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Title: SOIL FUNGAL HYPHAL DYNAMICS AND SEASONAL HYPOGEOUS SPOROCARP PRODUCTION IN WESTERN OREGON DOUGLAS-FIR FORESTS

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Total length and biomass of fungal mycelium in the soil of a young Douglas-fir stand in the central Oregon Coast Range were estimated over 27 months with the agar-film technique. In a second study, phenology and taxonomy of hypogeous (belowground) sporocarps were studied over 32 months in a nearby, young Douglas-fir stand. Mycelial mass was at maximum in fall and spring and significantly lower in summer. Melanized hyphae dominated those with other colors, averaging 66 percent of monthly litter and 73.7 percent of soil hyphal weight. The mycorrhizal fungus Cenococcum geophilum Fr. had significantly larger average diameter than other hyphae and contributed from 1.2 to 64.8 percent of monthly hyphal volume. Multiple regression analyses with temperature, moisture, and litterfall produced no adequate predictive equations for monthly fungal biomass.

Nine ascomycete and 21 basidiomycete species were collected during the sporocarp phenology study. Production was dominated by

a small number of species; taxa accounting for 5 percent or more of total annual dry weight were Gautieria monticola, Hysterangium crassum, H. separabile, and Melanogaster ambiguus. Annual productivity estimates ranged from 5,815 to 6,648 sporocarps $ha^{-1}$ and 2.0 to 3.2 kg dry weight $ha^{-1}$. Peaks in production generally resulted from a large contribution by one or two species. Pronounced seasonal trends in production were not evident, but sporocarp number and biomass were greater in spring than fall. Annual fruiting period for individual species ranged from only three months for some species to as much as 11 months for others.

Fungi produce the greatest biomass of all soil organisms in temperate coniferous forests. Mycelium and sporocarps are nutrient and energy sources for decomposers and consumers. In addition, they are essential as mycorrhizal symbionts to the growth of most forest-dwelling vascular plants. Consequently, ecosystem studies dealing with nutrient allocation, turnover rates, or mycophagy by soil fauna or vertebrate populations need to account for the contributions of fungal hyphae, sporocarps, and/or mycorrhizae. Because fungal biomass typically fluctuates widely over short periods, frequent sampling and long term study are needed to asses the importance of fungi in ecosytems.

# Soil Fungal Hyphal Dynamics and Seasonal Hypogeous Sporocarp Production in Western Oregon Douglas-fir Forests

by

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## INTRODUCTION

Studies of belowground processes of forests have shown that fungi are predominant agents of decomposition (Dickinson and Pugh 1974) and essential to the growth of forest trees as mycorrhizal symbionts (Trappe and Fogel 1977, Harley and Smith 1983). Moreover, fungi have the greatest biomass of all soil organisms in temperate coniferous forests and thus are important links in nutrient cycles by immobilizing plant nutrients (Baath and Soderstrom 1979; Fogel and Hunt 1979, 1983; Hunt and Fogel 1983), having rapid turnover, and serving as food for part of the soil fauna and vertebrate populations. Clearly, ecosystem studies dealing with biomass, nutrient allocation, and turnover must take into account the contributions of fungal hyphae, sporocarps, and mycorrhizae.

Gathering data for establishing the contribution of higher fungi (basidiomycetes and ascomycetes) to forest ecosystems presents challenges not encountered in study of aboveground forest components. Vascular plant communities are described by sampling a recognizable and relatively homogeneous and stable vegetation segment. By comparision, the mycoflora (mycota) consists of species groups distributed nonrandomly and separated spatially and temporally within many microhabitats in the general environment. Individuals cannot be delimited by vegetative structures, so collection of ephemeral sporocarps is the only means by which species populations can be studied. Sporocarp production is

generally erratic. Fungal species may fruit suddenly where they have not been seen before but presumably have been present for an indefinite time in the vegetative state.

Many if not most terrestrial species of higher fungi in forests are mycorrhizal and thus are root inhabitants that act as extensions of root systems and are required by forest trees for absorption of adequate nutrients from soil (Marks and Kozlowski 1973, Sanders et al. 1975, Trappe and Fogel 1977, Harley and Smith 1983).

Fungi producing sporocarps aboveground (epigeous) are easier to study than those that fruit belowground (hypogeous) fungi. As a result, many more studies have been done on the former (Hering 1966, Richardson 1970, Endo 1972, Lange 1978, Watling 1978). Fogel (1981) has reviewed the literature on epigeous sporocarp production. Description of ectomycorrhizal fungal communities requires determination of the species present and their relative abundance, yet few studies of hypogeous fungi have gathered these data or considered related areas of their ecology (Fogel 1981). Production by individual hypogeous species was reported in one study (Fogel 1976). The hypogeous mycota associated with different communities or geographical areas has been reported (Ceruti et al. 1967, Gross 1969, Fogel 1976, States 1983, 1984) and relationships of hypogeous sporocarp production to climatic or soil factors have been considered (Setchell and Watson 1926, Ceruti et al. 1967, Montacchini and Caramiello 1968, Fogel 1976).

The hypogeous fungi are members of the ascomycetes and basidiomycetes. A few members of the Endogonaceae (Zygomycetes)

produce small hypogeous sporocarps but are not generally abundant in coniferous forests. The hypogeous basidiomycetes and ascomycetes (excluding some secotioid forms) are characterized by having sporogenous tissues completely enclosed in a peridium and lacking forcible spore discharge. Most are subglobose in shape and all are presumed to be ectomycorrhizal (Miller 1983, Trappe 1971). Hypogeous fungi require animal mycophagy for spore dispersal and possess odor compounds which attract mammals (Marin et al. 1984, Trappe and Maser 1977). Some mammals strongly rely on hypogeous fungi as a primary food, and many use them as a supplemental food (Fogel and Trappe 1978, Maser et al. 1978a, Trappe and Maser 1977).

Data on species and production of hypogeous sporocarps are useful in developing important principles in community ecology (Seifert 1981). For example, determining ectomycorrhizal species richness in various plant communities and soil types permits inferences about the occurrence of specific host-fungus associations and their biogeographical distributions. Other research areas in which data on sporocarps are relevant include those relating environmental factors to sporocarp production, investigations of successional patterns of ectomycorrhizal fungi in plant communities (Watling 1981) and in physiological studies of interference and exploitation competition (Gadgil and Gadgil 1975, Marx 1972, Robinson 1972). Data on hypogeous sporocarp production are also potentially important in forest management, e.g., to establish the potential food resource for mycophagists (Fogel and Trappe 1978) or to determine the ectomycorrhizal species of potential value for commercial reforestation (Trappe 1977).

A primary goal of mycoecologists is to integrate studies of fungi into development of ecological theory and ultimately to reach an understanding of the contribution of fungi to the structure and function of whole ecosystems (States 1981). Descriptive studies designed to quantify both the vegetative fungal component (hyphae) and reproductive structures (sporocarps) in various plant communities are necessary preliminary steps in realizing this goal.

The objectives of my studies were (1) to assess seasonal total lengths and biomass of fungal mycelium in the soil of a young Douglas-fir stand in the central Oregon Coast Range (Chapter 1) and (2) to determine the species and phenology of hypogeous sporocarps in a second Douglas-fir stand (Chapter 2).

# CHAPTER I

# FUNGAL HYPHAL DYNAMICS IN A WESTERN OREGON DOUGLAS-FIR STAND

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## ABSTRACT

Total length and biomass of fungal mycelium in the soil of a young stand of second-growth Douglas-fir in the central Oregon Coast Range were estimated over 27 months with the agar-film technique. Mycelial mass was at maximum in fall and spring and significantly lower in summer. Melanized hyphae dominated other colors, averaging 66 percent of monthly litter and 73.7 percent of soil hyphal weight. The mycorrhizal fungus Cenococcum geophilum Fr. had significantly larger average diameter than other hyphae and contributed from 1.2 to 64.8 percent of the monthly hyphal volume. Multiple regression analyses with temperature, moisture, and litterfall produced no adequate predictive equations for monthly fungal biomass. Large biomass fluctuations over short periods necessitate frequent sampling and long-term study to fully assess the importance of fungal hyphae in ecosystems.


## INTRODUCTION

Little is yet known about the distribution of fungal hyphae in coniferous forest soils, though data on mycelial biomass are important to understanding the contribution fungi make in decomposition and nutrient cycling, and as mycorrhizal symbionts. We have reported the allocation of biomass and turnover time for fungi in a young, second-growth stand of western Oregon Douglas-fir

and have described the contribution of fungi to nutrient cycling in the same stand (Fogel and Hunt 1979, 1983). We here report an extended study of 27 consecutive months of litter and soil analysis, and describe monthly biomass fluctuations and seasonal changes in fungal hyphae throughout the soil profile.

## MATERIALS AND METHODS

### The site

The 1.2-ha Dinner Creek site is 11.3 km southwest of Philomath, Oregon, U.S.A. at 44°28'30"N, 123°29'W and at 305-m elevation. Aspect is south; slope ranges from 0 to 60 percent (mean 40 percent). The area is characterized by warm, dry summers and mild, wet winters without extensive snow cover (mean temperatures 2.7°C in January and 18.5°C in July). Annual precipitation averages 1905 mm but was substantially below average (848mm) during the first year of the study (September 1976 to August 1977) and slightly below (1775 mm) during the second year. Maximum predawn plant moisture stress of the overstory reached -1.35 MPa in September 1977 and -0.99 MPa in September 1978.

The stand, an overstocked, second-generation forest of 35- to 50-year old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), was established naturally after clearcutting and burning. Douglas-fir stems greater than 10.2 cm dia at 1.3 m aboveground number 1626 $ha^{-1}$ (basal area 4.59 $m^{-2}$ $ha^{-1}$ and bole volume

423 $m^{-3}$ $ha^{-1}$). A few golden chinquapin (Castanopsis Chrysophylla (Dougl.) A Dc.) and red alder (Alnus rubra Bong.) are scattered in the understory (basal area 3.2 $m^{-2}$ $ha^{-1}$). The sparse, shaded understory consists of a few Oregon grape (Berberis nervosa Pursh) and bear-grass (Zerophyllum tenax (Pursh) Nutt.).

The Bohannon soil type of the site is a well-drained, moderately deep (100 cm to bedrock), gravelly loam formed on colluvial materials weathered from Tyee sandstone (Knezevich 1975). Poorly developed organic layers, averaging 1.8 cm in depth, are a mull humus type. The $A_{00}$ (L) horizon, a thin layer of freshly fallen needles, is underlain by a scant $A_{01}$ (F) layer. The $A_{02}$ (H) horizon, well mixed with surface mineral soil by the activity of earthworms and microarthropods, forms a soft, friable $A_1$ horizon down to 25 cm. This zone of maximum rooting contains about 18 percent pebbles. The $A_3$ horizon extends from 25 to 45 cm and forms a smooth boundary with the B horizon, which extends to 90-110 cm. A distinctive feature of the Bohannon series is a buried A horizon found between 60-90 cm which contributes increased organic matter at the base of the profile. Average carbon (measured by loss on ignition at 850°C for 4 h) is 0-20 cm, 2.91 percent; 20-40 cm, 1.44 percent; 40-60 cm, 0.57 percent; 60-80 cm, 1.38 percent; 80-100 cm, 0.56 percent. All horizons are strongly acid: pH 5.5 in the litter layer and 5.7 in the $A_1$ horizon.

Sampling and preparation method

Mycelial length was measured by the Jones and Mollison (1948) agar-film technique as modified by Nagel-de Boois and Jansen (1971). Litter and mineral soil samples to 5 cm deep were collected on the first of each month at five sampling stations. Samples were also taken seasonally at 20 cm increments to a depth of 1 m at three randomly chosen locations. A portion of each sample (2 g litter or 5 g soil) was combined with 50 ml distilled water, then homogenized in a Waring knife blender at maximum speed (litter solutions 10 min and soil soulutions 5 min). The supernatant was added to 50 ml of hot 2.5 percent water-agar and mixed at low speed on a magnetic stirring plate as samples were pipetted into the well of a Howard mold-counting chamber producing a film 0.1 mm deep. The films were stained for 1 h in phenolic aniline blue, rinsed with 95 percent ETOH, and examined with phase-contrast microscopy (1000x).

Each month, 20 randomly chosen fields on each of two slides, one for litter and one for soil, from each of the five stations were observed. Hyphal lengths and diameters were measured with a net micrometer disc. All lengths were expressed as $mg^{-1}$ dry weight (dw) soil.

To convert mycelial length to biomass, the mean monthly biovolume over 20 sample fields of litter and surface soil was first calculated by computer with the formula of Baath and Soderstrom (1979b):

$$\text{mean biovolume } (\mu m^{-3} = \sum^{20} \frac{d_i^2}{2} \times \pi \times li/20,$$

where $d_i$ is diameter and $l_i$ is length of individual hyphal fragments in micrometers. The resulting values were converted to $mm^3 g^{-1}$ dw soil.

For seasonal samples from different depths in the soil profile, we used mean hyphal diameters determined from the agar-film preparations: 3.0 μm for 10, 30 and 50 cm and 2.7 μm for 70 and 90 cm. Thus, volume ($mm^3 g^{-1}$ dw soil) = hyphal length (m $g^{-1}$) x $r^2 x\ 10^{-3}$.

For conversion of biovolume to biomass (mg $g^{-1}$), we used the factors fresh weight hyphal density = 1.1 g $cm^{-3}$ (Saito 1955) and dry weight mycelium = 15 percent wet weight (Cochrane 1958, de Boois 1976). Thus, biomass (mg $g^{-1}$) = volume ($mm^{-3} g^{-1}$) x 1.1 x 0.15. Horizon weights from measurements of whole-soil bulk density, 1903.4 g $m^{-2}$ for litter and 34 x $10^3$ g $m^{-2}$ for soil surface, were used to convert hyphal biomass from mg $g^{-1}$ to g $m^{-2}$. Soil weights (based on bulk density samples) used for seasonal profile samples are given in Table I.1

## RESULTS

### Hyphae in litter and surface soil

Litter hyphal length (Fig. I.1a) was high in fall and spring and low in summer and winter throughout the study. Maximum length recorded (November 1976) was 12,502 ± 2131 m $g^{-1}$ dw litter. Minimum length (August 1978) was 2831 ± 271 m $g^{-1}$. Litter hyphal

weight (Fig. I.1b) peaked twice during the study: at 22.13 ± 5.8 mg $g^{-1}$ (November 1976) and 23.17 ± 7.2 mg $g^{-1}$ (March 1978), the maximum reached during the study. Minimum weight was 5.19 ± 1.2 mg $g^{-1}$ (August 1978).

Soil hyphae fluctuated seasonally but neither length nor weight decreased during winter 1977-1978. After July 1977, hyphal length (Fig. I.2b) followed a similar pattern, increasing during the winter of 1977-1978 to a peak in April of 1.50 ± 0.36 mg $g^{-1}$. The summer low occurred in Augut 1978 at 0.35 ± 0.11 mg $g^{-1}$.

Vertical distribution of soil hyphae

Hyphae were sampled to 1-m depth in winter, spring, and summer; but because fall samples were lost in an electrical failure, data for fall (to 50 cm) were estimated from linear regression equations with soil moisture and temperature as independent variables. Hyphal length fluctuated most near the surface--the annual range from 141 to 750 mg $g^{-1}$ (Fig. I.3). Distinct seasonal differences occurred down to 50 cm, where hyphal lengths ranged from 118 to 264 $mg^{-1}$. Below 50 cm, hyphal mass remained fairly stable, about 80 $mg^{-1}$ at 70 cm and 38 $mg^{-1}$ at 90 cm. The mean curve from six sampling dates shows a highly significant negative logarithmic correlation with depth (Fig. I.3). Maximum and minimum mycelial length and weight (Table I.1) generally decreased with increasing depth. Minimum weight increased from the surface down to 60 cm (6.47 - 28.12 g $m^{-2}$), then decreased to 2.19 $gm^{-2}$ at 90 cm.

Color groups

Hyphae were categorized by color after staining with phenolic aniline blue into "melanized" (brown, black and gray), "blue-stained," and "other" hyphae (primarily hyaline). For 19 months, melanized hyphae dominated (Table I.2). The weights of melanized litter hyphae ranged from 4.0 ± 0.22 mg $g^{-1}$ to a peak of 17.84 ± 1.33 mg $g^{-1}$. Blue-stained litter hyphae ranged from 0.55 ± 0.03 mg $g^{-1}$ to 8.44 ± 0.64 mg $g^{-1}$. Figure I.4 shows the monthly weight and the proportion of the total weight of melanized and blue-stained hyphae in litter.

