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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1. INTRODUCTION

Fungi are difficult to study in natural habitats because their minute mycelia ramify throughout terrestrial substrates. Most fungi cannot be identified by vegetative characteristics. In the field, even sporocarp-producing fungi whose taxonomy is based on morphology can be difficult 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 specific species from sites where reforestation is difficult can be used to artificially inoculate planting stock for similar sites. Fungi eaten by mycophages can be determined. Sporocarps can be used to compare different plant associations. Possible specific or obligate associations, such as that of Puccinellia distans with its mycorrhizal host L. argutus, 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 Entomophthoraceae. This morphologically 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). In 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 (Harms and Koslowski, 1973; Trappe and Fogel, 1977).

Epigeous fungi, those producing sporocarps aboveground, are easier to study than hypogeous fungi. Consequently, sporocarp production by hypogeous fungi has been re-
The subterranean habit of hypogeous fungi creates several problems in any systematic sampling scheme, because the sporocarps are not visible, simply locating the fungus 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. Hypogeous fungi also fruit in rotten logs that have been invaded by roots of ectomycorrhizal hosts. Pictures of dead grass and the presence of small flies (Hypomyzidae) foraging over ripe sporocarps are clues for Italian truffle collectors (Singer, 1974). The main published 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 taking 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 m²); (2) large (2-4 m²), 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. In Europe (Fig. 3) and Scotland, where sporocarp production is not limited by summer drought, production of hypogeous and presumably hypogeous species peaks in the fall (Grain, 1966; Richardson, 1970).

11. SAMPLING CONSIDERATIONS

Some of the sporocarps have rarely been reported (Richardson, 1970). Second, the structure of the fungus community has been analyzed, usually in relation to the vascular flora (e.g., West, 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 comparatively measured. The fungal florases of different communities have been summarized in species lists (Coret et al., 1945; 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 Arnold, 1926; Ceruti et al., 1967; Montacchini and Caramiello, 1968; Fogel, 1976). Hypogeous flora 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, 1973).

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 stumps larger than 4 cm dbh (diameter at breast height) at Woods Creek, Oregon. (From Fogel, 1976.)
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 inapplicable 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 m² between minimum and maximum production. Unfortunately, the time factor (4–6 man-hours needed to sample 100 m²) severely restrains the number of quadrats that can be thoroughly searched during maximum sporocarp production.

III. COMMUNITY AND POPULATION ATTRIBUTES

Data obtained by irregular collection 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). Haas 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, he collected 24 hypogeous species (11 ascomycetes, 13 basidiomycetes) in a young stand of Douglas-fir in western Oregon (Fogel, 1976); however, during the last year, he 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 mycorrhizal, hypogeous and epigeous floras can be compared better if only epigeous mycorrhizal species are considered. Of the 28 species listed by Richardson (1970), 12 (42.9%) were listed by Temple (1962) as possible mycorrhizal associates. Of the 134 species last year Maas and Stuntz (1970), 22 (16.1%) presumably were mycorrhizal. Sampling for more than 1 year may be necessary to reliably estimate total species number. For example, at Woods Creek, Oregon, I collected 68% of the theoretical hypogeous flora during the first year, 98% the second year, and 96% by the end of the third year. Parker-Hodes (1951) presented a statistical method useful for reducing the number of collections needed to estimate the total number of species per site.

S. 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.)

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 importance-value sequence (i.e., the Simpson index), or by an index of the relative evenness 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 proportion of the epigeous species are infrequently encountered. The low values might reflect 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 communities 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*:  

\[ c = \frac{200(s_{ij})}{s_i + s_j} \]  

28. Quantification of Sporocarps

For example, 87350 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 (9.0-19.4 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).
Table 1. Characteristics of fruiting by year for common species of hypogeous fungi in western Oregon.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gautieria sp.</td>
<td>24 May</td>
<td>21 May</td>
<td>12 Apr.</td>
<td>9 May</td>
</tr>
<tr>
<td>Scleroderma xerocolumellum</td>
<td>22 May</td>
<td>18 Nov.</td>
<td>14 Apr.</td>
<td>23 Jul.</td>
</tr>
<tr>
<td>Geoglossum marxwellii</td>
<td>9 May</td>
<td>12 Jan.</td>
<td>3 Apr.</td>
<td>30 Nov.</td>
</tr>
<tr>
<td>Hysterangium crassum</td>
<td>29 Apr.</td>
<td>26 Apr.</td>
<td>15 Apr.</td>
<td>24 Jul.</td>
</tr>
<tr>
<td>Hysterangium separabile</td>
<td>27 Apr.</td>
<td>9 Apr.</td>
<td>3 Apr.</td>
<td>11 Aug.</td>
</tr>
<tr>
<td>Tuber murinum</td>
<td>23 May</td>
<td>23 May</td>
<td>11 May</td>
<td>2 May</td>
</tr>
<tr>
<td>Total</td>
<td>39.4</td>
<td>77.6</td>
<td>55.9</td>
<td></td>
</tr>
</tbody>
</table>

*From Fogel (1976).*

The middate of fruiting F. Rarity of fruiting

The middate of fruiting, which permits comparison of different sites and prediction of seasonal occurrence of species, is calculated by the formula:

\[ m = \frac{1}{n} \sum F \times \frac{n}{2} \]

where \( F \) is the time spent in fruiting at Dinner Creek, and \( n \) is the number of species. In the case of species that fruit for a prolonged period, the middate is taken as the midpoint of the fruiting period.

