

STANDING CROP AND ANIMAL CONSUMPTION OF FUNGAL SPORO CARPS IN PACIFIC NORTHWEST FORESTS

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Abstract. Although fungal fruiting bodies are a common food supplement for many forest animals and an important dietary staple for several small mammals, changes in their abundance and consumption with forest succession or disturbance have not been quantified. Above- and belowground fungal fruiting bodies (epigeous and hypogeous sporocarps) were sampled for 46 mo in managed-young, natural-mature, and old-growth western hemlock (*Tsuga heterophylla*) stands in Washington State. Screen exclosures were placed over the surface of half of the sample plots to prevent aboveground predation of sporocarps. Standing crop of epigeous sporocarps was low in most seasons and then increased 30-fold to a mean of 2.28 kg/ha in the fall. Epigeous biomass varied little between stand types, and animal consumption of these sporocarps was low. Standing crop of hypogeous sporocarps was 0.78 kg/ha in managed-young stands, compared to 4.51 and 4.02 kg/ha in natural-mature and old-growth stands. In all stands, standing crop peaked in the summer and was lowest in the winter. Mean animal consumption of hypogeous sporocarps was 0.64 kg/ha, a value that exceeded the available standing crop quantity of 0.36 kg/ha in managed-young stands during the winter. In natural-mature and old-growth stands, truffle biomass remained high year-round and exceeded consumption in all seasons. Low hypogeous sporocarp biomass in the managed-young stands resulted from the general absence of large clusters of *Elaphomyces granulatus*, which made up >90% of the biomass in older stands. This absence in managed-young stands may be associated with the thin organic layer that has developed following harvest and burning 60 yr ago. The consistent level of animal consumption indicates that truffles may be an important and readily available year-round food source, compared to the ephemeral fruiting of epigeous sporocarps. Changes in forest composition and age due to natural disturbance or human management influence fungal sporocarp productivity and diversity and, consequently, affect food availability for animals dependent on hypogeous sporocarps.

Key words: *Elaphomyces granulatus*; epigeous fungi; exclosures; hypogeous sporocarps; mycophagy; northern flying squirrel; old growth; small mammals; truffles.

INTRODUCTION

Fungal communities form pervasive, but often unseen, links between many ecosystem functions. A mycorrhizal fungus essential to one plant's survival and growth can also provide food for many soil organisms (Warnock et al. 1982), increase nutrient availability (Fogel 1980), inhibit soil pathogens and bacteria (Marx 1972), facilitate primary succession (Schramm 1966, Miller 1987), and improve soil structure (Tisdall and Oades 1979). One of the less-studied aspects of these linkages is the role of fungal fruiting bodies (sporocarps) in the forest food chain. Mycorrhizal fungi form above- and belowground fruiting bodies known, respectively, as epigeous and hypogeous sporocarps, commonly called "mushrooms" and "truffles." Although many forest animals are mycophagous, opportunistic consumers of sporocarps (Fogel and Trappe 1978), several small mammals rely on mushrooms or

truffles for a substantial portion of their diet (Maser et al. 1978). Few studies, however, have examined how the standing crop of this food source varies with forest succession (Vogt et al. 1981, Luoma 1991, O'Dell et al. 1992), and no study has assessed the proportion of available sporocarps consumed.

Changes in forest composition due to succession, disturbance, or timber harvesting will produce changes in sporocarp abundance and diversity, because most sporocarps are produced by ectomycorrhizal fungi that rely on carbohydrates from their tree hosts (Harley and Smith 1983). Studies of epigeous and hypogeous sporocarps have revealed changes in the species composition of fruiting bodies as photosynthate production is altered with defoliation or thinning (Last et al. 1979, Termorshuizen 1991, Waters et al. 1994). Differences in hypogeous sporocarp abundance have also been found between young and old-growth conifer stands in the Pacific Northwest (Vogt et al. 1981, Luoma et al. 1991, O'Dell et al. 1992, Amaranthus et al. 1994, Clarkson and Mills 1994). These changes in sporocarp