Weights of melanized hyphae in soil ranged from 220 ± 8 $\mu g g^{-1}$. Blue-stained soil hyphae ranged from 400 ± 3 $\mu g g^{-1}$ to 330 ± 20 $\mu g g^{-1}$ (Table I.2, Fig. I.5)

The ubiquitous and morphologically distinctive mycorrhizal fungus Cenococcum geophilum Fr. (Trappe 1964) was recorded separately. In transmitted light, the thick-walled hyphae are bronze to purple. Data for Cenococcum and and all other hyphae for 1 yr show that Cenococcum composed a larger proportion of mycelial volume than of length (Table I.3). For 19 months, it contributed from 13.4 to 45.5 percent of litter mycelial volume and from 1.2 to 64.8 percent of soil hyphal volume.

# DISCUSSION

Results of different hyphal studies are not easily compared because of differences in techniques such as the preparation of Jones and Mollison slides (Thomas et al. 1965, Nagel-de Boois and Jansen 1971) or hyphal measurement, magnification, lighting (Frankland 1974), and calculation of hyphal volume (Baath and Soderstrom 1979b). Moreover, within-sample variation is typically large. For example, monthly coefficients of variation (standard deviation as a percentage of the mean) for litter hyphal length ranged from 16 to 65 percent during this study. In order to reduce this to an average 10 percent, monthly sampling should increase from 100 to 6588 fields, according to Stein's two-stage estimate of sample size for $P < 0.05$ (Steel and Torrie 1960). It should also be noted that the Jones-Mollison technique results in an underestimate of mycelial mass because of incomplete maceration of organic matter (inevitable in most homogenizers and tissue grinders) and incomplete separation of hyphal fragments from inorganic soil particles, so that hyphae are pulled to the bottom of the suspension by sinking particles. In addition, some hyphae are masked by soil particles incorporated in the finished preparations. The work of Baath and Soderstrom (1979a) may be most directly compared with our work because of similar techniques in knife blending, phenolic analine blue-staining, phase contrast microscopy and high magnification (1000x), and because we calculated biovolume by the same method.

Hyphal length

Despite pronounced fluctuation in hyphal length during the wet months of the year (Fig. I.1), seasonality is shown primarily by low summer values. The sharp drop in litter hyphal length and volume from November to December 1976 is apparently a "dilution effect" from a large input of uncolonized needle litter during November.

Comparison with other work is difficult because few studies have been extended over time. Nagel-de Boois and Jansen (1971) measured mycelial lengths monthly for 3 yr in an oak-beech forest and found no conclusive evidence of seasonal change. Hyphal length was maximum during autumn and winter in an English Scots pine forest (Nicholas et al. 1965) and in spring in a European black pine plantation (Parkinson et al. 1968). Seasonal samples in a Spanish beech forest (Martinez and Ramirez 1978) revealed a spring maximum in litter hyphae and a fall maximum in the $A_{11}$ horizon. Laursen and Miller (1977) found spring maxima and summer minima in tundra at Barrow, Alaska, seemingly a reflection of soil moisture and temperature.

The summer drop in hyphal length in Alaska and on our site indicates that seasonal drought influences hyphal biomass. However, it is important to note that monthly increment and decrement of total hyphae may not necessarily represent growth differences but may be influenced by decomposition and soil fauna grazing. Our measurements do not indicate whether the primary cause of fluctuation is rate of growth, mycophagy, or other processes.

Differences in vegetation, climate, and soils make between-site comparisons difficult (Table I.4 a,b). Different soil structures, for example, do not permit direct comparison of hyphal lengths of our study with those of Baath and Soderstrom (1979a). The mull humus of our site--$A_{01}$ and $A_{02}$ horizons (F and H respectively)--is inseparable and poorly developed compared to the distinct mor humus layers at the Swedish site; therefore, hyphal biomass of the litter there greatly exceeds ours. Our maximum value for surface soil ($A_1$) is the same order of magnitude as the $A_2$ value of the Swedish site.

Seasonal measurements of hyphal length through the soil profile (Fig. I.3) show the highest biomass in the fall, followed by spring, winter and summer. This surface hierarchy is maintained to 50 cm, which indicates that conditions fluctuate sufficiently at that depth to affect hyphal growth significantly. Soil moisture at 50 cm did not change significantly except during the driest part of summer--26.3 percent dw in August 1978, near 35 percent in other seasons. Below 50 cm, hyphal values are nearly the same in all seaons, reflecting the more buffered environment toward the bottom of the profile. The presence of hyphae at 90-100 cm shows that nutrient supplies are sufficient to sustain some growth. Although some nutrients may be transported from surface horizons to this depth, the hyphae may also derive nutrition from the buried A horizon. No comparable data for a seasonal profile are available for comparison, but several studies have documented a decrease in hyphae with depth (Burges and Nicholas 1961, Nagel-de Boois and

Jansen 1967, Nicholas and Parkinson 1967, Parkinson et al. 1968, Wadden and Parkinson 1973, Baath and Soderstrom 1979a).

Hyphal diameter

Baath and Soderstrom (1979a), in the only other publication of mean hyphal diameter through the soil profile that we know, report 2.63 μm in the organic layers and 1.90 μm in the mineral horizons ($A_2$ and B) of a Swedish Scots pine forest. They suggest three possible reasons for narrower hyphae in mineral soil: fewer nutrients, different fungal species inhabiting different horizons (Soderstrom 1975, Bissett and Parkinson 1979a), and abiotic conditions that may be less suitable for growth. Our data support the nutrient hypothesis, in that diameter does not change greatly through the profile. Mean diameter (3.01 μm) is the same to 50 cm, below which it decreases only modestly to 2.7 μm ($P < 0.2$). Moreover, the mean diamter of Cenococcum does not change significantly in the profile. These changes can be explained in terms of organic-matter distribution. Extensive mixing of humus with surface soil by arthropods and earthworms eliminates the distinct differentiation between organic layers and mineral soil apparent at the Swedish site, where most nutrients are in the mor humus layers. In addition, the buried A horizon of our study site means that organic matter increases slightly from 50 to 70 cm; thus, more uniform distribution may preclude diameter differences based on available nutrients. The mean diameter of 3.01 ± 0.05 μm of this study is at the top of the ranges 1.6-3.0 μm and 2.66-3.01 μm

reported respectively by Baath and Soderstrom (1979a) and Visser and Parkinson (1975).

Hyphal biomass

Biomass data best express fungal mass because they incorporate measures of diameter and thus volume. Baath and Soderstrom (1979 a,b) have discussed the importance of accurate measurement of hyphal diameter in calculating volume; because radius is squared, a relatively small difference in dimeter can result in a significant change in volume. For example, weight calculated from volume based on the overall mean dimater, 3.01 μm, and a length of 3366 m $g^{-1}$, is 10.21 g $m^{-2}$. Weight calculated with separate fragments is 15.80 g $m^{-2}$, 35 percent larger.

In our study, values based on mean dimeter of litter hyphae were 11-41 percent smaller than the values derived with the fragment-volume method. Corresponding decreases for surface soil hyphae were 1-47 percent. The difference in values apparently results from the thicker hyphae, which break into longer pieces during maceration (the longest fragments tend to be the widest). During 5 months, fragments 1-10 μm long averaged 3.02 ± 0.11 μm dia; those more than 50 μm long averaged 4.54 ± 0.26 μm dia. Use of a single mean diameter does not account for short-term changes which may occur with changes in species dominance. In May 1978, the mean diameter of litter hyphae 1-10 μm long was 2.60 ± 0.14 μm; in December 1977, the mean diameter was 3.09 ± 0.18 μm.

Although hyphal biomass and length fluctuate comparably from season to season, notable monthly differences reflect changes in mean volume of fragments. Between January and February 1977, mycelial length in the surface soil decreased 1.82 times, weight (mg $g^{-1}$) 3.47 times. This indicates an increase in the proportion of narrow hyphae.

The summer increase in mycelial weight (g $m^{-2}$) from the surface to 60cm (Table I.1) is probably a manifestation of greater soil bulk density, particularly from 20-40 cm where length decreases from 141 to 133 m $g^{-1}$ but biomass ($m^{-2}$) increases slightly. Extensive hyphal growth near the soil surface in the fall results in hyphal weight (g $m^{-2}$) decreasing down the profile despite the increase in soil bulk density from the surface to 60 cm. The effect of a moisture gradient on mycelial mass down the profile cannot be determined from our data, but the moisture gradient (percent dw) is minimal during wettest and driest periods. In August 1978, moisture was 21.65 ± 0.31 percent in the top 10 cm and 26.49 ± 0.20 percent at 90 cm, a range of only 4.84 percent. A similar narrow range, recorded in May 1978, was from 38.37 ± 0.66 percent at the surface to 34.50 ± 0.44 percent at 90 cm. In this clay soil, differences of this magnitude do not significantly change water availability.

Distribution of hyphal mass in the profile shifts distinctly with seasons (Table I.1), which indicates the importance of seasonal profile sampling to accurate description of distribution. During the fall, about 73 percent of the weight (g $m^{-2}$) is in the top 40 cm of soil, in the summer about 54 percent.

Our site may potentially produce 6666 kg $ha^{-1}$ $yr^{-1}$ of fungal mass, most of which turns over in one year (Fogel and Hunt 1979). The hyphae that decompose annually contain 2.1 percent of the total N stock for the stand (Fogel and Hunt 1983). Thus, soil hyphae constitute a rapidly cycling pool of nutrients and may contribute to ecosystem stability by immobilizing nutrients and thus reducing leaching from the root zone.

Table I.4 a,b shows data for mycelial biomass from other sites. Values from the only comparable study, a complete soil profile from Sweden (Baath and Soderstrom 1979a), generally agree with the Dinner Creek values for mineral soil if they are expressed in mg $g^{-1}$. A definite contrast appears, however, in the organic layers. Mean annual hyphal weight of litter from Dinner Creek is only one-fifth to one-third that of the Swedish sites, and the fall maximum of 15 mg $g^{-1}$ is only slightly over half of the Swedish value for Scots pine. However, total mycelial mass in the soil profile, expressed at g $m^{-2}$, is much greater at our site due to the greater depth (about 40 cm rather than 5 cm) and the greater hyphal productivity of the A horizon. The annual range of mycelial biomass at Dinner Creek is about 49 to 226 g $m^{-2}$, the value at the Swedish Scots pine site is 8.6 g $m^{-2}$. Hyphal biomass in the B horizon is similar at both sites--89 g $m^{-2}$ in Sweden and 41-82 g $m^{-2}$ at Dinner Creek. Clearly, the significantly greater mycelial mass at Dinner Creek (annual mean 216 g $m^{-2}$ vs 141 g $m^{-2}$) is due to the larger annual production in the A horizon.

Color groups

The amount of blue-stained hyphae in the litter and surface soil was recorded for comparison (Table I.2, Fig. I.5). The work of Frankland (1975) and Soderstrom (1979) has shown that blue-stained hyphae do not accurately represent the living fraction. Frankland reported that 34-60 percent of hyphae in an English deciduous forest stained blue (mean: 45 percent in litter, 54 percent in the A horizon); only 15-37 percent contained cytoplasm. Soderstrom found that the proportion of living hyphae (Fluorescein diacetate-active) was about 3-6.5 times less than the proportion of blue-stained hyphae. Melanized hyphae do not stain blue; apparently the stain is not taken up or is masked by other pigments. Length of blue-stained hyphae in Soderstrom's study was 12-16 percent of the total hyphal length in the $A_{01}$-$A_{02}$, $A_2$ and B horizons. Nagel-de Boois and Jansen (1971) reported a marked decrease in blue-stained mycelium from samples of the L, F, H and A horizons--80, 17, 5 and 4 percent of total length, respectively. Baath and Soderstrom (1979a) found that blue-stained mycelium ranged from 1-53 percent in four Swedish sites. Means for the Scots pine site were 17, 12 and 13 percent of total length in the organic layers, $A_2$ and B horizons, respectively.

Our percentages of blue-stained hyphae (Fig. I.5, Table I.2) are calclulated on total weight rather than length, but within this color group, mean total weight and length did not differ significantly ($P > 0.05$). Percentages ranged from 9 to 43 in litter and from 7 to 30 in the surface soil, decreasing slightly from

organic horizons to mineral soil. The values are reasonably close to those of the reports just cited.

Baath and Soderstrom (1979a) reported that melanized hyphae averaged 18 percent of the total hyphal length in the organic layers and 15 percent in the surface soil ($A_2$) at the Scots pine site. Burges and Nicholas (1961) reported that the number of melanized hyphal fragments decreased sharply from the H to the $A_1$ horizon in a glacial sand humus-podozol soil planted to Pinus sylvestris in England. Melanized hyphae comprised 91 percent of the fragments in a September sample of the H horizon and 76 percent in the $A_1$ horizon (calculated from Table I.5, Burges and Nicholas, 1961). Our data show a much higher contribution by the melanized group than that found in Sweden: 46.6-72.8 percent of the total length in litter (mean 59.9 ± 1.48 percent) and 52.0-90.4 percent in soil (mean 68.9 ± 2.5 percent). The proportion of melanized hyphae in litter, calculated on total weight (Table 2), differs significantly ($P < 0.05$) from the proportion of the total length (59.9 percent vs 66.0 percent). Comparable values for surface soil do not differ.

The high proportion of melanized hyphae at our site may be due to the summer drought conditions. Mycorrhizae of Cenococcum geophilum, a heavily melanized species more abundant during dry summers, apparently compete poorly with other fungi in moist soil (Palmer, unpublished data, 1954). Worley and Hacskaylo (1959) found that Cenococcum increased its mycorrhiza-forming capability as soil moisture was experimentally reduced. Meyer (1964) concluded that the abundance of Cenocuccum in strongly rooted mor humus results

from a widely fluctuating water economy. Mexal and Reid (1973) reported that Cenococcum tolerated low water potential and grew best at -1.5 MPa, unlike two hylaine species, Suillus luteus (Fr.) S.F. Gray and Thelephora terrestris (Ehrh.) Fr., which grew best at -0.5 MPa. The abundance of melanized hyphae in our seasonally dry climate may indicate that pigmentation is an adaptive advantage for surviving the droughty season. Mikola (1948) reported an optimum growing temperature of 25°C for Cenococcum, and we found that an isolate of Cenococcum from the central Oregon Coast Range grew best at 24°C, about 6°C higher than optimum temperature for a hyaline species from the same location, Laccaria laccata Fr. ex. Berk. and Br. (Hunt, unpublished data, 1981). Another factor contributing to this abundance may be that pigmented hyphae decompose more slowly than hyaline hyphae (Bloomfield and Alexander 1967, Kuo and Alexander 1967, Hurst and Wagner 1969).

Cenococcum hyphae compose a significantly larger proportion of total hyphal volume ($P < 0.05$) than of total length, which reflects a significantly larger diameter than that of other color categories (Table I.3). Clearly, when Cenococcum is abundant (maximum: 64.8 percent of total soil hyphal volume, December 1977), the mean hyphal diameter of soil samples would be significantly affected; therefore, calculations based on a single mean diameter might seriously underestimate biomass in some months.

The physiological significance of the larger diameter is unknown. Surface area is greater than that of most other hyphae, but the surface-to-volume ratio is smaller. Lumen volume is probably not significantly greater than that of most other hyphae.

Correlation with environmental factors

Monthly changes in hyphal biomass were analyzed through simple and multiple regression. Length (m $g^{-1}$) and weight (mg $g^{-1}$) for each substrate served as dependent variables, and 13 abiotic factors--which except for literfall were derived from temperature and moisture data--served as independent variables (Table I.5).

The 27 hyphal values for litter and soil (top 5 cm) were regressed against abiotic factors separately. Four curve types were fitted in each case: linear ($y = a + bx$), exponential ($y = ae^{bx}$), logarithmic ($y = a + b \ln x$), and power ($y = ax^{b}$). Coefficients of determination ($r^2$) did not exceed 0.39 for any pair tested. Multiple regression equations were generated by the stepwise addition of the Statistical Package for the Social Sciences available at Oregon State University. Each equation contained three to six independent variables.

Two environmental factors, maximum soil moisture and net precipitation, appeared in all four equations and nine of thirteen independent variables were used (Table I.5). The amount of variation accounted for was 41.84 percent (m $g^{-1}$) and 45.81 percent (mg $g^{-1}$) for litter hyphae, 54.92 percent (m $g^{-1}$) and 66.00 percent (mg $g^{-1}$) for soil hyphae. We know of only one other multiple regression analysis of hyphal mass. Dowding and Widden (1974) accounted for 44 percent of the variation in mycelial length in terms of soil moisture, pH and temperature.

