The
FUNGAL COMMUNITY

ITS ORGANIZATION AND ROLE IN THE ECOSYSTEM

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Chapter 28

QUANTIFICATION OF SPOROCARPS PRODUCED BY HYPOGEOUS FUNGI

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I. INTRODUCTION

Fungi are difficult to study in natural habitats because their minute hyphae ramify throughout their substrate. Most fungi cannot be identified by vegetative characteristics. In the field, even sporocarp-producing fungi whose taxonomy is based on morphology often are impossible to identify because of the important role of microscopic characteristics.

Despite the problems in defining individuals and identifying species as well as the ephemeral and seemingly irregular appearance of sporocarps, much can be learned by studying sporocarp production. For example, mycorrhizal fungi—difficult to isolate by dilution plating or other methods—can be identified, and those species from sites where reforestation is difficult can be used to artificially inoculate planting stock for similar sites. Fungi eaten by mycophagists can be determined. Sporocarps can be used to compare different plant associations. Possible specific or obligate associations, such as that of *Fuscoboletinus ochraceoroseus* (Snell) Pomerlau and Smith with its mycorrhizal host *Larix*, can be inferred. Finally, more can be learned about the reproductive biology of a species, range of variation in morphological characters, and environmental factors controlling sporocarp production.

The hypogeous fungi, those producing sporocarps underground, include members of the Ascomycetes, Basidiomycetes, and a few Endogonaceae. This phylogenetically diverse group not only produces macroscopic subterranean sporocarps but also generally lacks active spore discharge. Sterile tissue completely encloses sporogenous tissue, and many species are approximately spherical. Most hypogeous fungi are presumed to be ectomycorrhizal (Trappe, 1962, 1971). As mycorrhizal fungi, they play an important role in forest tree nutrition as extensions of the root system, directly draining photosynthates and contributing to soil respiration and nutrient mobilization (Marks and Kozlowski, 1973; Trappe and Fogel, 1977).

Epigeous fungi, those producing sporocarps aboveground, are easier to study than hypogeous fungi. Consequently, sporocarp production by epigeous fungi has been re-

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searched more extensively. Cooke (1948, 1953), Hueck (1953), and Hering (1966) reviewed much of the literature published prior to 1960, but much more has appeared since then, especially in Europe and Japan. Most of the research can be divided into three categories (Hering, 1966). First, the epigeous floras of different vascular plant communities have been summarized by species and by the numbers of sporocarps each produces (e.g., see Hofler, 1937; Arnolds, 1976). The associated biomass of epigeous sporocarps has rarely been reported (Richardson, 1970). Second, the structure of the fungus community has been analyzed, usually in relation to the vascular flora (e.g., see Haas, 1932; Cooke, 1955). Third, sporocarp phenology has been explained by graphs relating it to soil nitrate concentration, temperature, precipitation, and occasionally other environmental factors (e.g., see Wilkins and Harris, 1946; Lange, 1948; Guminska, 1962; Endo, 1972; Thoen, 1976). No statistical or regression analyses of sporocarp production have apparently been reported.

The ecology of hypogeous fungi has not been comparably researched. The fungal floras of different communities have been summarized in species lists (Ceruti et al., 1967; Gross, 1969), and associated biomass has been reported in one study (Fogel, 1976). Sporocarp production has been related to climatic or edaphic factors (Setchell and Watson, 1926; Ceruti et al., 1967; Montacchini and Caramiello, 1968; Fogel, 1976). Mycophagy also has been studied in very little detail (Fogel and Peck, 1975; Fogel and Trappe, 1978), although the subterranean habit, lack of active spore discharge, and sterile tissue enclosing spores make mycophagy crucial in spore dispersal. In turn, mycophagists have become dependent on hypogeous fungi. For example, fungi comprised from 1 to 72% of the food volume consumed yearly by nine species of rodents (Fogel and Trappe, 1978), and hypogeous fungi comprised 88% of the fungi in the stomachs of some small mammals (Maser et al., 1978). The importance of mycophagy to small mammals also is illustrated by squirrels who dry and cache sporocarps, including hypogeous species (Hardy, 1949).