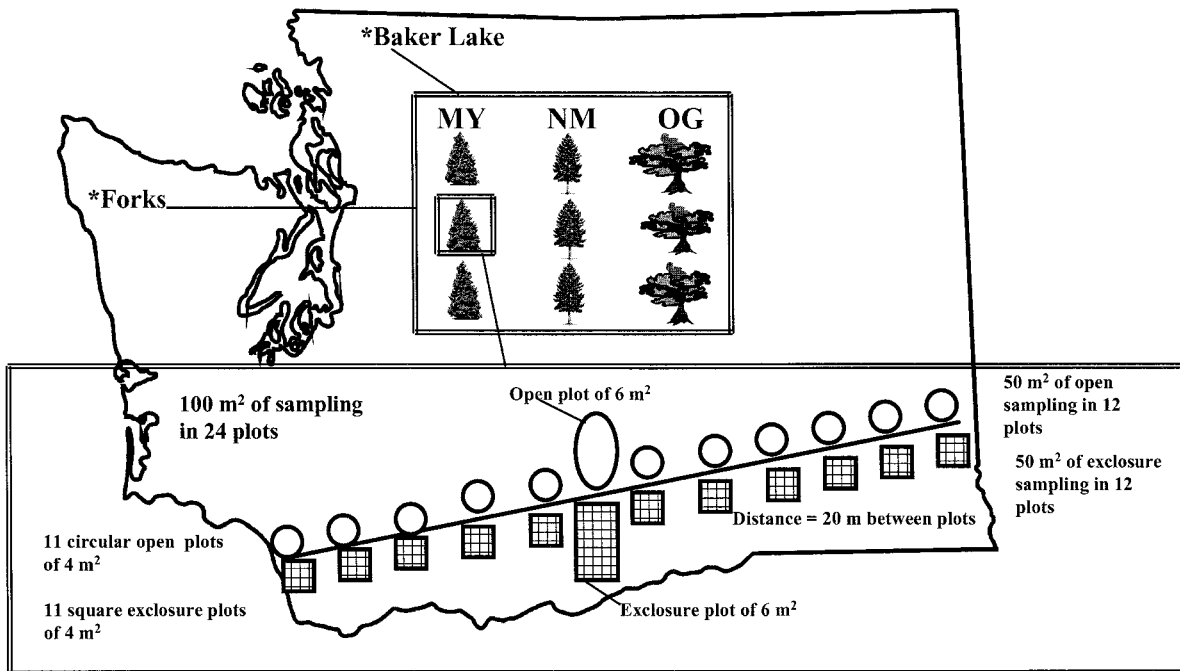


FIG. 1. Sampling design and stand locations in Washington State. At both Forks and Baker Lake, three managed-young (MY), three natural-mature (NM), and three old-growth (OG) stands were sampled, for a total of 18 stands. In each of these sample stands, fungal sporocarps were collected in 12 paired plots, 4 m² and 6 m² in area, distributed along a transect. The total area for each stand sample was 100 m²; 50 m² protected by enclosure and 50 m² open.

abundance and diversity affect animals that rely on fungal sporocarps for a substantial part of their diet.

Animal mycophagists include many species of Geomyidae (pocket gophers), most Microtidae (voles), and almost all Sciuridae (squirrels and chipmunks) in North America (Fogel and Trappe 1978, Maser et al. 1978), as well as many forest-dwelling marsupials in Australia (Seebeck et al. 1989, Johnson 1994, Claridge et al. 1996). Many of these species are a crucial food source for higher predators such as raptors, martens, and fishers (Grenfell and Fasenfest 1979; W. Zielinski, *personal communication*). For example, hypogeous sporocarps are the dominant food source for the northern flying squirrel (*Glaucomys sabrinus*) (McKeever 1960, Maser et al. 1985, Maser et al. 1986, Hall 1991) which, in turn, is the principal prey species for the Northern Spotted Owl (*Strix occidentalis caurina*) in mesic forests (Forsman et al. 1984, 1991). Although much research has been devoted to habitat requirements of the Northern Spotted Owl (Thomas et al. 1990), fundamental work is still needed on how truffle abundance and consumption changes with forest age and composition to determine how sporocarp availability may influence prey base populations of small mammals.

The goal of this study was to determine how the quantity and animal consumption of hypogeous and epigeous sporocarps vary with forest seral stage, using a long-term, large sampling of sporocarp standing crop. The study had two objectives: (1) to quantify differ-

ences in truffle and mushroom standing crop and diversity between managed-young, natural-mature, and old-growth stands; and (2) to assess the percentage of available sporocarp biomass that is consumed. The data were also used to estimate whether or not there is a correlation between epigeous and hypogeous sporocarp biomass in the same sample plot.

METHODS

Study areas

Eighteen stands were sampled, nine near Baker Lake in the North Cascades and nine near Forks on the Olympic Peninsula, both in Washington State (Fig. 1). The nine stands of each area were organized into three stand types with three replicates each: managed young, natural mature, and old growth. Managed-young stands were the oldest available sites that had been clear-cut and burned. Natural-mature stands had not been timber-harvested, but were disturbed by windstorms in the early part of the century. These stands retained $\approx 20\%$ of their original old-growth trees, were dominated by 70-yr-old advance regeneration, shade-tolerant trees, and had a high volume of coarse woody debris on the forest floor. Old-growth stands were ≥ 300 yr old and had no detectable significant disturbance since their inception (North 1993).

Sample stands were selected with special emphasis on finding comparable tree species composition, age

TABLE 1. Tree basal area by species, log volume, and organic layer depth for the three forest stand types in the two sample areas.

Characteristics	Forks, Olympic Peninsula			Baker Lake, North Cascades		
	Managed young	Natural mature	Old growth	Managed young	Natural mature	Old growth
Basal area (m ² /ha)	65.1	76.7	68.6	64.0	51.8	75.2
Basal area by species (%)						
<i>Tsuga heterophylla</i>	74	79	68	51	67	49
<i>Pseudotsuga menziesii</i>	21	0	0	29	2	14
<i>Thuja plicata</i>	0	2	1	15	20	31
<i>Abies amabilis</i>	0	18	26	0	10	4
<i>Picea sitchensis</i>	4	1	4	0	0	0
Other	1	0	1	5	1	2
Log volume (m ³ /ha)†	223	461	398	133	506	323
Organic-layer depth (cm)	3.1	3.9*	4.0*	3.1	4.8*	3.9*

* The organic layer differs significantly between managed-young and both natural-mature and old-growth stands (*t* test: *df* = 21, *P* < 0.05).

† Log volume is equivalent to "coarse woody debris" discussed in the text.

structure, and disturbance history, because the sporocarps are produced by mycorrhizal fungi symbiotic with the forest vegetation. Selected stands were also measured for a comparable organic layer depth and volume of coarse woody debris within replicates. Other soil properties and the understory vegetation were not assessed in stand selection (Table 1). Detailed measurements of forest structure in these stands were collected as part of a habitat analysis for the Northern Spotted Owl (North 1993).

The Olympic Peninsula sites were near Forks in the Sitka spruce (*Picea sitchensis*) zone (Franklin and Dyrness 1988) between 200 and 600 m in elevation. Soils were generally young spodosols and were slightly acidic. The dominant plant association was Sitka spruce/swordfern-oxalis (*Picea sitchensis*/*Polystichum munitum*-*Oxalis oregana*) (Henderson et al. 1989). In 1921, a storm with 250 km/h winds from the southwest hit the Forks area, uprooting $>16.5 \times 10^6$ m³ (seven billion board feet) of timber (Henderson et al. 1989). On windward slopes, some scattered residual trees survived the storm, but much of the affected area is now covered with naturally regenerated western hemlock (*Tsuga heterophylla*). Windblown areas were not salvage-logged because railroads had not yet reached the Forks area. Old-growth stands were on protected, leeward slopes close to the natural-mature stands and showed no sign of severe disturbance. The managed-young stands were the first areas to be logged and burned north of Forks in the early 1930s. These stands are a mix of young western hemlock, Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce, with little coarse woody debris. Managed-mature and natural-mature stands had comparable live tree compositions and structure (Table 1). The natural-mature stands, however, had the same or more coarse woody debris and organic layer depth as the old-growth stands.

