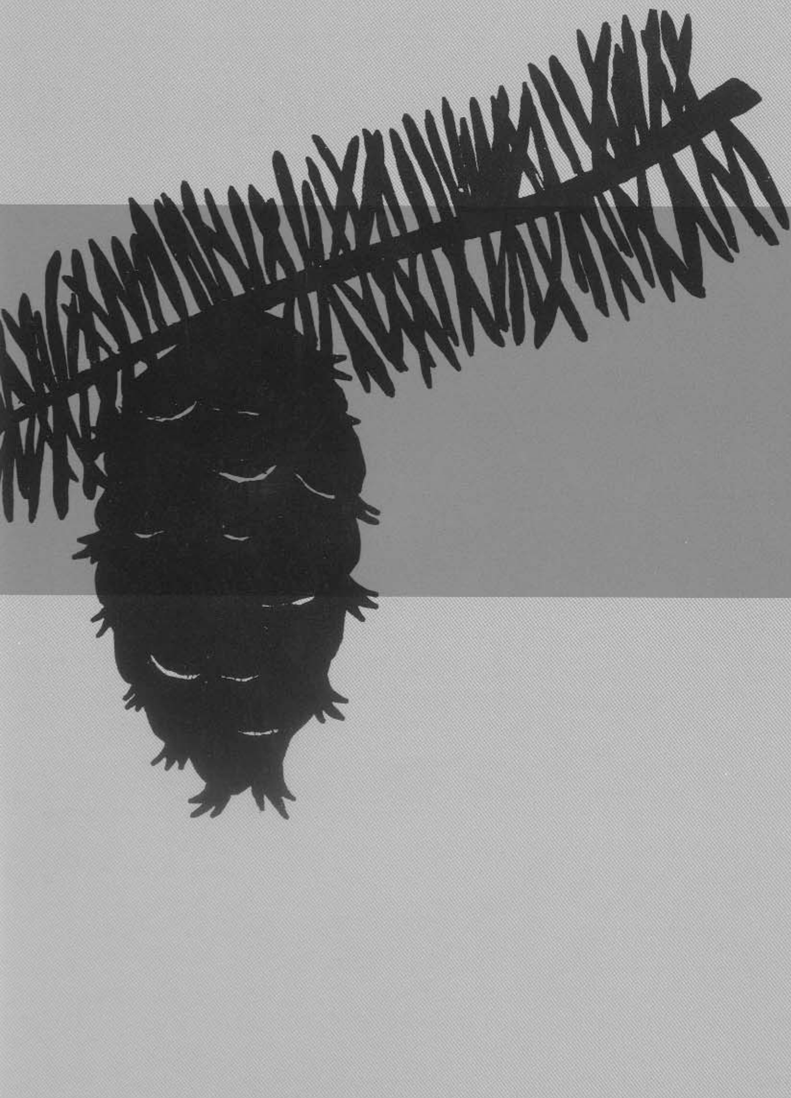

Part 3

Douglas-Fir Forests of Oregon and Washington

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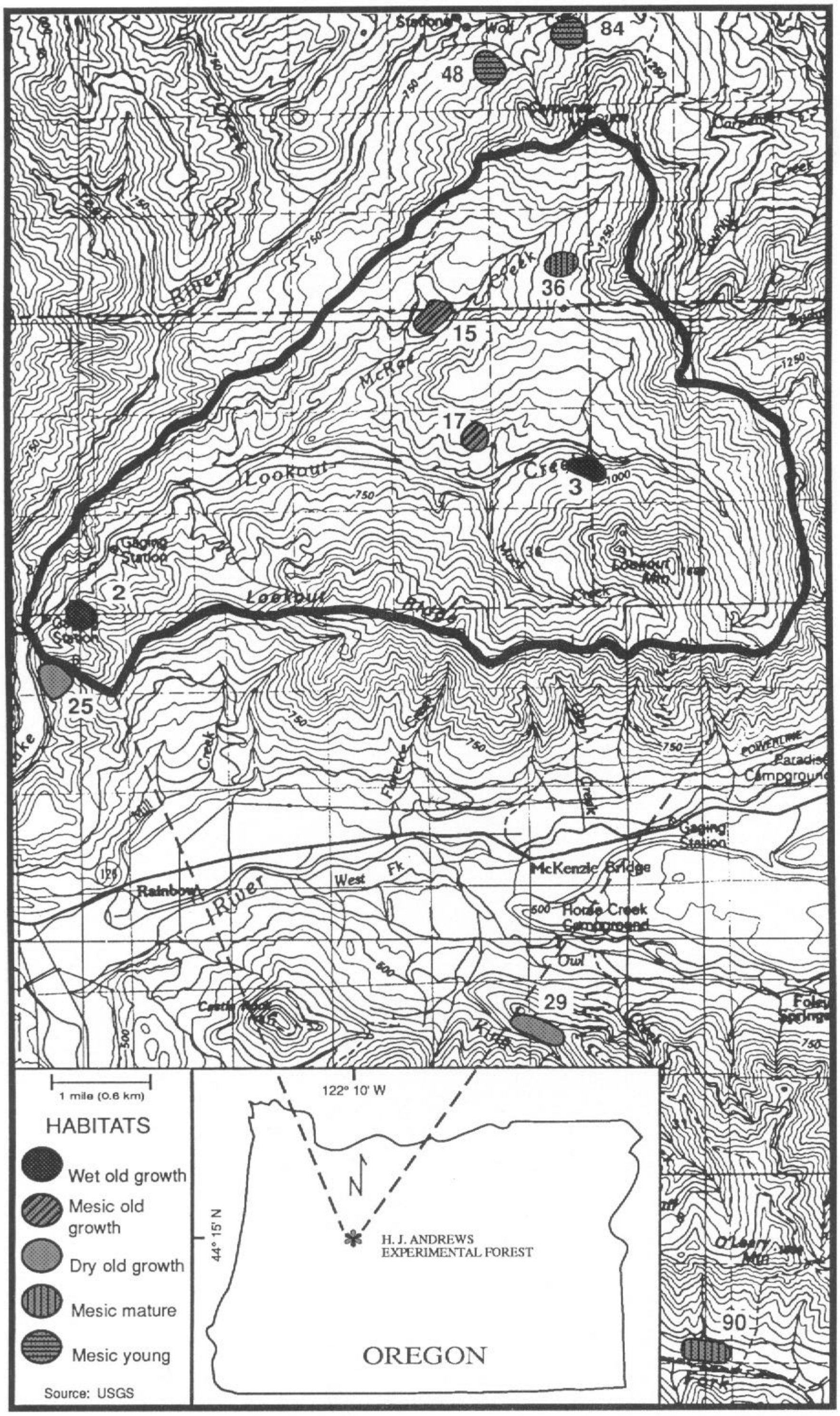

Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

Annual Changes in Seasonal Production of Hypogeous Sporocarps in Oregon Douglas-Fir Forests

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Abstract

Sporocarps of hypogeous ectomycorrhizal fungi were harvested from 10 Douglas-fir stands representing a variety of natural habitats. Results are presented in a landscape context by assuming that the reported sporocarp production is representative of Western Hemlock Zone forests in the central western Cascade Range of Oregon. Over all stands, sporocarps were harvested from 5400 m^2 and yielded a total dry standing biomass equivalent to 1.3 kg per ha. The maximum single-stand sample biomass equaled 9.9 kg per ha. Forty-seven species of hypogeous fungi were recorded. Elaphomyces granulatus, Gautieria monticola, Hysterangium coriaceum, Leucogaster rubescens, and Rhizopogon parksii accounted for 73 percent of the biomass.

In contrast to epigeous species in the study area, hypogeous sporocarp production was higher in spring than in fall, Individual fungal species showed strong seasonal trends; most had spring production peaks. Year-to-year variation in relative biomass for individual species was greater in spring than in fall. The major species in this study were also major species in studies from young Douglasfir stands in the Oregon Coast Range. Gautieria monticola, in particular, seems to be a widespread dominant species in Western Hemlock Zone forests of western Oregon.

Introduction

Cooke (1972) defines mycocoenologists as "mycologists with ecological orientation, [or] ecologists with mycological interests." Arnolds (1981) considers a mycocoenological approach to ecological research as one that usually uses sample plots (quadrats) to inventory macrofungi in stands of well-defined plant communities or selected habitats. The goals of such research are to describe the fungal composition of a particular plant community and to draw conclusions about relationships between fungi and vegetation on a quantitative and qualitative basis.

Vegetation has long been used to assess site quality and to help identify the importance of various environmental factors (Cajander 1949). In the Pacific Northwest, quantification and classification of vegetation in combination with autecological observations has furthered development of the plant association and habitat type concepts (Daubenmire 1968, Hemstrom and others 1987, Zobel and others 1976). The prevailing regional system of plant community classification in the

Pacific Northwest greatly facilitated the execution of myco-coenological research by freeing the investigator of the need to conduct elaborate vegetation studies to classify sample stands. This study was part of a regional characterization of Douglas-fir forests from which Spies and others (1988) provided the habitat classification.