Temperature and moisture are most often correlated with changing hyphal mass. Moisture and soil organic matter are highly

correlated, so their separate influence is nearly impossible to determine. Soil moisture (and organic matter) is cited as the primary controlling factor by Soderstrom (1979), Parkinson et al. (1968), Laursen and Miller (1977), and Dowding and Widden (1974). Flanagan and Van Cleve (1977) concluded that temperature was most important in an Alaskan black spruce taiga ecosystem. Bissett and Parkinson (1979b) used multiple regression analyses to determine the variables most affecting distribution and community composition of soil fungi in three Canadian alpine habitats. They concluded that temperature, moisture, available potassium, and soil pH were most important. Nicholas et al. (1965) noted an increase in mycelial production 1-2 months after maximum litterfall followed by rain leaching in England.

Our results indicate that available data cannot produce an adequate model to explain the biomass fluctuations observed. Several possibly confounding elements can be mentioned. First, large standard errors make monthly means difficult to ascertain. Second, the data set of 27 monthly values is too small for the number of independent variables; ideally, each independent variable would be represented by ten data points. Third, as we have noted, measurement of total hyphae does not necessarily indicate production because decomposition and grazing by soil fauna are not taken into account. Also, all possible influencing environmental factors have not been measured--for example, the effect of root exudates on growth of associated mycorrhizal fungi. Finally, a drought during the first year of this study (precipitation 45 percent of normal)

may have drastically altered typical fungal growth patterns. Our results support the view of Dowding and Widden (1974) that relationships between fungal growth and the environment are so complex that analyses of linear relationships are not likely to provide satisfactory explanations. Because fungal species vary greatly in their response to the complex of environmental factors, more useful information may be obtained by study of individual species.

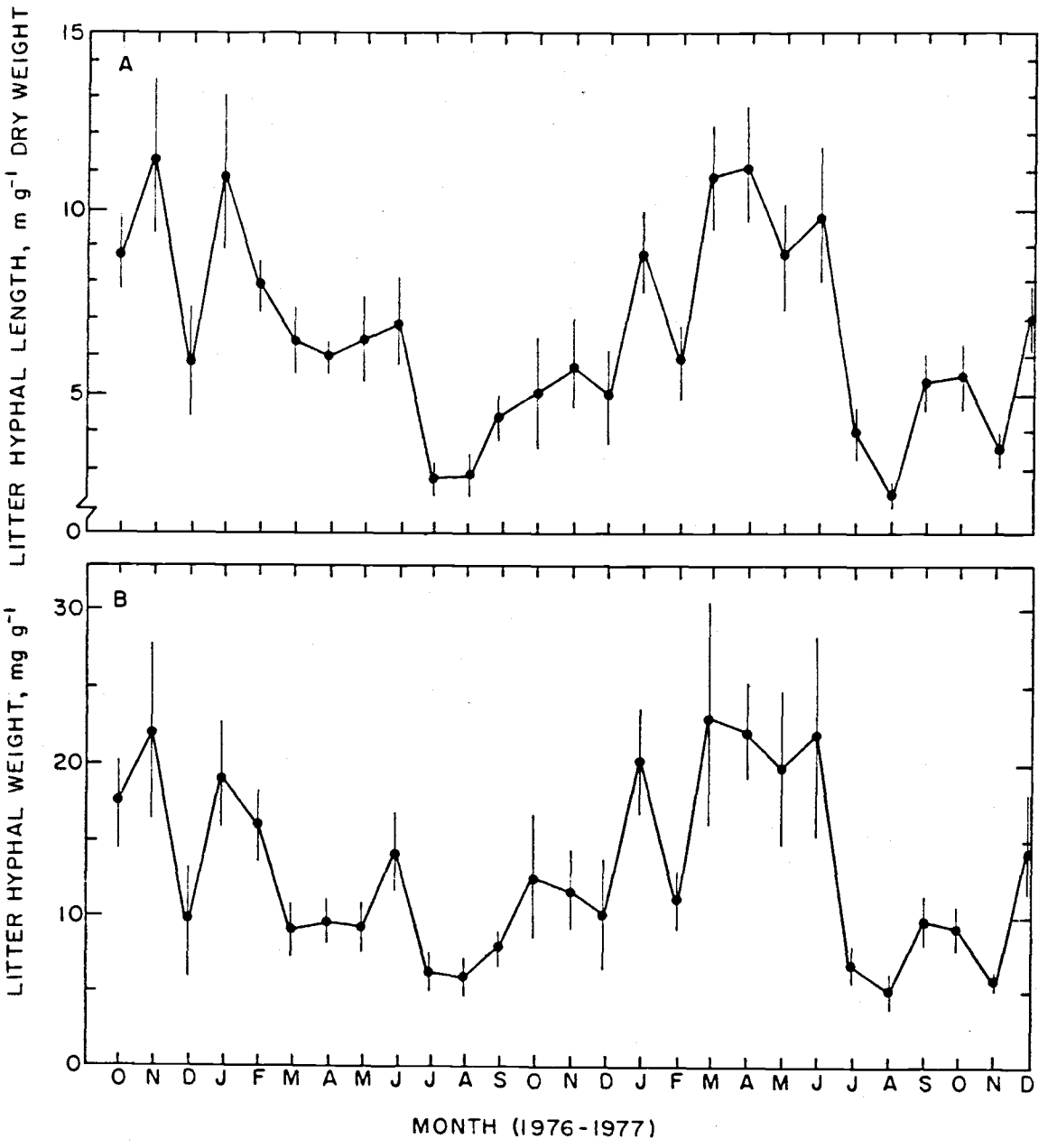


Figure I.1. Total monthly length (A) and weight (B) of hyphae in litter at Dinner Creek, Oregon. Bars indicate standard error of five samples

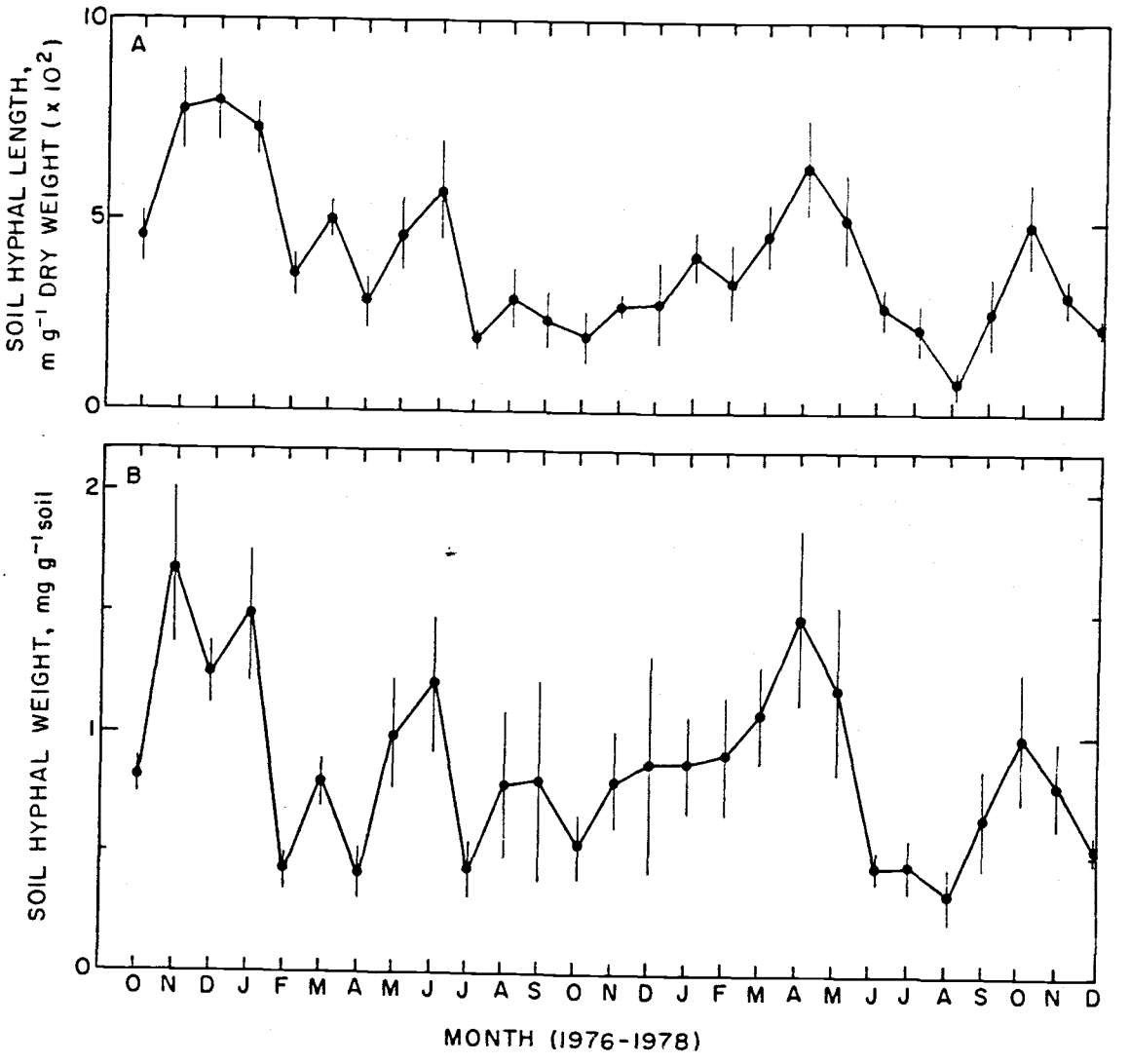


Figure I.2. Total monthly length (A) and weight (B) of hyphae in soil at Dinner Creek, Oregon. Bars indicate standard error of five samples.

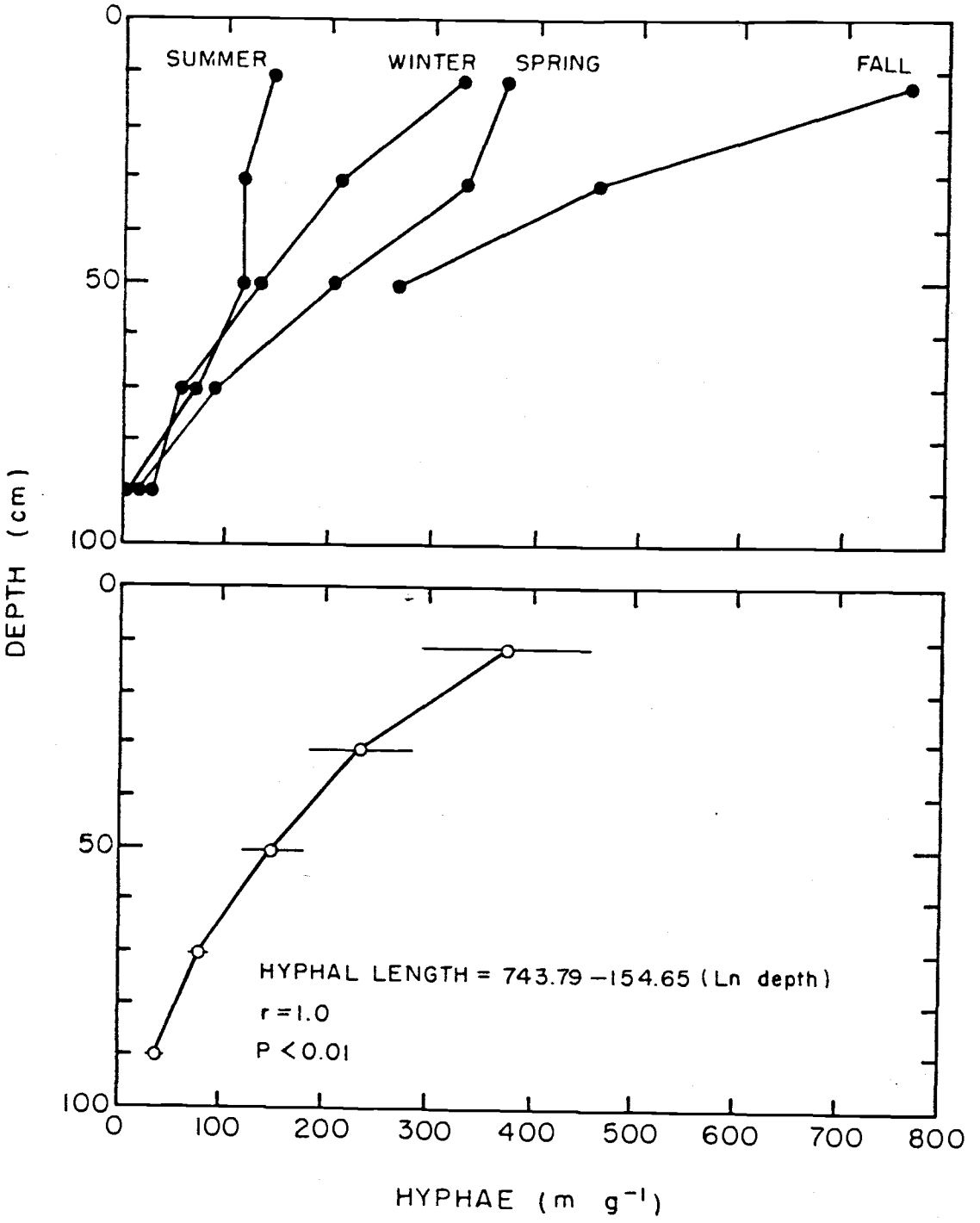


Figure I.3. Seasonal length (top) and mean annual length (bottom) of hyphae at different soil depths at Dinner Creek, Oregon. Horizontal bars are standard error of six samples.

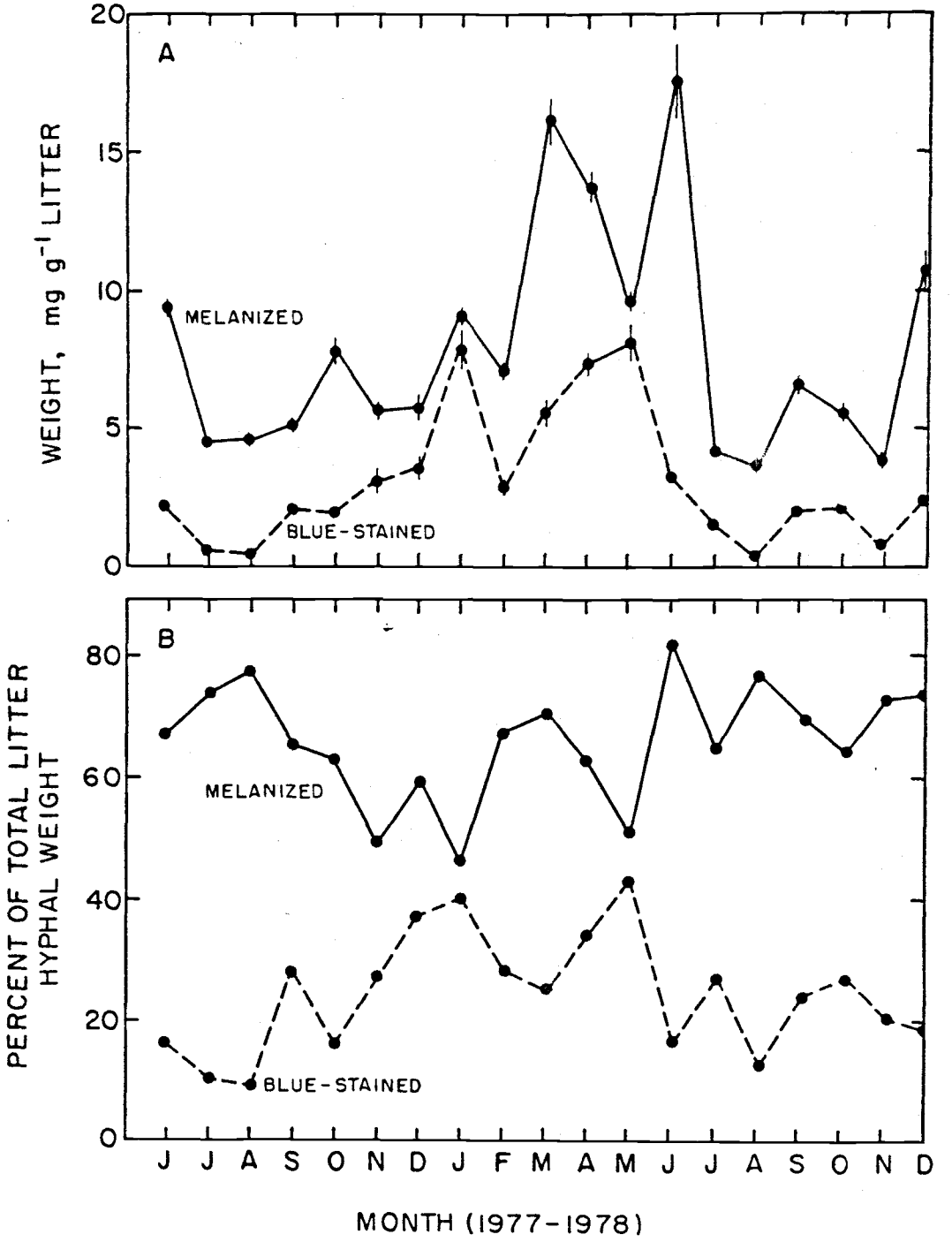


Figure I.4. Monthly weight (A) and percent of total weight (B) of melanized and blue-stained hyphae in litter at Dinner Creek, Oregon. Bars in A indicate standard error; missing bars indicate standard error is <4 percent of the mean.

