Biomass and Community Structure of Sporocarps Formed by Hypogeous Ectomycorrhizal Fungi within Selected Forest Habitats of the H. J. Andrews Experimental Forest, Oregon

by

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A THESIS

submitted to

Oregon State University

in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

Completed December 16, 1988

Commencement June 1989

"Some kinds of science dote on graphs, tables, and computer readouts. The finest naturalists have always known that biology without romance, without poetry, is not only incomplete but very often hopelessly distorted"

– Frank Graham Jr., 1983

AN ABSTRACT OF THE THESIS OF

Daniel L. Luoma for the degree of Doctor of Philosophy in Geography
presented on December 16, 1988.

Title: Biomass and Community Structure of Sporocarps Formed by Hypogeous Ectomycorrhizal Fungi within Selected Forest Habitats of the H. J. Andrews Experimental Forest, Oregon

Abstract approved: _____
Robert E. Frenkel

This study characterizes the production of hypogeous sporocarps (broadly referred to as truffles) by ectomycorrhizal fungi within Douglas-fir dominated forests that are considered typical of those found on the west slopes of the central Cascade mountains in Oregon. Three aspects of sporocarp production are addressed: 1) the distribution of total biomass and biomass of each species by season and habitat, 2) analysis of sporocarp biomass from the perspective of community structure, and 3) correlation of biomass production with sporocarp number and selected forest floor parameters.

Sporocarps with an equivalent dry standing biomass of 1.3 kg/ha were harvested from ten Douglas-fir stands in and near the H. J. Andrews Experimental forest. The maximum single stand sample biomass was equivalent to 9.9 kg/ha. Forty-seven species of hypogeous fungi were recorded during the study (although some collections are of uncertain taxonomic affinity and some taxa are of uncertain status). Fourteen species account for 93% of the total biomass. Five species account for 73% of the biomass (*Elaphomyces granulatus, Gautieria monticola, Hysterangium coriaceum, Leucogaster rubescens,* and *Rhizopogon parksii*).

Individual species showed strong differential trends in seasonal production of sporocarp biomass, with spring and summer production being greater than fall in contrast to fall fruiting epigeous species. Many species showed differences in sporocarp production by habitat. Sporocarp production was evaluated in five Douglas-fir habitats, (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young). The mesic mature forest habitat had the highest standing biomass value (2.2 kg/ha) of all the habitats. The dry old-growth forest habitat had the lowest (0.7 kg/ha). Analysis of the distribution of sample values indicates that samples of small total area overestimate biomass because of the strong skewing towards high values. Interspersion of the largest practical number of quadrats is required to reduce

overestimation of standing biomass (expressed on a kg/ha basis) when localized concentrations of biomass are included in samples.

Vegetation studies have shown that, for vascular plants, similar species combinations recur under similar habitat conditions. Also, species abundance and composition change more or less continuously over the landscape. This study found communities of hypogeous ectomycorrhizal fungi to be co-extensive with associated vascular plant communities and sensitive to subtle variations in habitats spanning wet-to-dry and young-to-old gradients.

A profound dichotomy in seasonal fruiting pattern between spring and fall precludes the use of single season sampling to reveal fungal community structure. Furthermore, yearly variation in weather patterns causes variation in sporocarp biomass production that tends to obscure community structure responses to environmental gradients. When fungal data collected over a number of years from a stand are integrated, subsequent classification and ordination closely reflect the vascular plant classification and subtle responses to a moisture gradient. A fungal community guild structure was delineated that reflected the subtle variation in the studied habitats. The guild of hypogeous ectomycorrhizal fungi has *Rhizopogon parksii* as the subterranean dominant counterpart to *Pseudotsuga menziesii* with *Gautieria monticola* nearly as wide spread and abundant. Changes in fungal community structure along the stand age gradient are noted, but the limited amount of replication in the present study makes this interpretation tentative.

Within three old-growth stands ranging from wet to dry, sporocarp biomass and numbers of hypogeous sporocarps were assessed in relation to each other, coarse woody debris, forest floor litter, and other selected forest floor parameters by use of regression models. Significant regressions between forest floor parameters are also examined.

Transformation of data values improved the normality of the distributions for most parameters. The regression of sporocarp biomass and number of sporocarps is significant, however, it is not a strong relationship and the use of numbers of sporocarps as a substitute for biomass is not recommended. The correlation between sporocarp biomass and forest floor depth was significant in the mesic old-growth stand only. Significant regression relationships between the parameters are highly individualistic within each stand. Over all stands, a slight tendency for forest floor depth to increase with coarse woody debris cover was noted.

Regression analysis may have been hampered by the old-growth status of all stands. Perhaps, due to centuries of development without catastrophic disturbance, within–stand variation in the chosen parameters has been reduced to the point that trends in the relations between selected parameters are difficult to detect. In designing future research, it would be advisable to include stands varying considerably in old-growth characteristics and to assess the degree to which "carry over" of characteristics into second growth stands affects sporocarp production.

ACKNOWLEDGMENT

The support, encouragement, and direction of Dr. Bob Frenkel is most gratefully acknowledged. A large amount of effort on his part greatly facilitated the completion of this thesis. This work is dedicated especially to my wife Alison and to our extended family for their continuing support and understanding over the years.

The research was supported by and done in cooperation with the Pacific Northwest Forest Research Station, Forestry Sciences Laboratory, Corvallis, Oregon and Forestry Sciences Laboratory, Olympia, Washington. Dr. Randy Molina provided assistance, guidance, and the use of facilities, his help is greatly appreciated. This project was initiated by Dr. Gary Hunt in the spring of 1983. I would especially like to thank Joyce Eberhart and John Chamard for their help with the considerable field work (in all kinds of weather) entailed in this project. Michelle Seidl, Wang Yun, Dr. Steve Miller, Efren Cazares, Mike McWillams, Jim Garha, Nola Mosier, Dr. Andy Moldenke, Ralph Crawford, Dr. C. Y. Li, Dr. Iwan Ho, Dr. Steve Carpenter, and Jenny Miller also assisted with the field work. Dr. Michael Castellano shared his knowledge on the genus *Hysterangium*. Bradley Smith provided expertise with the programs DECORANA and TWINSPAN and offered many helpful suggestions.

