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Hypogeous Sporocarps in Forest Remnants and Clearcuts in Southwest Oregon

Abstract

During June-August, 1991, we sampled hypogeous sporocarps on four late seral forest remnants ranging in size from 1.3 to 3.6 ha, and on clearcuts surrounding two of the remnants. In particular, our sampling of these southwestern Oregon sites (dominated by *Psuedotsuga menziesii/Abies concolor*) targeted three questions: 1) Are hypogeous sporocarps more abundant in remnants of late seral forest than in the surrounding clearcuts?; 2) Are hypogeous sporocarps more abundant under coarse woody debris?; 3) Is the California red-backed vole (*Clethrionomys californicus*) positively associated with areas having hypogeous sporocarps? Two forest remnants had twenty to forty times more hypogeous sporocarps than the young clearcuts which surrounded them. Hypogeous sporocarps were four times more abundant in plots having logs. Voles were more likely to be caught at traps having hypogeous sporocarps nearby. Remnant stands of late seral forest appear to provide a refuge for hypogeous sporocarps used by the California red-backed vole and other small mammals, and coarse woody debris may contribute to an abundance of hypogeous fungal sporocarps.

Introduction

The hypogeous sporocarps of mycorrhizal fungi (generally called "truffles"-Luoma 1988) are integral members of fully functioning Pacific Northwest coniferous forests. Truffles constitute the dominant food source of many small mammals, including 74%-89% of the diet of the California red-backed vole (*Clethrionomys californicus*) (Maser *et al.* 1978a; Ure and Maser 1982). Populations of *C. californicus* might become isolated on forest remnants in part because surrounding cutover areas lack truffles in early seral stages (Maser *et al.* 1978b; Ure and Maser 1982; Hayes *et al.* 1986). Although *C. californicus* is rarely found in young clearcuts (Gashwiler 1970; Mills In Press), it is not known whether suppressed truffle production might correlate with this absence of voles in clearcuts. Studying the distribution and abundance of truffles in a fragmented forest system will help foster understanding of the effects of fragmentation on *C. californicus*, and on other small mammals.

Furthermore, truffles have an ecological significance beyond supporting small mammals that rely on fungi in their diet. Nearly all hypogeous species form ectomycorrhizae with the roots of vascular plants, and are particularly abundant in association with conifers in the Pacific Northwest (Trappe and Molina 1986; Castellano *et al.* 1989; Molina *et al.* 1992). Mycorrhizae ("fungus roots") greatly increase the amount of water and nutrients available to a plant in exchange for the plant's photosynthate (Harley 1969; Trappe and Maser 1978; Allen 1991). This mutualistic symbiosis is thought to be necessary for the survival of conifers in the Pacific Northwest (Perry *et al.* 1987; Luoma *et al.* 1991; Molina *et al.* 1992). Because red-backed voles and other small mammal mycophagists serve as the primary dispersal vectors for hypogeous taxa, truffles and their dispersers are therefore notable members of the forest's functional diversity.

While knowledge of truffle taxonomy and phenology have greatly expanded in recent decades, the ecological issues of mycophagy pertinent to management of the Pacific Northwest's fragmented forests remain poorly understood. We investigate the abundance of truffles on four late-successional forest remnants and the clearcuts surrounding two of them during the summer to explore three questions: 1) are truffles more abundant in late seral forest remnants than in young clearcuts?; 2) are truffles more abundant in association with coarse woody debris?; 3) is the California red-backed vole, *Clethrionomys californicus*, associated with areas having truffles?

Study Area and Methods

The four sites studied (Figure 1) are in the Klamath Mountains physiographic province, in locations that