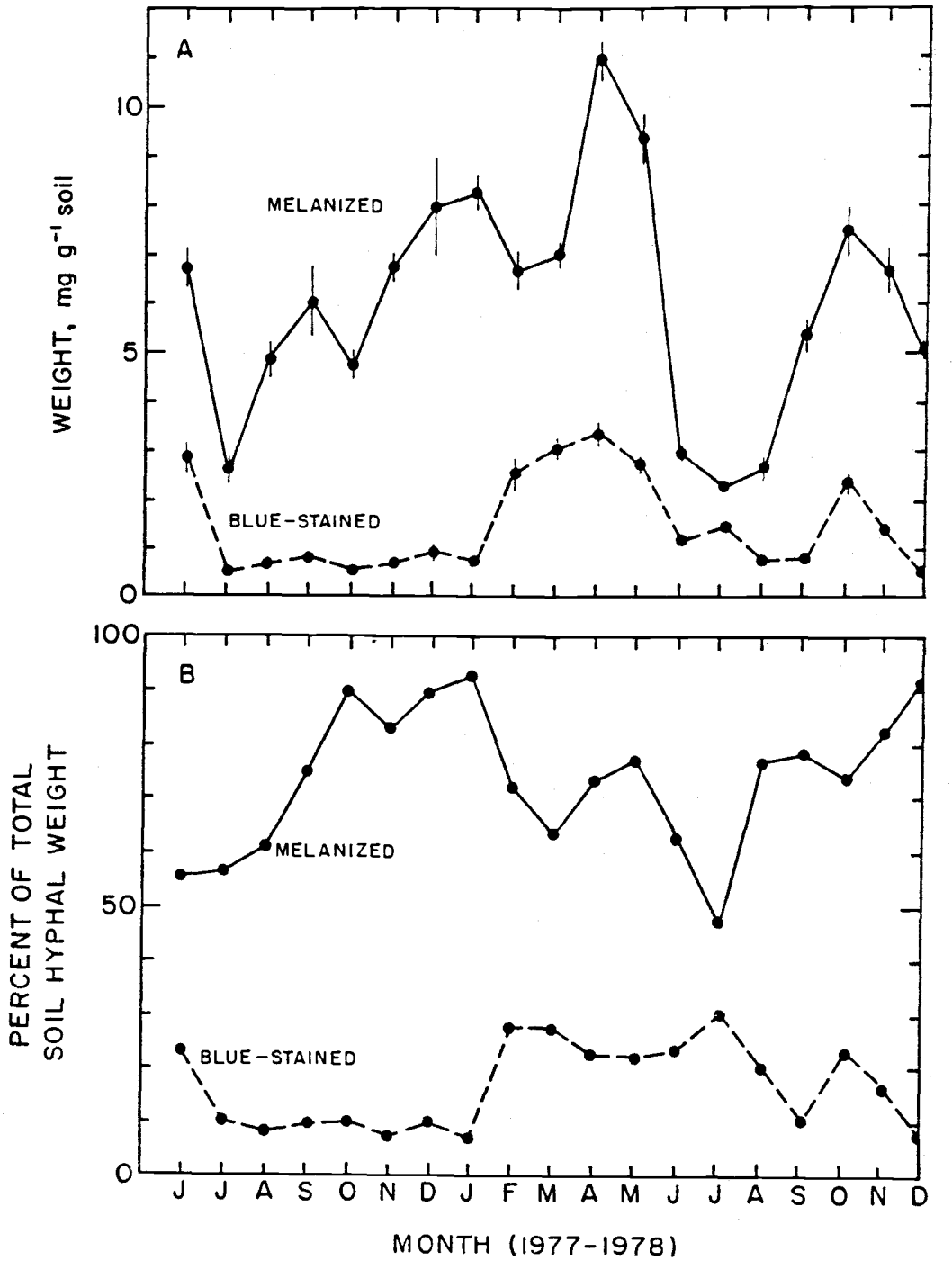


Figure I.5. Monthly weight (A) and percent of total weight (B) of melanized and blue-stained hyphae in litter at Dinner Creek, Oregon. Bars in A indicate standard error; missing bars indicate standard error is <4 percent of the mean.

Table I.1. Soil weight and range in hyphal length and weight in the soil profile at Dinner Creek, Oregon

| Sampling depth | Soil weight ($g\ m^{-2}$) | Hyphal length ($m\ g^{-1}$) | Hyphal weight ($mg\ g^{-1}$) | Hyphal weight ($g\ m^{-2}$)[1] |
|---|---|---|---|---|
| $A_{00}/A_{01}$ | 1903.4 | 2831 - 12,502 | 3.400 - 15.03 | 6.47 - 28.61 |
| $A_1$ 0- 20 cm | $136 \times 10^3$ | 141 - 750 | 0.170 - 0.90 | 23.12 - 122.40 |
| $A_1$ 20- 40 cm | $188 \times 10^3$ | 113 - 456 | 0.136 - 0.55 | 25.57 - 103.40 |
| B 40- 60 cm | $198 \times 10^3$ | 118 - 264 | 0.142 - 0.32 | 28.12 - 63.36 |
| B 60- 80 cm | $164 \times 10^3$ | 69 - 79 | 0.0672 - 0.077 | 11.02 - 12.63 |
| B 80-100 cm | $150 \times 10^3$ | 15 - 38 | 0.0146 - 0.037 | 2.19 - 5.55 |

[1] $g\ m^{-2} \times 10 = kg\ ha^{-1}$

Table I.2. Mean weight and proportion of total weight (% ± SE) of hyphae of three color categories at Dinner Creek, Oregon

| | Blue-stained | | Melanized | | Other | |
|---|---|---|---|---|---|---|
| | ($mg\ g^{-1}$) | (%) | ($mg\ g^{-1}$) | (%) | ($mg\ g^{-1}$) | (%) |
| Litter | 3.3(0.23) | 24.3 | 8.2(0.40) | 66.0 | 1.26(0.43) | 9.7 |
| Soil (top 5 cm) | 0.14(0.01) | 16.7 | 0.6(0.04) | 73.7 | 0.07(0.035) | 9.6 |

Table I.3. Mean diameter and proportion of total mycelial mass (% + SE) of *Cenococcum geophilum* and all other hyphae at Dinner Creek, Oregon

| | Litter | | | Soil | | |
|---|---|---|---|---|---|---|
| | Mean diameter | % volume | % length | Mean diameter | % volume | % length |
| *Cenococcum* | 4.52(0.10) | 23.7(1.7) | 12.4(0.7) | 4.17(0.12) | 29.4(4.0) | 16.4(1.9) |
| Other | 3.01(0.05) | 76.3(7.6) | 87.6(9.6) | 3.04(0.07) | 70.6(7.1) | 83.6(9.2) |

Table I.4a. Mycelial length for some temperate conifer forest sites (highest value from each source[1])

| Horizon | Eastern white pine Canada (1) | Lodgepole pine Canada (1) | Black spruce Canada (2) ($m\ g^{-1}$ dry weight) | Lodgepole pine Canada (3) | Scots pine Sweden (4) | Douglas-fir U.S.A. (4) |
|---|---|---|---|---|---|---|
| $A_{00}$ | | | | | 5,800 | 12,845[2] |
| $A_{01}$ | | | 28,600 | | 18,700 | |
| $A_{02}$ | 210 | 2,699 | | 2,749 | 7,500 | |
| $A_1$ | | | | 2,085 | | 909 |
| $A_2$ | 16 | 351 | | 384 | 650 | |
| B | | 140 | | 159 | 390 | 264 |

[1]Source: (1) Widden and Parkinson (1973); Visser in Baath and Soderstrom (1979a); (3) Widden and Parkinson (1973): (4) Baath and Soderstrom (1979a).

[2]$A_{00}$ and $A_{01}$ combined.

Table I.4b. Hyphal biomass from some temperate coniferous forest sites (highest value from each source[1])

| Horizon | Norway spruce Scots pine Sweden (4) ($mg\ g^{-1}$) | Scots pine Sweden (4) ($mg\ g^{-1}$) | Scots pine Sweden (4) ($g\ m^{-2}$) | Black spruce Alaska (6) ($g\ m^{-2}$) | Aspen Canada (7) ($g\ m^{-2}$) | Douglas-fir U.S.A. (5) ($mg\ g^{-1}$) | Douglas-fir U.S.A. (5) ($g\ m^{-2}$) |
|---|---|---|---|---|---|---|---|
| Organic | 54.4 | 29.3 | 43.4 | 5.7 | 34.0 | 9.2 | 17.5 |
| A | 1.3 | 0.3 | 8.6 | | | 0.82 | 137.2 |
| B | 1.4 | 0.2 | 89.0 | | | 0.33 | 61.4 |

[1]Source: (4) Baath and Soderstrom (1979a); (5) this study; (6) Flanagan and Van Cleve (1977); (7) Visser and Parkinson (1975).

Table I.5. Independent variables made available in multiple regression analyses

| Variables | Explanation |
|---|---|
| For the month | |
| Maximum air temperature | Maximum daily mean |
| [1]Minimum air temperature | Minimum daily mean |
| [1]Mean air temperature | Mean hourly temperature |
| [1]Maximum soil temperature | Maximum daily mean |
| [1]Minimum soil temperature | Minimum daily mean |
| Mean soil temperature | Mean hourly temperature |
| [1]Maximum soil temperature | Maximum weekly sample |
| [1]Minimum soil temperature | Mimimum weekly sample |
| [1]Mean soil moisture | Mean of weekly samples |
| [1]Throughfall | Total (mm) |
| Litterfall | Total dry weight captured (g) |
| [1]Net precipitation | Throughfall minus evaporation |
| For the season | |
| [1]Heat sum | Cumulative sum of mean soil temperatures |

[1]Used at least once in hyphal model equations.

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# CHAPTER II

# SEASONAL HYPOGEOUS SPOROCARP PRODUCTION IN A WESTERN OREGON DOUGLAS-FIR STAND

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## ABSTRACT

Hypogeous fungal sporocarps were collected in randomly located plots over 32 months in a 35- 50-year-old Douglas-fir stand in western Oregon. Nine ascomycete and 21 basidiomycete species were collected during the study. Production was dominated by a few species: taxa accounting for 5 percent or more of total annual dry weight were Gautieria monticola, Hysterangium crassum, H. separabile, and Melanogaster ambiguus. Annual productivity estimates ranged from 5,815 to 6,648 sporocarps $ha^{-1}$ and 2.0 to 3.2 kg dry weight $ha^{-1}$. Peaks in production generally resulted from a large contribution by one or two species. Pronounced seasonal trends in production were not evident, although standing crops decreased in winter. Annual fruiting period varied greatly between different species, ranging from 3 to 11 months.


## INTRODUCTION

Understanding the importance of fungal sporocarp production to forest ecosystems requires quantitative data on species abundance and phenological patterns of fruiting. Such data are needed to establish recognizable and consistent patterns in ectomycorrhizal fungal communities in different ecosystems. Scarcity of quantitative sporocarp data limits our understanding of the contribution by fungi to ecosystem nutrient cycling and their importance as a food resource to mammals and other forest animals.

Recent reports having quantitative data on epigeous (aboveground) sporocarp production include Richardson (1970), Endo (1972), Fogel and Hunt (1979), and Vogt et al. (1981). Earlier studies have been summarized by Lange (1948), and Cooke (1948, 1953). Fogel (1976) published the only quantitative study of belowground (hypogeous) sporocarps, combining data on species composition with estimates of production. He reported hypogeous sporocarp phenology over three years in a 40-65-year-old Douglas-fir stand in western Oregon. Vogt and others (1981) listed production estimates of hypogeous genera for one-year in 23- and 180-year-old Abies amabilis Dougl. (Forbes) stands in western Washington.

We herein present data describing the hypogeous mycoflora and phenological patterns of production over two years and eight months in a young Douglas-fir stand. Our data complement those of Fogel (1976) and, together, the two studies characterize the hypogeous fungal community of this young Douglas-fir forest type to a degree unattained for any other ecosystem.

## MATERIALS AND METHODS

### The site

The study site is located 14 km west of Philomath, Oregon (R7W, T12S) at an elevation of 381 m on the north side of Mary's Peak. Aspect is north and slope averages 40 percent.

The climate is characterized by mild winters and warm, dry summers (mean air temperature of 2.7 and 18.5°C in January and July, respectively). Annual precipitation averages 1905 mm; the occasional winter snowfall is seldom heavy. Neither temperature or precipitation patterns deviated substantially from normal during the study.

The stand is a second-generation (36-50 years old) Douglas-fir (Pseudotsuga menziesii) (Mirb.) Franco.) forest established after clear-cutting. The 600 live trees per hectare have a basal area of 60.5 $m^2$ $ha^{-1}$ and a bole volume of 808.8 $m^3$ $ha^{-1}$. Other tree species are scattered: red alder (Alnus rubra Bong.), western hemlock (Tsuga heterophylla (Raf.) Sarg.), and western red cedar (Thuja plicata Donn.). The patchy understory (resulting from openings caused by Phellinus weirii (Murr.) Gilb. root rot of Douglas-fir) consists of vine maple (Acer circinatum Pursh), Oregon grape (Berberis nervosa Pursh), Sword fern (Polystichum munitum (Kaulf.) Persl.), and bracken fern (Pteridium aquilinum (L.) Kuhn.). Fallen trees and stumps greater than 12.7 cm diam comprise a volume of 151 $m^3$ $ha^{-1}$ and debris between 2.5 and 12.7 cm diam was estimated (2 percent sample) to be 37.3 $m^3$ $ha^{-1}$.

The Slickrock gravelly loam soil of the site is a deep (100-150 cm to bedrock), well-drained colluvium soil weathered from sandstone (Knezevich 1975). Surface organic layers ($A_{00}$, $A_{01}$) are moderately well developed (averaging 3.2 cm in depth) and are associated with moss over most of the site. The $A_{02}$ (humus) layer is well mixed (mull humus type) with surface mineral soil by the activity of earthworms and microarthropods. The A horizon (the zone

of maximum rooting) extends to a depth of 15 cm and is friable, slightly sticky, and contains 20 percent fine pebbles. Both organic and mineral horizons are strongly acid ranging from pH 5.5 to 5.7.

Sampling and specimen processing

Monthly production was estimated from 12 randomly located 4 $m^2$ quadrats sampled without replacement. Litter was completely removed from each plot and the mineral soil turned to a depth of 5-10 cm with a rake. Sporocarps present were placed in waxed-paper bags for transport to the laboratory. A soft brush was used to remove adhering soil from sporocarps. Specimens were cut in half and dried in a forced-air oven at 60°C for 48 h; dry weight of each collection was then recorded.

## RESULTS

Eight ascomycete and 18 basidiomycete species were collected during the first two years of the study (Table II.1). Four more species (1 ascomycete, 3 basidiomycetes) were found during eight additional months of collecting: *Genea harknessii* Gilkey, *Rhizopogon colossus* A. H. Smith, *Rhizopogon hawkeri* A. H. Smith, and *Zelleromyces gilkeyae* Sing. and Smith. Genera represented by the most species were *Rhizopogon* with six species, and *Tuber* and *Hysterangium*, each with five. The single collection of *Tuber* sp. in year 1 was too immature for identification. Four undescribed

species were collected: one Tuber, one Rhizopogon, and two species of Hysterangium. One collection each of Hymenogaster and Martellia could not be identified to described species; further investigation is needed to determine if they are undescribed.