I would also like to thank the members of my committee. In addition to providing training on the taxonomy and identification of hypogeous ectomycorrhizal fungi, Dr. Jim Trappe contributed many insightful suggestions that improved the execution of this project and the resulting manuscript. Drs. Gordon Matzke and Charles Rosenfeld, also made helpful contributions to and criticisms of the thesis.

This endeavor represents a partial contribution (no. III e) of the project entitled "The Fallen Tree – an Extension of the Live Tree." The project is cooperative among the U.S.D.I., Bureau of Land Management; U.S.D.A., Forest Service, Pacific Northwest Research Station; Oregon State University, Department of Forest Science; U.S.D.A., Agricultural Research Service; and Oregon Department of Fish and Wildlife.

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Date thesis is presented December 16, 1988

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Biomass and Community Structure of Sporocarps Formed by Hypogeous Ectomycorrhizal Fungi within Selected Forest Habitats of the H. J. Andrews Experimental Forest, 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 the relationships between fungi and vegetation on a quantitative and qualitative basis. The central focus of this thesis is in the mycocoenological approach to biogeographic research.

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; Zobel et al., 1976; Hemstrom et al., 1987). The prevailing regional system of plant community classification in the Pacific Northwest greatly facilitates the execution of mycocoenological research by freeing the investigator of the

need to conduct elaborate prior vegetation studies in order to classify sample stands. This study is part of a regional characterization of Douglas-fir (*Pseudotsuga menziesii*) forests from which Spies et al. (1988) provide habitat classification of the stands used in this study.

Studies of the community ecology of macrofungi have lagged far behind those of those for vascular plants. Several daunting challenges face the would-be mycocoenologist. Arnolds (1981) provides a recent summary of some of these difficulties: (1) in many cases fungal species concepts are poorly understood and defined; (2) collections are difficult to identify morphologically and often require considerable research to reach independent taxonomic decisions; (3) research is limited to the study of sporocarps (fruiting bodies), which appear with a strong seasonal aspect (Hueck, 1953), are subject to yearly variation caused by variable weather patterns, and exhibit varying, largely unknown, rates of decay and predation; (4) sporocarp production is not necessarily related to the vegetative abundance or to the activity of the mycelial colony; and, (5) 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 inability of the investigator to confidently interpret conclusions in relation to field situations.

Fungi that produce hypogeous (below ground) 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 ground) fungi have been reported since at least 1932 (Haas), Fogel (1976) was the first to provide a quantitative assessment of hypogeous sporocarp production. Most of the fungi producing hypogeous sporocarps are thought to be ectomycorrhizal (fungi which develop mutually beneficial associations in the exterior layers of the roots of certain plants) (Trappe, 1962; 1971). Mycorrhizal fungi are important to the nutrition of forest trees by acting as extensions of the root system (Trappe and Fogel, 1978).

The most extensive previous studies of hypogeous sporocarp production are those of Fogel (1976), Fogel and Hunt (1979), and 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. Additionally, Hunt and Trappe (1987) calculated the mycofloristic similarity between forest stands of the three studies mentioned above. Those studies were confined to single stands and are from similar, relatively young (35-65 years), second growth (after clear-cut logging and burning) Douglas-fir forests located on Marys Peak, Oregon (two stands were only 250 m apart).

For this thesis, ten natural forest stands in the H. J. Andrews Experimental Forest and vicinity representing moisture and age gradients were studied. The study area is considered typical of the western slopes of the central Cascade Range in Oregon (Dyrness et al., 1974). The location of

this study and choice of stands greatly expands knowledge of the occurrence of hypogeous ectomycorrhizal fungi from a variety of natural habitats over a wide area of forest.

Hunt and Trappe (1987) were concerned with estimation of sporocarp production, determination of the phenology of production, and characterization of the hypogeous fungal species community for a given stand. Chapter 1 continues with the type of objectives that concerned Hunt and Trappe but extends their concerns to the characterization of species sporocarp production and distribution among various Douglas-fir habitats (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young), representing wet–to–dry and young–to–old-growth gradients. At one level, the discussion considers the results in a landscape context by generalizing sporocarp production as being representative of various mid-elevation Douglas-fir forests in the central Western Cascades of Oregon. At a second level, discussion considers the occurrence of individual fungal species within and by season and habitat. Previously neglected aspects in the analysis of sporocarp biomass production are also explored.

A major objective in Chapter 2 is to determine if communities of hypogeous ectomycorrhizal fungi occur: (a) co-extensively with associated vascular plant habitats; (b) more narrowly within vascular plant habitats; or, (c) broadly, over more than one vascular plant habitat. Chapter 2, then, applies multivariate analyses (Gauch, 1982) to the production of hypogeous sporocarps with respect to a moisture and development gradient. While

traditional approaches to the characterization of sporocarp production were used in a greatly expanded context in Chapter 1, the second chapter explores whether sporocarp biomass reveals an intrinsic fungal community structure. Two types of analysis are introduced, an ordination and a classification. Rather than merely characterizing and comparing the mycoflora of plant communities or habitats, the multivariate approach of detrended correspondence analysis (DCA) ordination (Hill, 1979a) considers the abundance of each fungal species across all habitats, together with the relative proportion of species within each habitat. This two-way iterative process allows the inherent complexity in the data set (each species sporocarp biomass in this case) to be reduced to relatively few values for each sample. The samples can then be ranked (ordinated) on independent axes on the basis of these multivariate scores. When the results of this DCA ordination are displayed along two perpendicular axes, the array of plots is said to be positioned on a community plane defined by two complex environmental gradients (Whittaker, 1967; Gauch, 1982).

As a second approach to understanding fungal community structure, the compositional data was classified by use of a companion methodology: two–way indicator species analysis (Hill, 1979b). Samples are first ordinated by reciprocal averaging, then grouped by species composition into ordinally hierarchical clusters. The technique is polythetic by use of quantitative measures of entity (sample) resemblance over all attributes (species scores) and divisive by progressively splitting the entire set of samples (and species)

into smaller groups at each level of the hierarchy (Boesch, 1977).

The attractiveness to mycocoenologists of these approaches is that the resulting ordination and classification (determined solely by individual fungal species sporocarp biomass) permit independent interpretation of the fungal community with reference to the preexisting habitat classification based on vascular plant species. This approach offers a chance to present empirical evidence that addresses long standing theoretical concerns (Cooke, 1979; Arnolds, 1981). Namely, what are the spatial, functional, and classification relations between fungi and vascular plant communities?