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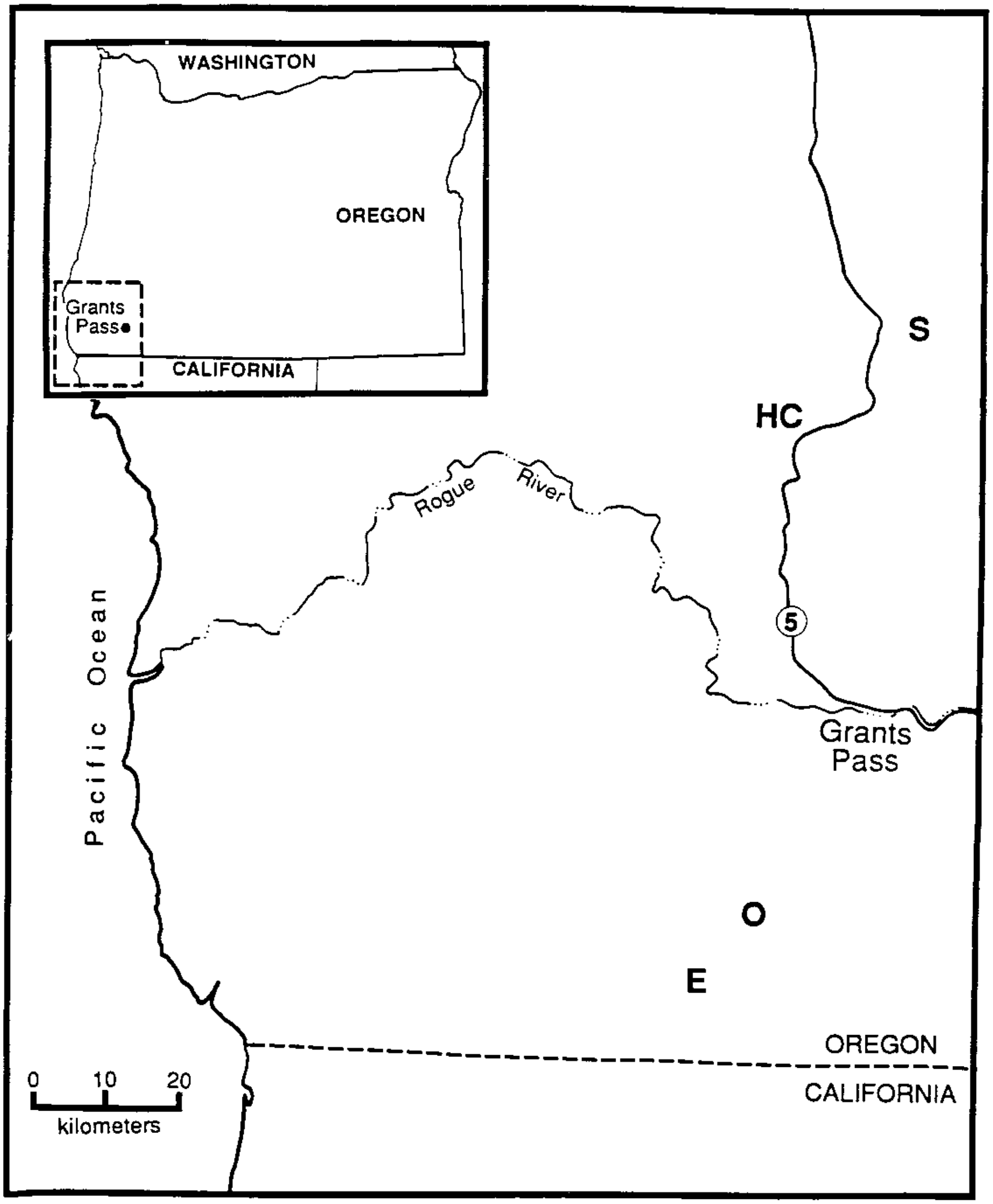

Figure 1. Location of four study sites sampled for truffles, 1991. The clearcuts surrounding sites E and O were sampled for forest-clearcut comparison. Map modified from Mills (In Press).

are relatively dry for the west side of the Cascades (mean annual rainfall 500-800 mm; Franklin and Dyrness 1973). Elevation, slope and aspect were variable, although all sites were steep and above 1,000 m (Table 1). All four sites were dominated by Douglas-fir (*Pseudotsuga menziesii*); the two higher sites (E and O) also had white fir (*Abies concolor*), and site HC had a tanoak (*Lithocarpus*

TABLE 1. Characteristics of sites sampled for truffles in southwestern Oregon, 1991. Modified from Mills (1993).

Site	Size (ha)	Number of truffle plots	Number of different trap sites with truffle plots[1]	Time since last cut	Distance (m) to nearest forest >7 ha	Slope	Aspect	Elevation (m)
S	1.3	24	10	1977	150	33°	E	1032
HC	2.5	32	27	1974	95	24°	S	1007
E	2.5	40	40	1987	100	38°	W	1280
O	3.6	40	40	1981	150	31°	W	1402

[1] On sites HC and S, a small mammal trap site might have more than one truffle plot: for the vole-truffle question, one of these truffle plots was randomly chosen for each trap site.

densiflorus) understory. All remnants, which ranged in size from 1.3 to 3.6 ha (Table 1), were completely surrounded by clearcuts <28 years old (see below).

We sampled truffle plots from mid-June until mid-August, 1991. For all three questions, each of the two treatments was sampled on alternate 1-4 day periods (if not on the same day) in order to eliminate the potentially confounding effects of weather. Each plot was 1x1 m in size, and was sampled by raking down to the organic-mineral soil interface. Truffles were weighed for fresh biomass within 24 hours and identified to genus.