Number of sporocarps collected monthly ranged from 625 (November 1981) to 16,664 per hectare (April 1982) while monthly biomass ranged between 0.15 (November 1981) and 17.5 (October 1980) kg dry weight $ha^{-1}$ (Fig. II.1). Annual productivity estimates (Table II.1) ranged from 5,815 to 6,648 sporocarps $ha^{-1}$ and 2.0 to 3.2 kg dry weight $ha^{-1}$. Sporocarp number and weight fluctuated greatly between consecutive sample dates throughout the study. Numbers remained relatively constant during only two periods: September through December 1981 and September through December 1982. Biomass fluctuated little over the last 15 sample dates. Peaks in production frequently resulted from a large contribution by one or two species, most often Hysterangium crassum, H. separabile, or Gautieria monticola. For example, 53 percent of the 65 sporocarps collected for September 1980 were Hysterangium crassum. Hysterangium crassum and H. separabile were the only species collected in April 1982 when the highest number (80) of sporocarps were collected. October 1980, and June and July 1981 had higher biomass production than other months of the study. For these months, Gautieria monticola composed 89 percent, 70 percent, and 57 percent, respectively, of monthly production. Neither weight or number of hypogeous sporocarps showed the distinct seasonal peaks characteristic of epigeous sporocarps (Fig. II.1), but a decrease in number and weight of hypogeous sporocarps occurred each winter.

Correlation between number and weight of sporocarps is low, reflecting the high variability of mean sporocarp dry weight both between and within species (Table II.1). The correlation coefficient of determination ($r^2$) was 0.15 for number and weight data over the entire study.

Species contributing five percent or more to total annual weight or sporocarp number (Table II.2) were considered major species (Hering 1966). Biomass of Hysterangium crassum was surpassed the first year by Gautieria monticola, but was highest in year 2, contributing 40.4 percent of annual production. The high value for Gautieria monticola in year 1 resulted largely from one month of high biomass (October 1980). Number of major species are few (7 in year 1, 4 in year 2), but compose a high percentage of annual production; percentage by weight ranged from 77.6 to 91.3.

Seasonal productivity on individual species (Table II.3) can be examined by obtaining middates of fruiting from the formula

$$m = (d(n)/N)$$

where m is the midpoint in days after the starting point, n is the number or weight of sporocarps collected d days after the starting point and N is the total number or weight recorded. Average middates for spring (March-June) and fall (September-December) peaks were 16 April and 12 October, respectively. Individual species middates generally did not differ more than 7 wks between years except for Hysterangium crassum and Melanogaster ambiguus. Hysterangium crassum and H. separabile appear to be capable of fruiting any month while others are restricted to fall (e.g.,

Truncocolumella citrina) or spring (e.g., Barssia oregonensis). Sporocarp number and biomass were greater in spring than in fall for 1981 and 1982 (Fig. II.1, Table II.9). Average middate for all ascomycetes (12 July) compared to all basidiomycetes (2 August) did not differ significantly ($P > 0.05$).

The species-area curve for our study (Fig. II.2) shows species number was still increasing at the end of the study. Twenty species were collected by the end of year one, 26 species after two years, and 30 by the end of the study.

## DISCUSSION

### Sampling considerations

Sampling hypogeous sporocarps presents problems not encountered in sampling aboveground components of plant communities, because sporocarp populations are ephemeral and constantly change both quantitatively and qualitatively. No good method for predicting sporocarp location is known. In addition, individuals are typically distributed in clusters rather than homogeneously. Fogel (1976, 1981) described three types of sporocarp clustering occurring in the Oregon Coast Range. Stand size may limit sample size because quadrats cannot be resampled during a study. New quadrats are required each sampling date because harvesting by raking disturbs litter layers and surface mineral soil.

While no absolutely objective guide exists for establishing sample size or number, a "minimal area" quadrat size (i.e., the smallest area on which species composition of a community can be adequately represented) can be estimated from a species-area curve (Mueller-Dombois and Ellenberg 1974). Cain's method (in Mueller-Dumbois and Ellenberg 1974), for example, establishes a point on the curve at which an increase of 10 percent in total sample area yields 10 percent more species of the total recorded for the study; this is a sample of 509 $m^2$ for our stand. Another method is to set an objective standard based on total number of species collected and require the sample quadrat to contain 95 percent of that number. From our species-area curve, this is 1402 $m^2$. While these methods can be used as general guides to establishing sample size, technically they cannot be applied to sampling hypogeous sporocarps because two basic criteria are not met. Minimal area can only be determined in communities which are not fragmented (i.e., not lacking species usually present in the recurring assemblage) and are relatively homogeneous in distribution (Mueller-Dombois and Ellenberg 1974). Moreover, only species-area curves that level off can be used for minimal area determination. Thus, for hypogeous sporocarps, sample area and quadrat size are determined by what is practical and manageable given stand size, stand composition, and time limitations. Consequently, our relatively small sample of 48 $m^2$/mo sample may underestimate sporocarp production. Because sampling of hypogeous fungi requires considerable time and area, data sets can seldom meet the

assumptions for standard statistical procedures. Data reported by Fogel (1981) suggest that larger quadrats are better to quantify biomass or numbers, while a large number of smaller quadrats is best for documenting species number. Because many hypogeous fungi do not fruit every year and some may fruit only once in five or ten years, collecting over extended time may be more important than the area sampled.

Large biomass fluctuation between monthly samples partly reflects sampling technique but also expresses the highly variable spatial and temporal distribution of sporocarps. Rapid biomass decreases can result from senescence influenced by weather conditions or harvesting by mammals. Biomass peaks are most often attributable to one or two species. Documenting the occurrence of biomass peaks and low points could be improved with information on sporocarp longevity. While no studies of longevity have been reported, our field observations and herbarium data show high variability between species. Most ascomycetes have a longer period of maturation than basidiomycetes. Tuber gibbosum, for example, typically first appears in October, when most specimens are immature, having little odor and a pale gleba. Maturation continues over four to five months; most collections from late December and January are fully mature with noticeable odor and gleba dark from matured spores. Sporocarps of the ascomycete Elaphomyces (not collected in this study, but occurring in the Coast Range) probably last many months because they have a thick, firm peridium and mature slowly (Trappe 1976). The basidiomycete Truncocolumella citrina, by

contrast, is much more ephemeral. Fully mature and senescent specimens can be found within two weeks after fruiting begins. While sporocarps of most basidiomycete species in the Oregon Coast Range may last about a month, a few species probably last much longer. Sporocarps of Hysterangium crassum and Gautieria monticola, major species both years of our study (Table II.7), are associated with dense rhizomorph mats (Cromack et al. 1979) that are hydrophobic and may protect sporocarps from high moisture levels reached in adjacent soil.

Variation between samples might be reduced by sampling twice monthly or stratifying samples. Occasionally, a large biomass change occurs in a short time that may be missed by monthly sampling. Fogel (1976) found a decrease form 3.9 to 0.1 kg $ha^{-1}$ in samples taken 17 days apart during December. Samples could be stratified to reflect microhabitat variation in a stand. For example, habitats such as drainages, open spaces, or areas adjacent to woody debris could be sampled systematically and compared.

Peaks in biomass frequently result from "blooms" of one species. The large crop of Gautieria monticola in October 1980, for example, (89 percent of October biomass) resulted in that month contributing 49 percent of total annual production. Without this large fruiting, October would have had 29.5 percent of the annual production. Fogel and Hunt collected 78.1 g dry weight/100 $m^2$ (201 sporocarps) of Truncocolumella citrina in November 1976 from a Douglas-fir stand at Dinner Creek, 3 km from our site. This sample comprised 35 percent of the total hypogeous sporocarp biomass for the year.

Comparison of taxa

Similarity of taxa between two stands can be examined by calculation of the Jaccard Similarity Coefficient, s (Janson and Vegelius 1981):

$$s = a/a + b + c$$

where a is the number of taxa in common to both stands, b the number of taxa in stand one but not in stand two, and c, the number in stand two but not one. Multiplying s x 100 gives the percentage of taxa in common to two stands.

Species data are available from two other studies conducted longer than one year (Fogel 1976, Fogel and Hunt unpublished data 1978). Fogel found 24 species (11 ascomycetes, 13 basidiomycetes) over three years of monthly collecting in a Douglas-fir stand located 250 m from our site. Because our stand and that of Fogel have a comparable environment and are of similar age and composition, our study can be considered an extension of his and the total data applicable to this Douglas-fir habitat type. The combined species list totals 36 (13 ascomycetes, 23 basidiomycetes) representing five years and eight months of study. Our species-area curve (Fig. II.2) did not reach a stable plateau during this study, indicating that not all species were recorded. Inability to document all species is not unique to mycologists and occurs in ecosystem level taxonomic studies of most all organism groups. So long as sampling methods are standardized, however, it is generally valid to compare species lists from different locations and studies.

Available data permit comparison of species occurrence in three stands on Mary's Peak by use of the Jaccard Similarity Coefficient. The three stands can be considered as two pairs; the two north side stands on Woods Creek (ours and Fogel's (1976)) and the second pair consisting of our stand and the Dinner Creek stand on the south side of Mary's Peak (Fogel and Hunt 1979). Our Woods Creek stand was not far from Fogel's and the two resembled each other much more closely than either resembled the Dinner Creek stand in overall habitat and structure. Thus we hypothesized that the hypogeous mycota of our stand was more like that of Fogel's Woods Creek stand than that of Dinner Creek. A comparison of the mean percentages of total taxa in common and major taxa in common shows some trend in support of the hypothesis (Table II.4).

Similarity of total and major species between the Woods Creek stands is lower than expected. High year-to-year variability in sporocarp abundance appears to explain differences in major species between the two stands (Table II.5). Consequently, a species may dominate production one year and be of little consequence other years. For example, five species of ascomycetes were among major producers during Fogel's study, but no ascomycetes were major species during our study. The pattern of occasional fruiting exhibited by numerous species suggests one reason why lists of total species for the two stands are dissimilar. Of thirteen species not shared by the two stands, ten fruited once in three years. Hysterangium occidentale Harkn. is an example of a species which fruits rarely. Only two collections of this species have been

recorded from the Coast Range, one obtained in 1966 by J. Trappe on the north side of Mary's Peak and the second collected by Fogel (1976). Fruiting periodicity data indicate that long term studies are essential to documenting species occurrence, even in small stands.

Fruiting periodicity is controlled by numerous factors (Fig. II.3) including conditions of the general environment as well as those of microhabitats. Although the general environment of the Woods Creek stands is similar, differing climatic conditions during the two studies may have contributed to differences in mycota. Fogel's site is less steep than ours and has a northwest aspect, conditions that would make his site dryer and influence microhabitat conditions important to fruiting.

The alternative explanation for dissimilarity in species between the Woods Creek stands is that the mycotas may actually be dissimilar and continued sampling would not result in highly similar species lists. This would imply that some species are restricted to narrowly defined microhabitats and are not readily established away from these areas. Moreover, it suggests a danger in generalizing research results from one stand to others even though sites are generally similar.

Major differences in the hypogeous mycota exist between our north-facing stand and the south-facing Dinner Creek stand. Fewer species were found at Dinner Creek, 15 in total (one ascomycete, 14 basidiomycetes) over 27 months of collecting (see Appendix). Monthly sample size at Dinner Creek was 100 $m^2$. Major species

differed greatly between the two stands (Table II.4): none were in common for major species by weight and only one (Truncocolumella citrina) of nine was the same for major species by number. Leucogaster rubescens Zeller and Dodge and Leucophleps magnata Harkn. (Fogel 1979) occurred abundantly (major species both years) at Dinner Creek, but were absent at our site. Herbarium records indicate that these genera have not been collected from the north side of Mary's Peak. The two stands have major differences that could influence species composition and production. Amount of precipitation is similar (about 1900 mm mean/yr) but was substantially below normal (848 mm) the first year of the Dinner Creek study. While soils are similar at both sites (gravelly loam; 18-20 percent pebbles) soil moisture is lower at Dinner Creek due to the south aspect and scant litter layer.

Few studies have documented species of hypogeous fungi in forests and none have compared epigeous and hypogeous species in one stand. States (1983, 1984) has recorded six ascomycetes and 18 basidiomycetes to date in an ongoing study of pure and mixed stands of Pinus ponderosa (Laws.) in Arizona. Over two years of spring and fall sampling, Hunt and Luoma (unpublished data 1984) have collected nine species of ascomycetes and 36 basidiomycetes from ten stands representing a range of age classes and moisture conditions. These are mixed conifer stands dominated by Douglas-fir in the central Oregon Cascades. Terwilliger (1985) collected seven ascomycetes and 15 basidiomycetes over four months of sampling in an Abies grandis (Dougl.) Lindl. dominated stand (1463 m elev.) in western Idaho.

Number of aboveground (epigeous) mushroom species is probably greater than hypogeous species in a given area, but this requires confirmation. Because all hypogeous species are probably ectomycorrhizal (Trappe and Maser 1977, Miller 1983) comparison to epigeous ectomycorrhizal species is the most meaningful. Maas and Stuntz (1970) reported 134 epigeous species from a mixed conifer (Pseudotsuga, Abies, Pinus) stand on serpentine soil in the Washington Cascades. Of these, 22 (16 percent) were putative ectomycorrhizal species (Trappe 1962a). Twelve of 28 (43 percent) epigeous species from a Scots pine stand in Scotland listed by Richardson (1970) were presumably mycorrhizal. Vogt and others (1981) reported numbers of epigeous species and hypogeous genera from two stands of Abies amabilis (Dougl.) Forbes in central Washington. During six months of collecting they recorded 48 epigeous species and two hypogeous genera (Rhizopogon and Genea) in a 23-year-old stand and 50 epigeous species and one hypogeous genus (Elaphomyces) from a 180-year-old stand. Fogel (1981) reviews fungal taxa lists from studies in Europe and Japan.

Evidence indicates that diversity of putative ectomycorrhizal epigeous and hypogeous species increases with stand age. This suggests that fungal succession proceeds toward increased diversity as host trees mature, at least up to a point. Studies of epigeous fungi conducted by Miller (1983) in western white pine (Pinus monticola Dougl. ex D. Don) revealed five, 37, and 78 putative ectomycorrhizal species in 15, 30-40, and 175-215 year-old stands, repectively. Hunt and Trappe (unpublished data 1983) have

identified one hypogeous species from five-year-old clear-cut and planted stands, 13 species from 85 year-old stands, and 15 and 32 species from 120 and 250 year-old stands, respectively, after two seasons of collecting in stands dominated by Douglas-fir. While reasons for increased fungal species diversity with stand age remain to be enumerated, data suggest several possible influencing factors. Specificity between some ectomycorrhizal fungi and their hosts is well documented although little is known about mechanisms of recognition between compatable partners (Molina 1981). For example, Alnus and its ectomycorrhizal fungi are strongly specific. This specialization may limit species of ectomycorrhizal fungi on sites dominated by alder (Molina 1981). Competition among ectomycorrhizal fungi for root colonization sites may influence fungal species composition in a stand, but this is not known. Fine root biomass varies with stand age (Karizume 1968; Persson 1978, 1980; Grier et al. 1981; Vogt et al. 1981) and productivity (Vogt et al. 1983). Vogt and others (1983) found that fine root biomass in Abies amabilis reached maximum near the time of canopy closure (stands 40-70 years old) and thereafter decreased substantially in more productive stands (site class II). Less productive sites (nutrient poor, site class IV) showed a decrease in fine root biomass after canopy closure, but maintained significantly higher fine root mass compared to class II sites. The authors attribute these biomass differences to lower nutrient availability in low site quality stands, a condition requiring more roots to obtain adequate nutrients. Growing evidence indicates that succession in higher

plant communities is not the driving force of ectomycorrhizal succession but that fungi, by influencing interactions between roots of plants, may act as agents of changing ecosystem structure (Bowen 1980, Janos 1985, Perry 1985).

Success of ectomycorrhizal fungi on a particular site is influenced by numerous factors including competition with other ectomycorrhizal fungi (Perry 1985), light and temperature (Pilz and Perry 1984), soil-litter chemistry (Handley 1963, Shoenberger and Perry 1982, Rose et al. 1983, Gardner and Malajczuk 1985), and site productivity and disturbance (Shoenberger and Perry 1982, Pilz and Perry 1984, Perry 1985). Growth of ectomycorrhizal fungi in pure culture may be stimulated, suppressed, or unchanged by presence of litter leachates, the response depending on species of fungus, litter type, and leachate concentration (Rose et al. 1983). Buildup of litter and consequent biochemical changes may alter types of fungi present (Gardner and Malajczuk 1985) and produce stratified rooting zones in litter, humus layers, and mineral soil (Cole 1981). Trappe (1962b) found that Cenococcum geophilum becomes increasingly dominant in sites with increasing hazard of temperature or moisture stress. In addition, ectomycorrhizal fungi may alter their own biochemical environment by influencing foliage terpene concentration (Perry 1985).