In general, multivariate ordination and classification allow the interpretation of community composition in relation to a wide variety of complex gradients. Samples of vascular plant communities are frequently related to their relative position along moisture and temperature gradients (Whittaker, 1967; Dyrness et al., 1974; Luoma, 1987), but placement with respect to gradients of successional change and spatial variation in disturbance intensity have also been noted (Curtis and McIntosh, 1951; van der Maarel, 1969; Halpern, 1987). It is reasonable to expect the interpretation of fungal communities would benefit from this type of analysis; however, even recent ecological studies of ectomycorrhizal fungi have made little use of multivariate techniques (e.g., Bills et al., 1986) to relate fungal community structure to vascular plant communities and their habitats.

Chapter 3 is mainly concerned with two further aspects of hypogeous sporocarp production. First, the relationship between sporocarp biomass and

the number of sporocarps in a sample plot is investigated. Most workers have used counts of sporocarps to quantify fungal species relative "importance" (Orłoś, 1966; Arnolds, 1981; Winterhoff, 1984; Bills et al., 1986; Cibula and Ovrebo, 1988) or have used sporocarp number in addition to sporocarp weight (Fogel, 1976; 1981; Hunt and Trappe, 1987), despite well known reservations as to the appropriateness of the approach due to variation in sporocarp size between and within species (Hering, 1966).

Second, the quantitative relationship of sporocarp biomass production to selected forest floor parameters is explored. An assessment of this relationship is particularly important because of the documented utilization of hypogeous sporocarps by mycophagous animals (Fogel and Trappe, 1978). Spores of hypogeous fungi are often dispersed via consumption by animals (mycophagy). The overwhelming importance of these sporocarps in the diet of small mammals has been documented by investigators in different regions of the world (Durrieu et al., 1984; Hunt and Trappe, 1984; Malajczuk et al., 1987). Even though Tevis (1952) recognized the importance of small mammals to spore dispersal more than three decades ago, the attributes of coarse woody debris critical to the life history of many small mammals are just beginning to be understood (Maser and Trappe, 1984). Mycophagous small mammals are particularly active around coarse woody debris. Their movement between microhabitats has been hypothesized as a mechanism for spore dispersal into logged habitats (Hayes et al., 1986).

Deposition of spore–rich fecal pellets by small mammals in and around coarse woody debris is thought to play an important role in the establishment of tree seedlings on such substrates (Maser et al., 1978b; Trappe and Maser, 1978). Coarse woody debris has been found to be the most frequent (or only) site of active ectomycorrhizae on dry and disturbed sites (Harvey et al., 1979; Amaranthus et al., 1989). *Rhizopogon vinicolor* is common (vegetatively) in decaying wood (Zak, 1971) and is adapted to increasing drought resistance in its associated host (Parke et al., 1983).

Given this complex of interdependent biological symbioses, coarse woody debris and associated forest floor characteristics can be generally hypothesized to contribute structurally and functionally to the formation and development of hypogeous sporocarps. Although sporocarp production has been recognized as potentially important to the reforestation of disturbed sites (Maser et al., 1978b; Perry et al., 1987), the role of fallen trees and decaying woody debris with regard to the production of hypogeous sporocarps has not been investigated previously.

Chapter 1

Seasonal and Habitat Variation of Sporocarp Production by Hypogeous Ectomycorrhizal Fungi in Douglas-fir Forests of the Central Western Cascades, Oregon

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SUMMARY

To characterize the occurrence of hypogeous (fruiting below ground) ectomycorrhizal fungi from a variety of natural habitats over a wide area of forest, sporocarps were harvested from ten Douglas-fir stands in and near the H. J. Andrews Experimental forest. Over all stands, the dry standing biomass was equivalent to 1.3 kg/ha. The maximum single stand sample biomass was equivalent to 9.9 kg/ha. Forty-seven species of hypogeous fungi were recorded during the study. Fourteen species account for 93% of the total biomass. Five species account for 73% of the biomass (*Elaphomyces granulatus, Gautieria monticola, Hysterangium coriaceum, Leucogaster rubescens,* and *Rhizopogon parksii*). Counts of sporocarps are a poor substitute for biomass data.

In contrast to epigeous (fruiting above ground) species in the study area, hypogeous sporocarp production was higher in spring than in fall. Sporocarp production was evaluated in five Douglas-fir habitats, (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young), forming two gradients, wet to dry and young to old-growth. The mesic mature forest habitat had the highest standing biomass value (2.2 kg/ha) of all the habitats studied. The dry old-growth forest habitat had the lowest (0.7 kg/ha).

Individual species showed strong trends in seasonal production of sporocarp biomass. Most species had spring or summer production peaks. Some species also showed differences in sporocarp production by habitat.

For example, *Leucogaster rubescens* had peak biomass in the dry old–growth habitat while the peak biomass of *Leucophleps magnata* was in non-old–growth habitats. Conversely, *Rhizopogon vinicolor* was well distributed throughout all habitats.

Analysis of sample value distributions indicated that samples of small total area (≤ 800 m^2) tend to overestimate sporocarp biomass on a grams per hectare basis because biomass is strongly skewed towards high values. Additionally, interspersion of the largest practical number of quadrats is required to reduce the tendency of localized biomass concentrations to further overestimate standing biomass when data are expressed on a grams per hectare basis.

INTRODUCTION

Currently, the only practical method to assess the relative functional importance of hypogeous ectomycorrhizal fungi in an ecosystem on a species by species basis is through estimation of sporocarp production. Potential functional roles of ectomycorrhizal fungi range from essential symbiosis with the roots of overstory trees (Harley and Smith, 1983) to sporocarps serving as a food source for small animals (Fogel and Trappe, 1978).

Several recent studies have focused on aspects of sporocarp production by hypogeous mycorrhizal fungi in the Coast Range of western Oregon (Fogel, 1976; Fogel and Hunt, 1979; Fogel, 1981; Hunt and Trappe, 1987). Fogel (1976) was the first to report a quantitative analysis of the seasonal distribution of hypogeous sporocarps in which sporocarp dry weight and number were used to calculate mid-dates of fruiting for individual species and populations.

