Post	Δ%	Pre	Post	Δ%	Pre	Post	Δ%	Pre	Post	Δ%	Pre	Post	Δ%
Mushroom	61	40	−34	72	33	−54	65	25	−62	71	20	−72	58	6	−90	68	15	−78
Truffle	20	24	20	25	21	−16	25	15	−40	29	15	−48	23	8	−65	22	10	−55

Data are cumulative across three blocks with five samples before treatment and six samples after treatment.

Table 4
MANOVA repeated measures tests of the time × treatment interaction

Season	Group	Exact F[a]	P-value
Spring	Mushrooms	3.3276	0.05
	Truffles	6.4385	0.006
Fall	Mushrooms	3.2229	0.05
	Truffles	12.1171	0.0006

[a] Degrees of freedom for each test were 5 for the numerator and 10 for the denominator.

retention treatments (Fig. 4). The 15%D and 75%A treatments showed the least reduction in spring truffle biomass as compared to the control (Table 5).

Total fall mushroom biomass decreased significantly in the 40%A, 15%D, and 15%A treatments as compared to the other treatments (Fig. 5). No treatment effect was detected on the fall mushroom standing crop in the 40%D treatment (Fig. 5). Total fall truffle biomass was significantly reduced in the 40%A, 15%D, and 15%A treatments as compared to the control, 75%A, and 40%D treatments (Fig. 6). No treatment effect was detected on the fall truffle standing crop in the 40%D treatment (Fig. 6).

In general, the among-treatment comparisons showed the 15%D and 15%A retention treatments to have the greatest reduction in sporocarp biomass standing crop as compared to the control (Table 5). The 15% retention levels were also different from the 75 and 40% retention levels in some cases. The 40%A treatment differed from the control except for spring mushroom biomass (Table 5). The 40%D treatment differed from the control only for spring truffle biomass (Table 5). The 75%A treatment differed from the control in spring truffle biomass and fall mushroom biomass (Table 5).

4. Discussion

The pre-treatment EMF sporocarp biomass values reported here (Table 2) are consistent with the values reported in previous studies from the Pacific Northwest (Fogel, 1976; Fogel and Hunt, 1979; Hunt and Trappe, 1987; Luoma et al., 1991; Waters et al., 1994; Waters et al., 1997; Luoma et al., 1997; North et al., 1997; Colgan et al., 1999; O'Dell et al., 1999; Carey et al., 2002; Smith et al., 2002). Also consistent with other studies from our region was the heavy preponderance of fall fruiting by EM mushroom species (Fogel and Hunt, 1979; O'Dell et al., 1999; Smith et al., 2002). Two of three blocks in our study had substantially greater hypogeous standing-crop biomass in fall as compared to spring (Table 2). This seasonal variability is also consistent with the range of findings in other studies (Fogel, 1976; Fogel and Hunt,

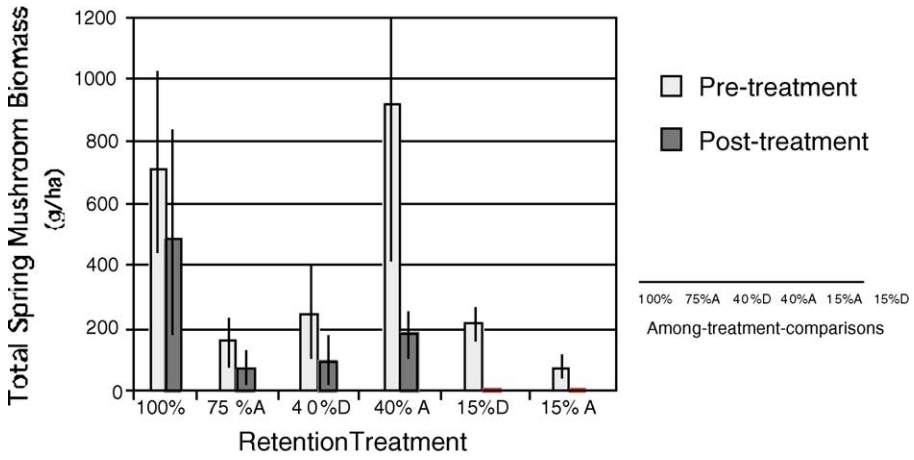

Fig. 3. Mean total ectomycorrhizal mushroom standing-crop biomass for the spring samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from MANOVA repeated measures contrasts of the time × treatment interaction using transformed data. Treatments without a shared horizontal bar above them are significantly different at $P \leq 0.1$ (see Table 5 for specific P-values).

