Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas Fir stand

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Sporocarp phenology of hypogeous or subterranean fruiting fleshy fungi was studied between March 1972 and March 1975 in a 40- to 65-year-old Douglas fir stand in western Oregon. Estimates of yearly productivity ranged from 11 052 to 16 753 sporocarps ha^{-1} and 2.3 to 5.4 kg dry weight ha^{-1}. The productivity curve was bimodal as a result of temperature and moisture effects, with peaks in May–June and October. Eleven hypogeous ascomycete species and 13 hypogeous basidiomycete species were collected during the study. Major species that each accounted for 5% or more of the total weight were *Tuber murinum*, *Hymenogaster parksii*, *Hysterangium crassum*, *H. separabile*, and *Truncocolumella citrina* var. *citrina*. Sporocarp moisture content as determined for several species presumably varied with sporocarp age and soil moisture content and ranged from 17.4 to 88.6%. Hypogeous sporocarps had substantially higher macronutrient contents of N, P, and K plus the micronutrients Fe and Al than did epigeous sporocarps of *Fomes pinicola*. Sporocarp numbers increased exponentially with distance from nearest live Douglas fir stem to a peak at 160 to 200 cm, beyond which numbers dropped sharply. The optimum sporocarp zone was slightly less than the average midpoint between tree stems (205 cm).

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Entre mars 1972 et mars 1975, l'auteur a étudié la phénologie du sporocarpe de champignons charnus hypogés ou souterrains, dans un peuplement de sapin de Douglas âgé de 40–65 ans dans l'ouest de l'Orégon. Les estimés de productivité annuelle vont de 11 052 à 16 753 sporocarpes ha^{-1} et de 2.3 à 5.4 kg ha^{-1} en poids sec. Suite aux effets de la température et de l'humidité, la courbe de productivité est bimodale, avec des pics en mai–juin et en octobre. Onze espèces hypogées d'ascomycètes et 13 espèces hypogées de basidiomycètes ont été récoltées durant ce travail. Les principales espèces, chacune contribuant 5% ou plus du poids total, sont les suivantes: *Tuber murinum*, *Hymenogaster parksii*, *Hysterangium crassum*, *H. separabile* et *Truncocolumella citrina* var. *citrina*. La teneur en eau du sporocarpe, déterminée chez plusieurs espèces, s'étend de 17.4 à 88.6% et varie présumément avec l'âge du sporocarpe et la teneur en eau du sol. Chez les sporocarpes hypogés, la teneur en N, P et K et en Fe et Al est substantiellement plus élevée que chez les sporocarpes épigés de *Fomes pinicola*. Le nombre de sporocarpes augmente de manière exponentielle avec la distance à partir du tronc du sapin de Douglas vivant le plus proche, jusqu'à un pic situé à une distance de 160 à 200 cm; au-delà, le nombre de sporocarpes diminue brusquement. La zone optimale pour les sporocarpes se trouve à une distance légèrement inférieure à la mi-distance moyenne (205 cm) entre les arbres.

[Traduit par le journal]

Introduction

The scarcity of quantitative estimates of sporocarp production by fungi hinders efforts to simulate energy flow and nutrient cycling in ecosystems. Such estimates appear to be scarce because study sites are usually not visited often enough to provide adequate quantitative data. Moreover, the importance of mycophagy to small mammals and insects (Fogel 1975, unpublished; Fogel and Peck 1975) is not widely appreciated. Investigations of epigeous sporocarp phenology, including several well designed quantitative studies, have been summarized by Lange (1948) and Cooke (1948, 1953). Richardson (1970) has recently presented results of a 5-year study in a plantation of *Pinus sylvestris* L., as has Endo (1972) for a Japanese evergreen broad-leaved forest.

No quantitative study of hypogeous sporocarp production has been reported. Gross (1969) listed the number of hypogeous sporocarps found during monthly visits to beech and spruce forests in southwest Germany. His data suggested that the production curve was bimodal with peaks in May–June and October–November separated by a summer decline as a result of drought. A qualitative study by Ceruti *et al.* (1967) in northern Italy indicated that temperature mostly influenced fruiting, availability of mycorrhizal hosts and soil moisture were important, soil pH was not important, and each species had a characteristic phenology. Montacchini and Caramiello (1968) reported that July–August precipitation was important in the commercial production of *Tuber magnatum* Pico in the Po River Basin of Italy.

The data presented here are from a study designed to evaluate the applicability of phytosociological methods to study of hypogeous fungi. The main objectives were to quantitatively estimate sporocarp production, to characterize species and phenology, and to evaluate the influence of precipitation and temperature on production.