Studies of the community ecology of macrofungi have lagged far behind those of vascular plants. Several daunting challenges face the would-be mycocoenologist. Arnolds (198 1) provides a summary of some of these difficulties: fungal species concepts are often poorly understood and defined; collections are difficult to identify morphologically and often require considerable research to reach independent taxonomic decisions; research is limited to the study of sporocarps (fruiting bodies), which are strongly seasonal (Hueck1953), are subject to yearly variation caused by variable weather patterns, and exhibit varying, largely unknown, rates of decay and predation; sporocarp production is not necessarily related to the abundance or activity of the mycelial colony; and, autecological research is lacking both in the field, where it is hampered by the concealed nature of the fungal colonies and in the laboratory where it is constrained by the investigators' inability to relate the conclusions to field situations with confidence.

Fungi that produce hypogeous (belowground) sporocarps (broadly referred to as truffles) pose additional challenges. The sporocarps are not only hidden from view, but are also often preferentially sought and consumed by small animals (Ure and Maser 1982). Although quantitative community studies of epigeous (fruiting above the ground) fungi have been reported since at least 1933 (Haas), Fogel (1976) was the first to provide a quantitative assessment of hypogeous sporocarp production. Most of the fungal species producing hypogeous sporocarps are thought to be ectomycorrhizal (fungi which develop mutually beneficial associations in the exterior layers of the roots of certain plants) (Castellano and others 1989; Trappe 1962, 1971). Mycorrhizal fungi act as extensions of the root system in forest trees and are thus important to their nutrition (Tmppe and Fogel1978).

Currently, the only practical way to compare the relative functional importance of species of ectomycorrhizal fungi in an ecosystem is by estimating sporocarp production. Potential functional roles of hypogeous species range from essential symbiosis with the roots of over-story trees (Harley and Smith 1983) to provision of sporocarps as food for animals (Vogel and Trappe 1978).

Several recent studies focused on sporocarp production by hypogeous fungal species in the Coast Range of western Oregon. Fogel (1976) was the first to quantitatively analyze the seasonal distribution of hypogeous sporocarps; he used sporocarp dry weight and number to calculate mid-dates of fruiting for individual species and populations.

In a 13-month study including the end of a severe winter drought, Fogel and Hunt (1979) observed a strong fall peak in total sporocarp dry weight. Fogel (1981) reviews techniques for quantifying hypogeous sporocarps and correlates sporocarp production with temperature and moisture. Hunt and Trappe (1987) point out that documenting all species of hypogeous fungi in a forest stand requires longterm collecting over several years. Underestimation of species richness due to small stand samples and infrequent fruiting of some species was noted by Hunt and Trappe (1987). After 32 months of collection with a total sample area of 1536 m^2, their species-area curve still had not stabilized.

The cited studies were confined to single, similar, second-growth Douglas-fir stands on Marys Peak in the Oregon Coast Range, which had all developed over 35 to 65 years after clearcut logging and burning. An obvious need existed to characterize the occurrence of hypogeous sporocarps in a landscape context from a variety of natural habitats over a wider forest area.

This research aims at broadening the data on year-to-year changes in the seasonal distribution of sporocarp production and reports the sporocarp abundance of major species (Hering 1966) of hypogeous fungi found in 10 forest stands in the H. J. Andrews Experimental Forest (Oregon Cascade Range physiographic province). Standing crop sporocarp biomass was measured within five Douglas-fir forest habitats covering a range of moisture- and age-classes. To obtain a representative sample of the major species and to document the differences in sporocarp production that are largely induced by yeartoyear changes in weather patterns, the study spanned a 4-year period. Seasonal variation in fruiting pattern was anticipated through intensive spring and fall sampling. The following specific objectives were addressed: identification of the major fungal species that produce hypogeous sporocarps in Douglas-fir stands typical of the central Oregon Cascades; characterization of the seasonal fruiting aspect as determined by the major species; and determination of yeartoyear changes in the seasonal distribution of each major species as measured by sporocarp biomass.

Materials and Methods

Study Area

The H. J. Andrews Experimental Forest occupies the 6400-ha drainage of Lookout Creek, a tributary of the McKenzie River (see frontispiece). Elevations range from 420 to 1630 m. The area is typical of the western slopes of the central Cascade Range in Oregon. The experimental forest has been administered by the USDA Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948.