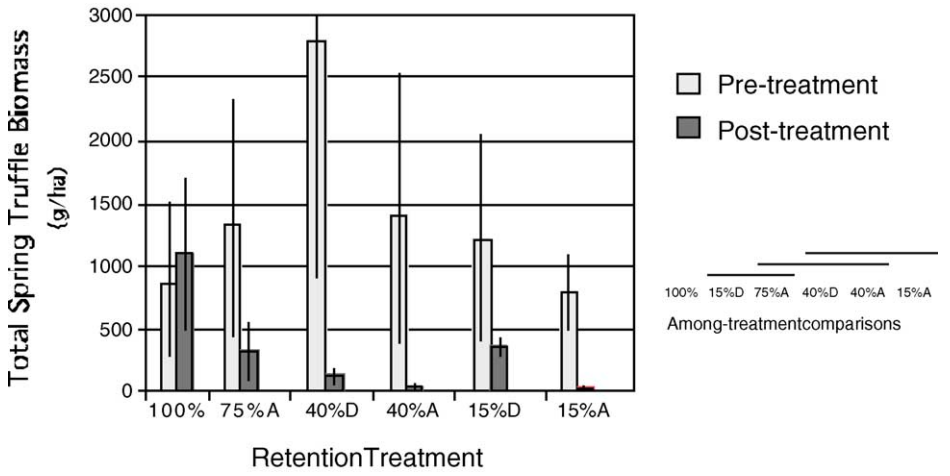

Fig. 4. Mean total truffle standing-crop biomass for the spring samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from MANOVA repeated measures contrasts of the time × treatment interaction using transformed data. Treatments without a shared horizontal bar above them are significantly different at $P \leq 0.1$ (see Table 5 for specific P-values).

1979; Hunt and Trappe, 1987; Luoma et al., 1991; Colgan et al., 1999; Claridge et al., 2000b; Smith et al., 2002). Based on our findings and those of other researchers, it seems that truffle production is generally more equably distributed between the spring and fall seasons than mushroom production. However, local micro-climate controls on soil temperature and moisture conditions combined with annual variation in weather patterns are likely responsible for the departures from that generalization encountered in some of the previous, relatively short-term studies, noted above. Longer-term studies will help resolve conflicting reports by examining sporocarp production temporally in a broader context of physical and biotic conditions.

Although we found total pre-treatment standing crops of mushrooms and truffles to be comparable (Table 2), Smith et al. (2002) found that truffle biomass exceeded mushroom biomass. Both studies, however, found about twice as many mushroom taxa as truffle taxa. Therefore, truffle taxa seem to be disproportionately successful in the production of sexual propagules (spores).

4.1. Treatment effects

Ours is the first study from the Pacific Northwest to examine the effects of a forest management experiment on both EM mushroom and truffle production that also includes pre-treatment data as basis for comparisons. We found that even though green-tree retention can preserve EMF diversity on root-tips (Stockdale, 2000), aspects of sporocarp production were significantly reduced at all levels of basal area removal examined in this study (Figs. 3–6, Table 5). Notably important among abiotic influences on sporocarp production are temperature and moisture, particularly as they affect the soil ecosystem (Wilkins and Harris, 1946; Hering, 1966; Fogel, 1976, 1981; Last et al., 1981; Mehus, 1986; Luoma, 1991; States and Gaud, 1997; Claridge et al., 2000a; Castellano et al., 2004).