The North Cascade sites are located between 250 and 700 m in elevation in the western hemlock forest

zone (Franklin and Dyrness 1988). Soils are weakly defined spodosols or inceptisols, often with a shallow depth to bedrock (Henderson and Peter 1985). The dominant plant association is western hemlock/swordfern-foamflower (*Tsuga heterophylla*/*Polystichum munitum*-*Tiarella trifoliata*). Although western hemlock is considered the "climax" species, long-lived Douglas-fir and western red cedar (*Thuja plicata*) are common. Managed-young stands were selected in an area that was clear-cut and burned in the early 1930s. Natural-mature stands were chosen from three areas that were blown down by one of two windstorms in 1911 or 1917. Old-growth stands appear to be free of significant stand-regenerating disturbance.

Sampling considerations

Representative sampling of fungal sporocarps is difficult because standing crop and species composition change seasonally and annually (Richardson 1970, Hunt and Trappe 1987, Vogt et al. 1992). Sporocarps may fruit individually or in sporadically spaced clusters, and locating hypogeous sporocarps is difficult except for animals with a keen sense of smell (Fogel 1976). Moreover, the sporocarp longevity of most species is unknown. Effective sampling needs to account for seasonal and annual fluctuations, as well as spatial variability and turnover within the forest stand being sampled. Accurate estimates of sporocarp production require long-term, extensive sampling to collect an unbiased representation of the sporocarp population.

Previous studies provide some sampling guidelines for normalizing the seasonal and annual variability of sporocarp production. To effectively sample fungal sporocarps at peak biomass and species diversity, low-elevation collections in the Pacific Northwest should concentrate in the spring and fall, when sporocarps are most abundant. Epigeous sporocarp productivity greatly increases after the first rains of fall; many species produce sporocarps only during fall (Richardson 1970;

J. Ammirati, *personal communication*). Hypogeous sporocarp productivity at lower elevations in the Pacific Northwest generally peaks in the spring and fall, although sporocarps of several species either persist through summer and winter, or are produced during these seasons (Fogel 1976, Hunt and Trappe 1987, Luoma 1991). Annual changes in sporocarp production are common (Parker-Rhodes 1951, Hering 1966, Luoma 1991), and particularly high variance in epigeous fungi has been reported (Ohenoja 1978, Mehus 1986). Results of some studies recommend sampling for at least three years (Vogt et al. 1992) or collecting on at least 800 m² (Luoma et al. 1991) to effectively characterize sporocarp production.

To normalize seasonal and annual variation, fungal sporocarps were collected over 46 months. An area of 100 m² (50 m² open and 50 m² under exclosures) was sampled in each of 18 stands. Over the course of the study, the total sample area for each stand ranged from 1100 to 1600 m². In 1992, stands were sampled twice in the spring and twice in the fall; from 1993 to 1995, one sampling during each summer and winter was added each year. Some winter and spring sample collections did not include every stand, because short daylight hours and snow limited work hours and access. With this large sample, the variance of each collection had little effect on mean biomass values for each sample stand by the 3rd yr of sampling.

Within a stand, the sampling design must provide a representative collection of sporocarps that may be variably distributed, ranging from scattered individuals to widely dispersed clusters (Fogel 1976, 1981, States 1985). Large sporocarp clusters can bias biomass calculations if a single, large plot is used for sampling. Many small plots summed to provide a stand-sample value may better represent a stand's sporocarp population. Following Hurlbert (1984), Luoma et al. (1991) suggest that systematic plot placement can provide better interspersions than strict randomization, which can produce collections from spatially segregated populations. Luoma et al. (1991) used 25 4-m² plots placed 25 m apart along three transects within a stand. For epigeous sporocarps, O'Dell et al. (1995) also found that dispersed, small plots provide a better sample of stand-level species richness than do large, aggregated plots.

Following these recommendations, we sampled each stand using a transect along which 12 paired plots were systematically spaced 20 m apart. Twenty-two 4-m² plots in 11 pairs and the two 6-m² plots of the remaining pair gave a total stand sample of 100 m² (Fig. 1). Each of the 12 plot pairs included one unprotected plot and one protected by an exclosure. Exclosures consisted of 4 m² or 6 m² areas of aluminum screen fastened to the ground with 16 penny duplex nails every 10 cm. These exclosures effectively excluded surface access to fungal sporocarps (North and Trappe 1994), but did not prevent potential consumption of sporocarps by fos-

orial animals. Exclosures were kept in place for the period between stand samples (6–12 wk), so that the sporocarps could develop without predation (North and Trappe 1994).

Within these plots, all epigeous sporocarps were collected; then the area was raked down to mineral soil and all hypogeous sporocarps were collected. Sporocarps were placed in wax paper bags and labeled. After each sampling, exclosures were moved; no excavated plots were resampled.

In the lab, hypogeous sporocarps were identified to species, cut in half, and dried in a dehumidifier cabinet. Epigeous sporocarps were classified into general morphological types (agaric, bolete, cup, chanterelle, polypore, jelly, or coral fungi) and dried. After 3 d of drying, all sporocarps were weighed to the nearest 0.01 g.

Analysis

The sampling was a nested split-plot design. The standing crop and frequency (presence or absence in sample plots) were calculated for both hypogeous and epigeous sporocarps. The basic unit of comparison, the stand sample, was calculated by summing sporocarp biomass for each visit and standardizing the value to kilograms per hectare per year. Mean values were calculated for replicates of the same stand type. These variables were compared between seasons, stand types, and exclosure vs. open plots. Animal consumption of sporocarps was estimated by calculating the difference in standing crop between the open and exclosure plots for each stand sample. Absolute productivity cannot be calculated because sporocarp longevity is unknown. Sample collections may have missed some short-lived species while double-counting species that decay slowly. Standing crop biomass can be compared between treatments, however, using systematic, equal-sized samples taken nearly simultaneously in all stands. The biomass, rather than the number, of sporocarps was used, because the two are weakly correlated (Luoma et al. 1991) and biomass more directly measures food source value for animals.