Locality and Habitat

The study site is located 10 mi (16.1 km) west of Philomath, Oregon, at 44°35′ N latitude, 123°30′ W longitude, at an elevation of 1500 ft (460 m). The site is situated on a bench of about 20 ha with a west aspect and slight slope. The soil is derived from weathered sedimentary rock, has good drainage, and varies from shallow and stoney to deep and fine textured.

The climate is characterized by mild winters (January mean temperature 2.7 °C) and warm, dry summers (July mean temperature 18.5 °C). Annual precipitation totals 1905 mm, mostly as rain. Precipitation during the study averaged 369.2 mm for January and 13.8 mm for July with none in July 1972 or 1973. Climatic data were collected by the Corvallis Water Bureau about 1.6 km SE of the study site and 280 m lower in elevation (Anonymous 1972–1975).

The stand is a well stocked second-generation forest of Douglas fir (*Pseudotsuga menziesii* (Mirb) Franco) 40–65 years old that established after clear-cutting and burning. Scattered shrubs of *Acer circinatum* Pursh (vine maple) and *Berberis nervosa* Pursh (Oregon grape) are present, and the ground cover is a mixture of *Polystichum munitum* (Kaulf.) Presl. (sword fern) and bryophytes. *Phellinus weirii* (Murr.) Gilb. root rot of Douglas fir has caused some openings in the stand. These openings have a ground cover of grasses and *Pteridium aquilinum* (L.) Kuhn. var. *lanuginosum* (Bong.) Fern. (bracken fern). Some wind-toppled trees and dead poles have been salvage-logged.

Methods

Monthly production was estimated from 50 randomly located 1-m^2 quadrats sampled without replacement. A rake was used to carefully remove the litter from each quadrat and then to dig 5–10 cm into the mineral soil, exposing any sporocarps present. Sporocarps of each species from each quadrat were placed in wax-paper bags; all specimens were taken to the laboratory, cleaned of adhering soil, and dried in a forced-air oven at 60 °C for 48 h. Fresh weights were also occasionally recorded.

In addition, a total of four 10 × 10 m quadrats, subdivided into four 5 × 5 m subplots, were used to investigate sporocarp clustering and estimate minimal sampling area. Procedure was the same as in the monthly sample except location of sporocarps and tree stems larger than 4 cm diameter at breast height (dbh) were mapped.

For selected species, those with 1.5 g dry weight from one visit, total sporocarp nitrogen was determined by the micro-Kjeldahl method, and K, P, Ca, Mg, Mn, Fe, Cu, B, Zn, and Al were determined after ashing and dissolution in HCl on a Jarrell-Ash Model 750 atom counter AC spark emission spectrophotometer.

Results

The number of species collected (Table 1) was small compared with floristic lists of epigeous species (Hering 1966; Parker-Rhodes 1951) but was representative of the hypogeous flora of a young western Oregon Douglas fir stand (Fogel, unpublished). *Balsamia nigrens*, a species not previously reported from Oregon was collected twice. Species infrequently encountered in western Oregon otherwise but found during the study included *Melanogaster ambiguus* and *Hydnotyra tulasnei*. One species thought to be rare before the study, *Genea harknessii*, proved to be common. Eleven ascomycete and 13 basidiomycete species were found during the study.

Species contributing 5% to the total annual weight production (Table 2) were considered major species, as was done by Hering (1966). Major species were generally not the same among the 3 years of the study; the same was true of those species contributing 5% to total sporocarp number. Major species by weight accounted for 16 to 24% of the total species. A number of commonly occurring species were not major contributors to sporocarp biomass production.

Seasonal Productivity

The middates of fruiting (Table 3) for individual species and the spring and fall populations as a whole were obtained by the formula

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

where m is the midpoint in days after the starting point, n is the number of sporocarps collected at

TABLE 1. Species list and yearly productivity estimates for hypogeous fungi in western Oregon