In a thirteen month study, Fogel and Hunt (1979) observed a fall peak in total sporocarp dry weight. A strong spring peak was not observed but their spring sample occurred at the end of a severe drought. Fogel (1981) provides an excellent review of techniques for the quantification of hypogeous sporocarps and correlates sporocarp production with temperature and moisture parameters. Hunt and Trappe (1987) point out that documenting all species of hypogeous ectomycorrhizal fungi in a forest stand requires long–term collecting spanning several years. After 32 months of collection

and a total sample area of 1536 m^2, their species–area curve had not stabilized.

The previous studies were confined to single stands of Douglas-fir located on Marys Peak and are from similar, relatively young second growth forests developing 35-65 years after clear-cut logging and burning (two of their stands were only 250 m apart). An obvious need to characterize the occurrence of hypogeous sporocarps from a variety of natural habitats over a wide area of forest exists.

This paper, aimed at broadening the data on seasonal and habitat distribution of sporocarp production, reports the abundance of sporocarps for the major species of hypogeous ectomycorrhizal fungi found in ten forest stands of the H. J. Andrews Experimental Forest and vicinity. Standing crop sporocarp biomass production within five Douglas-fir forest habitats covering a range of moisture and age classes was measured. In order to obtain a representative sample of the major species and to integrate the variation in sporocarp production that is induced by year to year changes in weather patterns, the study spanned a four year period. Seasonal variation in fruiting patterns was anticipated by spring and fall sampling. Limited summer sampling was undertaken to provide a glimpse at production during the usually dry season. The broad scope of this study allows the following specific objectives to be addressed: (1) to identify the major species of hypogeous ectomycorrhizal fungi (as indicated by sporocarp biomass) found in Douglas-fir stands typical of the central Western Cascades; (2) to

characterize the seasonal fruiting aspect as determined by the major species; (3) to characterize the sporocarp biomass distribution among stands of various moisture and age classes; (4) to determine the seasonal and habitat distribution of each major species as measured by sporocarp biomass and species frequency; and (5) to analyze the distribution of sample values of sporocarp biomass with respect to previous estimates of annual productivity and standing crop production.

METHODS

Study area

The H. J. Andrews Experimental Forest occupies the 6,000 ha drainage of Lookout Creek, a tributary of the McKenzie River, in Lane Co., Oregon The area is considered typical of the western slopes of the central Cascade Range in Oregon. The forest has been administered by the U. S. Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948. The location of the study stands in the experimental forest and vicinity is presented in Figure 1.1.

The regional climate is classified as Temperate Oceanic by Trewartha and Horn (1980) or Csb (cool–summer Mediterranean) by Köppen (1936). Average annual precipitation varies from about 2,300 to 2,800 mm, depending on topography. About 90% of the precipitation occurs from October through April. Above 900 m elevation, winter snowpacks accumulate to a depth of 1 m or more. Summers are dry. Temperatures are moderate with a range from -3° (mean January minima) to 29° C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Franklin and Dyrness, 1971).