RESULTS

Hypogeous sporocarps

Over the 46 mo of sampling, 7242 sporocarps were harvested from 23 100 m² of forest floor. The total dry mass was 6900.87 g, producing a standing crop mean of 2.99 kg/ha over all stand samples. The maximum single-stand sample was 274.7 g dry mass, or 27.47 kg/ha, in an old-growth stand near Baker Lake in the North Cascades. Thirty-nine known species of hypogeous fungi and four undescribed species were identified from collected specimens. One species, *Elaphomyces granulatus*, accounted for 92.8% of total standing crop; another 11 species contributed 6.6% of the total, and 27 species made up the remaining 0.6% of the standing crop (Table 2). Palatability varied among

TABLE 2. Biomass, percentage contribution of each species to the total biomass, frequency, and palatability of the 12 most common species of hypogeous sporocarps by stand type and for all stands.

Species	Dry mass						Total, all stands	Fre- quen- cy† (% of plots)	Palata- bility‡ (% con- sumed)	
	Managed young		Natural mature		Old growth					
	g	%	g	%	g	%				
<i>Elaphomyces granulatus</i>	459.23	76.5	2939.18	93.9	3007.16	94.8	6405.57	92.8	13.3	13.5
<i>Elaphomyces muricatus</i>	15.46	2.6	70.94	2.3	86.09	2.7	172.49	2.5	2.1	27.1
<i>Rhizopogon parksii</i>	18.47	3.1	19.84	0.6	8.60	0.3	46.91	0.7	1.3	4.5
<i>Melanogaster tuberiformis</i>	24.97	4.2	15.65	0.5	3.41	0.1	44.03	0.6	0.6	55.0
<i>Leucogaster rubescens</i>	0		24.9	0.8	15.62	0.5	40.52	0.6	1.0	16.1
<i>Martellia vesiculosa</i>	7.90	1.3	20.06	0.6	11.32	0.4	39.28	0.6	1.7	29.1
<i>Rhizopogon vinicolor</i>	20.45	3.4	5.29	0.2	11.09	0.3	36.83	0.5	1.0	41.3
<i>Hydnotrya variiformis</i>	7.57	1.3	6.37	0.2	6.84	0.2	20.78	0.3	1.7	37.8
<i>Truncocolumella citrina</i>	15.92	2.7	0.43	0	0.10	0	16.45	0.2	0.2	98.6
<i>Rhizopogon subcaerulescens</i>	12.26	2.0	0.62	0	1.44	0	14.32	0.2	0.3	87.4
<i>Hysterangium coriaceum</i>	6.42	1.1	6.88	0.2	0		13.3	0.2	0.1	14.8
<i>Gauteria monticola</i>	3.17	0.5	2.97	0.1	4.84	0.2	10.98	0.2	0.6	11.0
All other species§	8.36	1.4	16.93	0.5	14.12	0.4	39.41	0.6		
Total	600.18		3130.06		3170.63		6900.87			

† Frequency is calculated as the percentage occurrence in the total number of 4-m² and 6-m² sample plots ($n = 5544$ plots).

‡ Palatability is the percentage of the available standing crop that was consumed in the open plots, calculated by comparing biomass in open and enclosure plots.

§ These data are from 27 species pooled.

the 12 most common species, from a consumption rate of 99% of the *Truncocolumella citrina* biomass in the open plots, to a low of 4.5% for *Rhizopogon parksii*. Three species, *Elaphomyces granulatus*, *E. muricatus*, and *Leucogaster rubescens*, were more abundant in natural, older stands, whereas four species, *Melanogaster tuberiformis*, *Rhizopogon subcaerulescens*, *R. vinicolor*, and *Truncocolumella citrina*, were more abundant in managed, young stands.

Stand samples from the north Cascades and the Olympic Peninsula were combined by stand type, because fungal standing crop within stand type did not differ significantly between the two areas. For the sample period, species richness was highest in the old-growth stands, which had seven and five more species than the managed-young and natural-mature stands, respectively. Truffle standing crop in natural-mature and old-growth stands was significantly higher than in managed-young stands ($P < 0.01$) (Table 3), averaging more than five times as much in the former as in the

latter. Truffle standing crop was higher under enclosure plots in all stand types ($P < 0.05$).

By comparing enclosure plots to open plots, we estimate that 60% of the truffle biomass in managed-young stands was being consumed by mycophagists, compared to 12% and 17% in natural-mature and old-growth stands, respectively. Mean consumption of the standing crop of truffles across all stands over the course of the study was 0.64 ± 0.18 kg/ha (mean \pm 1 SD). This consumption level varied little, even as the period between sample collections varied from 6 wk to 12 wk.

Truffle availability varied between seasons, but differed significantly between season only in the managed-young stands. In all stand types, truffle standing crop was lowest in winter and highest in summer (Fig. 2). Truffle consumption by mycophagists also differed by season, being lowest in fall for the natural-mature and old-growth stands when epigeous sporocarps were abundant, and lowest in winter for the managed-young stands when the standing crop of truffles was low (Fig. 3).

Epigeous sporocarps

Aboveground sporocarps were collected for 44 mo of sampling from a total area of 21 300 m² (the first collection in the spring of 1992 did not include epigeous sporocarps). The total dry mass was 2215.12 g, producing a mean standing crop of 1.04 kg/ha over all stand samples. The maximum single stand sample was 90.34 g dry mass, or 9.03 kg/ha, in a managed-young stand near Baker Lake in the North Cascades. Specific differences in epigeous diversity could not be assessed, because sporocarps were not identified to genus and species. However, morphological types provided in-

TABLE 3. Species richness and standing crop of truffles by stand and plot type.