Species	Year	Total in 12 × 50 m²	Equivalent no./ha	Mean dry weight of sporocarps, g	Equivalent dry weight, g/ha
Total	1	1005	16 753	0.32	5408
	2	663	11 052	0.27	2975
	3	784	13 069	0.17	2267
Balsamia nigrens Harkn.	1	2	33.3	0.20	7
	2	0	0.0	0.00	0
	3	1	16.7	0.13	2
Barssia oregonensis Gilkey	1	56	933.5	0.18	168
	2	34	566.8	0.23	130
	3	29	483.4	0.20	97
Elaphomyces granulatus Fr.	1	0	0.0	0.00	0
	2	0	0.0	0.00	0
	3	12	200.0	0.45	90
Genabea cerebriformis (Harkn.) Trappe	1	5	83.4	0.01	1
	2	63	1050.2	0.02	21
	3	5	83.4	0.08	7
Genea harknessii Gilkey	1	137	2283.8	0.08	183
	2	27	450.1	0.12	54
	3	12	200.0	0.10	20
Genea intermedia Gilkey	1	13	216.7	0.02	4
	2	2	33.3	0.04	1
	3	0	0.0	0.00	0
Geopora cooperi Harkn. f. *cooperi*	1	4	66.7	0.19	13
	2	2	33.3	0.20	7
	3	0	0.0	0.00	0
Hydnotrya tulasnei (Bk.) Bk. & Br.	1	0	0.0	0.00	0
	2	0	0.0	0.00	0
	3	1	16.7	0.12	2
Tuber gibbosum Harkn.	1	30	500.1	0.76	380
	2	7	116.7	0.63	74
	3	0	0.0	0.00	0
Tuber murinum Hesse	1	100	1667.0	0.22	367
	2	124	2067.1	0.12	248
	3	48	800.2	0.20	160
Tuber rufum Fr. var. *rufum*	1	4	66.7	0.30	20
	2	7	116.7	0.37	43
	3	0	0.0	0.00	0
Tuber sp.	1	24	400.1	0.05	20
	2	0	0.0	0.00	0
	3	0	0.0	0.00	0
Gautieria sp.	1	4	66.7	0.20	13
	2	32	533.4	0.81	432
	3	2	33.3	3.16	105
Hymenogaster parksii Zeller & Dodge	1	58	966.9	0.45	435
	2	70	1166.9	0.31	362
	3	24	400.1	0.19	76
Hysterangium crassum (Tul. & Tul.) Fischer	1	262	4375.4	0.18	788
	2	172	2872.4	0.18	517
	3	516	8617.2	0.14	1206

TABLE 1. (*Concluded*)

Species	Year	Total in 12 × 50 m²	Equivalent no./ha	Mean dry weight of sporocarps, g	Equivalent dry weight, g/ha
Hysterangium occidentale Harkn.	1	0	0.0	0.00	0
	2	3	50.0	0.28	14
	3	0	0.0	0.00	0
Hysterangium separabile Zeller	1	188	3139.6	0.16	502
	2	73	1216.9	0.47	572
	3	110	1837.0	0.16	294
Martellia ellipsospora (Zeller) Sing. & Sm.	1	0	0.0	0.00	0
	2	1	16.7	0.60	10
	3	6	100.0	0.34	34
Martellia parksii Sing. & Sm.	1	0	0.0	0.00	0
	2	1	16.7	0.72	12
	3	0	0.0	0.00	0
Martellia sp.	1	4	66.7	0.11	7
	2	0	0.0	0.00	0
	3	0	0.0	0.00	0
Melanogaster ambiguus (Vitt.) Tul. & Tul.	1	0	0.0	0.00	0
	2	1	16.7	1.93	32
	3	0	0.0	0.00	0
Rhizopogon parksii Sm.	1	5	83.4	0.52	43
	2	5	83.4	0.97	81
	3	0	0.0	0.00	0
Rhizopogon villosulus Zeller	1	12	200.0	0.23	46
	2	8	133.4	1.28	171
	3	4	66.7	1.58	105
Rhizopogon vinicolor Sm.	1	0	0.0	0.00	0
	2	9	150.0	0.22	33
	3	5	83.4	0.47	39
Truncocolumella citrina Zeller var. *citrina*	1	96	1600.3	1.46	2336
	2	20	333.4	0.28	93
	3	9	150.0	0.20	30
Zelleromyces gilkeyae Sing. & Sm.	1	1	16.7	4.48	75
	2	2	33.3	2.03	68
	3	0	0.0	0.00	0

d days after the starting point, and N is the total number of sporocarps observed (Richardson 1970). End points for the seasonal midpoint calculations were those sample dates with no sporocarps.