Depending on remnant size, we sampled between 24 and 40 truffle plots on each remnant (Table 1). Placement of truffle plots was based on the systematic small mammal trapping grid of Mills (1993; In Press), which featured markers at measured 15-m intervals, indicating the locations of Sherman live traps. All truffle plots on remnants were placed within 5 m of randomly chosen trap markers, with exact placement constrained by avoiding rocky or densely vegetated areas.

To address our first question, whether truffle abundance in forest remnants differed from surrounding clearcuts, we also sampled the clearcuts around the two largest remnants (O and E, Table 1). The clearcuts were broadcast burned within two years of harvest and were 10 to 27 years old. These clearcuts are dominated by Douglas fir and white fir, although the percent cover by ectomycorrhizal host species is only about one-quarter that of the forest remnants (M. Amaranthus, U.S. Forest Service, Grants Pass, OR., unpubl. data). Because both remnants had 40 truffle plots each, we placed 40 plots throughout each surrounding clearcut. The clearcuts lacked a grid for systematic plot location, so each plot was located in the most promising microsites using the same criteria for placing plots within 5m of our randomly chosen locations on the forest remnants. Thus, we intentionally biased our test in favor of finding more truffles in clearcuts than in the remnants, which makes for a stronger test of the hypothesis that clearcuts have fewer truffles. Instead of performing pseudoreplicated statistical analysis of 80 plots in each of 2 remnants (Hurlbert 1984), we present our data for this question as graphical trends.

Second, we tested whether truffles are significantly associated with coarse woody debris within the forest remnants. If a downed log 10-70 cm in diameter was present within 5 m of a chosen marker flag, it was removed and the plot was placed underneath it. In this fashion, nearly half (43%) of all truffle plots were placed under logs. The proportion of log and no-log plots with at least one truffle present (occurrence) was compared using a 2X2 contingency test for binomial proportions (Rice 1988). To test whether fresh-weight biomass differed between log and no-log treatments we used a Behrens Fisher T-test (Rice and Gaines 1989). This test is preferred because it is robust to the unequal variances which commonly occur in ecological mycology research (Luoma 1988; 1991), including ours.

Finally, we asked if there was an association between truffle presence and the presence of California red-backed voles on the forest remnants. Based on small mammal trapping data collected the same summer as this study (Mills In Press), and on the conservative assumption that the home range of voles is 15 m in diameter (Tallmon and

Mills 1994), we tested whether plots with truffles tend to fall within vole home ranges more often than expected by chance. We first classified each truffle plot in all remnants as a "truffle present" or "truffle absent" plot. We then noted whether a California red-backed vole was captured in four nights of sampling in any of the five traps within 15 m of the plot. The null hypothesis, that plots with and without truffles have the same probability of having a vole present within 15 m, was tested with a 2x2 contingency test for comparing binomial proportions (Rice 1988).

Results and Discussion

We sampled a total of 136 truffle plots on four forest remnants, and 80 plots in clearcuts surrounding two of the forest remnants (E and O, Table 1). On the four remnants, 29 of 136 plots (21%) had at least one truffle, for a total of 82 sporocarps from 12 identified genera (Table 2). Weights varied greatly, with 3 of the 29 plots netting 51% of the total fresh-weight biomass on all remnants of $119.8g/136m^2$.

TABLE 2. Total biomass and number of sporocarps for hypogeous sporocarp genera[1] found in 136 plots on four forest remnants sampled in June-August, 1991.

General	Total Biomass (g)	Number of Sporocarps
Melanogaster	40.5	6
Hysterangium	23.2	26
Gautieria	16.0	4
Genabea	10.0	20
Rhizopogon	3.7	4
Martellia	3.6	2
Gymnomyces	2.6	4
Genea	1.0	3
Octavianina	0.4	1
Tuber	0.2	1
Endogone	0.1	1
Leucophleps	0.1	1
Unidentified	18.3	9
TOTAL	119.8	82

Truffle Production in Forest Remnants versus Adjacent Clearcuts

Late seral forest remnants "O" and "E" produced substantially more truffles than the clearcuts surrounding them (Figure 2). Nineteen of 80 plots on the two forest remnants had a total of 67 sporocarps, for a mean weight of 1.02 g (s.e. = 0.44) per plot. In contrast, the 80 clearcut plots had only a single truffle. To our knowledge, these are the first data to corroborate the "conventional wisdom" that hypogeous sporocarps are largely absent from young, slowly regenerating clearcuts.