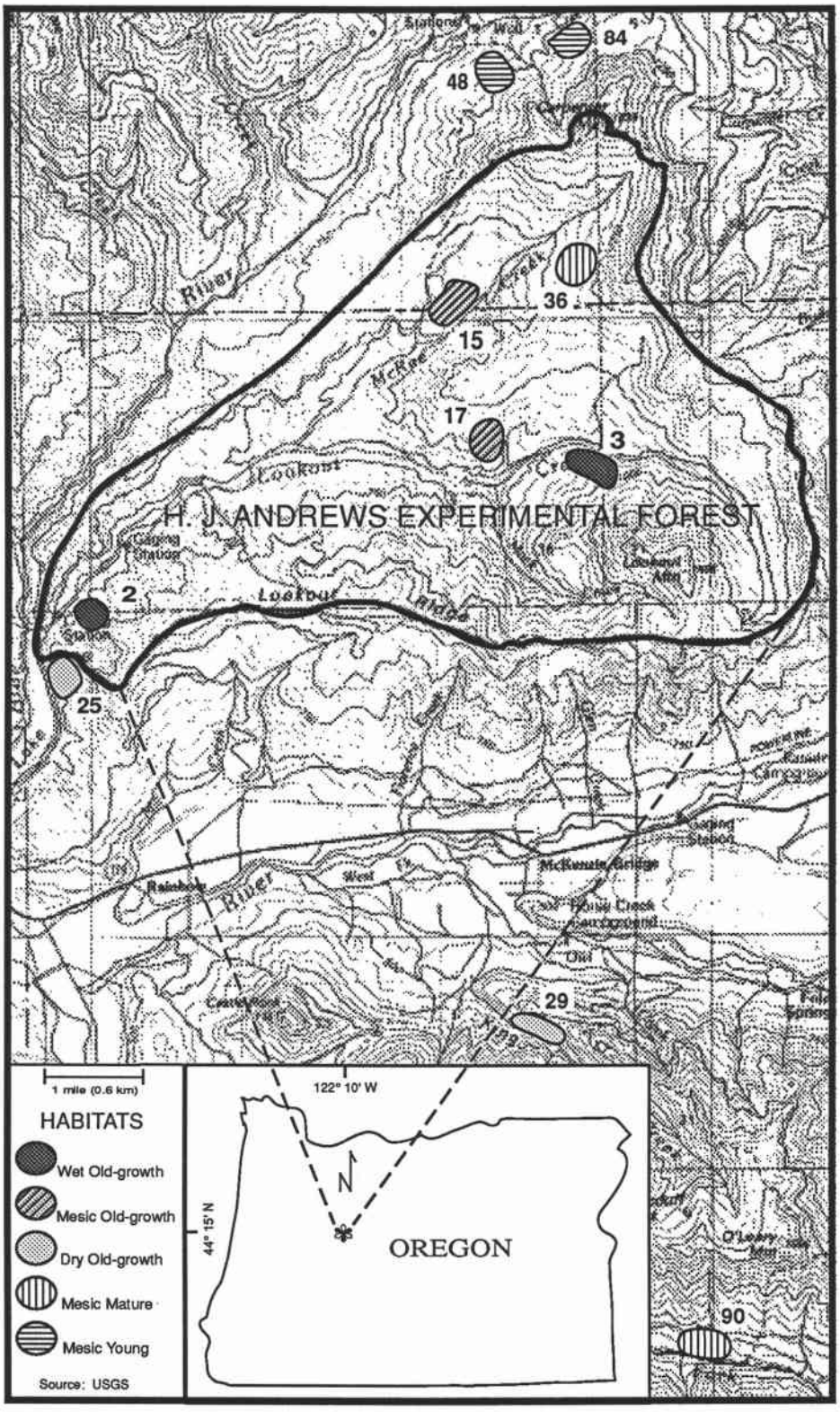


Figure 1.1. Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

Three general soil types are characteristic of the experimental forest (Berntsen and Rothacher, 1959; Franklin and Dyrness, 1973; Dyrness et al., 1974). Steeper slopes and ridgetops often support a residual Brown Podzolic gravelly clay loam formed from andesite or basalt (usually classified as Haplorthods or Xerumbrepts). Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams (generally classified as Haploxerults and 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 *Tsuga heterophylla* Zone of Franklin and Dyrness (1973). Studies of forest communities within the *Tsuga heterophylla* Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Franklin and Dyrness, 1973; Dyrness et al., 1974; Zobel et al., 1976). Characteristic understory species are used to describe the community types. *Lysichitum americanum* indicates extremely wet forest sites with the water table near or seasonally above the surface. Abundant *Polystichum munitum* and *Oxalis oregana* typify moist sites. Mesic sites may be occupied by *Berberis nervosa* and/or *Rhododendron macrophyllum*. Towards the dry end of the scale, *Gaultheria shallon* increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities belonging to the *Pseudotsuga menziesii* series. In these communities Douglas-fir is often considered climax and *Holodiscus discolor* is an important shrub (Hemstrom et al., 1987). A temperature gradient reflecting elevation has also been noted (Zobel et al., 1976). The coolest

extreme is represented by the *Tsuga–Abies amabilis/Linnaea borealis* association, transitional to associations in the *Abies amabilis* Zone.

Dyrness et al. (1974) found classification of communities to be challenging because of the wide geographic and ecologic distribution of most plant species. In modal (with respect to moisture and temperature gradients) communities, the difference in relative abundance of shared species was the basis for community recognition.

Sampling

Ten Douglas-fir forest stands were selected for sampling on the basis of age and moisture status. Age classes were 75, 150, and 300+ years of age and are referred to respectively in this paper 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 et al. (1988):

Pseudotsuga menziesii / Polystichum munitum / Oxalis oregana (**wet**)

Pseudotsuga / Acer circinatum / Berberis nervosa (**mesic**)

Pseudotsuga / Gaultheria shallon–Rhus diversiloba (**dry**)

Five habitats were selected: wet old-growth, mesic old-growth, dry old-growth, mesic mature and mesic young. Two stands of each of the five habitats shaded in the matrix (Figure 1.2) were sampled.

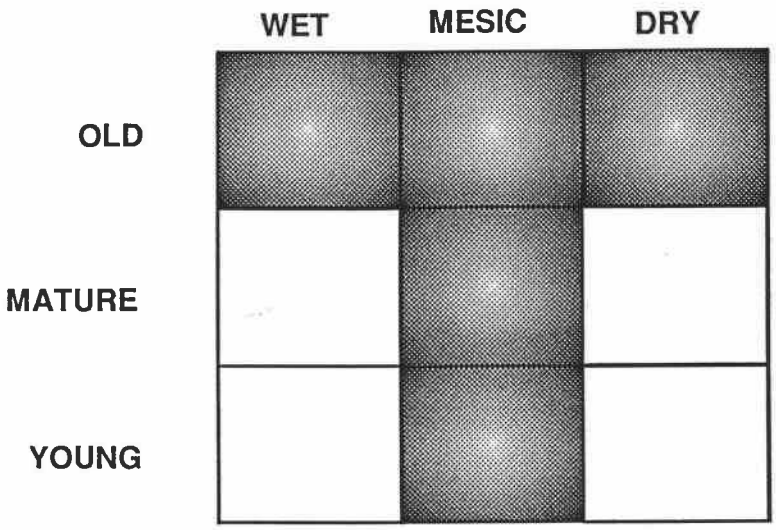


Figure 1.2. Sampling matrix for five chosen Douglas-fir habitats, H. J. Andrews Experimental Forest, Oregon.

Consisting of approximately five hectares of relatively homogeneous forest, the chosen stands represent a subset of typical stands originally located by other researchers as part of a regional forest characterization (Spies et al., 1988). Selected descriptive characteristics of each stand are presented in Table 1.1.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps, because fruiting varies so much by species and abundance in time and space. Fogel (1976, 1981) and States (1985) also report the clustered distribution of fruitbodies. Given the clumped distribution of sporocarps, the sampling strategy in this study was to use well–distributed small plots to obtain a representative stand sample. Random sampling requires many more plots than does systematic, interspersed sampling to achieve this goal (Hurlbert, 1984). Ideally, with more resources, random sampling stratified by microsite would have been employed.

Stand sampling in each season occurred over a period of six to seven weeks. For spring and summer samples, stands on lower elevation south slopes were sampled first, and those on higher elevation north slopes sampled last. This procedure allowed the sample period to be condensed relative to the temperature and moisture controlled fruiting phenology. The fall sampling strategy was reversed with stands on higher, northerly slopes sampled first. Because personnel were limited in summer, only old–growth stands were sampled.

Table 1.1. Selected stand characteristics by habitat from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Habitat[1]	Stand (#)	Basal[2] Area (m^2/ha)	Stem[2] Density (#/ha)	Coarse[2,3] Soil (% vol.)	Median Elevation (m)	Aspect	Slope[4] (°)
WOG	2	81	280	47	550	NNE	30-35
	3	101	526	19	800	N	0-35
MOG	15	146	392	8	800	SW	0-15
	17	108	670	13	770	SSE	10-30
DOG	25	49	443	55	550	W	30-35
	29	47	463	52	700	SW	30-40
MM	36	71	408	33	1160	W	15-30
	90	38	433	25	930	SSW	10-30
MY	48	58	1410	48	1050	NW	20-30
	86	52	1535	59	930	NW	20-30

[1] WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

[2] T. Spies, personal communication.

[3] Fragments > 2mm.

[4] Wet old-growth stand 3 occupied a series of slumps causing high slope variability.