The dependence of the fall crop on precipitation (Figs. 1, 2) might explain the greater variability in its population midpoint (Table 3, Fig. 3) compared with the spring crop. Comparison of the 1974 fall peak with the two previous years' fall peaks and their associated precipitation patterns (Fig. 1) clearly shows this dependence. The spring production peak shows a logarithmic increase when the mean minimum temperature exceeds 0 °C (6 °C mean maximum temperature) until it reaches 6 °C (23 °C mean maximum temperature). During this period, precipitation is usually less than 5 cm and evaporative demand steadily depletes the moisture content of the soil and litter. The fall

TABLE 2. Species accounting for 5% or more of productivity of hypogeous fungi in western Oregon

Species	Percentage of total weight		
	Year 1	Year 2	Year 3
Gautieria sp.	—	14.5	—
Hymenogaster parksii	8.0	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	88.9	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	5.8	10.6	—
Hysterangium crassum	26.1	25.9	65.8
Hysterangium separabile	18.7	11.0	14.0
Truncocolumella citrina var. *citrina*	9.6	—	—
Tuber murinum	10.0	18.7	6.1
Total	89.4	77.6	85.9

production peak begins when precipitation is at least 0.5 cm month^{-1} and gradually increases until the mean minimum temperature drops to 4 °C (18 °C mean maximum temperature).

Although fewer sporocarps were found (Fig. 1) during fall, the variance (Table 3) was less than for spring and the biomass was comparable with spring. Small, lightweight sporocarps of vernal ascomycetes, i.e., *Genabea cerebriformis* and *Genea harknessii*, accounted for the larger number of sporocarps found during the spring than fall. No difference in the relative frequency of Ascomycetes and Basidiomycetes was discernible. Three different phenological species groups (Table 3, Fig. 2) were identified. *Truncocolumella citrina* var. *citrina* and *Rhizopogon parksii* were characteristic fall species. Spring species included *Rhizopogon vinicolor*, *Barssia oregonensis*, *Genabea cerebriformis*, and *Tuber murinum*. Winter was represented by *Hymenogaster parksii*, although it continued to fruit during spring. Opportunistic species that fruited whenever conditions were suitable included *Hysterangium separabile* and *H. crassum*.

Sociology

Production of sporocarp clusters (Fig. 3) is characteristic of hypogeous as well as epigeous fungi. Depending on species, three distinct patterns (Fig. 3) of sporocarp clustering were identified. The first pattern was the wide scattering of single or a few sporocarps over a large area, i.e., *Hymenogaster parksii*, *Barssia oregonensis*, and *Tuber murinum*. A second pattern was of large, loose, gregarious clusters formed by *Genabea cerebriformis*. The third pattern was of arcs and partial arcs, 'fairy rings,' produced by the tight sporocarp clusters characteristic of *Hysterangium crassum*. Gregarious species such as *Genabea cerebriformis* and *Hysterangium crassum* had smaller sporocarps than those with isolated sporocarps. However, a relationship between sporocarp size and clustering is coincidental to the study area since gregarious hypogeous species with large sporocarps also exist, e.g. in *Rhizopogon* and *Elaphomyces*.

TABLE 3. Middates of fruiting by year for common species of hypogeous fungi in western Oregon

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.	56	Nov.–June
Hymenogaster parksii	—	18 Jan.	9 Nov.	14 Dec.	50	Oct.–June
Hysterangium crassum	29 Apr.	28 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.	20 Oct.	25	Sept.–Dec.
Tuber murinum	28 May	6 May	10 June	22 May	15	Feb.–July
Spring peak	—	23 Apr.	11 May	2 May	13	—
Fall peak	10 Oct.	30 Oct.	8 Dec.	5 Nov.	30	—