	Managed young	Natural mature	Old growth
Richness (no. species)	27	29	34
Standing crop (kg/ha)			
Open plots	0.44	4.21	3.69
Enclosure plots	1.11*	4.81*	4.34*
Mean	0.78	4.51**	4.02**

* Significant difference (one-tailed t test: $df = 77$, $P < 0.05$) between enclosure and open plots.

** Standing crop value differs significantly ($P < 0.01$) between managed-young stands and both natural-mature and old-growth stands.

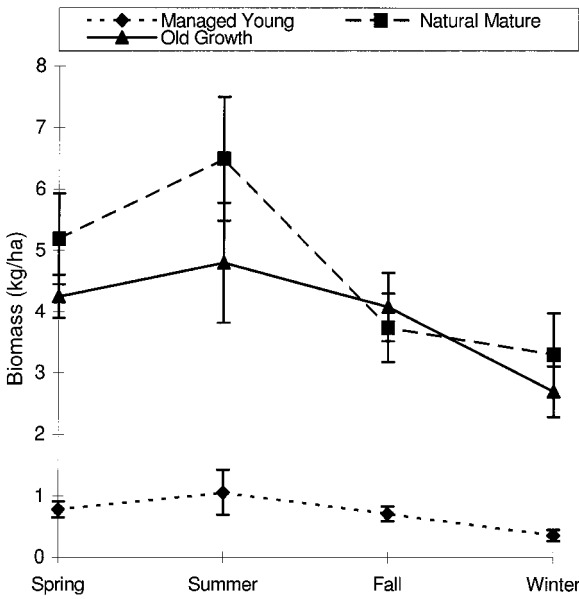


FIG. 2. Mean (± 1 SE) hypogeous sporocarp standing crop of managed-young, natural-mature, and old-growth stands by season. Biomass values have been standardized to kg/ha.

formation about general changes in sporocarp diversity with stand type. The proportions of different groups differed significantly among the three treatment types (Table 4). The percentage of agarics was significantly higher in managed-young than in old-growth stands ($P < 0.05$). The percentage of boletes was higher in natural-mature and old-growth stands than in managed-young stands ($P < 0.03$). Chantrelles were higher in managed-young stands than in natural-mature and old-growth stands ($P < 0.05$). By morphologic type, coral and chanterelle fungi were the epigeous sporocarps most preferred for consumption. Agaric and bolete sporo-

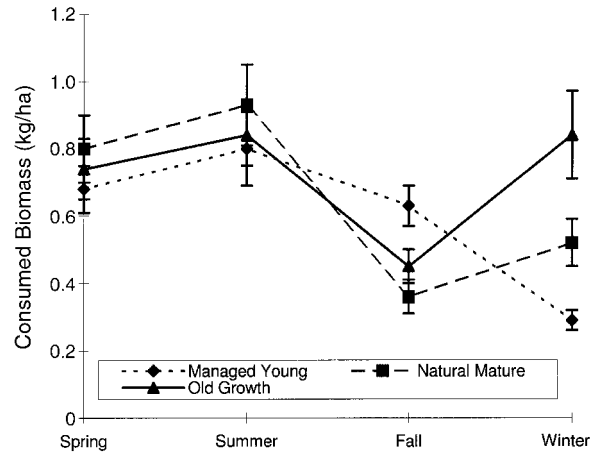


FIG. 3. Mean (± 1 SE) biomass of hypogeous sporocarps consumed by aboveground animals. The seasonal means for managed-young, natural-mature, and old-growth stands have been standardized and expressed as kg/ha.

carps were moderately consumed, and no difference in polypore and jelly sporocarp biomass was found between open and enclosure plots.

The standing crop of epigeous sporocarps did not differ significantly between stand treatment or plot type (Table 5). The lack of significant consumption, as measured by the biomass difference between open and enclosure plots, may relate to the seasonality of epigeous sporocarp production. Mycophagists may rely on a more constant food source than epigeous sporocarps, which fluctuated from relative rarity for most of the year (0.08 kg/ha) to abundance in the fall (2.28 kg/ha; Fig. 4).

Of 5544 plots sampled, 1274 contained hypogeous sporocarps, 946 contained epigeous sporocarps, and 262 contained both. In plots with both above- and be-

TABLE 4. Percentage of total epigeous sporocarp standing crop by morphological type for each of the three stand types. Palatability of the different forms was determined as indicated in Table 2.

Sporocarp form	Percentage of total standing crop			Palatability (% consumed)
	Managed young	Natural mature	Old growth	
Agaric	79.55*,†	76.15	68.23	5.3
Bolete	2.12	14.0*,§	17.85*,§	2.1
Chanterelle	8.34*,‡	1.64	3.15	21.1
Coral	6.22	3.70	8.54	30.3
Polypore	3.11	2.93	1.50	0
Cup	0.58	1.22	0.51	17.9
Puffball	0.07	0.31	0.21	14.4
Jelly	0.01	0.05	0.01	0
Total	100	100	100	

* Differences are statistically significant at $P < 0.05$ (Tukey-type multiple proportions test: $df = 3$).

† Significant difference between managed-young and old-growth stands.

‡ Significant difference between managed-young and both natural-mature and old-growth stands.

§ Significant difference ($P < 0.03$) between managed-young and both natural-mature and old-growth stands.

TABLE 5. Standing crop of epigeous sporocarps by stand and plot type, standardized to kg/ha.

Plot type	Managed young	Natural mature	Old growth
Open	1.09	0.90	1.00
Exclosure	1.23	0.92	1.08
Mean	1.16	0.91	1.04

lowground sporocarps, the biomass values were compared with a correlation analysis. A plot of the biomass values indicated that they were not normally distributed or linearly related, so Spearman rank correlation analysis was used (Norusis 1996). No significant relationship between above- and belowground biomass was found ($r_s = -0.01$, $P = 0.87$).