For each stand sample, sporocarps were harvested from 25 circular four-square-meter plots for a total sample area of 100 m^2. Plots were placed systematically approximately every 25 m along three transects spaced equidistantly (about 75 m) and arranged parallel to the slope contour. New transects were established for each stand sample; no plots were reraked. In the conifer forests of western Oregon, most hypogeous sporocarps are produced at or above the mineral/organic soil interface (personal observations, J. Trappe, G. Hunt, D. Luoma, M. Castellano). In each plot, the forest floor was raked back to a 5 to 10 cm depth, exposing sporocarps in the upper layers of the soil. The number of sporocarps of each species in a plot was recorded. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain < 15% relative humidity, and weighed to the nearest 0.01 g to determine biomass.

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. Over four years, data were collected from 59 stand samples in all. Twenty-eight were taken in spring, five in summer, and 26 in fall. Seasons were defined by equinox and solstice calendar dates. Thirteen stand samples were taken in wet old-growth (WOG), 12 in mesic old-growth (MOG), 14 in dry-old growth (DOG), 8 in mesic mature (MM), and 12 in mesic young (MY) habitats.

Analysis

The percentile distribution of sporocarp biomass sample values was graphically displayed as "box and whiskers" symbols (Tukey, 1977) that depict five percentiles for each species (see, for example, Figure 1.4, p. 30). The top of each box represents the 75th, the line within the box the 50th, and the bottom of the box the 25th percentile. Therefore, the middle 50% of the sample values are contained within the range spanned by the box. The lines extending above and below each box range to the 90th percentile and the 10th percentile, respectively. Small circles represent observed values above and below the 90th and 10th percentiles, respectively. The percentile distributions are used to provide perspective to the interpretations of sporocarp production values in landscape, seasonal, habitat, and species specific contexts. They are also used to evaluate the results of previous workers.

Due to the unequal number of stand samples in the various seasonal and habitat categories, sporocarp biomass values were standardized to equivalent biomass expressed in grams per hectare and used to report seasonal and habitat results. 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. Use of the terms “dominant” and “subdominant” within categories refers to sporocarp biomass as an indicator of a species importance relative to other species and was restricted to those species with more than five percent of the total biomass within a seasonal or habitat category.

Each species relative biomass was calculated as a percentage of a species total biomass (equivalent g/ha within each category) for all seasons or habitats. The number of stand samples (*n*) in which a species occurred within a given seasonal or habitat category was determined. Each species percent frequency within categories was calculated as *n* divided by the total number of stand samples for each category (*N*) multiplied by 100.

RESULTS

Total sporocarp production

Sporocarps were harvested from a total of 5,900 m^2, yielding a dry weight sporocarp biomass of 777 grams. This is equivalent to a standing biomass of 1.3 kg/ha. The maximum single stand sample total biomass was 99 g dry weight, equivalent to 9.9 kg/ha. Approximately 47 species of hypogeous fungi were recorded during the study (some collections are of uncertain taxonomic affinity and some taxa are of uncertain status). Fourteen species account for 93% of the total biomass. Five species account for 73% of the biomass. The 14 major species are listed in Table 1.2 with species biomass, percent total biomass, frequency, and species acronyms. Species with 5% or more of the total biomass are ranked in Table 1.3.

The correlation between the number of sporocarps of a species in a plot and their total dry weight produced an *r* value of 0.51 (Figure 1.3). This indicates sporocarp number is a poor substitute for sporocarp biomass as a measure of species relative importance, and therefore numbers of sporocarps were not used in further analyses (see also Chapter 3). Sporocarp distribution tended to be clumped with sequential plots along a transect having sporocarps and other plots in sequence lacking them, though spatial distribution of sporocarps was not formally tested or described.

Table 1.2. Sporocarp biomass, percent of total biomass, frequency in stand samples, and acronyms of major hypogeous fungal species obtained from a 5,900 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Species	Dry weight (g)	Percent of total	Freq.[1] (%)	Species acronym
Alpova trappei	7.9	1	15	ALTR
Elaphomyces granulatus	201.5	26	39	ELGR
Elaphomyces muricatus	17.4	2	15	ELMU
Gautieria monticola	146.4	19	37	GAMO
Hysterangium coriaceum	46.0	6	37	HYCO
Hysterangium crassirhachis	24.2	3	46	HYCR
Hysterangium setchellii	13.8	2	27	HYSE
Leucogaster rubescens	49.0	6	47	LERU
Leucophleps magnata	13.7	2	32	LEMA
Leucophleps spinispora	18.9	2	31	LESP
Rhizopogon parksii	122.6	16	41	RHPA
Rhizopogon subcaerulescens	22.6	3	34	RHSU
Rhizopogon vinicolor	28.5	4	51	RHVI
Truncocolumella citrina	21.6	3	24	TRCI
Total	734.1	95		

[1] Frequency determined as a percent of the total number of stand samples (59).

Table 1.3. Equivalent grams per hectare dry weight of sporocarps of hypogeous fungi each accounting for five percent or more of the biomass from a 5,900 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Species	g/ha
Elaphomyces granulatus	341.5
Gautieria monticola	248.1
Rhizopogon parksii	207.8
Leucogaster rubescens	83.0
Hysterangium coriaceum	78.0