II. SAMPLING CONSIDERATIONS

The subterranean habit of hypogeous fungi creates several problems in any systematic sampling scheme. Because the sporocarps are not visible, simply locating the fungi can be difficult. Ectomycorrhizal hosts on a study site indicate the possible hypogeous flora. Other clues include small pits excavated by rodents and small mounds raised by sporocarps fruiting at the soil-litter interface. Sporocarps also fruit in rotten logs that have been invaded by roots of ectomycorrhizal hosts. Patches of dead grass and the presence of small flies (Mycetophilidae) hovering over ripe sporocarps are clues for Italian truffle collectors (Singer, 1961). The much publicized use of pigs and dogs to locate truffles depends on their ability to smell ripe sporocarps of a few truffle species, and the animals probably could not efficiently locate immature sporocarps in quantitative studies.

Once the sporocarps are located, sampling requires removing the forest floor and raking the top 10 to 20 cm of mineral soil. This seriously disturbs quadrats, and new quadrats are needed for each sampling date.

Other sampling considerations include species differences in spatial distribution and sporocarp phenology. Sporocarp distribution is aggregated, not random, and sporocarp fruiting occurs in three distinct patterns (Fogel, 1976): (1) single sporocarps or a few widely scattered over a large area (e.g., 25 m^2); (2) large (2-4 m^2), loose clusters; and (3) arcs and partial arcs ("fairy rings") formed by tight clusters of sporocarps (Fig. 1).

The fruiting of individual species and of the population as a whole varies seasonally, and it apparently depends on the climate of the study area. In western Oregon, for instance, production is bimodal (Fig. 2) with winter and summer valleys due to summer drought and cold winter temperatures (Fogel, 1976). In England (Fig. 3) and Scotland, where sporocarp production is not limited by summer drought, production of epigeous and presumably hypogeous species peaks in the fall (Grainger, 1946; Richardson, 1970).
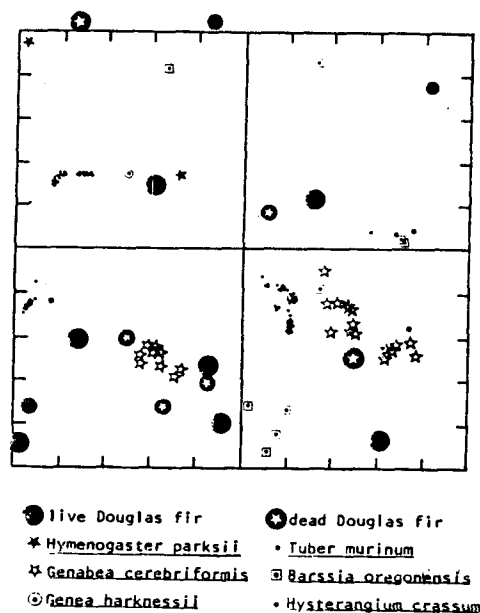

● live Douglas fir	◉ dead Douglas fir
✱ Hymenogaster parksii	• Tuber murinum
✿ Genabea cerebriformis	▣ Barssia oregonensis
◉ Genea harknessii	• Hysterangium crassum