DISCUSSION

The spores of fungal sporocarps have been found in the stomach contents or scat of most forest mammals (Fogel and Trappe 1978, Maser et al. 1978, Claridge et al. 1996). The potential food value of truffles and mushrooms for consumers depends on sporocarp abundance and availability: are sporocarps abundant enough to meet consumers needs, and are they available in different forest types and during all times of the year? Most herbivore food sources in the forest, such as forbs and seeds, are highly seasonal. Therefore, fungal sporocarps, which are relatively abundant year-round, are an important seasonal food source and may be nutritionally important year-round.

Standing crop by stand type

The standing crop of truffles was significantly higher in natural-mature and old-growth than in managed-young stands. Smaller but significant differences in truffle biomass with stand age were also found in the western Oregon Cascades by a similar sampling scheme. Luoma et al. (1991) reported truffle standing-crop means of 1.2, 2.2, and 1.6 kg/ha in mesic, natural-young, natural-mature, and old-growth stands, respectively, at the H. J. Andrews Experimental Forest. In a comparison of truffles in 23-yr-old managed and 180-yr-old natural Pacific silver fir (*Abies amabilis*) stands, Vogt et al. (1981) found 1 kg/ha in the former and 380 kg/ha in the latter. However, problems with the sampling design in this study (Luoma et al. 1991, Vogt et al. 1992) indicate that the values were strongly skewed toward high biomass values. These comparisons did not include managed-young stands that had been previously clear-cut and slash-burned. Amaranthus et al. (1994) did compare standing crop of hypogeous fungi in 180-yr-old Douglas-fir patches with those in surrounding plantations 4–27 yr old. The 180-yr-old stands had from 6.8 to >100 times the dry mass of standing crop as did the plantations.

Three other studies have sampled in managed stands

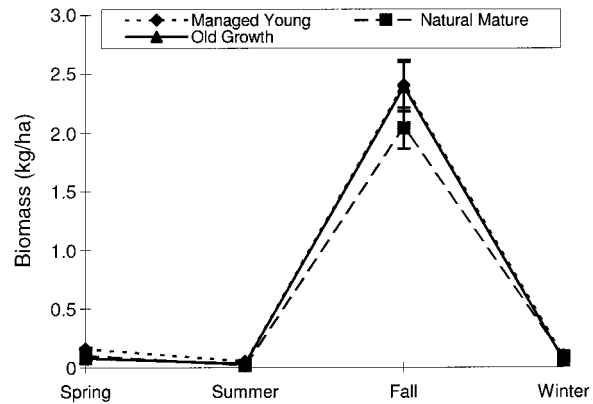


FIG. 4. Mean (± 1 SE) epigeous sporocarp standing crop of managed-young, natural-mature, and old-growth stands by season. Biomass values have been standardized to kg/ha.

alone. Sampling a 40–65 yr-old Douglas-fir stand established after a clearcut and burn in Oregon's Central Coast Range, Fogel (1976) found standing crops of 2.3–5.4 kg/ha of hypogeous sporocarps. In the same area and in a similar stand type, Hunt and Trappe (1987) reported a 2.0–3.2 kg/ha standing crop. In a comparison of selectively logged vs. selectively logged and burned stands of white and red fir (*Abies concolor* and *A. magnifica*) in northern California, Waters et al. (1994) found a mean of 1.56 kg/ha of hypogeous standing crop. These values are within the range of standing crop biomass found in our study's managed-young (0.78 ± 0.29 ; mean and 95% CI), natural-mature (4.51 ± 1.50), and old-growth (4.02 ± 1.06) sample stands.

The disparity in standing crop between managed and natural stands in our study may be due to the composition of the hypogeous community sampled. In our sample stands, most of the difference between managed and natural stands results from the presence and abundance of *Elaphomyces granulatus*. Managed-young stands had low standing crop values resulting from occurrence of only three large clusters of *E. granulatus*. Luoma et al. (1991) found only one large cluster of *E. granulatus* in 5400 m² of sampling over four years. However, in the central Washington Cascades, Vogt et al. (1981) also reported large clusters of *E. granulatus* in old-growth Pacific silver fir (*Abies amabilis*).

The reason for the large standing crop of *E. granulatus* in natural, older stands in Washington State is not clear. In general, this species becomes increasingly common with an increase of latitude north of $\approx 45^\circ$ to far northern forests (J. M. Trappe, unpublished data). Although *E. granulatus* may be the most common hypogeous fungus in North America (Smith et al. 1981), little is known about its autecology. Over the course of this study, field crews noted that large clusters of *E. granulatus* were found in plots with a thick organic layer comprised of dense mats of fine roots. In a study in which truffle locations, soil type, and stand structures were mapped and analyzed using a GIS, M. North and

J. Greenburg (*unpublished manuscript*) found a highly significant correlation between *E. granulatus* and thick, dry organic layers with a high density of fine roots. Generally, managed-young stands lack this soil structure because organic matter has accumulated only since their past slash burn. The three large clusters of *E. granulatus* found in managed-young stands were all found in moist depressions that had not burned and that did have a deep organic layer. Thick organic mats of fine roots are common in unburned stands of surface-rooting species such as western hemlock and silver fir.

Standing crop and abundance of *E. granulatus* did not differ significantly between natural-mature and old-growth stands. In contrast, however, truffle standing crop differed significantly between natural-mature and managed-young stands. Although most of the trees are of similar age and composition in these two stand types, managed-young and natural-mature stands have different disturbance histories. The absence of past clear-cut harvest and burning in the natural-mature stands has left a legacy of some old-growth features, such as a well-developed organic layer, abundant coarse woody debris, and a few large, old trees. These soil and structural legacies may be important to the productivity of *E. granulatus* and the abundance of food for mycophagists. Further research, including manipulation studies, is needed to determine the influence of particular stand structures, age, disturbance histories, or soil conditions on the fungal community.