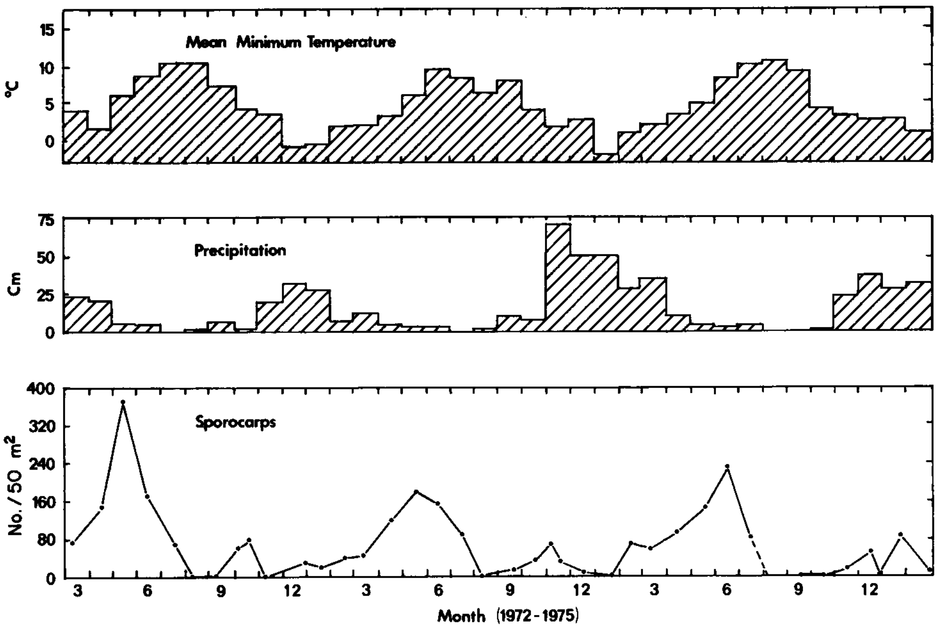

FIG. 1. A 3-year comparison of sporocarp production by hypogeous fungi with corresponding temperature and precipitation in western Oregon. Summer drought and cold winter temperature appear to control sporocarp number.

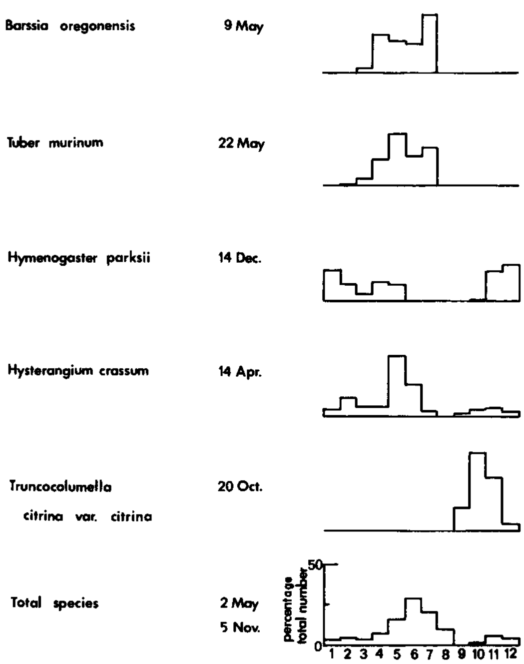

FIG. 2. Sporocarp phenology and midpoint of fruiting for several major species and the total species population of hypogeous fungi in western Oregon.

Distribution maps of the four 10 × 10 m quadrats provided additional information on sporocarp clusters and their relationship to Douglas fir stems larger than 4 cm dbh. Numbers of sporocarps increased logarithmically in distance from the nearest live tree to an optimum at 160 to 200 cm, then decreased sharply beyond 200 cm (Fig. 4). The optimum sporocarp zone was slightly less than half the mean distance between tree stems (410 cm). The number of sporocarp clusters was similarly related to distance from the nearest live tree stem.

Water and Nutrient Content of Common Species

Sporocarp moisture content of selected species ranged from 17.4 to 88.6% dry weight with a mean of 80.3% and a standard deviation of 4.7% (Table 4). Moisture content apparently varied with sporocarp age and soil moisture content. A *Hysterangium crassum* sporocarp collected 10 August 1972 after a 57-day dry period, for example, had a moisture content of 17.4% compared with the average of 75.2% (Table 4).

Sporocarps of hypogeous fungi from western Oregon had substantially higher macronutrient contents of nitrogen, phosphorus, and potassium