A cool-summer Mediterranean climate prevails in the study area. Average annual precipitation ranges from about 2300 to 2800 mm, depending on topography. About 90 percent of the precipitation occurs from October through April; summers are dry. Above 900-m elevation, winter snowpacks accumulate to a depth of 1 m or more. Temperatures are moderate and range from -2 (mean January minima) to 28 ^{o}C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Bierlmaier and McKee 1989, Franklin and Dyrness 1971).

Inceptosols dominate the three general soil types that are characteristic of the experimental forest (Bemtsen and Rothacher 1959, Brown and Parsons 1973, Dymess and others 1974, Franklin and Dymess 1973). Steeper slopes and ridgetops often support a residual Brown Podzolic gravelly clay loam formed from andesite or basalt. Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams associated with breccia and tuff parent material are commonly found on midslopes. Gentle slopes and benches are often occupied by a colluvial clay loam.

The study area lies generally within the Western Hemlock Zone of Franklin and Dymess (1973). Studies of forest communities within the Western Hemlock Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Zobel and others 1976). Characteristic understory vascular plant species are used to describe the community types. For example, abundant sword fern and Oregon oxalis typify moist sites. Mesic sites may be occupied by Oregongrape and Pacific rhododendron. Towards the dry end of the scale, salal increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities of the Douglas-fir series. In these communities, Douglas-fir is often considered climax and oceanspray is an important shrub (Hemstrom and others 1987). A temperature gradient reflecting elevation is also noted (Zobel and others 1976). The coolest extreme is represented by the Western Hemlock-Pacific Silver Fir/Twinflower association, transitional to associations in the Pacific Silver Fir Zone.

Sampling

Ten Douglas-fir forest stands were selected for sampling by age and moisture status. Age-classes were <80,80 to 199, and 2200 years of age and are referred to in this paper, respectively, as young, mature, and old-growth. Relative moisture-classes prevailing at these sites were identified by generalized vascular plant habitat or community types by Spies and others (1988).

Five habitat combinations were selected (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young); two stands of each were sampled. Each stand, occupying about 5 ha of relatively homogeneous forest, represented a subset of typical stands originally located by other researchers as part of a regional forest characterization (Spies and others 1988). Stand locations (see frontispiece) and selected descriptive characteristics of each stand (table 1) are presented.

Stands were sampled in each season over 6 to 7 weeks. In spring, stands on lower elevation south slopes were sampled first, those on higher elevation north slopes last. We thereby condensed the sample period relative to temperature and moisture conditions that strongly influence fruiting. The fall sampling strategy was reversed with stands on higher, northerly slopes sampled first. Field work was initiated in the spring of 1983 and continued through spring of 1986.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps because fruiting differs so much by species and abundance in time and space. Additionally, Fogel(1976, 1981) and States (1985) report the clustered distribution of fruit bodies. Accordingly, welldistributed small plots were used in the conduct of this study.

For each stand sample, sporocarps were harvested from 25 circular 4-m^2 plots for a total sample area of 100 m^2. Plots were placed systematically about every 25 m along three transects running parallel to the slope contour and spaced about 75 m apart. New transects were established for each stand sample; no plots were resampled. In western Oregon conifer forests, most hypogeous sporocarps are produced at or above the mineralorganic soil interface (M. Castellano, G. Hunt, D. Luoma, J. Trappe, pers. obs.). In each plot, the forest floor was raked back to a 5- to IO-cm depth, thereby exposing sporocarps in the upper soil layers. The number of sporocarps from each collection in a plot was recorded. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain <l5 percent relative humidity, and weighed to the nearest 0.01 g to determine biomass. Major species are those with 25 percent of the total biomass in the study (Hering 1966).

The terms “dominant” and “subdominant” within categories refers to sporocarp biomass as an indicator of a species’ importance relative to other species. Cooke (1955) measured the dominance of epigeous sporocarp by estimating fruiting body volume, and concluded his measure had “physiognomic rather than competitive significance.” Cain and Castro (1959) note that the term “dominance” is applied to different phenomena but argue against restrictive meanings because the

Table 1—Selected characteristics by habitat of 10 Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon

Habitat[a]	Stand (#)	Age[b] (yr)	Basal area[b] (m^2/ha)	Stem density[b] (#/ha)	Coarse soil[b, c] (% vol.)	Median elevation (m)	Aspect	Slope[d] (deg.)
WOG	2	450	81	280	47	550	NNE	30-35
	3	450	101	526	19	800	N	0-35
MOG	15	450	146	392	8	800	SW	0-15
	17	450	108	670	13	770	SSE	10-30
DOG	25	200	49	443	55	550	W	30-35
	29	200	47	463	52	700	SW	30-40
MM	36	130	71	408	33	1160	W	15-30
	90	84	38	433	25	930	SSW	10-30
MY	48	69	58	1410	48	1050	NW	20-30
	86	79	52	1535	59	930	NW	20-30