Fig. 1 Distribution of hypogeous sporocarps on a 10-m X 10-m quadrat subdivided into 5-m X 5-m subplots in relation to Douglas-fir stems larger than 4 cm dbh (diameter at breast height) at Woods Creek, Oregon. (From Fogel, 1976.)
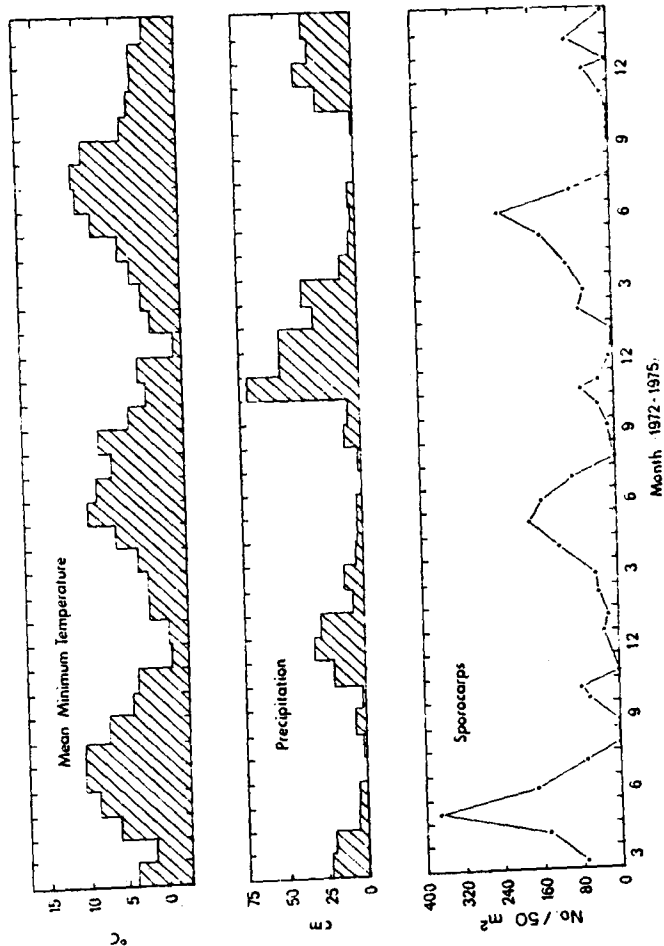
Fig. 2 A 3-year comparison of sporocarp production by hypogeous fungi with corresponding temperature and precipitation in western Oregon. (From Fogel, 1976.)
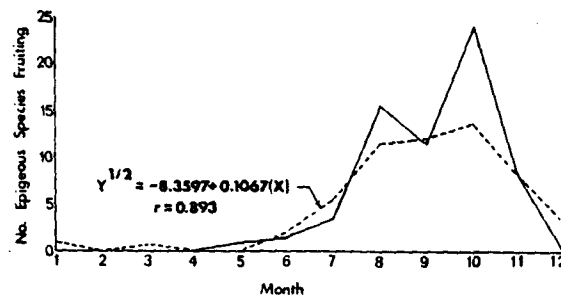

Fig. 3 Simulation of the number of epigeous species fruiting in England. Solid line is the observed number fruiting, and the broken line is the predicted number. (After Grainger, 1946.)

Seasonal and spatial differences in sporocarp production make the minimal area for sampling difficult to determine. Mueller-Dombois and Ellenberg (1974) defined minimal area for population sampling either as the quadrat size that contains 90-95% of one species or as the species number asymptote derived from a species-area curve. The former definition is inoperable for hypogeous fungi because the community represented by sporocarps constantly changes. The asymptote derived for hypogeous populations depends on the seasonal abundance of sporocarps. For example, species-area curves constructed from data collected on 10-m X 10-m quadrats in western Oregon indicate that the minimal area ranges from 0 to 100 m^2 between minimum and maximum production. Unfortunately, the time factor (4-6 man-hours needed to sample 100 m^2) severely restrains the number of quadrats that can be thoroughly searched during maximum sporocarp production.

III. COMMUNITY AND POPULATION ATTRIBUTES

Data obtained by irregular collecting of sporocarps can be used to compile species lists for different areas, but the usefulness of such information is limited. Much more can be learned by simply sampling quadrats at periodic intervals. This section begins by comparing hypogeous floras, then explores several attributes of the hypogeous community that can be examined if data are collected periodically.

A. Flora

A given area probably has more epigeous than hypogeous species, although this has not been substantiated. Floristic lists contain far more epigeous than hypogeous species. Epigeous floras in Europe and Japan include 28 to 205 species (Parker-Rhodes, 1951; Hering, 1966; Richardson, 1970; Endo, 1972; Smarda, 1973; Thoen, 1976). Maas and