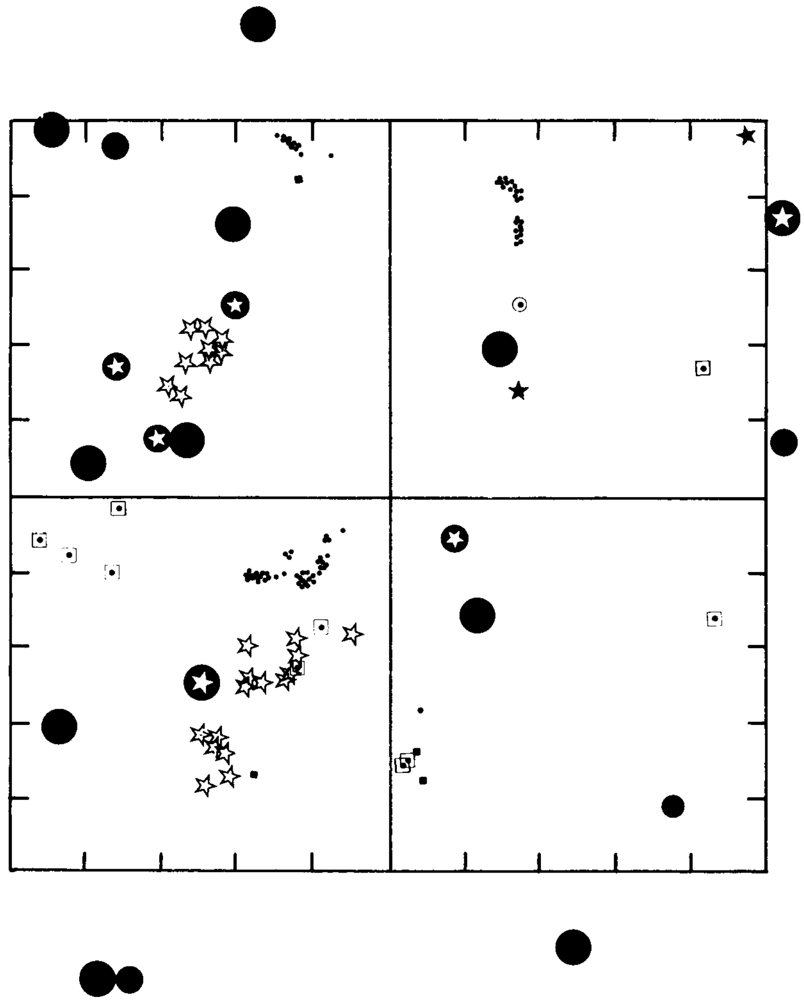

FIG. 3. Distribution of hypogeous sporocarps on a 10 × 10 m quadrat subdivided into 5 × 5 m subplots in relation to Douglas fir stems larger than 4 cm dbh in western Oregon. Plot sampled 16 May 1973. ●, live Douglas fir; ✪, dead Douglas fir; ★, *Hymenogaster parksii*; ☆, *Genabea cerebriformis*; ■, *Tuber murinum*; ⊡, *Barssia oregonensis*; ⊙, *Genea harknessii*; ●, *Hysterangium crassum*.

plus the micronutrients iron and aluminum than sporocarps of the wood-rotting fungus *Fomes pinicola* (Table 5). The higher macronutrient concentration of hypogeous sporocarps might be due to their higher proportion of reproductive tissue: spores should be particularly rich in nitrogen, phosphorus, and potassium. It might also be due to the growth of *F. pinicola* on a nutrient-poor substrate.

Discussion

Sampling hypogeous sporocarps presents certain problems since it is analogous to sampling the ephemeral fruit of an apple tree with the tree hidden from view. Removal of sporocarp-concealing litter and humus can be hard work, and no consistently good method of predicting sporocarp location has existed. Mueller-Dombois and Ellenberg (1974) define minimal area for population sampling as the quadrat size that contains 90 to 95% frequency for one species or as the species number asymptote derived from a species–area curve. The first approach is impractical for hypogeous fungi since the species population as represented by sporocarps is constantly changing. By using a species–area

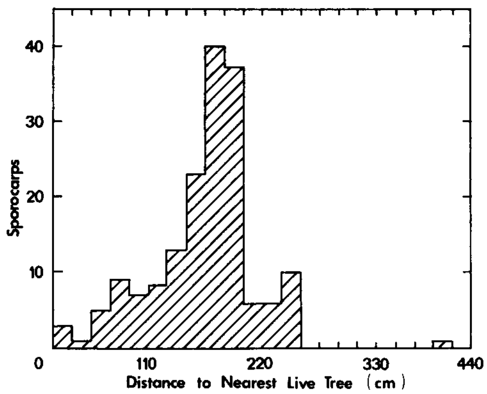

FIG. 4. Distance of hypogeous sporocarps from nearest live Douglas fir stem in western Oregon, calculated from data from three 10 × 10 m quadrats sampled 23 October 1972, 4 April 1973, and 16 May 1973.

TABLE 4. Sporocarp moisture content of hypogeous fungi in western Oregon

Species	Mean percentage dry weight	Standard deviation	Samples
Barssia oregonensis	76.6	9.12	10
Balsamia nigrens	76.6		1
Gautieria sp.	79.8		1
Genea harknessii	77.3	6.22	11
Geopora cooperi f. *cooperi*	87.7		1
Hymenogaster parksii	85.6	3.54	17
Hysterangium crassum	75.2	7.98	28
Martellia sp.	81.9	8.84	2
Rhizopogon parksii	88.6	3.71	3
Truncocolumella citrina var. *citrina*	82.3	3.93	16
Tuber gibbosum	81.1	6.72	6
Tuber murinum	74.8	6.21	22
Zelleromyces gilkeyae	76.7		1
Total	80.3	4.70	13

curve constructed from three of the four 10 × 10 m quadrats, I determined that the minimal area is 100 m^2 at the peak of sporocarp production. Careful removal of litter and humus and raking 5–10 cm into mineral soil in a young Douglas fir stand free of understory vegetation requires 4 to 6 man-hours for an area of this size. As a result of time limitations, the monthly estimates presented in this paper are based on an area of 50 m^2. Consequently, because of time limitations and mycophagy, sporocarp numbers and biomass may be underestimated.