Diversity and stability of ectomycorrhizal communities in the Oregon Cascades are influenced by degree and type of disturbance resulting from differing logging practices (Schoenberger and Perry 1982, Pilz and Perry 1984, Perry 1985). Soil structure probably

influences distribution of some fungal species. Our observations of species that produce abundant rhizomorphs (e.g., Hysterangium crassum and Gautieria monticola) indicate that they occur more commonly in loose clay loam soil than in compact or heavy clay soil.

Individual trees and whole ecosystems undergo various changes as they progress from juvenile to mature and finally to senescence (Bormann and Likens 1979, Kramer and Kozlowski 1979). As trees age, orderly and progressively degradative physiological changes occur (Kramer and Kozlowski 1979) and may directly or indirectly influence ectomycorrhizal symbionts. Changes in food, water, mineral, and hormonal relations resulting from declining photosynthetic output and increased respiration from accumulating sapwood contribute to a metabolic shift. Decreasing metabolism results in declining rates of shoot, cambial,and root growth and decreasing annual dry weight increment. Successional changes in ecosystems may be related to a successional sequence of ectomycorrhizal fungi (Mason et al. 1983). It is logical to assume that changes in fungal species richness would occur as ecosystems pass through major structural changes. Major stages in stand development, by increasing age, have been named (Bormann and Likens 1979): "Reorganization," "Aggradation," "Transition," and "Shifting-Mosaic Steady State." Because different ectomycorrhizal species are adapted to different conditions (Perry 1985), it follows that increased habitat diversity would increase species richness. Habitat diversity remains fairly low during Aggradation, the stage of relatively even-aged trees, low plant species diversity, and uniform environmental conditions. Habitat

diversity increases as dominants fall and openings are created (Transition stage). Greatest habitat diversity occurs during the attainment of the Shifting-Mosaic Steady State which is characterized as an array of irregular forest patches composed of relatively diverse vegetation of different ages, well developed litter layers, and abundant woody debris. Richness of ectomycorrhizal species probably peaks in forests of this type.

Ecosystem development from young to mature stages gives rise to the hypothesis that young stands favor ectomycorrhizal fungi (and vascular plants) with high growth and reproductive potential, those species better adapted to disturbance and comparatively rapidly changing environmental conditions ("r" selection). More mature stages of ecosystem development would favor species ("K" selection) having lower growth and reproductive potential but with higher capability of competitive survival in older, "fully occupied" forests (Odum 1969, Bormann and Likens 1979, Grime 1979). Whether this range of "strategies" actually exists within ectomycorrhizal fungi is unexplored.

## Production

Estimates of net hypogeous sporocarp production are not possible because losses cannot be measured. Biomass losses occur from decompositon, grazing by soil fauna, and consumption by mammals (mycophagy). Consequently, production values are obtained by summing totals or calculating means from sample plots. Estimates of annual production can be derived by three methods: (1) by

converting monthly standing crops (biomass or sporocarp number) to a hectare basis and summing all months for the year, (2) by accumulating monthly standing crops (grams or number collected) and the area sampled for all months and converting to a hectare basis at years end, and (3) by calculating the mean of monthly standing crops (kg $ha^{-1}$) for the year.

Calculating monthly standing crops of sporocarps by averaging individual plot values or deriving annual production as a mean of monthly standing crops is of limited use because variation is typically high and significant differences between means are seldom evident. Method one is the most commonly used of the three, but probably gives an overestimate of production in most cases. Use of method one assumes that the sporocarp population is completely replaced each sampling period, probably an uncommon occurrence. The equivalent annual totals per hectare in Table II.1 were derived by method two, which gives a lower annual production value compared to method one. In year one of our study, for example, method one results in a production of 35.4 kg $ha^{-1}$ $yr^{-1}$ (Table II.6) and method two, 3.2 kg $ha^{-1}$ $yr^{-1}$. We feel method one overestimates production in our stand because longevity of highly productive Hysterangium and Gautieria species likely exceeds one month.

Available estimates of hypogeous sporocarp standing crops and production (Table II.6) range from 1.4 to 142 kg $ha^{-1}$ for single sample estimates and 22 to 380 kg $ha^{-1}$ $yr^{-1}$ for annual production (calculated as a sum of monthly kg $ha^{-1}$). Annual production in Douglas-fir ranges from 24 to 43.9 kg $ha^{-1}$ $yr^{-1}$.

The high value for Pacific Silver fir (Vogt et al. 1981) is probably due to two factors. Elaphomyces, the only hypogeous taxon collected in their 180-year-old stand, produces exceptionally heavy sporocarps. Data from the Oregon Cascades show that mean sporocarp dry weight of Elaphomyces granulatus was 1.12 g compared to 0.37 g for all other species combined (Hunt unpublished data 1983). In addition, the authors calculated annual production as a sum of monthly crops (method one above) which probably substantially overestimates production of these long-lived sporocarps.

Maximum standing crops of sporocarps produced by hypogeous species compared to epigeous mycorrhizal species (Table II.7) were similar in range. Peak monthly biomass over three years ranged from 3.2 to 17.5 kg $ha^{-1}$ and 8.7 to 19.6 for hypogeous and epigeous sporocarps, respectively. However, large differences in biomass occurred between hypogeous and epigeous mycorrhizal species during two of three years (Table II.7). Available data show that hypogeous sporocarp biomass can peak any month from May to November, but epigeous sporocarps consistently reach maximum only during fall months (October to December). Peak production in biomass of hypogeous sporocarps occurred in July or October in our study but maxima for epigeous sporocarps (Table II.7) were always in fall (October or November). Biomass of hypogeous and epigeous mycorrhizal sporocarps peaked (10.1 and 16.8 kg $ha^{-1}$, respectively) during November in the first year of a study by Fogel and Hunt (1979, and unpublished data 1978) but hypogeous sporocarps peaked in August (2.7 kg $ha^{-1}$) and epigeous in October (33.4 kg

$ha^{-1}$ during year two. Hypogeous sporocarp biomass peaked in May during two of three years and in June one year during Fogel's (1976) study. Large differences in peak standing crops between epigeous and hypogeous sporocarps in the same year were found by Fogel and Hunt (unpublished data 1978). In 1977, for example, maximum monthly standing crop of hypogeous sporocarps was 2.7 kg $ha^{-1}$ (August) whereas sporocarps of epigeous mycorrhizal species peaked at 33.4 kg $ha^{-1}$ in October. In contrast, peak sporocarp standing crops of hypogeous and epigeous mycorrhizal species were similar in the first year of the Fogel and Hunt (1979) study when maxima were 10.1 and 16.8 kg $ha^{-1}$, respectively, both occurring in November.

Comparison of annual epigeous and hypogeous sporocarp production (Table II.8) shows high variablity. Biomass of hypogeous sporocarps was greater than the weight of epigeous mycorrhizal species both years of our study; 76 and 18 percent greater for year one and two, respectively. By contrast, weight of epigeous mycorrhizal species was substantially higher than hypogeous (48 and 633 percent higher for year one and two, respectively) during a study by Fogel and Hunt (1983). The large decrease in hypogeous sporocarp production (from 21.1 to 6.2 kg $ha^{-1}$) during the second year of that study may reflect the abnormally dry year preceeding this drop (rainfall was 45 percent of normal), however weight of both total and mycorrhizal species of epigeous sporocarps increased modestly the year following the drought (Table II.8).

Most available data indicate that a substantial majority of epigeous sporocarp biomass results from mycorrhizal species. Of the

total epigeous sporocarp biomass in our study (Table II.8), 71.1 to 79.7 percent resulted from mycorrhizal species. This compares with a range of 73.7 to 96.3 percent recorded by Fogel and Hunt (unpublished data 1978). Vogt and others (1981) reported that in two stands of Abies amabalis, 71 percent (23-year-old stand) and 87 percent (180-year-old stand) of epigeous sporocarp dry weight was produced by mycorrhizal fungi. Of the total epigeous sporocarp biomass (16-30 kg $ha^{-1}$ $yr^{-1}$) reported by Richardson (1970), over half (9.8-19.4 kg $ha^{-1}$ $yr^{-1}$) resulted from mycorrhizal species.

## Seasonality

The relationship of sporocarp production to temperature and precipitation seems empirical, but clearly many other factors affect fruiting (Fig. II.3). Major factors likely to influence seasonal abundance of sporocarps include energy and nutrient reserves of host plants and mycelium (Krueger and Trappe 1967), mycophagy, and physiological interactions of the mycorrhizal association (Hatch 1937, Handley and Sanders 1962). Fogel (1976) found that spring and fall peaks in hypogeous sporocarp production were associated with temperature and precipitation patterns. Production in spring seemed dependent on temperature and began when mean minimum air temperature exceeded 0°C (6°C mean maximum temperature). Production ceased when mean minimum and maximum air temperature reached 6°C and 23°C, respectively, which occurred after precipitation dropped below 5 cm $month^{-1}$ and evaporative demand was relatively high. Fall production began when precipitation was at least 0.5 cm $month^{-1}$

and increased until mean minimum air temperature dropped to 4°C (18°C mean maximum). Although Fogel (1981) found significant linear correlations between sporocarp biomass and temperature, and biomass with temperature plus precipitation, $r^2$ values did not exceed 0.685.

Hypogeous sporocarp production in our study was not well defined seasonally compared to epigeous sporocarps (Fig. II.1). Epigeous sporocarps showed a consistent fall peak in October, November, or December, followed by rapid decline and low production through spring, reaching zero (or nearly so) in summer. No epigeous sporocarps appeared in 13 of 30 months (43.3 percent). Production of hypogeous sporocarps, in contrast, was more uniform. Production showed no seasonal peaks and never reached zero at any sample month. Data collected by Fogel and Hunt (1979, unpublished data 1978) showed a similar trend; epigeous sporocarp production was zero during 41.4 percent of sample months (12 of 29 months) compared to 7.4 percent of (2 of 27 months) for hypogeous sporocarps. Greater uniformity in monthly production by hypogeous fungi compared to epigeous is partly because some hypogeous species fruit consistently during winter, summer, or both seasons. Hymenogaster parksii (Table II.3), for example, is a winter and early spring fruiting species in the coast range. Leucogaster rubescens can fruit any season (Fogel and Hunt unpublished data 1979), but is often present during the driest months (July-September). Three species common on our site (Gautieria monticola, Hysterangium crassum, H. separabile) appear to be fruiting "opportunists" and capable of fruiting any month. They

produce dense rhizomorph mats that not only modify the physical and chemical soil environment (Cromack et al. 1979), but may store substantial amounts of nutrients and energy that can be relatively quickly mobilized for sporocarp production. In contrast, Truncocolumella citrina, a species having a very restricted fruiting period (Table II.3) produces little if any supporting rhizomorph network so that fruiting may depend on a flux of nutrients or other materials from host trees.

Our data on fruiting periods for common hypogeous species (Table II.3) can be extended with results obtained by Fogel (1976). Tuber murinum, for example, fruited from May to September during our study and from February to July during Fogel's study. Thus, the documented occurrence for this species is February to September in these adjacent stands. Fruiting periods for five additional species (Barssia oregonensis, Hymenogaster parksii, Hysterangium crassum, H. separabile, and Truncocolumella citrina) were likewise extended by Fogel's data.

Calculation of fruiting middate for a species over a number of years indicates consistency of fruiting habit. For five years (combining our data with that of Fogel (1976)), the middate of fruiting for Hysterangium separabile was in April, even though the fruiting period extends all year for this species. Fruiting of Truncocolumella citrina is always restricted to fall (September-December) so fruiting middate consistently fell during the period from September to November. Four species collected in both our study and that of Fogel (1976) (Barssia oregonensis, Tuber

murinum, Hymenogaster parksii, and Hysterangium crassum) had mean fruiting middates that differed between years by more than one month. For the three years in which Hymenogaster parksii occurred (combining data for the two studies), fruiting middate varied from 9 November to 14 March. Comparably, middate for Hysterangium crassum ranged from 28 March to 13 July. Clearly, there is a high degree of variability in annual fruiting patterns both between and within some species.

Comparative data for each of six years (Table II.9) show biomass and number of hypogeous sporocarps was always higher in spring than in fall although seasonal means did not differ significantly ($P > 0.05$) for weight or number of sporocarps. Sporocarp numbers ranged from 2.8 (1977) to 8.0 (1981) times greater in spring than in fall (mean of 3.1 times more). Greater sporocarp numbers in spring compared to fall is partly due to fruiting of spring ascomycetes (e.g., Genabea cerebriformis and Genea intermedia) which tend to be smaller than sporocarps of most basidiomycetes. In addition, some hypogeous species that fruit both spring and fall produce smaller sporocarps in spring. Comparison of spring and fall mean sporocarp weights for the genus Hysterangium, for example, showed a significant difference ($P < 0.05$). Mean sporocarp weight for all Hysterangium species combined was 0.19 in spring compared to 0.39 in fall. Mean sporocarp dry weight of all hypogeous species combined did not differ ($P > 0.05$) between spring and fall.

Reasons for seasonal fruiting patterns are not clear. Although hypogeous ascomycetes, as a group, are generally thought of as

spring fungi, the fruiting middate for all ascomycetes in our study (12 July) did not differ significantly ($P > 0.05$) from the middate for basidiomycetes (2 August). If there are fruiting "strategies," they are probably adaptations of species rather than genera or larger groups. Species capable of fruiting year around may have sufficient stored nutrients and energy in rhizomorphs to permit fruiting during brief periods of favorable weather. Species that fruit only in fall or spring may be responding to a combination of abiotic and biotic factors such as changing temperature and moisture conditions, cold conditioning, or a nutrient and/or hormonal flux from roots of host plants. Winter and early spring fruiting species (e.g., Hymenogaster parksii) may have a lower optimum metabolic temperature compared to other species and thus avoid fruiting at times when competition for nutrients is high. In addition, spores of winter fruiting species may be readily dispersed by small mammals because sporocarps of most other fungi are in short supply.

It is clear that a strong interdependence exists between mammals and hypogeous fungi. This relationship appears to be highly evolved in many cases and may have developed over more than one hundred million years of coexistance between gymnosperms and mammals (Trappe 1977, Raven et al. 1981). Substantial evidence indicates that hypogeous fungi are derived from epigeous taxa (Savile 1968). Evolution of the hypogeous habit was accompanied by notable morphological changes from epigeous forms. Sporogenous tissue of hypogeous fungi is typically enclosed in a continuous peridium and most species lack the ability to forcibly discharge spores. Unlike

epigeous fungi, hypogeous taxa need not uplift spore bearing tissue above ground so somatic stipe and pileal tissues are absent or greatly reduced. This allows diversion of energy and nutrient resources to production of spores and hymenial tissues. A chemical change which may have evolved with the hypogeous habit is production of new odor compounds but this remains unexplored. Clearly, odor is the primary means by which mammals locate hypogeous fungi. There is little detectable odor on immature sporocarps, but as spores mature, odor intensifies often becoming nearly overwhelming to humans. The diversity and structure of mushroom odor compounds is poorly understood, but a few have been identified (Benedict and Stuntz 1975, Claus et al. 1981, Marin et al. 1984). For example, eight-carbon alcohol compounds such as oct-1en-3-ol are common in both epigeous and hypogeous mushrooms (Marin et al. 1984). A steroid identical to a sexual pheromone of the boar has been identified from the European black truffle, (Tuber melanosporum) (Claus et al. 1981). This suggests that this truffle has evolved an odor compound that specifically attracts mammalian mycophagists. Although hypogeous fungi depend on mycophagy for spore dispersal, it is unknown if any require spores to pass through a digestive tract before germination. Spores are viable as ectomycorrhizal inoculum after passing through digestive tracts of Tassel-eared squirrels (Kotter and Farentinos 1984), white-footed mice (Miller 1985), bear, elk, and deer (Trappe unpublished data 1985). Because spores of ectomycorrhizal fungi germinate poorly under any conditions, effects of passage through a digestive tract are difficult to determine,

although fresh Rhizopogon spores are as effective a mycorrhizal inoculum as those that have gone through an animal (Trappe and Castellano, unpubl. data 1985). Inducing spore germination often requires stress treatment such as low temperature or wetting and drying (Sussman and Halvorson 1966, Lamb and Richards 1974). Spore dormancy can sometimes be broken by exposure to extracts or living roots, or co-culture with other organisms and activated charcoal (Bowen and Theodorou 1973; Fries 1981, 1983; Fries and Birraux 1980). While mycophagy has not been demonstrated to affect spore dormancy, digestive tract conditions such as heat, enzymatic action, and co-culture with microorganisms may potentially stimulate germination (Fogel and Trappe 1978).