Stuntz (1970) collected 134 epigeous species from a nonserpentine mixed conifer
(*Pseudotsuga-Abies-Pinus*) stand in the Cascade Mountains of Washington. Over a 3-
year period, I collected 24 hypogeous species (11 ascomycetes, 13 basidiomycetes) in
a young stand of Douglas-fir in western Oregon (Fogel, 1976); however, during the
past year, I found only 11 species in a nearby stand, possibly the result of drought
last year in the Pacific Northwest. Seventeen hypogeous species have been reported
for an Italian oak stand, 12 for a German red beech stand, and 17 for a German spruce
stand (Ceruti et al., 1967; Gross, 1969). Because hypogeous fungi appear mycorrhi-
zal, hypogeous and epigeous floras can be compared better if only epigeous mycorrhi-
zal species are considered. Of the 28 species listed by Richardson (1970), 12 (42.9%)
were listed by Trappe (1962) as possible mycorrhizal associates. Of the 134 species
listed by Maas and Stuntz (1970), 22 (16%) presumably were mycorrhizal.

Sampling for more than 1 year may be necessary to reliably estimate total spe-
cies number. For example, at Woods Creek, Oregon, I collected 68% of the theoreti-
cal hypogeous flora during the first year, 88% the second year, and 96% by the end
of the third year (Fig. 4) (Fogel, 1976). Parker-Rhodes (1951) presented a statis-
tical method useful for reducing the number of collections needed to estimate the
total number of species per site.

B. Abundance: Number of Sporocarps and Biomass

Yearly production of hypogeous sporocarps ranged from 11,052 to 16,753 ha^{-1} in a
young Douglas-fir forest in western Oregon (Fogel, 1976). Other hypogeous studies
(Ceruti et al., 1967; Gross, 1969) did not specify plot size, so the three studies
cannot be compared. Estimates of epigeous sporocarp numbers range from 7000 to
489,000 sporocarps ha^{-1} year^{-1} (Hering, 1966; Richardson, 1970). Epigeous sporocarp
numbers closely approximate hypogeous numbers if mycorrhizal species are compared.
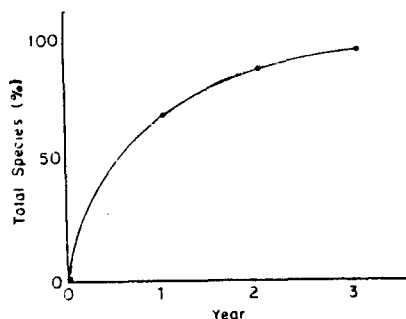

Fig. 4 Percentage of total number of hypogeous species fruiting in each year of a
3-year study at Woods Creek, Oregon. (Author's unpublished data.)

For example, 8750 to 20,250 (1.8-8.5%) of the 239,000 to 489,000 epigeous sporocarps
produced annually per hectare in Richardson's (1970) study are mycorrhizal compared
to the 11,052 to 16,753 hypogeous sporocarps per hectare reported by Fogel (1976).

The dry weight produced by hypogeous sporocarps ranges from 2.3 to 5.4 kg ha^{-1}
year^{-1} (Fogel, 1976). Hering (1966) estimated that epigeous species would produce
0.19 to 19.2 kg dry weight ha^{-1} year^{-1} [using Richardson's (1970) conversion factor
of 6.36% to convert fresh weight to dry weight]. Dry weight of epigeous mycorrhizal
species (9.8-19.4 kg ha^{-1} year^{-1}) accounted for slightly more than half of the total
sporocarp biomass (16-30 kg ha^{-1} year^{-1}) reported by Richardson (1970).

C. Frequency

Frequency of individual species is difficult to measure due to the large minimal area
required for sampling and the constant change in fruiting species. Total frequencies
of all species ranged from 0 to 68% and species number ranged from 0 to 10 when 50
new 1-m X 1-m quadrats were sampled monthly; when four new 5-m X 5-m quadrats were
sampled monthly, the total frequency ranged from 0 to 100%, representing from 0 to 5
species per month (R. Fogel, unpublished data). Therefore, large quadrats with a
higher frequency of sporocarps should be used to quantify biomass or numbers, and a
large number of small quadrats should be used in floristic studies where the goal is
to maximize species number.