Comparison of cumulative number of species observed versus year shows that the theoretical species number or floristic list is closely approximated by an asymptote of 25 species. During the first year, 68% of the theoretical flora was collected, 88% in the second year, and 96% in the third year. The corresponding percentages for species numbers found in each year are 68, 84, and 60%.

The 24 species comprising the Woods Creek hypogeous flora compares favorably with the 17 species reported from an Italian oak stand, 12 from a German red beech stand, and 17 from a German spruce stand (Ceruti *et al.* 1967; Gross 1969). Floristic lists of epigeous species in European and Japanese forests have ranged from 28 to 190 species (Richardson 1970; Endo 1972; Hering 1966; Parker-Rhodes 1951); no comparable data are available for Douglas fir forests. Undoubtedly all nutritional groups of fungi were included in the epigeous floristic lists. Of the 28 epigeous species listed by Richardson (1970), for example, 12 or 42.9% of the total species are presumably mycorrhizal like hypogeous fungi (Trappe 1962).

The middates of fruiting for individual species and the population as a whole (Table 3) can be used to compare different studies and as a guide in collecting. Richardson's (1970) population midpoints for 5 years range from 11 to 26 September, indicating a single peak in sporocarp production with a standard deviation of 6 days. The Woods Creek population has two middates, which reflects the bimodal production of sporocarps resulting from summer drought. The greater variance in the Woods Creek population middates is probably due to the greater variability in western Oregon climate. The large standard deviations in middates of *Genea harknessii*, *Hymenogaster parksii*, and *Genabea cerebriformis* may be due to climate, longer fruiting seasons, greater individual variance in the number of sporocarps produced by hypogeous fungi, or an inadequate sample.

The Woods Creek dry weight production of 2.3 to 5.4 kg ha^{-1} $year^{-1}$ has to be compared with epigeous studies since there are no published data on weight production by hypogeous fungi. Hering (1966) estimates fresh weight production by epigeous species, based on his work and four literature reports, to range from 3 to 302 kg ha^{-1} $year^{-1}$. By using Richardson's (1970) conversion figure of 6.36% dry weight content for epigeous species, the range in epigeous production would be from 0.19 to 19.2 kg dry weight ha^{-1} $year^{-1}$,

TABLE 5. Nutrient content of hypogeous fungi in western Oregon

Species	Percentage dry weight					PPM						
	N	K	P	Ca	Mg	Mn	Fe	Cu	B	Zn	Al	Samples
Gautieria sp.	1.66	1.40	0.41	0.02	0.12	4	203	27	5	37	482	2
Hymenogaster parksii	2.21	2.21	0.88	0.29	0.12	38	1427	34	9	96	1433	3
Hysterangium crassum	1.53	0.77	0.48	0.45	0.11	65	1102	15	6	66	1359	1
Rhizopogon occidentalis	2.00	1.77	0.53	0.01	0.03	5	434	5	1	48	641	1
Truncocolumella citrina var. *citrina*	1.53	1.79	0.52	0.03	0.02	24	818	14	8	24	1445	1
Average content	1.79	1.59	0.56	0.16	0.08	27	797	19	6	54	1072	8
Fomes pinicola	0.47	0.10	0.03	0.07	0.14	62	163	6	0	45	176	3

slightly lower than Richardson's (1970) estimate, based on more visits, of 16 to 30 kg dry weight ha^{-1} $year^{-1}$ (9.8 to 19.4 kg dry weight ha^{-1} $year^{-1}$ mycorrhizal). A direct comparison of sporocarp numbers with other studies on hypogeous fungi is not possible because Gross (1969) and Ceruti *et al.* (1967) did not use plots with specified area. Estimates of epigeous sporocarp numbers range from 7 000 to 489 800 sporocarps ha^{-1} $year^{-1}$ compared with 11 052 to 16 753 sporocarps ha^{-1} $year^{-1}$ observed during this study (Hering 1966; Richardson 1970). There is greater similarity between epigeous and hypogeous sporocarp numbers if epigeous mycorrhizal species are used for the comparison. Reexamination of Richardson's (1970) data, for example, showed that his estimated 239 000 to 489 800 sporocarps ha^{-1} $year^{-1}$ only included 8 750 to 20 250 sporocarps of epigeous mycorrhizal species or 1.8 to 8.5% of the total sporocarps.