A number of morphological and behavioral adaptations of small mammals may directly relate to mycophagy. For example, highly developed olfaction allows detection of fungal odor compounds. Fossorial animals not only can extract sporocarps from soil efficiently but also can defecate in burrows thereby placing fungal inoculum near host roots (Fogel and Trappe 1978, Trappe 1977). In addition, some mammals in which ectomycorrhizal fungi compose a significant part of the diet have molars which are rooted rather than ever-growing (C. Maser, pers. comm.). These mycophagists include members of the Sciuridae (chipmunks and squirrels), Cricetidae (native mice), and some members of the family Aricolidae (voles). Apparently one set of rooted molars lasts a life-time when the primary diet is soft food such as fungi or mast (nuts). Analysis of small mammal stomach and fecal samples shows a clear

feeding preference for hypogeous over epigeous fungi (Maser et al. 1978a, Sanders 1984). Maser and others (1978a) found a preponderance of hypogeous taxa compared to epigeous (88 percent frequency compared to 9 percent, respectively) in animals sampled when both types of sporocarps were abundant. This suggests that odor, palatability, or nutritional value may be involved in preferential selection of hypogeous fungi. Data on food value of fungi compared to nuts and fruits show that on a dry weight basis, fungi compare favorably with fruits and nuts in protein, carbohydrates, and minerals (Fogel and Trappe 1978). Fungi have less fat than nuts so caloric value is correspondingly less. However, concentrations of minerals, niacin, and riboflavin in fungi exceed most nuts and fruits. Comparative food value data alone are of limited value in determining the relative dietary importance of fungi because little is known about digestibility of different fungal and plant tissues. Fungal hyphal cell walls and cytoplasm are digested but apparently spores are not (Fogel and Trappe 1978). Limited available data (Fogel and Trappe 1978, Sanders 1984) show food value of epigeous compared to hypogeous fungi does not differ significantly. Clearly, by what ever means, hypogeous fungi have evolved as a more attractive food source to small mammals than epigeous fungi.

Phenological patterns of hypogeous fungus fruiting may to some degree reflect the compelling interdependence of small mammals and fungi. Clearly, hypogeous fungi are a primary or important alternative food source for numerous mammal species (Fogel and

Trappe 1978; Maser et al. 1978a, 1978b; Ure and Maser 1982; McIntire 1984; Maser et al. in press). Despite inadequate quantitative data for many mammal species, it is clear that mycophagy is a significant energy source and nutrient transfer mechanism in many ecosystems. Extremes in abiotic factors of the environment are probably important "driving forces" in the natural selection and evolution of hypogeous fungi (Savile 1968). Harsh conditions present at high elevations, for example, would obviously be buffered in the belowground environment. In contrast, it seems unlikely that the comparatively mild climatic conditions characteristic of the Oregon Coast Range could produce dramatically contrasting selective pressures favoring the hypogeous habit. It is possible, in areas of mild climate, that mycophagy has significantly influenced evolution toward the hypogeous habit. Spore transfer by mammals may be significantly more efficient than haphazard dispersal by wind. This could be due to more strategic placement of spore inoculum as well as possible favorable effects of mycophagy on spore germination and viability. An additional advantage in dispersal by animals may have come about with reduction of supportive somatic tissues resulting in more spores per unit weight of sporocarp. The hypogeous habit is conducive to an extended fruiting period resulting in greater year around sporocarp availability for mycophagists. Thus, annual dispersal period is lengthened and total number of spores dispersed is increased. Fruiting during the "off-seasons" (winter and summer) may have evolved partly as a response to competition from other fungi during the growing season, but also could have been influenced

by mycophagy. Demand for sporocarps by mycophagists intensifies as fungus production decreases when winter and summer climatic conditions arrive. During late fall near timberline on Mt. Hood, for example, "soil pits" where mammals have dug for fungi are abundant, but we seldom find sporocarps. Apparently sporocarps are virtually all consumed this time of year. It follows that fungi able to fruit during comparatively unfavorable times would be assured of spore dispersal by mammals.

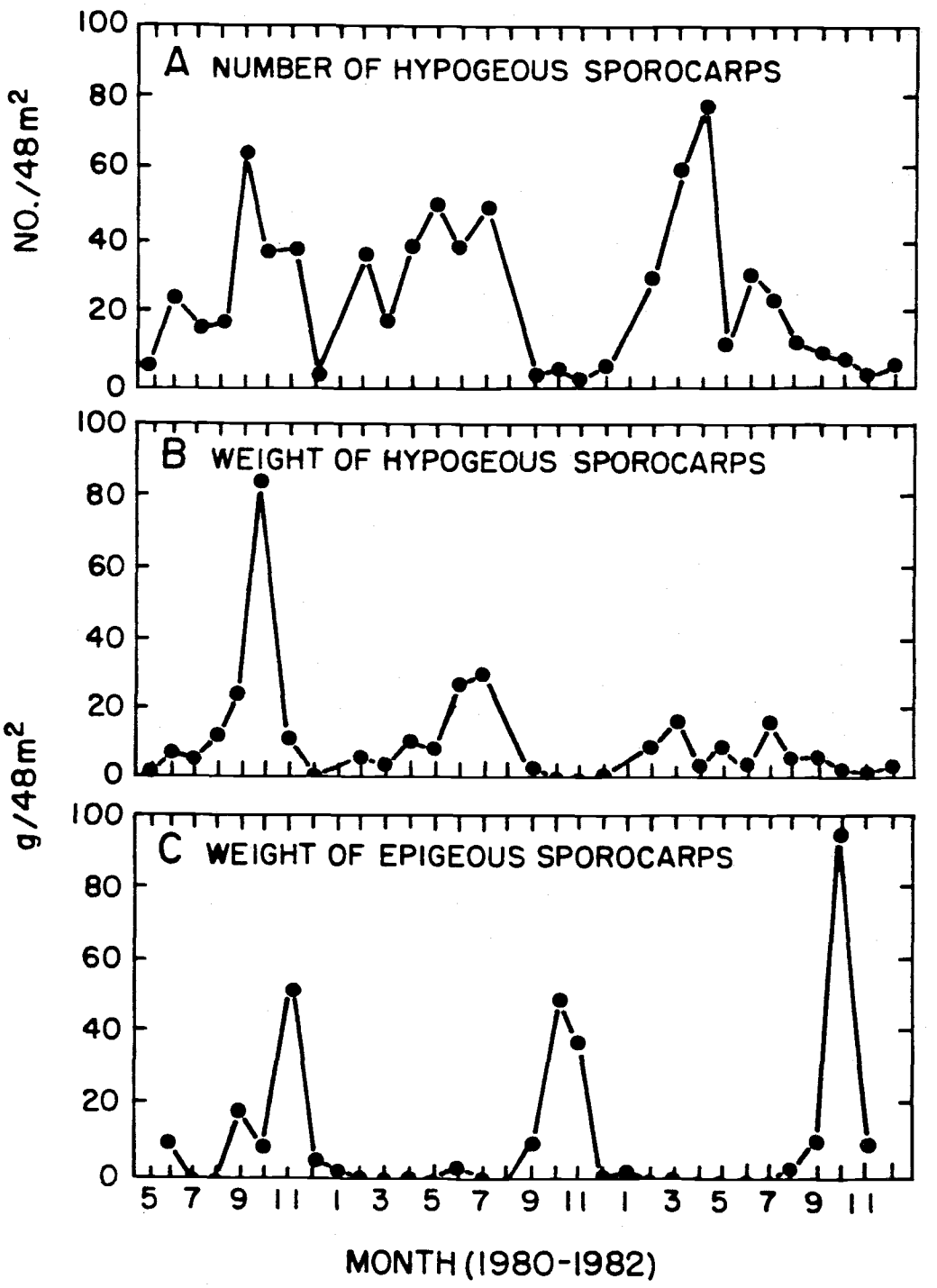


Fig. II. 1. Monthly production of hypogeous and epigeous sporocarps in a western Oregon Douglas-fir stand.

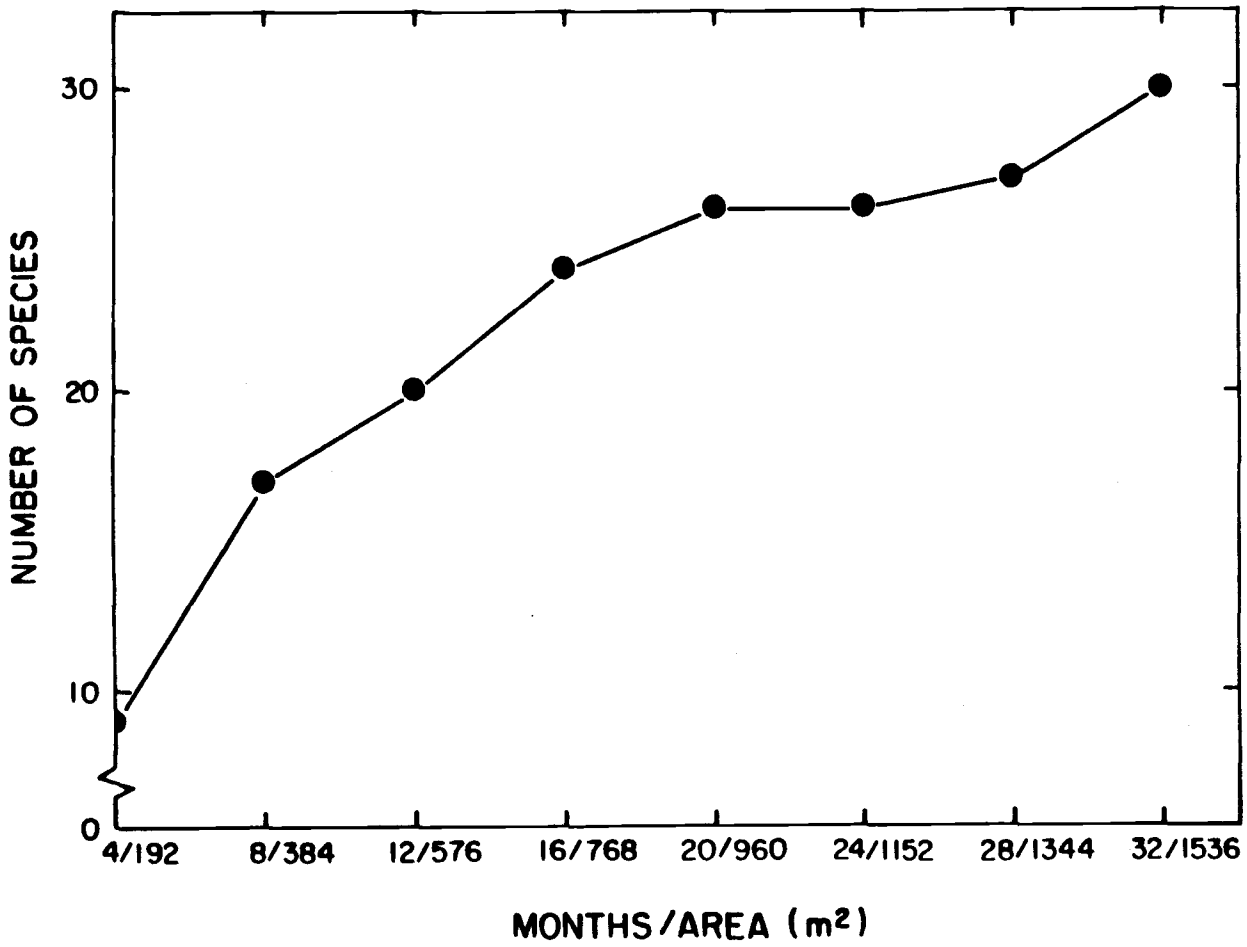


Fig. II.2. Cumulative number of hypogeous fungal species with time and area sampled in a western Oregon Douglas-fir stand.

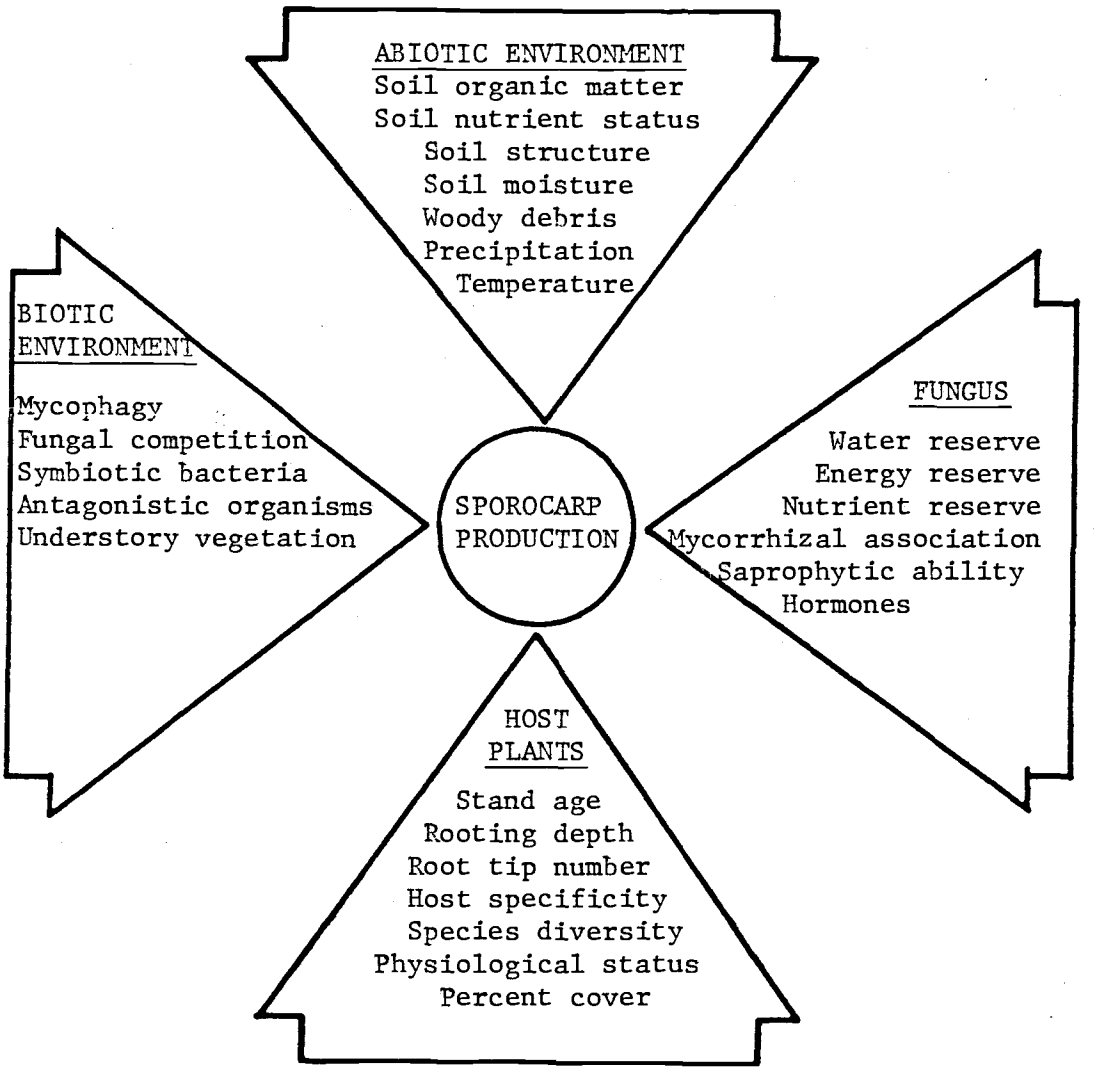


Fig. II.3. Major factors influencing hypogeous sporocarp production in western Oregon.