Several interacting explanations probably account for our observation of truffles being virtually absent in clearcuts. First, decreased soil moisture on cutover areas may depress truffle production. Clearcutting and burning exacerbate soil dessication during the Northwest's summer drought (Chen *et al.* 1993), and truffle production tends to be lowest during hot and dry seasons (Fogel 1981). Similarly, the decrease in organic soil depth following clearcutting and burning can generate negative ecological effects (see Rosenberg *et al.* In Press), which could include a decrease in sporocarps normally found in the organic soil layer.

Low truffle abundance in clearcuts may also reflect reduced spore dispersal. In southwest Oregon, two primary dispersal vectors of hypogeous propagules, the California red-backed vole and Townsend's chipmunk (*Eutamias townsendii*), are significantly less likely to be captured in clearcuts than in forest remnants (Mills 1993, In Press). Finally, depressed truffle production may reflect the loss of plant hosts in these clearcuts. Most hypogeous fungi rely on ectomycorrhizal associations with conifers and ericaceous plants for nutrition (e.g., *Arctostaphylos spp., Arbutus menziesii*) (Trappe 1962; Trappe and Maser 1978; Perry *et al.* 1987; Molina *et al.* 1992), and a decrease of these hosts on clearcuts can greatly reduce ectomycorrhizae (Perry *et al.* 1987).

It is possible that other managed forests having substantive regeneration of ectomycorrhizal hosts may not show such dramatic losses of hypogeous fungal sporocarps. It is also possible that ectomycorrizae may have formed on the few regenerating plants on our sites, but that the parent mycelia has not yet obtained sufficient photosynthate for fruiting. There is a great need for

[1] Identified by Michael Amaranthus, U.S. Forest Service, Grants Pass, OR.

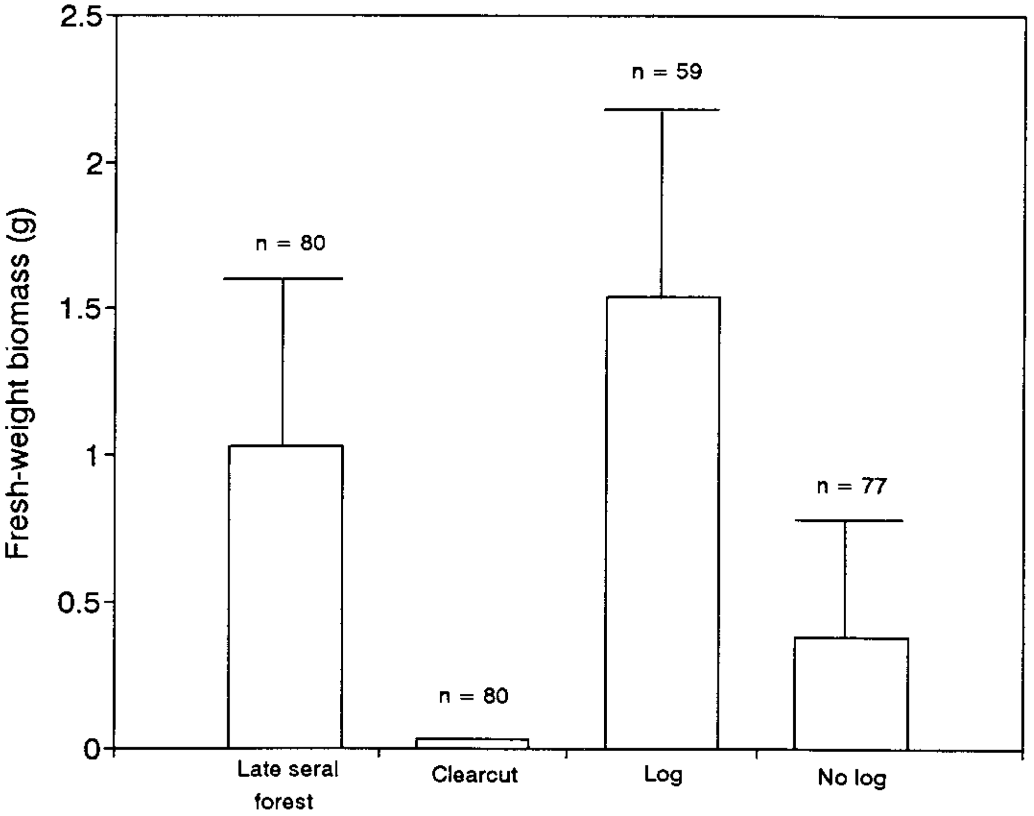

Figure 2. Mean (and standard error) of truffle fresh-weight biomass (grams). Comparisons include two late seral forest remnants versus their surrounding clearcuts, and log versus no-log plots on four forest remnants. Sample sizes refer to number of plots.

long-term study on mycorrhizal fungi in a variety of stand ages in order to determine the extent of fungal decline and regeneration in managed forests.