Sporocarp production was nearly eliminated from the 15%A retention treatment (Figs. 3–6). A combination of removing most host trees and severe edge effects (alteration of temperature and moisture regimes) in the two 1-ha retained aggregates likely accounts for this effect. Though mushroom production and truffle production were significantly reduced in the 15%D treatment, spring truffle biomass was maintained at 33% of the pre-treatment value (Fig. 4). We speculate that three habitat attributes were important in maintaining this level of truffle production: (1) soils were moist in spring; (2) the dispersed pattern of retention increased insolation to the soil facilitating soil warming; and (3) living tree root systems were distributed over a greater area than the in aggregated 15% pattern. The combination of these

Table 5
Between-treatment comparisons of the difference (percentage of first treatment in the pair) in the change in mean sporocarp standing-crop biomass from the pre-treatment values for ectomycorrhizal mushrooms and truffles

Season and sporocarp group	Difference in biomass change over time (%)	*P*-value[a]
Spring		
Mushrooms		
100% vs. 15%D	−69	0.01
75%A vs. 15%D	−48	0.01
40%D vs. 15%D	−42	0.008
40%A vs. 15%D	−21	0.009
15%A vs. 15%D	−6	0.1
Truffles		
100% vs. 75%A	−108	0.02
100% vs. 40%D	−131	0.002
100% vs. 40%A	−132	0.001
100% vs. 15%D	−102	0.08
100% vs. 15%A	−130	0.0008
75%A vs. 15%A	−21	0.1
40%D vs. 15%D	29	0.06
40%A vs. 15%D	30	0.04
15%A vs. 15%D	28	0.02
Fall		
Mushrooms		
100% vs. 75%A	−34	0.05
100% vs. 40%A	−47	0.03
100% vs. 15%D	−48	0.02
100% vs. 15%A	−48	0.02
75%A vs. 40%A	−13	0.07
75%A vs. 15%D	−14	0.04
75%A vs. 15%A	−14	0.05
40%D vs. 40%A	−30	0.09
40%D vs. 15%D	−32	0.06
40%D vs. 15%A	−32	0.06
Truffles		
100% vs. 40%A	−54	0.01
100% vs. 15%D	−59	0.001
100% vs. 15%A	−64	0.0001
75%A vs. 40%A	−48	0.02
75%A vs. 15%D	−53	0.002
75%A vs. 15%A	−58	0.0002
40%D vs. 40%A	−65	0.07
40%D vs. 15%D	−70	0.007
40%D vs. 15%A	−75	0.0006
40%A vs. 15%A	−10	0.02

The *P*-values were derived from MANOVA repeated measures contrasts of the time × treatment interaction using transformed data. Only contrasts having *P*-values ≤0.1 are shown. See Figs. 3–6 for sporocarp mean standing-crop biomass values and a graphical summary of among-treatment comparisons.

[a] Degrees of freedom for each test were 1 for the numerator and 10 for the denominator.

influences likely contributed to the spring truffle biomass being reduced 28% more in the 15%A treatment as compared to the 15%D treatment (Table 5).

The spring fruiting truffle *Rhizopogon vinicolor* (*sensu lato*, Kretzer et al., 2003) in particular, a known stress-tolerant species (Parke et al., 1983a,b; Castellano and Trappe, 1985; Castellano and Molina, 1989) was able to maintain (or perhaps expand) reproductive populations in this treatment. However, the 15%D treatment showed the most decrease in total number of

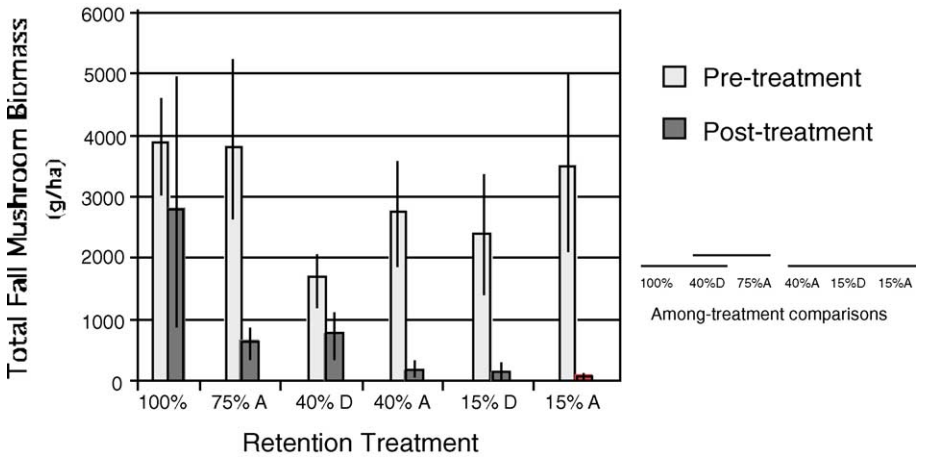

Fig. 5. Mean total ectomycorrhizal mushroom standing-crop biomass for the fall samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from MANOVA repeated measures contrasts of the time × treatment interaction using transformed data. Treatments without a shared horizontal bar above them are significantly different at $P \leq 0.1$ (see Table 5 for specific P-values).