D. Diversity

A floristic list also reflects a site's species richness. Diversity can be estimated
by the number of species in a sample of standard size, by the steepness of the impor-
tance-value sequence (i.e., the Simpson index), or by an index of the relative even-
ness of the importance values through a sequence (i.e., the Shannon-Wiener index)
(Whittaker, 1972). Shannon-Wiener index values (base 2) for hypogeous fungi from
the Fogel (1976) site (Woods Creek) and for a new site located 3 km from the original
(Dinner Creek) are 3.14 and 2.17. The value for Dinner Creek epigeous fungi was
3.67. For the first year of each study, Woods Creek had 13 hypogeous species, and
Dinner Creek had 12 hypogeous and 55 epigeous species. Apparently, a larger propor-
tion of the epigeous species are infrequently encountered. The low values might re-
flect the low diversity of the vascular plant flora, i.e., four tree species per
site. Beta diversity, defined by Whittaker (1972) as the differentiation of communi-
ties along gradients, has not been estimated.

E. Coefficient of Community

The similarity in species composition between two sites can be calculated using the
coefficient of community, c_c:

$$c_c = \frac{200(s_{xy})}{s_x + s_y}$$

(1)

Table 1 Middates of fruiting by year for common species of hypogeous fungi in western Oregon[a]

Species	Year 1	Year 2	Year 3	Mean	Standard deviation	Fruiting period
Barssia oregonensis	24 May	21 May	12 Apr.	9 May	23	March-July
Genabea cerebriformis	--	12 Feb.	22 May	2 Apr.	70	March-July
Genea harknessii	9 May	18 Mar.	14 Dec.	15 Mar.	58	Nov.-June
Hymenogaster parksii	-	18 Jan.	9 Nov.	14 Dec.	50	Oct.-June
Hysterangium crassum	29 Apr.	26 Mar.	15 Apr.	14 Apr.	16	Sept.-July
Hysterangium separabile	27 Apr.	9 Apr.	30 Apr.	22 Apr.	11	Sept.-Aug.
Truncocolumella citrina var. citrina	10 Oct.	1 Oct.	17 Nov.	23 Oct.	25	Sept.-Dec.
Tuber murinum	28 May	6 May	16 June	23 May	15	Feb.-July
Spring peak	-	23 Apr.	11 May	2 May	13	--
Fall peak	10 Oct.	30 Oct.	6 Dec.	5 Nov.	30	--

[a] From Fogel (1976).

Table 2 Species accounting for 5% or more of productivity of hypogeous fungi in western Oregon[a]

Species	Percentage of total weight		
	Year 1	Year 2	Year 3
Gautieria sp.	--	14.5	--
Hymenogaster parksii	3.0	12.2	--
Hysterangium crassum	14.6	17.4	53.2
Hysterangium separabile	9.3	19.2	13.0
Truncocolumella citrina var. citrina	43.2	--	--
Tuber gibbosum	7.0	--	--
Tuber murinum	6.8	8.3	7.1
Total	83.9	71.6	73.3

Species	Percentage of total sporocarp no.		
	Year 1	Year 2	Year 3
Barssia oregonensis	5.6	5.1	--
Genabea cerebriformis	--	6.3	--
Genea harknessii	13.6	--	--
Hymenogaster parksii	5.3	10.6	--
Hysterangium crassum	26.1	25.9	65.8
Hysterangium separabile	18.7	11.0	14.0
Truncocolumella citrina var. citrina	5.6	--	--
Tuber murinum	10.0	13.7	6.1
Total	89.4	77.6	85.9

[a] From Fogel (1976).

where s_x and s_y are the number of species in quadrats x and y (Pielou, 1975). In the first year of the Fogel (1976) study and the Dinner Creek study, 64.5% of species collected at each site occurred at both. Normally I would expect more similarity because the sites, only 3 km apart, have comparable aspect and stand structure, but the 1976-1977 drought in the Pacific Northwest may have reduced the number of species fruiting at Dinner Creek.