[a] WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.
[b] Unpublished data from T. Spies (see Spies and others 1988).
[c] Fragments >2 mm.
[d] Wet old-growth stand 3 occupied a series of slumps causing high slope variability.

differences are clear enough in context. Dominance (also co- and subdominance) of a species indicates predominance as expressed by some measure that may or may not reflect ecological influence in the dynamics of the community.

The term "stand sample" refers to the total 100-m^2 collection area (from 25 plots) for a given stand at a given seasonal harvest in a given year. This report uses data collected from 54 stand samples over 4 years, 28 stand samples in spring and 26 in fall. Seasons were defined by equinox and solstice calendar dates. Twelve stand samples were taken in wet old growth, 10 in mesic old growth, 12 in dry old growth, 8 in mesic mature, and 12 in mesic young habitats.

Analysis

Because of the unequal number of stand samples in the various seasonal categories, sporocarp biomass values were standardized to equivalent biomass, expressed in grams per hectare, and used to report seasonal results and relative values. The total biomass for a species in a category was divided by the appropriate fraction of a hectare sampled in that category to obtain equivalent biomass. Relative annual biomass of each species by season was calculated as a percentage of a species' total seasonal biomass (equivalent g/ha within each year).

Results

Total sporocarp production

Sporocarps were harvested from 5400 m^2 and yielded a dry weight biomass of 697 g, equivalent to a standing biomass of 1.3 kg per ha. The maximum single-stand-sample total biomass was 99 g dry weight or 9.9 kg per ha. Forty-seven species of hypogeous fungi were recorded during the study. Fourteen species accounted for 94 percent of the total biomass. Five major species—*Elaphomyces granulatus* Fr., *Gautieria monticola* Harkn., *Hysterangium coriaceum* Hesse, *Leucogaster rubescens* Zeller & Dodge, and *Rhizopogon parksii* Smith—accounted for 73 percent of the biomass.

Year-to-year variation

Spring fruiting was dominated by a different fungus each year: *Hysterangium coriaceum* in year one, *Gautieria monticola* in year two, and *Elaphomyces granulatus* in year three (table 2). Eighty percent of the spring biomass of *Elaphomyces granulatus* in year three was attributable to one extreme stand sample of 99 g. This value represents a particularly interesting outlier because it was obtained from a single 4-m^2 plot containing 54 sporocarps. If a more "reasonable" (for this sample size, 1000 m^2) stand-sample value of 35 g for *E. granulatus* were assumed, then *Gautieria* would have been the spring biomass dominant in year three also. *Elaphomyces granulatus* was a subdominant in year two. *Rhizopogon parksii* was not found in spring.

Fall sporocarp production was dominated by *Rhizopogon parksii* with >50 percent of the total biomass (table 2) in all years. In each year, one stand sample contributed a large proportion of *R. parksii's* fall biomass (29, 36, and 70 percent in years 1, 2, and 3, respectively). *Elaphomyces granulatus* was a fall subdominant in years one and two. *Leucogaster rubescens* was a fall subdominant in year three. *Hysterangium coriaceum* was not found in fall. Year one, with the least biomass, had relatively equal distribution of fall and spring biomass (table 2).

Table 2—Annual sporocarp biomass (equivalent g per ha) of major species by season in a 5400-m^2 total sample from 10 Douglas-fir stands, H.J. Andrews Experimental Forest, Oregon

Species	YEAR 1 Spring (n = 8)	YEAR 1 Fall (n = 8)	YEAR 2 Spring (n = 10)[a]	YEAR 2 Fall (n = 9)	YEAR 3 Spring (n = 10)	YEAR 3 Fall (n = 9)
Elaphomyces granulatus	65	109	231	82	1234	87
Gautieria monticola	4	30	790	19	525	19
Hysterangium coriaceum	293	—	142	—	80	—
Leucogaster rubescens	10	21	84	43	13	131
Rhizopogon parksii	—	170	—	672	—	491
Seasonal g per ha	372	330	1247	917	1852	728
Yearly g per ha	351		1091		1319	

[a] 3 spring stand samples from a 4th year were included.