fruiting species (Table 3) suggesting a change in dominance favoring disturbance adapted species. The aggregates of the 15%A treatment seem to be important for maintaining fruiting of a greater number of species than the 15%D treatment, despite lower truffle production.

The 40%A retention treatment showed significantly reduced fall mushroom and truffle biomass as compared to the control, whereas the 40%D treatment did not (Figs. 5 and 6). Again, the greater area occupied by the root systems of the remaining trees is an important factor in the continued fall fruiting of sporocarps in the 40%D treatment. Also, the physical spacing of the trees allows the initial fall rains, critical to fruiting (Fogel, 1976), to reach the forest floor as opposed to being intercepted by the canopy in the aggregates. In contrast to the 15% aggregated retention, the aggregated pattern of the 40% retention treatment did not retain a higher number of fruiting EMF species. This may indicate that the higher level

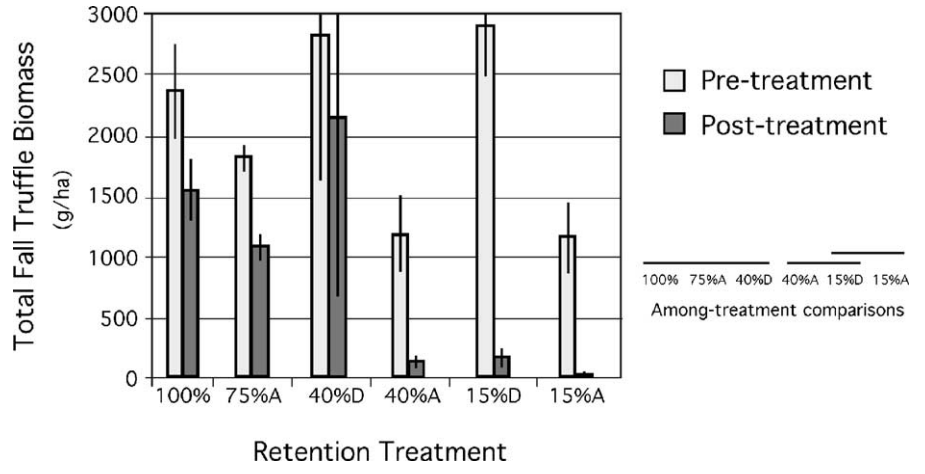

Fig. 6. Mean total truffle standing-crop biomass for the fall samples from three DEMO blocks. Standard errors are indicated by vertical bars. Among-treatment comparisons were derived from MANOVA repeated measures contrasts of the time × treatment interaction using transformed data. Treatments without a shared horizontal bar above them are significantly different at $P \leq 0.1$ (see Table 5 for specific P-values).

of retention did not precipitate a shift in dominance to a few stress-tolerant species. Another important consideration in the context of this experiment is the generally more mesic site conditions of the 40%D treatment units within their respective blocks. Had those treatment units been on more stressful sites, sporocarp production would likely have been lower (Luoma, 1988; Luoma et al., 1991).

The disparity in response to the treatments between EM mushrooms and truffles is particularly apparent in the 75%A retention treatment. The post-treatment mean fall truffle standing crop was 61% of the pre-treatment value (Fig. 6). This level of production was relatively proportional to the basal area retained given the similar post-treatment decrease in the control treatment and was not significantly different (Fig. 6). However, mean fall mushroom standing crop dropped to about 20% of the pre-treatment value and was significantly different from the control (Fig. 5). For mushrooms, this result was strongly contrary to our hypotheses that sporocarp biomass production would be proportional to the retained green-tree basal area. In the 75%A treatment, total number of EM mushroom species dropped to less than 50% of the pre-treatment condition while total number of truffle species maintained 84% of the pre-treatment value (Table 3). Notice, however, that the total number of mushroom species fruiting in the control treatment dropped by 34% during the post-treatment sampling period (Table 3). This was due to the exceptional fall mushroom fruiting in 1997, a pre-treatment period for two of the three blocks. In that context, the number of mushroom species in the 75%A treatment is only 20% below the value based on adjusting for the decline in the control and therefore, the number of species retained by the 75%A treatment was approximately proportional to the aggregate area remaining uncut. Total number of truffle species was also roughly proportional to basal area retained as compared relative to the post-treatment species richness increase in the control treatment (Table 3).