F. Middate of Fruiting

The middate of fruiting, which permits comparison of different sites and prediction of species abundance on a given date, is calculated by the formula:
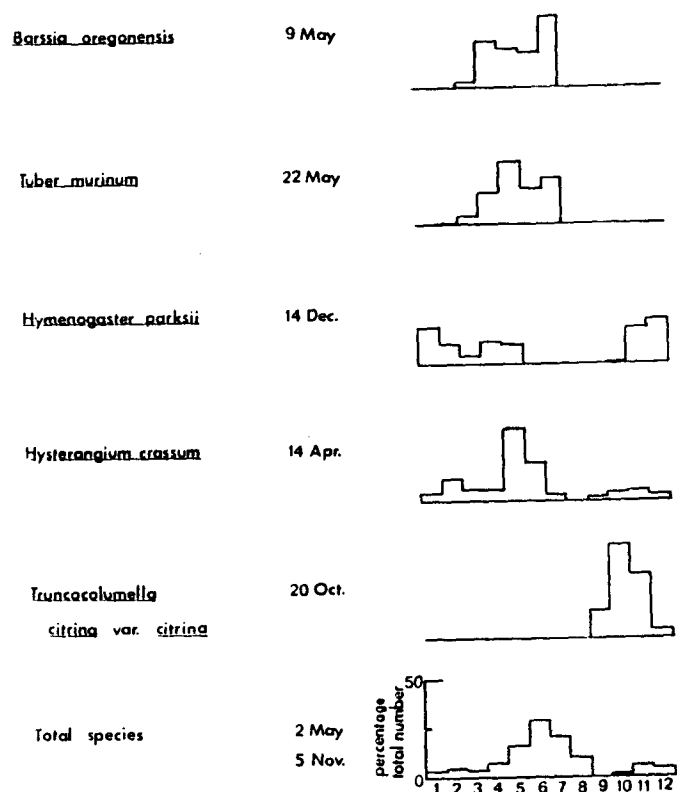
$$m = \frac{d(n)}{N}$$

(2)

Fig. 5 Sporocarp phenology and midpoint of fruiting for major species and the total species population of hypogeous fungi at Woods Creek, Oregon. (From Fogel, 1976.)

where m is the midpoint in days after the starting point, n is the number of sporocarps collected d days after the starting point, and N is the total number of sporocarps collected (Richardson, 1970). Richardson's (1970) epigeous population midpoints for a 5-year study in Scotland range from September 11 to 26, with a standard deviation of 6 days; production peaked in the fall. The mean midpoints for a 3-year study of hypogeous production in Oregon (Table 1) were May 2 and November 5, with standard deviations of 13 and 30 days. The two dates reflect the bimodal production of sporocarps due to summer drought and winter cold, and the standard deviations might reflect the greater variability of western Oregon's climate. The fall middate in Oregon, for

instance, is determined by the timing of the first heavy fall rain and the elapsed time to the first freezing temperatures (Fig. 5).

G. Sporocarp Longevity

Richardson (1970) also reported a linear relationship between mean epigeous sporocarp longevity and the slope of the population decay curve for sporocarps of _Russula emetica_ (Schaef. ex. Fr.) S. F. Gray. The population decay curve was a function of the percentage of total sporocarps observed for a species and the mean time interval between observations. The calculated sporocarp longevity closely corresponded to observed maximum life of marked sporocarps. Hypogeous species have not been similarly analyzed.

H. Major Species

Hering (1966) classified as major species those contributing 5% to the total number of species or biomass production (Table 2). The major species by weight or number generally differed among the 3 years of the Oregon hypogeous study (Fogel, 1976). Major species by weight comprised some 16-24% of the total species, but many commonly occurring species--especially those with small, hollow ascocarps--did not contribute greatly to total sporocarp biomass.

IV. PHENOLOGY

Most mushroom collectors intuitively sense that sporocarp production is related in some way to temperature, precipitation, or both. Fruiting and environmental factors have been graphically compared many times, but apparently only one study has attempted to predict production. Matveev (1972) developed a method to predict the date for mass fruiting of epigeous species in a birch forest near Leningrad. The method, basically a heat-sum approach, also uses the average period for development of sporocarps for each species and the dates of warm ($\geq 12°C$) spring rains. Unfortunately, Matveev did not quantitatively define mass fruiting (numbers or biomass), and he did not compare observed and predicted fruiting dates.