Hypogeous sporocarp richness was highest in old-growth stands during the sample period. Sampling in southern Oregon, Amaranthus et al. (1994) also reported higher richness in old-forest fragments than in young plantations. Although these results provide a comparison of sporocarp diversity during the sample period, the collections probably missed sporocarps that fruit infrequently (Hering 1966, Hunt and Trappe 1987), and sporocarps may not be representative of total fungal diversity (Gardes and Bruns 1996).

Although epigeous sporocarp diversity varied by stand type, the mean sporocarp biomass did not differ significantly between stand types. Standing-crop biomass values differed by only 0.25 kg/ha, whereas the proportion of four morphological types differed significantly between stand types. Variance in epigeous sporocarp biomass was associated with seasonal and annual changes, rather than with differences in stand age or disturbance history. The standing-crop comparison for epigeous sporocarps is essentially a comparison of autumn production, because standing-crop values are low at other times of the year. Variability in standing crop may result from annual fluctuations in the timing and amount of autumn precipitation (Wilkins and Harris 1946, Last et al. 1981, Wasterlund and Ingellog 1981, Mehus 1986). The mean (and 95% CI) epigeous standing crop was 3.01 ± 0.73 , 0.93 ± 0.29 , and 2.94 ± 1.02 kg/ha for the fall sampling in 1992, 1993, and 1994, respectively. Within this annual vari-

ability, however, the relative equality between stand type, and open vs. exclosure plots did not change significantly.

The mean fall standing crop value of 2.28 kg/ha is lower than values given in other studies (Richardson 1970, Vogt et al. 1981, Garbaye and Le Tacon 1982, Mehus 1986, Ohtonen 1986), probably because we collected only two samples each year, during peak fall productivity. Sampling was designed to compare standing crop among stand and plot types, and did not sample epigeous sporocarps frequently during their prime period of production to permit comparison with more intensive studies. Consequently, epigeous biomass may be underestimated relative to hypogeous biomass, because epigeous sporocarps decay more rapidly than hypogeous sporocarps. Changes in the relative proportion of epigeous morphological type with stand type agree with studies suggesting that the composition and age of the forest influences the diversity of the fungal community (Last et al. 1981, Wasterlund and Ingellog 1981, Chu-Chou and Grace 1982, Mason et al. 1984, Dighton and Mason 1985, Dighton et al. 1986, Jansen and Denie 1988, Hilton et al. 1989, Termorshuizen 1991).

Consumption

Estimates of the standing crop and productivity of fungal sporocarps have always been conservative, because the quantity of fruiting bodies eaten by animals has been unknown (Fogel 1976, Luoma et al. 1991). Consequently, estimates have been biased downward, and the relative importance of fungal sporocarps in the forest food chain has not been quantified. Although this study provides some information on animal consumption, it is limited to predation by aboveground animals. Hypogeous sporocarps are also eaten by soil invertebrates and larger fossorial animals, such as various voles and gophers (Fogel and Trappe 1978, Maser et al. 1978). Over the 2.31 ha of area sampled in this study, only a few instances of tunneling under exclosure screens were observed. However, partial consumption of several hypogeous species with soft peridium by soil invertebrates was not uncommon. No invertebrate consumption of *E. granulatus* was found, possibly due to its tough peridium.

Palatability preferences in this study should be compared with caution, because differences in the percentage consumed also reflect differences in species abundance between stand types. Species with the highest consumption percentages, such as *Truncocolumella citrina*, *Rhizopogon subcaerulescens*, *Melanogaster tuberiformis*, and *R. vinicolor*, were most abundant in managed-young stands, where total standing-crop biomass was low. Consumption preferences probably change in response to both the abundance and the diversity of sporocarps and alternative food available at any one time and place. Controlled cafeteria experiments with small-mammal mycophagists would provide a better comparison of consumer preferences.

Consumption values did not differ significantly among stand types, averaging 0.67, 0.60, and 0.65 kg/ha for managed young, natural mature, and old growth, respectively. Variation in mycophagy rates appeared to be an interaction of season and truffle abundance. Mycophagy was highest in all stand types in the summer, when hypogeous sporocarps were most abundant. Consumption in natural-mature and old-growth stands was lowest in the fall, when epigeous sporocarps are also abundant. In managed-young stands, consumption was lowest in winter, when truffles were scarce and also when some small mammals hibernate.

Truffle biomass for animal consumption did not appear to be limiting for animal consumption in the natural-mature and old-growth stands. The mean standing crop of hypogeous sporocarps in the natural-mature and old-growth stands was 4.72 kg/ha in spring, 5.65 kg/ha in summer, 3.91 kg/ha in fall, and 3.0 kg/ha in winter. The lowest single stand-sample biomass value of 2.7 kg/ha in old-growth during the winter was well above the mean consumption of 0.64 kg/ha. The evenness in standing crop among seasons is due to the dominance of *Elaphomyces granulatus*, which is slow to decay and may persist in the soil for many months. This year-round availability may be important to opportunistic as well as to obligate mycophagists, because alternative food sources such as epigeous sporocarps, seeds, and legumes are highly seasonal.

The mean consumption rate (0.64 kg/ha) was close to the truffle standing-crop values of 0.78 kg/ha in spring, 1.06 kg/ha in summer, 0.71 kg/ha in fall, and 0.36 kg/ha in winter in the managed-young stands. Several of the exclosures that did contain truffles in managed-young stands showed evidence of failed attempts to chew through the screens. All attempted entries were found on exclosures that were in place over winter, when the truffle standing crop dropped below the mean consumption level. No examples of screen chewing were observed in the natural-mature and old-growth stands during any season.

Although *E. granulatus* may provide a year-round food source, its nutrient value may not be high despite its high nitrogen content. Most of the nitrogen in *E. granulatus* is in indigestible forms, and its digestible energy content is lower than that of most conifer seeds (Cork and Kenagy 1989). Nine of the 12 most common hypogeous species were more heavily preyed upon than was *E. granulatus* (Table 2), suggesting that these seasonal truffles may have greater nutritional value. However, studies of small-mammal stomach and fecal contents indicate that *E. granulatus* is one of the most commonly consumed sporocarps (Fogel and Trappe 1978, Maser et al. 1978, 1985). Although perhaps not as nutritious as other food items, *E. granulatus* may still be a staple food because it is easy to locate, abundant, and available year-round (Cork and Kenagy 1989).