Sampling would be more efficient if areas of sporocarp concentration could be identified. The relationship between sporocarp clusters and distance to nearest live tree (Fig. 4) suggests that such an approach is feasible. It might be further refined if cluster location could be related to root distribution, logs, or perhaps drainage patterns. Ogawa (1969) has described 'fairy ring' colonies produced by the epigeous mycobiont *Tricholoma matsutake* (Ito and Imai) as consisting of a high concentration of rhizomorphs and mycorrhizae on the growing front of the colony and decaying hyphae on the trailing edge. Most or all of the hypogeous fungi collected at Woods Creek are probably mycorrhizal species (Trappe 1962, 1971, and unpublished data) and might exhibit a similar relationship to fine roots. *Hysterangium crassum*, for example, forms large distinctive beds of white flocculose rhizomorphs and mycorrhizae, a metre or more in diameter, that can be identified without the presence of sporocarps.

Environmental control of sporocarp production, particularly by temperature and moisture, is known to all mushroom collectors. Wilkens and Patrick (1940) report a bimodal fruiting pattern for grassland fungi and suggest that the "well known summer and autumn fungus seasons are due to the fact that only at these two periods of the year does synchronization of favorable factors make sporophore production possible." They suggest, in addition, that the minimum temperature for production should be above 5 °C, the maximum temperature below 30 °C, and the soil water content above 20%. Setchell and Watson (1926) state that the temperature for production of *Hysterangium* sp., a hypogeous fungus, ranges from 8.9 °C to 13.3 °C and that sporocarp production varies with moisture supply. Wilkens and Harris (1946) report that sporocarps could be produced in a beech forest when the water content of the litter exceeds 50% and the mean minimum temperature is above 4 °C. Overall sporocarp production in Oregon (Fig. 1) has similar environmental limits. The fruiting of an individual species (Fig. 2) is not as easily explained and may depend on cold conditioning, energy reserves in mycorrhizal host roots, or other stimuli since similar ranges of temperature and moisture are present in both spring and fall.

The reproductive tissue of hypogeous fungi is enclosed within somatic tissue and most species lack forcible spore discharge. Consequently, they must depend on mycophagy or physical movement, i.e., rainwater, for spore dispersal. Reported mycophagists include arthropods, slugs, small mammals, deer, bears, and baboons (Buller 1909; Fogel 1975; Fogel and Peck 1975;

Strode 1954). Mycophagists in turn have evolved a dependence on fungi with yearly dietary volume for several small species ranging from 1 to 72% (Fogel, unpublished). Another indication of the importance of mycophagy is the drying and caching of fungi by squirrels (Cram 1924; Hardy 1949).

During this study *Truncocolumella citrina* var. *citrina* and a *Gautieria* species were found cached from 30 to 60 cm above the ground in rotten stump and log cavities. On one occasion a *Tamiasciurus douglasii* (Bachman) (Douglas squirrel) was observed eating a *Truncocolumella citrina* var. *citrina* sporocarp while perched on a stump 1 m above the ground. Douglas squirrels were also observed digging in the forest floor and on one occasion a squirrel was chased away from a *Rhizopogon vinicolor* sporocarp it was unearthing. Judging from the number of pits dug in the forest floor of the study area by rodents, hypogeous fungi were an important food item at least seasonally and may have affected quantitative sporocarp estimates, but no attempt was made to quantify rodent consumption.

The food value of hypogeous fungi is difficult to assess. Tevis (1952) reports that *Eutamias* stomachs containing hypogeous fungi only are heavier than those of animals feeding on non-fungal material. He also reports that when chipmunks begin to acquire hibernation fat, those that eat fungi become fat sooner. The lower content of N, P, and K in the wood-rotting fungus *Fomes pinicola* (Table 5) compared with hypogeous fungi emphasizes that some fungi may have less food value than others.

The fallacy of regarding fungi as either saprophytes or parasites in natural ecosystems has already been exposed by Harley (1971), but I would like to reinforce his point by estimating the amount of energy needed to produce sporocarps of hypogeous ectomycorrhizal fungi. Assuming a 10% conversion efficiency, 23 to 54 kg dry weight of photosynthate is needed to produce the annual crop of hypogeous sporocarps in the young western Oregon Douglas fir stand at Woods Creek. Only a small portion of the photosynthate utilized by mycorrhizal fungi is accounted for in hypogeous sporocarps since epigeous sporocarps and vegetative hyphae in soil are not included.

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