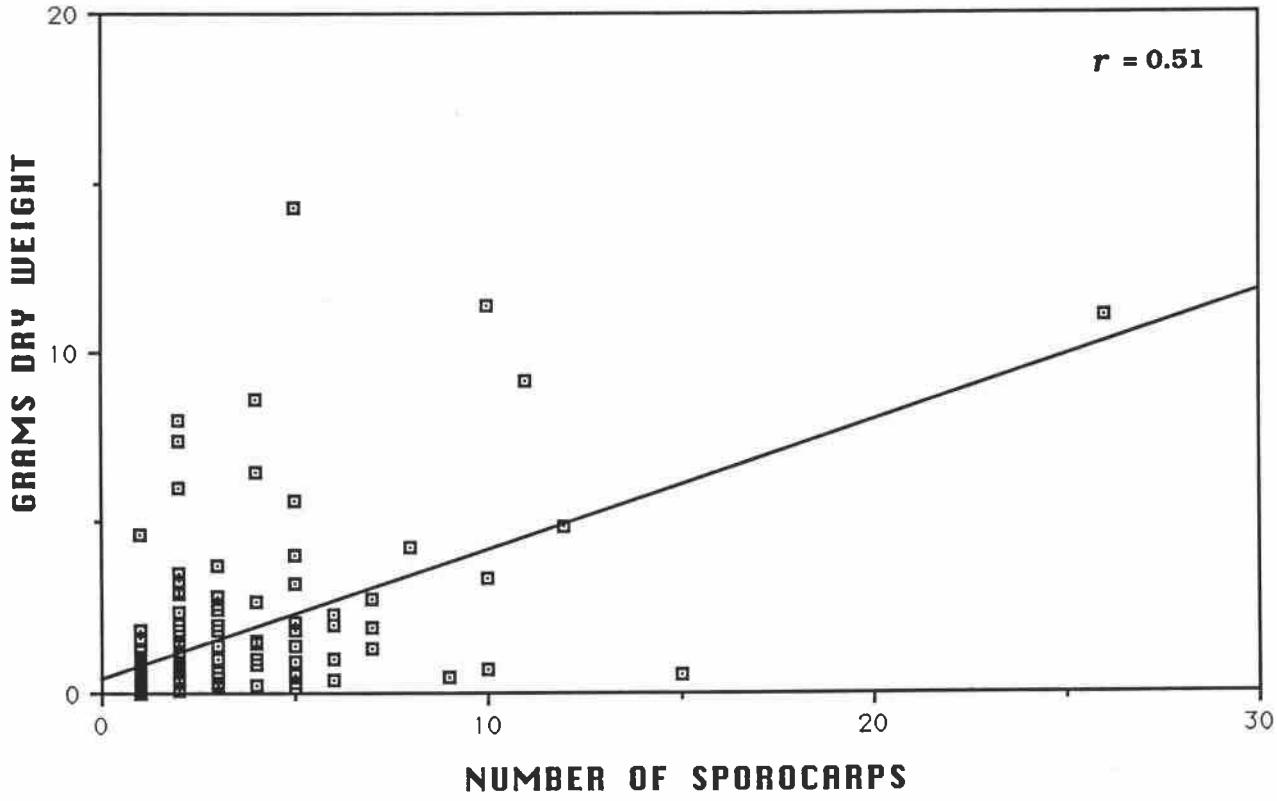


Figure 1.3. Correlation between number of sporocarps by species in a plot sample and species sample dry weight from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The distribution of stand sample biomass values by species, for all ten stands, is presented in Figure 1.4. The distribution of sample values is strongly skewed towards high values. Many sampling design considerations and analytical techniques become problematical because the non-normal distribution of the biomass values makes analysis by comparison of means difficult to interpret. The box representing the range from the 25th to the 75th percentile presents typical expected biomass values. The relative contribution of a particular sample value (as displayed in Figure 1.4) to a species' total biomass can be ascertained by comparison with dry weight totals in Table 1.2. The number of stand samples (*n*) in which a species occurred indicates the number of observations included in each percentile distribution.

Fifty percent of the total biomass of *Elaphomyces granulatus* is attributable to one extreme stand sample of 99 g (Table 1.2 and Figure 1.4). The value represents a particularly interesting outlier because it was obtained from a single 4 m^2 plot containing 54 sporocarps. If a high biomass typical for the overall sample area (30 to 35 g) had been collected instead, then the total biomass values for *Elaphomyces granulatus, Gautieria monticola,* and *Rhizopogon parksii* would have been similar. The three species form a group of biomass codominants with similar 50th percentile values each of which exceed the 75th percentile value of any other single species. The codominants also share similar frequencies (Table 1.2).