Table II.1. Species list and productivity estimates for hypogeous fungi collected during two years in a western Oregon Douglas-fir stand.

| Species | Year | Total sporocarps | Equivalent no./ha | Mean dry weight of sporocarps g | Equivalent dry weight g/ha |
|---|---|---|---|---|---|
| Total | 1 | 307 | 5815 | 0.55 | 3221 |
| | 2 | 351 | 6648 | 0.30 | 1998 |
| Barssia oregonensis Gilkey | 1 | 5 | 95 | 0.54 | 51 |
| | 2 | 2 | 42 | 0.19 | 8 |
| Genabea cerebriformis (Harkn.) Trappe | 1 | 1 | 19 | 0.14 | 3 |
| | 2 | 2 | 42 | 0.06 | 3 |
| Genea intermedia Gilkey | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 6 | 125 | 0.08 | 10 |
| Tuber gibbosum Harkn. | 1 | 1 | 19 | 0.12 | 2 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Tuber levissimum Gilkey | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 1 | 21 | 0.07 | 1 |
| Tuber murinum Hesse | 1 | 7 | 133 | 0.22 | 30 |
| | 2 | 11 | 229 | 0.16 | 37 |
| Tuber rufum (Vitt.) Fischer | 1 | 11 | 208 | 0.15 | 31 |
| | 2 | 3 | 62 | 0.08 | 5 |
| Tuber sp. | 1 | 4 | 76 | 0.06 | 5 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Tuber sp. nov. | 1 | 4 | 76 | 0.32 | 24 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Gautieria monticola (Harkn.) Harkn. | 1 | 28 | 530 | 2.88 | 1527 |
| | 2 | 17 | 354 | 2.11 | 769 |
| Hymenogaster gilkeyae Zeller & Dodge | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 1 | 21 | 0.22 | 5 |
| Hymenogaster parksii Zeller & Dodge | 1 | 9 | 170 | 0.49 | 83 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Hymenogaster sp. | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 2 | 42 | 0.58 | 24 |
| Hysterangium crassirhachis Zeller & Dodge | 1 | 10 | 189 | 0.72 | 136 |
| | 2 | 1 | 21 | 0.52 | 11 |
| Hysterangium crassum (Tul. & Tul.) Fisher | 1 | 129 | 2443 | 0.31 | 746 |
| | 2 | 181 | 3770 | 0.22 | 842 |
| Hysterangium separabile Zeller | 1 | 20 | 379 | 0.28 | 106 |
| | 2 | 88 | 1833 | 0.11 | 204 |
| Hysterangium sp. nov. 1 | 1 | 24 | 455 | 0.18 | 82 |
| | 2 | 6 | 114 | 0.27 | 34 |
| Hysterangium sp. nov. 2 | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 3 | 62 | 0.17 | 13 |
| Martellia brunnescens Sing. & Sm. | 1 | 1 | 19 | 0.07 | 1 |
| | 2 | 1 | 21 | 0.71 | 15 |
| Martellia ellipsospora (Zeller) Sing. & Sm. | 1 | 6 | 114 | 0.05 | 6 |
| | 2 | 0 | 0 | .00 | 0 |
| Martellia sp. | 1 | 3 | 57 | 0.05 | 3 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Melanogaster ambiguus (Vitt.) Tul. & Tul. | 1 | 7 | 133 | 1.70 | 225 |
| | 2 | 3 | 62 | 1.73 | 108 |
| Rhizopogon parksii Sm. | 1 | 3 | 57 | 0.22 | 13 |
| | 2 | 3 | 62 | 0.15 | 9 |
| Rhizopogon villosulus Zeller | 1 | 16 | 303 | 0.10 | 31 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Rhizopogon vinicolor Sm. | 1 | 2 | 38 | 0.06 | 2 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Rhizopogon sp. nov. 1 | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 2 | 42 | 0.12 | 5 |
| Truncocolumella citrina Zeller | 1 | 16 | 303 | 0.37 | 112 |
| | 2 | 5 | 104 | 0.03 | 4 |

Table II.2. Species accounting for 5 percent or more of productivity of hypogeous fungi in a western Oregon Douglas-fir stand.

| Species | Percentage of total weight year 1 | year 2 |
|---|---|---|
| *Gautieria monticola* | 47.4 | 35.9 |
| *Hysterangium crassum* | 23.2 | 40.4 |
| *Hysterangium separabile* | -- | 9.8 |
| *Melanogaster ambiguus* | 7.0 | 5.2 |
| Total | 77.6 | 91.3 |

| | Percentage of total sporocarp no. | |
|---|---|---|
| *Gautieria monticola* | 9.1 | 5.0 |
| *Hysterangium crassum* | 42.0 | 53.6 |
| *Hysterangium separabile* | 6.5 | 26.0 |
| *Hysterangium* sp. nov. 1 | 7.8 | -- |
| *Rhizopogon villosulus* | 5.2 | -- |
| *Truncocolumella citrina* | 5.2 | -- |
| Total | 75.8 | 84.6 |

Table II.3. Middates of fruiting for selected species of hypogeous fungi in a western Oregon Douglas-fir stand.

| Species | Year 1 | Year 2 | Mean | Standard deviation | Fruiting period |
|---|---|---|---|---|---|
| Barssia oregonensis | 2 July | 5 June | 18 June | 19 | June-July |
| Tuber murinum | 23 July | 15 June | 3 July | 27 | May-Sept. |
| Gautieria monticola | 21 July | 16 June | 3 July | 25 | Apr.-Nov. |
| Hymenogaster parksii | 14 Mar. | -- | -- | -- | Nov.-Apr. |
| Hysterangium crassum | 13 July | 10 Apr. | 26 May | 66 | Feb.-Dec. |
| Hysterangium separabile | 29 Apr. | 17 Apr. | 22 Apr. | 8 | Feb.-Nov. |
| Melanogaster ambiguus | 20 July | 3 June | 16 June | 33 | May-Aug. |
| Rhizopogon parksii | 3 Nov. | 4 Dec. | 18 Nov. | 22 | Sept.-Dec. |
| Truncocolumella citrina | 16 Oct. | 26 Sept. | 5 Oct. | 14 | Sept.-Nov. |
| Spring peak | 26 Apr. | 5 Apr. | 16 Apr. | 15 | |
| Fall peak | 30 Sept. | 23 Oct. | 12 Oct. | 16 | |

Table II.4. Similarity of hypogeous fungal taxa between different stands of Douglas-fir in western Oregon.

| Stand pairs[2] | Total taxa in common (%) | | Major taxa[1] in common (%) by weight | | Major taxa[1] in common (%) by number | |
|---|---|---|---|---|---|---|
| | Species | Genera | Species | Genera | Species | Genera |
| North slope no. 1, North slope no. 2 | 54 | 75 | 38 | 33 | 27 | 22 |
| North slope no. 1, South slope | 32 | 69 | 0 | 17 | 11 | 40 |

[1]Taxa composing 5% or more of annual production on the basis of weight and number of sporocarps, respectively.

[2]Data for stand 1 are this study, data for stand 2 and the south slope are from Fogel 1976 and Fogel and Hunt 1979, respectively.

Table II.5. Variability in annual production by some major species of hypogeous fungi over five years in western Oregon.

| Species | Grams/ha/yr high | low | mean |
|---|---|---|---|
| Genabea cerebriformis | 21 | 1 | 7 |
| Tuber gibbosum | 380 | 2 | 152 |
| Hysterangium crassum | 1206 | 517 | 820 |
| Gautieria monticola | 1527 | 13 | 569 |
| Hymenogaster parksii | 435 | 76 | 239 |
| Truncocolumella citrina | 2336 | 4 | 515 |

Table II.6. Hypogeous sporocarp production in some coniferous forests.

| Single sample maximum kg/ha | Annual production kg/ha/yr[1] | Forest type | Reference |
|---|---|---|---|
| 9.6 | 43.9 | Douglas-fir | Fogel 1976 |
| 10.1 | 24.0 | Douglas-fir | Fogel and Hunt 1979 |
| 1.4 | --- | Douglas-fir | Luoma (unpubl. 1984) |
| 1.7 | --- | Douglas-fir | Hunt (unpubl. 1983) |
| 17.5 | 35.4 | Douglas-fir | This study |
| 4.6 | --- | Grand fir | Terwilliger 1985 |
| 142.0 | 380.0 | Pacific Silver fir | Vogt et al. 1981 |
| --- | 22.0 | Ponderosa pine | States 1985 |

[1]Calculated by summing monthly kg/ha.

Table II.7. Peak standing crops of sporocarps produced by hypogeous and epigeous mycorrhizal species in a western Oregon Douglas-fir stand.

| | Hypogeous | | Epigeous | |
|---|---|---|---|---|
| Year | kg/ha | month | kg/ha | month |
| 1 | 17.5 | Oct. | 9.0 | Nov. |
| 2 | 6.1 | July | 8.7 | Oct. |
| 3 | 3.2 | July | 19.6 | Oct. |

Table II.8 Comparison of annual epigeous and hypogeous sporocarp production in two stands of Douglas-fir in western Oregon.

| | Epigeous | | | Hypogeous | |
|---|---|---|---|---|---|
| | weight (kg/ha/yr) | | percent | weight | |
| Year | total | mycorrhizal | mycorrhizal | (kg/ha/yr) | Reference |
| 1 | 21.4 | 15.3 | 71.1 | 35.4 | This study |
| 2 | 23.4 | 18.7 | 79.7 | 22.0 | This study |
| 1 | 42.6 | 31.4 | 73.7 | 21.1 | Fogel and Hunt 1983 |
| 2 | 45.4 | 43.7 | 96.3 | 6.2 | Fogel and Hunt 1983 |

Table II.9. Comparison of spring and fall production of hypogeous sporocarps in western Oregon.

| | Spring[1] | | Fall | | |
|---|---|---|---|---|---|
| | Number[2] | weight[2] | Number | weight | |
| Year | no./ha | kg/ha | no./ha | kg/ha | Reference |
| 1972 | 153,600 | 23.35 | 21,200 | 13.18 | Fogel 1976 |
| 1973 | 83,400 | 17.36 | 19,200 | 8.98 | Fogel 1976 |
| 1974 | 105,200 | 14.75 | 13,800 | 5.83 | Fogel 1976 |
| 1976 | --- | -- | 36,100 | 17.14 | Fogel and Hunt 1979 |
| 1977 | 12,700 | 3.37 | 4,600 | 2.72 | Fogel and Hunt 1979 |
| 1978 | 1,300 | 0.34 | --- | -- | Fogel and Hunt 1979 |
| 1980 | --- | -- | 30,412 | 24.98 | This study |
| 1981 | 31,662 | 10.40 | 3,958 | 1.14 | This study |
| 1982 | 38,953 | 7.45 | 6,457 | 3.26 | This study |

[1]Spring includes March-June. Fall includes September-December.
[2]Values are sums of monthly production per hectare

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# SUMMARY AND CONCLUSIONS

Hyphal length is easier to measure than hyphal biomass, but the latter best expresses the amount of fungal mass in soil because measures of diameter and thus volume are included. Hyphal volume should be calculated from each fragment separately, rather than by use of a mean diameter of all hyphae, to avoid underestimates of mycelial mass.

Hyphal biomass fluctuated greatly during the study, but was higher in fall and spring than in summer and winter. Hyphal biomass in litter ranged from 5.19 to 23.17 mg $g^{-1}$ and from 0.35 to 1.5 mg $g^{-1}$ in soil. High within-sample variation made significant differences between means in hyphal biomass difficult to demonstrate. Significantly lower mycelial mass in summer apparently results from seasonal drought conditions. Weight of mycelium in the soil profile to a depth of 100 cm shifted significantly with season and was highest in fall and lowest in summer.

Melanized hyphae composed more than 50 percent of total hyphal weight throughout most of the study. This may indicate that pigmentation is an adaptive advantage for surviving the droughty season. Also, melanized hyphae probably decompose more slowly than hyaline hyphae.

Multiple regression analyses, with independent variables derived from temperature, moisture, and litterfall data produced no adequate

predictive equations for monthly hyphal biomass.

The large mycelial mass in soils of coniferous forests constitutes a rapidly cycling pool of nutrients which contributes to ecosystem stability by immobilizing nutrients and thus reducing leaching from the root zone.

Gathering data for establishing the contribution of higher fungi to forest ecosystems is difficult compared to study of aboveground forest components. The community of higher fungi consists of species groups distributed nonrandomly and separated spatially and temporally within many microhabitats in the general environment. Moreover, individuals cannot be delimited by vegetative structures so collection of sporocarps is the only means by which populations can be studied. Documenting all species of hypogeous fungi in a forest stand requires collecting over a long period. New species were recorded during the final four months of our study. Erratic fruiting and patchy distribution of sporocarps indicate that hypogeous fungi respond to microhabitat conditions within the seemingly uniform general environment of the forest. Because of difficulty in sampling, identification of sporocarps, and time required, few quantitative or taxonomic studies of hypogeous fungi have been conducted.

Nine ascomycete and 21 basidiomycete species were recorded over 32 months of sporocarp collecting. Production was dominated by relatively small number of species. Species accounting for 5 percent or more of annual sporocarp number or dry weight were Gautieria monticola, Hysterangium crassum, H. separabile, H. sp. nov., Melanogaster ambiguus, Rhizopogon villosulus, and Truncocolumella citrina.

Estimates of monthly hypogeous sporocarp standing crop ranged from 0.15 to 17.51 kg $ha^{-1}$ and estimates of annual production were 22.0 and 35.4 kg $ha^{-1}$ $yr^{-1}$ (calculated as a sum of monthly production).

In contrast to epigeous sporocarps, biomass and number of hypogeous sporocarps showed no well defined seasonal peaks, and was more uniform throughout the year. Monthly standing crops of both hypogeous and epigeous sporocarps decreased in winter. Fruiting period of some hypogeous species is strictly seasonal (e.g., Barssia oregonensis in spring and Truncocolumella citrina in fall) while a few are capable of fruiting year-around (e.g., Hysterangium crassum). Ability to fruit during any month may partly result from nutrients and energy stored in rhizomorph mats produced by these species. The middate of fruiting for all ascomycete species compared to basidiomycetes did not differ significantly. Data for six years show that biomass and number of hypogeous sporocarp were higher in spring than in fall, but spring and fall means did not differ significantly ($P > 0.05$).

Data on species and production of hypogeous sporocarps are useful in developing important principles in community ecology. Examples include determining fungal species richness, making inferences about the occurrence of specific ectomycorrhizal host-fungus associations, relating sporocarp production to environmental factors, determining successional patterns of ectomycorrhizal fungi, and establishing the potential food resource for mycophagists.

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# APPENDIX

## APPENDIX

Species list and yearly productivity estimates for hypogeous fungi at Dinner Creek, Oregon

| Species | Year | Total sporocarps | Equivalent no./ha | Mean dry weight of sporocarps g | Equivalent dry weight g/ha |
|---|---|---|---|---|---|
| Total | 1 | 508 | 4232 | 0.44 | 1855 |
| | 2 | 85 | 850 | 0.68 | 578 |
| Gautieria sp. | 1 | 4 | 33 | 0.24 | 8 |
| | 2 | 4 | 40 | 2.13 | 85 |
| Hymenogaster parksii Zeller & Dodge | 1 | 5 | 42 | 0.18 | 7 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Hysterangium crassum (Tul. & Tul.) Fisher | 1 | 3 | 25 | 0.08 | 2 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Hysterangium separabile Zeller | 1 | 8 | 67 | 0.62 | 41 |
| | 2 | 3 | 30 | 0.33 | 10 |
| Leucogaster rubescens Zeller & Dodge | 1 | 70 | 583 | 0.54 | 316 |
| | 2 | 35 | 350 | 0.97 | 338 |
| Leucophleps magnata Harkn. | 1 | 62 | 516 | 0.37 | 189 |
| | 2 | 10 | 100 | 0.21 | 21 |
| Martellia parksii Sing & Sm. | 1 | 2 | 17 | 0.75 | 12 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Melanogaster sp. | 1 | 1 | 8 | 1.46 | 12 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Rhizopogon parksii Sm. | 1 | 93 | 775 | 0.60 | 463 |
| | 2 | 31 | 258 | 0.37 | 116 |
| Rhizopogon vinicolor Sm. | 1 | 5 | 42 | 0.25 | 10 |
| | 2 | 1 | 10 | 0.11 | 1 |
| Rhizopogon sp. | 1 | 0 | 0 | 0.00 | 0 |
| | 2 | 1 | 10 | 0.65 | 6 |
| Truncocolumella citrina Zeller | 1 | 247 | 2058 | 0.36 | 749 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Tuber sp. | 1 | 3 | 25 | 0.13 | 3 |
| | 2 | 0 | 0 | 0.00 | 0 |
| Zelleromyces gilkeyae Sing. & Sm. | 1 | 5 | 42 | 0.98 | 41 |
| | 2 | 0 | 0 | 0.00 | 0 |