4.2. Comparisons of spatial pattern

The dominant pattern found by among-treatment comparisons was that the 15% retention treatments were most different from the other treatments (Table 5). This is an expected result since sporocarp production by ectomycorrhizal fungi should be greatly reduced by removal of 85% of the carbon source for the fungi. With the 15% retention, sporocarp production was differentiated by lower spring truffle production in the aggregated treatment. Spatial pattern of retention within the 40% retention level showed that the dispersed retention maintained higher levels of sporocarp production in the fall but spatial pattern showed no effect in the spring. However, this comparison must be considered in the context of pre-existing differences between the treatments. The 40%D experimental units were all situated on more mesic sites than the 40%A units. Thus, an unknown portion of the difference between the spatial patterns may be attributable to lower moisture stress experienced on the 40%D experimental units during the summer drought period that is typical of our climate (Köppen, 1931).

4.3. Relevance to ecosystem management

Standing-crop data are useful to interpret the role of fungal species as a food source for animals (Luoma et al., 2003). When both epigeous and hypogeous fruiting species are simultaneously assessed, new understanding of overall diversity phenomena emerges. For example, the more equable biomass distribution of truffles compared to mushrooms between spring and fall (Table 2, see also Smith et al., 2002) has important implications to mycophagous mammals. Fungal diversity in the diet of such animals appears to be nutritionally important (Maser et al., 1978; Johnson, 1994; Claridge et al., 1999). Clearly in our region, animals that depend on fungi as major food items (Fogel and Trappe, 1978; Luoma et al., 2003) could not rely on epigeous fungi for diet diversity over the spring. Other research suggests that the decline in populations of some mycophagous animals is related to a decline in diversity of the fungal populations due to habitat disturbance (Claridge et al., 1996; Pyare and Longland, 2001).

Results from another part of the DEMO study show that truffle genera important in the diets of small mammals were significantly affected by the treatments (Jacobs, 2002). *Rhizopogon* spore frequency in the diet of *Clethrionomys* was reduced by the 15%A retention treatment, potentially reflecting the reduced ability of these animals to obtain *Rhizopogon* truffles in those treatment units (Jacobs, 2002).

Maintenance of EM fungal diversity is important for ecosystem health and resilience (Amaranthus and Perry, 1987, 1989; Perry et al., 1990; Amaranthus, 1997). Disturbance, whether natural or man caused, can drastically alter populations of EM fungi (Schoenberger and Perry, 1982; Pilz and Perry, 1984; Amaranthus et al., 1990, 1994, 1996; Colgan, 1997). Management implications include the need to address the conservation of rare truffle and mushroom species with the knowledge that they exhibit different sporocarp production responses to forest disturbance. We have shown that 85% basal area removal significantly reduces EM sporocarp production during the first 3 years following cutting and that the relative amount of the reduction was generally greater than the proportion of basal area removed.

4.4. Future directions

While all harvested treatments showed some reduction in sporocarp production compared to the control, the 75 and 40% basal area retention generally maintain higher sporocarp production than 15% retention (Table 5). However, these analyses do not fully account for year-to-year variation in sporocarp biomass production that is a result of annual variation in weather patterns or other natural, non-treatment related variation (Fogel, 1976; Fogel, 1981; Luoma, 1991; O'Dell et al., 1999; Nara et al., 2003). Pre-existing differences among treatment units or annual variation in weather patterns that affect sporocarp production may influence the results (Cazares et al., 1999). Because sporocarp formation is strongly influenced by weather patterns (particularly variation in temperature and moisture) and is species specific (Fogel, 1976; States and Gaud, 1997; Colgan et al., 1999) we perceive a need to develop statistical models that incorporate these species-specific biological factors when analyzing treatment effects.