Truffles and Logs

Log plots were more than twice as likely to contain truffles than no-log plots ($P=0.007$). Similarly, truffle biomass was four times greater in log than in no-log plots (Figure 2), although high variance made statistical significance marginal ($P=0.08$).

Harvey *et al.* (1976) had a similar finding in western Montana, where mycorrhizae were found in greater amounts underneath logs. However, Luoma (1988) was the first to investigate any relationship between production of sporocarps and logs; his multi-year, year-round study in the relatively mesic westside Cascades found no significant correlation between logs and increased truffle production. This at first seems unexpected since logs are primary habitat for mycophagous small mammals who presumably inoculate these areas with feces laden with spores of mycorrhizal fungi (Franklin *et al.* 1981; Luoma 1988).

Nevertheless, logs may be uniquely important for truffles and voles in southwestern Oregon since the soils are relatively dry and poor (Franklin and Dyrness 1973; Hayes *et al.* 1986). Because logs provide a reservoir of moisture for surrounding soils during months of little precipitation, they serve increasingly vital ecological functions in drier regions (Franklin *et al.* 1981; Maser and Trappe 1984). For example, radio-telemetry on California red-backed voles on one of our sites (Site E) during the same summer found that 98% of telemetry locations for four voles were under logs, even though logs covered only 7% of the vole home range area; also, more highly decayed logs were preferred (Tallmon and Mills 1994). Preferential log use by this mycophagist would inoculate log-covered soils with spores of hypogeous taxa, explaining in part why more sporocarps are found there as well. We find it likely that this study found a positive log-truffle relationship where Luoma did not because the drier summer climate of southwestern Oregon tends to result in association of both moisture and mycophagy around coarse woody debris.

Truffle Occurrence Related to Vole Occurrence

Of the 136 total truffle plots, 19 were deleted from this analysis (with the deleted plot chosen randomly) because they represented multiple samples at the same trap location (Table 1). Of the 117 truffle plots at different trap locations, we found that red-backed voles were more likely to occur in areas with truffles than in those lacking them ($P<.05$; Table 3). For plots with truffles, 78% (28 of 36) had voles within a 15 m radius around the truffle plot. For plots lacking truffles, 46% (37 of 81) had voles within a 15 m radius.

TABLE 3. Contingency table showing plots with or without truffles having California red-backed voles within 15 m.

	vole	no vole	total
truffle	28	8	36
no truffle	37	44	81
total	65	52	117

The finding that voles tend to be found near truffles corroborates earlier research showing that the California red-backed vole's fecal pellets are composed mostly of spores from hypogeous sporocarps (Maser *et al.* 1978a; Ure and Maser 1982). The finding that voles are often found near truffles, coupled with our observations that both voles (Mills In Press) and truffles are nearly absent from clearcuts, strengthens earlier suggestions that "dependence on [hypogeous] ectomycorrhizal fungi by the western red-backed vole probably accounts for the latter's disappearance from deforested sites" (Ure and Maser 1982: 3307).

Although our results are limited to the summer period, this is the time for both maximum truffle consumption for the California red-backed vole in southwestern Oregon (Hayes *et al.* 1986), and the most limited period of fruiting of hypogeous fungi in general (Fogel 1976; 1981). Thus, these small remnants of forest may be especially important to red-backed voles during the dry season.

Conclusion

We found that during the summer of 1991 truffles were practically absent from young clearcuts in comparison to adjacent forest remnants. On remnants, truffles were more often found under logs and near red-backed voles. Our findings may be most relevant to the drier forests of southwestern Oregon and northwestern California, and there is certainly need to examine these questions over a wide variety of sites, seasons, and years. Nevertheless, it appears that small remnants of late seral forest can serve, at least seasonally, as vital refuges for hypogeous sporocarps and the small mammal mycophagists (Mills 1993) which eat and disperse them. Logs seemed to be an important structure for maintaining an abundance of truffles and red-backed voles on our forest remnants (see also Tallmon and Mills 1994, Mills In Press). Our study strengthens other suggestions that coarse woody debris may be central to maintaining biological and functional diversity across fragmented landscapes, in both managed and unmanaged forests (Franklin *et al.* 1981; Spies *et al.* 1988; Spies and Cline 1988; Hansen *et al.* 1991, Tallmon and Mills 1994).

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