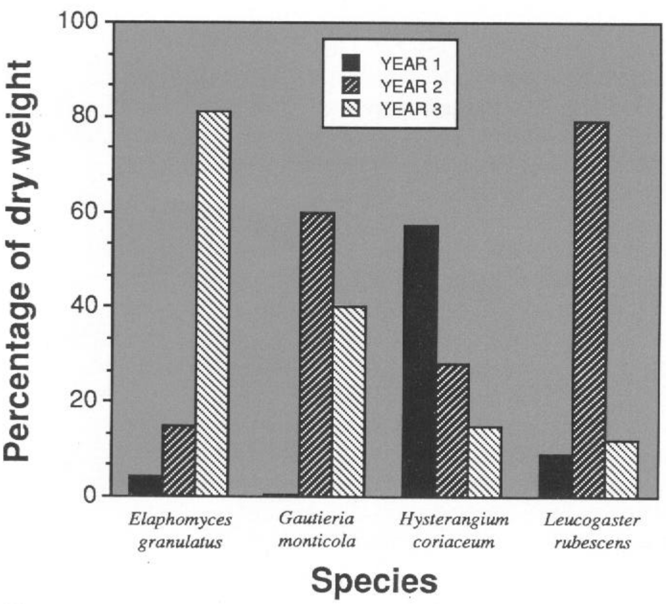

Figure 1—Major species year-to-year variation in spring relative sporocarp biomass in a 2800 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

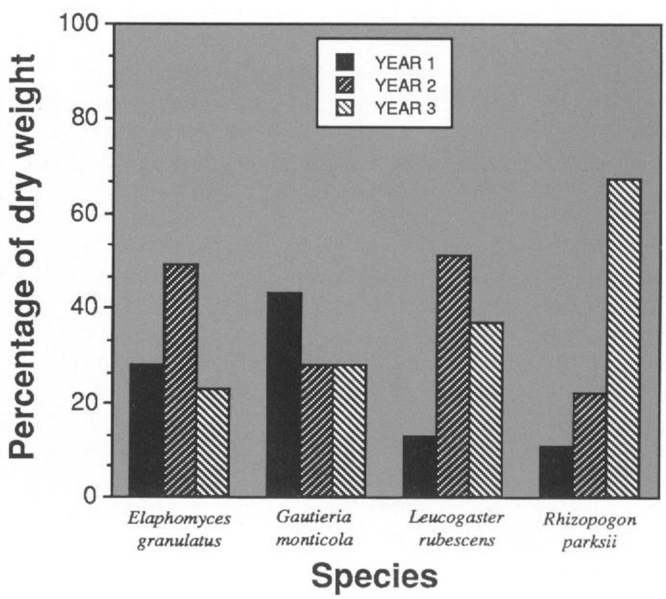

Figure 2—Major species year-to-year variation in fall relative sporocarp biomass in a 2600 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The yearly proportion of each species seasonal sporocarp biomass is shown (figs. 1, 2). Variation in relative biomass from yeartoyear for individual species was greater in spring than in fall. Three spring species had one year with >60 percent of their total seasonal biomass. In fall, only *Rhizopogon parksii* had such a strong single-year dominance.

Discussion

This paper seeks to put the results in a landscape perspective by generalizing seasonal sporocarp production as being representative of Western Hemlock Zone forests in the central Cascade Range of Oregon. The most extensive previous studies of hypogeous sporocarp production were confined to single stands (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). Their major goals were to quantitatively estimate sporocarp production, to determine phenology of production, and to characterize the hypogeous fungal-species community composition.

Fogel (1976) and Hunt and Trappe (1987) show that sporocarp biomass production of single species differs from year to year. In a 3-year study with small (50-m^2) monthly samples, Fogel (1976) had four major species in common with this study. The species and biomass ranges of the annual standing crop were as follows: *Elaphomyces granulatus, 0* to 90 *g* per ha; *Gautieria monticola,* 13 to 432 g per ha; *Hysterangium coriaceum* (as *H. separabile* Zeller), 294 to *572 g* per ha; and *Rhizopogon parksii, 89* to 252 g per ha. Other major species of Fogel's (1976) study include: *ffymenogasterparksii* Zeller *&* Dodge, 76 to 435 g per ha; *Hysterangium setchellii* Fischer (as *H. crassum* [Tul. *&* Tul.] Fischer), 517 to 1206 *g* per ha; *Truncocolumella citrina* Zeller, *30* to *2336 g* per ha; and *Tuber* spp., 0 to 380 g per ha. *Hysterangium setchellii* and *Truncocolumella citrina* were moderately important, while *Hymenogaster parksii* and *Tuber* spp. were minor species in Luoma (1988).