It remains unclear how short-term reduction in sporocarps and reproductive propagules (spores) will affect either EMF population dynamics and survival or actual inoculum for future trees. After disturbance, spores are a form of legacy from the previous stand and are key to species' future adaptations in the face of environmental change. Spores can also disperse into disturbed areas from adjacent intact forests, however. The relative importance of residual (legacy) spore banks versus incoming spores as they affect future EMF populations and functions is unknown. The experimental silvicultural treatments imposed by the DEMO study will allow long-term assessment of EM fruiting to determine how community composition changes and at what rate recovery takes place.

4.5. Sampling Implications

Arnolds (1981), Fogel (1981), Luoma (1991), Claridge et al. (1993), O'Dell et al. (1995), Colgan (1997), North et al. (1997), Castellano et al. (2004) and others have addressed the problems of sampling sporocarps for estimation of diversity and standing crop of EMF. Our results on differences between seasons and among and within blocks confirm the conclusions of those authors. The more frequently one can sample an area during the year and the more years such sampling can be conducted, the better the estimates represent ecosystem conditions. Although axiomatic for any sampling, this conclusion pertains especially to fungal sporocarps, which are extremely weather dependent and erratic in their fruiting, temporally and spatially. A useful example applicable to surveys for rare mushrooms can be found in our study. If we consider the pre-treatment data from the permanent mushroom plots, we can track the presence or absence of sporocarps on each square meter separately. Taken across all the non-control experimental units, sampled twice-yearly for 3 years prior treatment, 4500 individual square meters were inventoried. Of those, only 1246 (28%) ever contained a sporocarp of any EM species. For comparison, the control experimental units were sampled twice-yearly for 6 years with 900 individual square meters inventoried. Of those, only 346 (38%) ever contained a sporocarp. Yet we know from studies of EM root tips that the forest soil of our study has highly diverse and abundant populations of EMF averaging 10 EM types in each 350 cm^3 soil sample (Stockdale, 2000).

For reasons noted above, it is clear that studies of effects of forest management practices on EMF fruiting must be relatively long-term and involve frequent sampling. However, studies solely of sporocarp production do not reveal the full picture of EMF community structure. Alternative approaches to answer questions about populations of EMF entail

estimation of their actual occupation of rootlets in the soil. This can be based on mycorrhiza morphotypes and on DNA analysis of mycorrhizae (Agerer et al., 1996; Eberhart et al., 1996; Eberhart and Luoma, 1996, 1997; Gardes and Bruns, 1996; Horton and Bruns, 2001) Molecular approaches are presently costly, but are becoming less so as the technology develops. In order to more fully examine the ecosystem functions and community structure of EMF, comprehensive studies that encompass assessment of mycorrhizae and sporocarps are needed. Such research holds promise as a great improvement over present approaches to determining effects of natural or anthropogenic disturbance on populations of EMF in forests (Dahlberg, 2001).

5. Conclusions

We found that overstory removal significantly reduced EMF sporocarp production but, in contrast to our initial hypothesis, the effects were not always proportional to basal area retained. We speculate that *Rhizopogon vinicolor* in particular, was able to maintain reproductive populations in the most heavily cut and disturbed areas due to its ability to tolerate environmental stress (Parke et al., 1983a,b; Castellano and Trappe, 1985; Castellano and Molina, 1989). The continued presence of *R. vinicolor* in severely disturbed areas could have positive effects on seedling recruitment and survival (Parke et al., 1984). The effect of spatial pattern of retention varied between retention levels and mushroom and truffle sporocarp groups. Though not directly studied in this experiment, our results lend support to the use of dispersed green-tree retention in combination with aggregated retention when maintenance of sporocarp production is a goal. Such a mix would overcome the effects of clear cutting as demonstrated in this study and maintain higher levels of sporocarp production in the aggregates by ameliorating edge effects. Taken together, the 40% green-tree retention treatments maintained higher levels of EM sporocarp biomass and total number of fruiting species than the 15% retention treatments. Continuing study of these relationships is important for development of scientifically sound silvicultural techniques for use in the pursuit of ecosystem-based forest management.

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