The standing crop of epigeous sporocarps did not

differ significantly between open and exclosure plots during any season. The mean standing crop of epigeous sporocarps was 2.28 kg/ha during the fall season, compared to a mean 0.08 kg/ha for the remainder of the year. Field observations of partially eaten sporocarps in the fall suggest that when epigeous sporocarps are available, some are consumed. Differences in consumption rates between morphological types suggest that some epigeous sporocarps, such as corals and chanelles, may be preferred by mycophagists over sporocarps that may have lower nutritional value, such as polypore and cup fungi.

Sampling

Fruiting of both hypogeous and epigeous sporocarps varies greatly in space and time. Assessments of standing-crop biomass can be biased upward when values are standardized from a small sample size that contains a few large sporocarp collections. In this study, standing-crop values for stand samples had large variability (0–27.45 kg/ha for hypogeous and 0–9.03 kg/ha for epigeous sporocarps). However, by the study's third year, sample variance did not significantly alter mean standing-crop values for each stand type.

Standing crops of above- and belowground sporocarps did not correlate significantly. A positive correlation would improve the chances of locating truffles from aboveground sporocarp patterns, and would suggest that there might be particular edaphic conditions that synergize sporocarp production for mycorrhizae. A negative correlation might indicate antagonism between above- and belowground sporocarps. Some mycologists have suggested that competition in the fungal community produces spatial separation of sporocarps by different species (Murakami 1987, Cibula and Ovrebø 1988). This type of competition may still operate between individual epigeous and hypogeous species, but there was no correlation between above- and belowground sporocarp biomass in our study.

Implications for mycophagists

In this study, fungal sporocarp availability was determined by season and stand type. As a food source for mycophagists, epigeous biomass was relatively equal in all stand types, but was abundant only in autumn following the onset of rain. The belowground environment, however, remains more constant between seasons; therefore, hypogeous fungi potentially have a longer season for sporocarp production. Our study found truffles to be available year-round and more abundant than the amount consumed in older stands. In managed-young stands, however, hypogeous sporocarps may be limiting as a food source, especially in winter. This seasonal shortage in managed-young stands may influence populations of mycophagists that rely principally on hypogeous sporocarps.

Studies of eight small-mammal species of the forest floor (Carey and Johnson 1995) and three sciurids (Ca-

TABLE 6. Forest floor small-mammal and sciurid species surveyed (Carey and Johnson 1995, Carey 1995) in the same area from which truffles were collected (10 stands common to all three studies). The percentages (by volume) of fungi found in stomach contents are from studies in Washington and Oregon. Abundance values are reported as either CPU (no. captures/100 trap nights) or density estimates (no./ha).

Species	Fungi in stomach contents (% by volume)†	Abundance, by stand type			
		Young managed		Old growth	
		CPU‡	no./ha§	CPU‡	no./ha§
<i>Clethrionomys gapperi</i>	72	0.98		0.93	
<i>Glaucomys sabrinus</i>	78		0.2		0.5
<i>Microtus oregoni</i>	36	0.55		0.45	
<i>Neurotrichus gibbsii</i>	0	0.56		0.74	
<i>Peromyscus maniculatus</i>	8	0.33		0.40	
<i>P. oreas</i>	...	1.10		1.71	
<i>Sorex monticolus</i>	...	1.00		1.58	
<i>S. trowbridgii</i>	5	1.65		2.12	
<i>S. vagrans</i>	7	0.30		0.30	
<i>Tamias townsendii</i>	77		0.2		0.4
<i>Tamiasciurus douglasii</i>	70		0.01		0.01

† All fungal content values are from Maser et al. (1978), except for *Neurotrichus gibbsii* (Whitaker et al. 1979) and *Sorex vagrans* (Whitaker and Maser 1976).

‡ All CPU values are from Carey and Johnson (1995).

§ All density values are from Carey (1995).

|| Indicates a significant difference ($P < 0.10$) in old-growth vs. young-managed values. P values from Carey and Johnson (1995) are calculated using an ANOVA on the log-transformed CPU values. P values from Carey (1995) are calculated using the Levene statistic.

rey 1995), in some of the same forest stands sampled in this study, included four species that are predominantly mycophagist (Table 6). Two of these species, *Glaucomys sabrinus* and *Tamias townsendii*, were more abundant in old growth, although the density value for *Tamias townsendii* was not significant due to high capture variance (A. Carey, personal communication). In Washington State, *Clethrionomys gapperi* replaces *C. californicus*, and has a more diverse diet and wider habitat range (Ure and Maser 1982, Gunther et al. 1983) than the strictly mycophagist, forest-dwelling *C. californicus* (Hayes et al. 1986). Carey and Johnson (1995) note that it was difficult to compare the relative abundance of *C. gapperi* between young and old forests because capture rates were highly variable between different stands. No difference in *Tamiasciurus douglasii* density was found between young and old stands, possibly due to annual variation in local populations and the squirrel's avoidance of the *G. sabrinus* and *T. townsendii* habitat that was sampled (Carey 1995). Many factors can influence small-mammal abundance, such as vegetation structure and composition (Wells-Gosling and Heaney 1984, Gilbert and Allwine 1991, Carey and Johnson 1995), understory shrubs (Carey 1995), and predator density. However, higher hypogeous sporocarp abundance and availability in the sampled old-growth stands corresponded with higher densities for the two small-mammal species that most rely on fungal sporocarps. Natural or human disturbance that alters the age or composition of a forest stand will probably affect hypogeous sporocarp abundance, the small mammals that rely on truffles for a substantial portion of

their diet, and the higher predators of these mycophagists.

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