Visual comparison of hypogeous sporocarp production versus mean monthly temperature and total monthly precipitation (Fig. 2) shows that summer drought and cold winter temperature appear to control sporocarp production in western Oregon (Fogel, 1976). Time-series analysis of my Oregon data failed to detect any pattern (R. H. Strand, Oak Ridge National Laboratory, Oak Ridge, Tennessee, personal communication, 1975), and simple linear regressions of sporocarp biomass, mean monthly temperature, and total monthly precipitation were not significant (Table 3). I then stratified the data by assuming that precipitation was limiting during the summer (mean monthly air temperature > 14°C) and that precipitation and temperature were limiting during the rest of the year. The correlation between biomass and temperature was highly significant ($r = -0.818$, $p > 0.01$), as was the multiple correlation between biomass

Table 3 Correlation between biomass of hypogeous sporocarps, mean monthly air temperature, and total monthly precipitation[a]

Variable	$\bar{X}$ monthly air temperature (°C)	r	n	Site[b]
Temperature	≤14	0.646**	20	WC
	≤14	0.711*	3	DC
	>14	-0.818**	12	WC
	>14	-0.754*	6	DC
	1.7 to 19.9	-0.034	16	WC
	3.0 to 19.9	0.079	14	DC
Precipitation	≤14	-0.417*	24	WC
	≤14	-0.333	3	DC
	>14	0.676*	12	WC
	>14	-0.520	6	DC
	1.7 to 19.9	-0.157	16	WC
	3.0 to 19.9	-0.221	14	DC
Temperature and precipitation	≤14	0.646**	20	WC
	>14	-0.828**	11	WC

[a] The data have been analyzed as collected and stratified into summer (temperature > 14°C) and winter (temperature ≤ 14°C) periods.

[b] Site abbreviations are WC for Woods Creek, Oregon (Fogel, 1976) and DC for Dinner Creek, Oregon (Fogel, unpublished data).

and temperature plus precipitation (r = -0.828, p > 0.01). The correlation between biomass and total precipitation of the previous month was slightly less significant (r = 0.676, p > 0.05). During the rest of the year, when the temperature was equal to or less than 14°C, the correlation between biomass and temperature was highly significant (r = 0.646, p > 0.01), as was the multiple correlation with temperature and precipitation (r = 0.665, p > 0.01) (Table 3). The correlation between biomass and precipitation was slightly less significant (r = -0.417, p > 0.05).

I then used a simple model incorporating two of the linear regression equations to predict hypogeous sporocarp biomass in western Oregon (Fig. 6). The correlation between the data used in the regressions and the predicted production was highly significant (r = 0.648, p > 0.01, n = 32), and the visual fit of the two curves was good, although the amplitude of the predicted production was consistently lower than that observed. The model was then used to predict the sporocarp production of Dinner Creek. The correlation was highly significant between observed and predicted production for Dinner Creek, but the fit was poor (Fig. 7). This might be due to the severe drought during the sampling period, because the only significant correlation
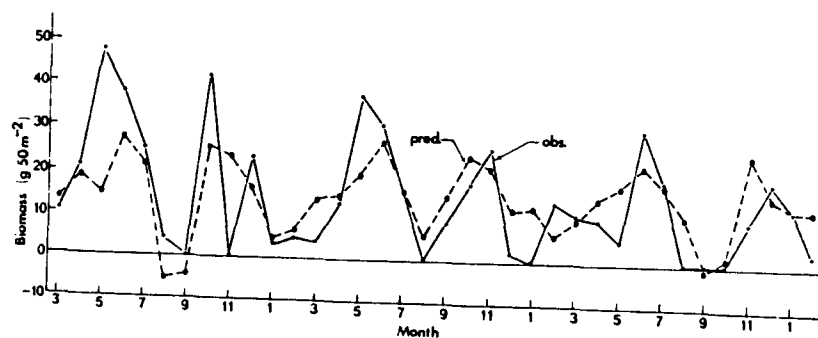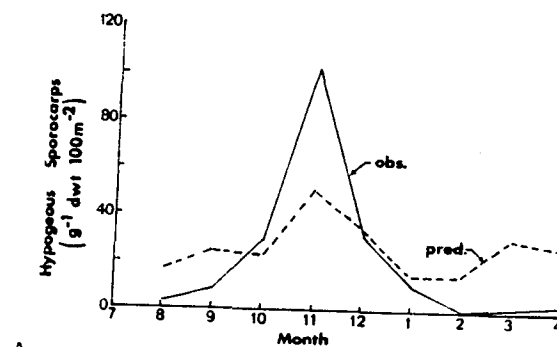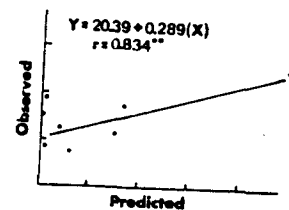
Fig. 6 Simulation of Woods Creek hypogeous sporocarp production from 1972 to 1975. (Author's unpublished data.)