*From Fogel (1976).*
**B. Quantification of Sporocarps**

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* (Schaeff. 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 ascohcarps—did not contribute greatly to total sporocarp biomass.

**IV. PHYSIOLOGY**

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, based on a heat-sum approach, also uses the average period for development of sporocarps for each species and the dates of warm (>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. 21) shows that summer drought and cold winter temperature appear to control sporocarp production in western Oregon (Fogel, 1976). Linear series of analysis of my Oregon data failed to detect any pattern (R. H. Strand, Oak Ridge National Laboratory, Oak Ridge, Tennessee, personal communication, 1975). 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 ($r = -0.91$, $p < 0.01$), as was the multiple correlation between biomass
Fogel

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

<table>
<thead>
<tr>
<th>Variable</th>
<th>Temperature (°C)</th>
<th>r</th>
<th>n</th>
<th>Site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Temperature &gt; 14°C</td>
<td>0.646**</td>
<td>20</td>
<td>WC</td>
</tr>
<tr>
<td></td>
<td>Temperature &lt; 14°C</td>
<td>0.711*</td>
<td>3</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>&gt;14</td>
<td>-0.016**</td>
<td>12</td>
<td>WC</td>
</tr>
<tr>
<td></td>
<td>&gt;14</td>
<td>-0.754*</td>
<td>6</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>1.7 to 19.9</td>
<td>0.024</td>
<td>20</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>1.0 to 19.9</td>
<td>0.079</td>
<td>14</td>
<td>DC</td>
</tr>
<tr>
<td>Precipitation</td>
<td>&gt;14</td>
<td>-0.417*</td>
<td>24</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>&gt;14</td>
<td>-0.333</td>
<td>3</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>&gt;14</td>
<td>0.076*</td>
<td>12</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>&gt;14</td>
<td>-0.520*</td>
<td>6</td>
<td>DC</td>
</tr>
<tr>
<td></td>
<td>1.7 to 19.9</td>
<td>-0.157</td>
<td>36</td>
<td>WC</td>
</tr>
<tr>
<td></td>
<td>1.0 to 19.9</td>
<td>-0.221*</td>
<td>14</td>
<td>DC</td>
</tr>
<tr>
<td>Temperature and</td>
<td>&gt;14</td>
<td>0.646**</td>
<td>20</td>
<td>WC</td>
</tr>
<tr>
<td>Precipitation</td>
<td>&gt;14</td>
<td>-0.923**</td>
<td>11</td>
<td>DC</td>
</tr>
</tbody>
</table>

Table data have been analyzed as collected and stratified into summer (temperature > 14°C) and winter (temperature ≤ 14°C) periods. Site abbreviations are WC for Woods Creek, Oregon (Fogel, 1976) and DC for Dinner Creek, Oregon (Fogel, unpublished data).

The data were analyzed using a simple model incorporating two of the linear regression equations to predict hypogeous sporocarp biomass in western Oregon (Fig. 6). The correlation between biomass and mean temperature of the previous month was slightly less significant (r = 0.028, p > 0.01). 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 = 0.065, 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 > 0.01).

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 = 0.34, 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 between observed and predicted production was slightly 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 between observed and predicted production was slightly 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...
such as cover and aspect might also have had an effect.

Grulke'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 epispermic species fruiting and mean monthly air temperature (Fig. 1). The correlation between production and precipitation was not significant. Precipitation was not limiting in Grulke'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 correlate 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, fruits of spores, 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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REFERENCES


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 relatively newcomer to biological sciences, the work of Adametz (1912) being the starting point for serious soil mycological studies. The communications of Jensen (1922 and 1923) 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 ecological 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. Hayman and Bunker (1927) presented a comprehensive review of the activities of fungi in hydrolysis of cellulose, hemi-cellulose, pectin, and gums.

During more recent years numerous publications have proven the ubiquitous occurrence of fungi in soils. Lists of taxonomic groups within and between different soils are common to the literature of fungal ecology, i.e., mycology. 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, nitrification, nitrogen translocation, cellulose decomposition, and humification. These investigations concerned themselves with organisms isolated from the soil. The methods and approaches used in different sites by different workers varied, thus fore-stalling comparative studies among different soils. Until Jones and Allison (1940), soil fungi were quantified in terms of the number of their occurrences on soil dilution 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...