Fogel (1976) provides seasonal information on *Hysterangium coriaceum* by reporting fruiting period (monthly range) and mean calender day of fruiting with number of days standard deviation. *Hysterangium* taxonomy was not well known at the time of his study so that *H. separabile* is the species reported and may not entirely equate with what is now accepted as *H. coriaceum*. Fogel(1976) made collections of *H. separabile* throughout the year and lists it as an "opportunistic" species. The mean fruiting date, however, in each of 3 years was in April with a standard deviation of 11 **days**—the smallest of the eight species reported. Fogel(1976) lists *Rhizopogon parksii as* a characteristic fall species.

Data from Dinner Creek, Oregon (Fogel and Hunt 1979, Hunt and Trappe 1987), gathered over 2 years, revealed five major species. *Three-Gautieria monticola, 8* to 85 g per ha; *Leucogaster rubescens,* 316 to *338 g* per *ha:* and *Rhizopogon parksii,* 116 to 463 g per ha-were also major species in the current study. *Two-Leucophleps magnata Harkn.,* 21 to *189 g* per ha; and *Truncocolumella citrina, 0 to 749 g* per ha-had moderate importance in Luoma (1988).

Hunt and Trappe (1987) sampled sporocarp production in a 1.5-ha stand for 21 months. Monthly production was estimated from twelve **4-m^2** plots. Major species in common with the present study were *Gautieria monticola, 769* to 1527 g per ha and *Hysterangium coriaceum, 106* to 204 g per ha. Other major species were *Hysterangium setchellii, 746 to 842 g* per ha and *Melanogaster* sp. nov., 108 to 225 g per ha.

Hunt and Trappe (1987) also report fruiting middate mean, and standard deviation for selected species. Over 2 years, *Hysterangium coriaceum* was collected from February to December but its middate was in April with a standard deviation of *8* days. *Rhizopogon parksii* was found only from September to December.

In this study, total spring equivalent biomass ranged from 0.4 to 1.8 kg per ha. These values were consistently greater than or equal to the fall range of 0.3 to 0.9 kg per ha (table 2) and contrast with Fogel and Hunt's (1979) marked fall biomass peak in the 1st year of sampling at Dinner Creek. Hunt and Trappe (1987) found comparable biomass between spring and fall during the 2d year of sampling at Dinner Creek. Fogel(1976) reports that spring and fall biomass were comparable but data in Hunt and Trappe (1987) show that Fogel had a marked spring biomass peak in each of 3 years. The single-sample maximum biomass of 9.9 kg per ha reported here supplants the unpublished values (1.4, 1.7 kg per ha) of Luoma and Hunt cited in table 6 of Hunt and Trappe (1987).

Total sporocarp biomass was substantially less in both spring and fall of year one compared to the other years. The low spring values may have been influenced by record high temperatures in May 1983. A 14-day period with only a trace of rain encompassed 12 days in which high temperatures reached more than 25 °C (mean monthly high = 18.7 °C) and included the highest May temperature (40°C) recorded at the H. J. Andrews station. Low sporocarp production in fall was coincidental with well below average September and October precipitation in 1983 (Bierlmaier and McKee 1989; F. Bierlmaier, unpubl. data).

Year one had the maximum production for one species in spring and another species in fall (figs. 1.2). Year two showed highest relative sporocarp biomass for two species in spring and two species in fall. One species had maximum spring biomass and one species had maximum fall biomass in *year three. Hysterangium coriaceum* was not found in the fall and *Rhizopogonparksii* was not found in spring; otherwise, no strong trends were in these data. In this data set, a single year with maximum relative biomass of two species occurring in the same season is the nominal distribution. Year two had both such species maximums for spring and fall.

Weather patterns (particularly the timing and duration of drought periods) likely account for much of the yeartoyear seasonal variation observed in this and other studies (Fogel 1981). Although it is ecologically meaningful for a given year, such variation detracts from attempts to characterize general trends in importance or dominance (as measured by sporocarp biomass) by season and habitat. Such a characterization will be presented elsewhere in the scientific literature (Luoma and others, in press).