Y = 20.39 + 0.289(X)
r = 0.834**

Fig. 7 (A) Simulation of Dinner Creek hypogeous sporocarp production by the Woods Creek model. (B) Correlation between predicted and observed sporocarp biomass. (Author's unpublished data.)

was between biomass and temperature ($r = -0.754$, $p > 0.05$) (Table 3). Site factors such as cover and aspect might also have had an effect.

Grainger's (1946) data of sporocarp production and environmental data for a different climatic area had a highly significant correlation ($r = 0.693$, $p > 0.01$) between the square root of the number of epigeous species fruiting and mean monthly air temperature (Fig. 3). The correlation between production and precipitation was not significant. Precipitation was not limiting in Grainger's study because of the characteristic high level of summer precipitation in England, contrasting markedly with western Oregon's dry summers.

In summary, sporocarp production by hypogeous and epigeous fungi apparently correlates with environmental factors, and those that are limiting vary with season and climatic region. Other factors, perhaps site or floristic, will have to be incorporated into any general sporocarp production model.

V. SUMMARY

Systematic and periodic sampling of hypogeous sporocarps can yield more information than can collection methods conventionally used by mycologists. Systematic collection permits determination of spatial distribution, phenology, flora, abundance, frequency, species diversity, coefficient of community, middate of fruiting, sporocarp longevity, and major species. Most of these attributes have been investigated only in one western Oregon stand, and different climatic regions or variation along gradients cannot be compared without further research.

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Chapter 29

FUNGAL TAXA, PHYSIOLOGICAL GROUPS, AND BIOMASS:
A COMPARISON BETWEEN ECOSYSTEMS

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I. INTRODUCTION

Fungi in the form of yeasts, mushrooms, toadstools, and molds have occupied man's
general interest for a long time. However, scientific investigation of fungi,
especially invisible soil fungi, is a relative newcomer to biological sciences, the
work of Adametz (1886) being the starting point for serious soil mycological studies.
The communications of Jensen (1912) and Waksman (1916a,b, 1917) ask the question as
to whether there is any fungus flora of the soil and further attest to the recency
of soil mycological studies. Adametz and several others including Reinitzer (1900)
and Nikitinsky (1902) studied their isolates for clues to their biochemical or eco-
logical role in soil.

    As soon as soil fungi were accepted as natural entities in soils, their role
therein became of interest, especially to those investigating soil fertility. Thay-
sen and Bunker (1927) presented a comprehensive review of the activities of fungi in
hydrolysis of cellulose, hemicellulose, pectin, and gums.

    During more recent years numerous publications have proven the ubiquitous occur-
rence of fungi in soils. Lists of taxonomic groups within and between different soils
are common to the literature of fungal ecology, i.e., mycoecology. But taxonomic
listings tell us little of the role played by soil fungi in ecosystem development and
maintenance and nothing of the composite fungal niche in ecosystems.

    From the beginning of the twentieth century fungal activities in the soil have
been discussed and investigated in relation to their role in ammonification, nitrifi-
cation, nitrogen transformation, cellulose decomposition, and humification. These
investigations concerned themselves with organisms isolated from the soil. The meth-
ods and approaches used in different sites by different workers varied, thus fore-
stalling comparative studies among different soils. Until Jones and Mollison (1948),
soil fungi were quantified in terms of the number of their occurrences on soil dilu-
tion agar plates. The inadequacy of such quantification need not be stressed here,
but it should be pointed out that the use of the soil dilution isolation technique
for fungi probably led to the generally held concept that soil bacteria were the