Conclusions

Relatively few species (five) of hypogeous fungi accounted for most of the total biomass (73 percent). Many species showed strong seasonal variation in relative biomass production. For the major species, spring had greater year-to-year variation in sporocarp production and higher total biomass production than did fall. The range of standing biomass values for the species reported in this study is similar to the values reported for hypogeous sporocarps by other researchers. All of the major species in this study were also major species in one or more of the studies from young Douglas-fir stands in the Oregon Coast Range (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). In Western Hemlock Zone forests of western Oregon, *Gautieria monticola* seems to be a widespread sporocarp dominant, *Hysterangium coriaceum* a predominantly spring species, and *Rhizopogon parksii* characterizes the fall fruiting aspect. In contrast to epigeous mycorrhizal fungi, hypogeous sporocarp production is generally higher in spring than in fall (Fogel 1976; Hunt, unpubl. data).

Acknowledgments

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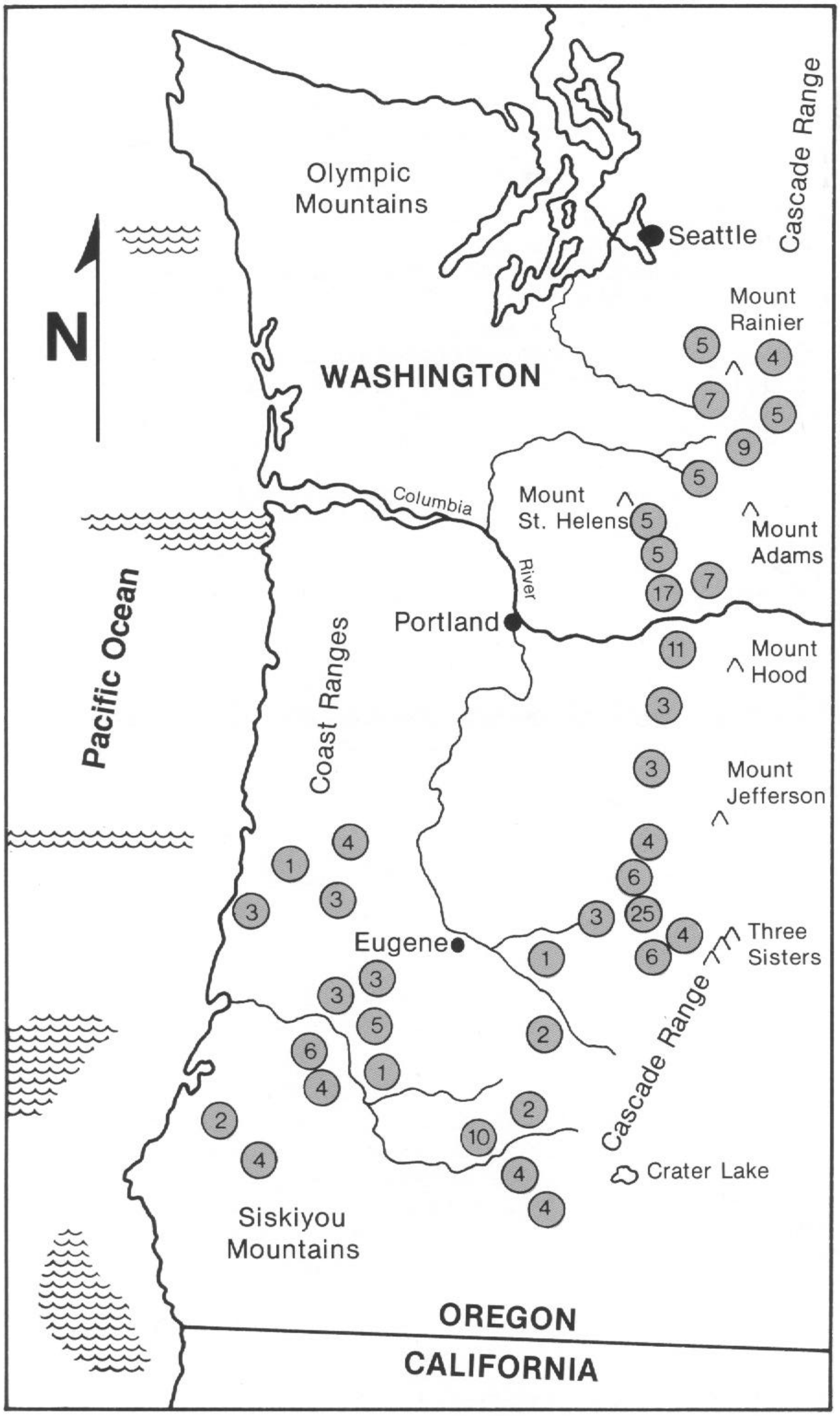

Location of stands in western Oregon and Washington. Numbers indicate total number of stands in an area.