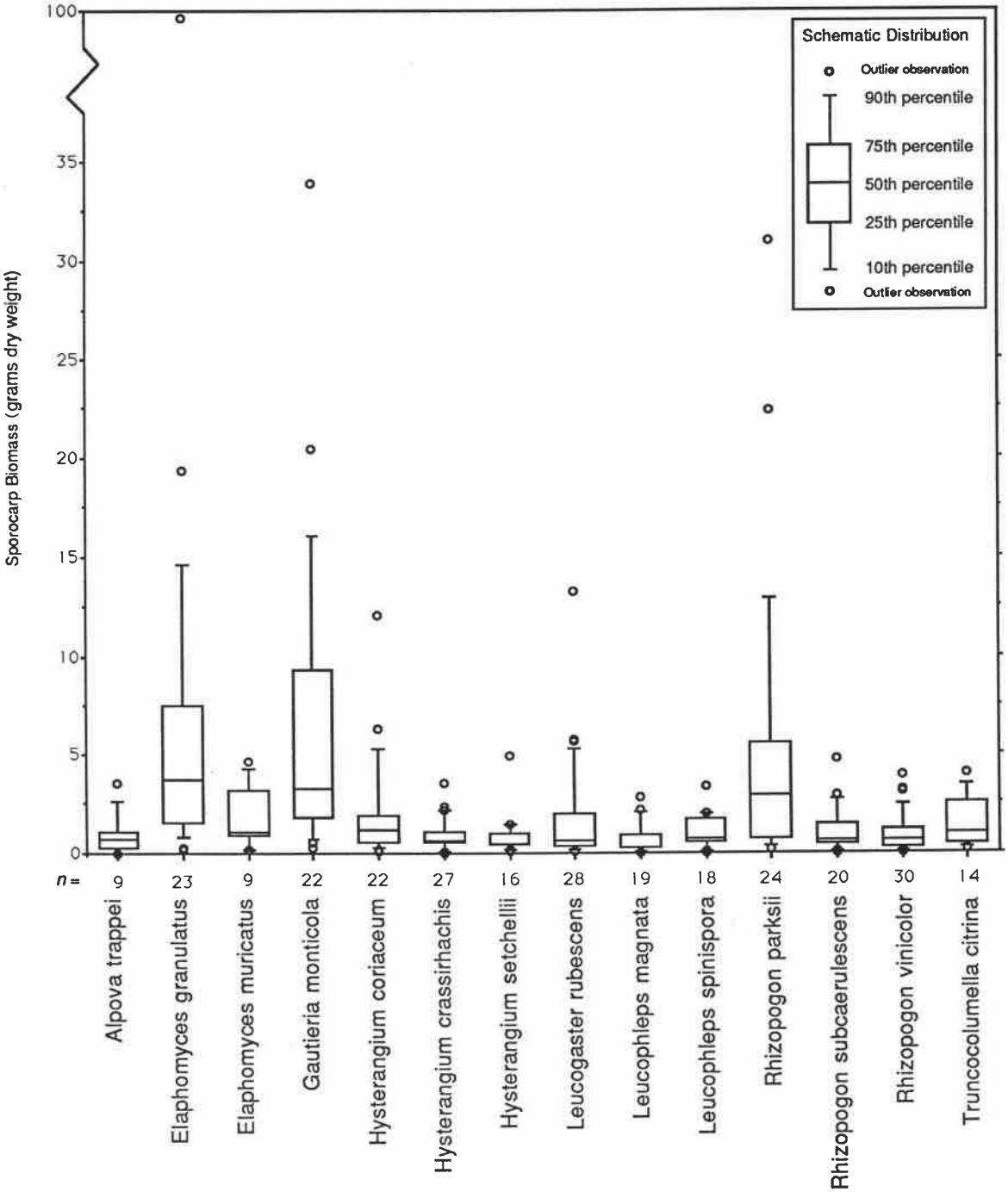


Figure 1.4. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for all stand samples (total $N = 59$) from a 5,900 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Hysterangium coriaceum and *Leucogaster rubescens* are two other species contributing five percent or more to the total biomass. Each has a single high sample value which is responsible for the species subdominant status. Otherwise, their 50th percentile values are not much different from those of the remaining species. *Hysterangium coriaceum* also has a frequency (37%) similar to that of the dominant species, while *Leucogaster rubescens* has the second highest frequency (47%, Table 1.2).

Alpova trappei and *Elaphomyces muricatus* share the lowest frequency (15%, Table 1.2) and *Alpova trappei* has the lowest total biomass of the major species. *Rhizopogon vinicolor* occurred in the most stand samples (51%) and *Hysterangium crassirhachis* had the third highest frequency (46%); yet, each had relatively low total biomass among the 14 major species. If relatively high frequency conveys some measure of importance, then *R. vinicolor* and *H. crassirhachis* could also be considered subdominant species.

The remaining species are not particularly distinctive in biomass. *Elaphomyces muricatus* and *Truncocolumella citrina* show relatively expanded ranges from the 50th to 75th percentile, with their 75th percentile values above those of *Hysterangium coriaceum* and *Leucogaster rubescens*.

Seasonal sporocarp production

Spring, summer, and fall sporocarp biomass stand sample values are shown by species in Figures 1.5–1.7. The percentile diagrams show strongly skewed species biomass distributions in all seasons. Comparisons of species abundance between and within seasons are shown in Table 1.4. Changes in the relative importance of a species between seasons can be seen by examining the percentage data (Table 1.4). The number of stand samples in which a species was encountered (frequency) is shown as a percentage of the total number of stand samples in the various seasonal and habitat categories (Table 1.5).

The spring fruiting is dominated by *Elaphomyces granulatus* and *Gautieria monticola* (Table 1.4). As discussed earlier, the extreme biomass value of *E. granulatus* is due to a single outlier and if a more "reasonable"(for this sample size, 2,800 m^2) high stand sample value of 35 g for *E. granulatus* were assumed, then *Gautieria* would have higher total spring biomass. *Hysterangium coriaceum* and *Rhizopogon vinicolor* are spring biomass sub-dominants and also have the two highest frequencies. The low spring biomass of *Elaphomyces muricatus* is attributable to moderately high sample values (Figure 1.5) but low frequency (14%, Table 1.5). Spring and summer were nearly equal in total sporocarp biomass, each season with an equivalent of 1.6 kg/ha standing biomass, however, with the adjustment for *Elaphomyces granulatus*, the spring equivalent biomass, is 1.3 kg/ha.

Table 1.4. Seasonal sporocarp equivalent biomass and percent (%) of total seasonal biomass for the 14 most important species from a 5,900 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Species	Spring g/ha	Spring %	Summer g/ha	Summer %	Fall g/ha	Fall %
Alpova trappei	7	<1	**92**	**6**	5	<1
Elaphomyces granulatus	**545**[1]	**35**	**320**	**20**	**127**	**15**
Elaphomyces muricatus	39	3	20	1	21	2
Gautieria monticola	**471**	**30**	**176**	**11**	22	3
Hysterangium coriaceum	**163**	**10**	—	—	2	<1
Hysterangium crassirhachis	50	3	24	2	34	4
Hysterangium setchellii	19	1	**108**	**7**	12	1
Leucogaster rubescens	37	2	**426**	**27**	**67**	**8**
Leucophleps magnata	49	3	—	—	—	—
Leucophleps spinispora	66	4	10	<1	—	—
Rhizopogon parksii	—	—	**238**	**15**	**426**	**51**
Rhizopogon subcaerulescens	27	2	**116**	**7**	36	4
Rhizopogon vinicolor	**88**	**6**	46	3	7	<1
Truncocolumella citrina	—	—	16	1	**80**	**9**
Seasonal total g/ha	1561		1592		839	
Adjusted values (g/ha)[2]	(1329)		(1354)		(885)	

[1] Values for dominant and subdominant species (sporocarp biomass > 5%) are shown in bold type.

[2] One *Elaphomyces granulatus* sample value was reduced and one *Rhizopogon parksii* sample value was moved from the summer to the fall catatgory. Details are in the results.

Table 1.5. Species frequency in stand samples by season and by habitat, expressed as percentage of the total number of stand samples in a catagory, for the 14 most important species from a 5,900 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Species	Season			Habitat				
	Spring	Summer	Fall	WOG	MOG	DOG	MM	MY
Alpova trappei	21	40	4	8	8	14	38	17
Elaphomyces granulatus	39	40	38	46	58	7	50	42
Elaphomyces muricatus	14	20	15	23	25	0	38	0
Gautieria monticola	57	60	12	15	33	36	63	50
Hysterangium coriaceum	75	0	4	46	33	21	50	42
Hysterangium crassirhachis	53	40	38	23	67	79	63	0
Hysterangium setchellii	36	40	15	23	42	36	25	8
Leucogaster rubescens	43	100	42	38	33	50	63	58
Leucophleps magnata	68	0	0	23	42	14	50	42
Leucophleps spinispora	61	20	0	8	33	43	38	33
Rhizopogon parksii	0	20	88	46	42	36	38	42
Rhizopogon subcaerulescens	29	60	31	23	42	43	50	17
Rhizopogon vinicolor	79	60	15	62	50	50	38	50
Truncocolumella citrina	0	20	50	15	42	0	25	42

[1]WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

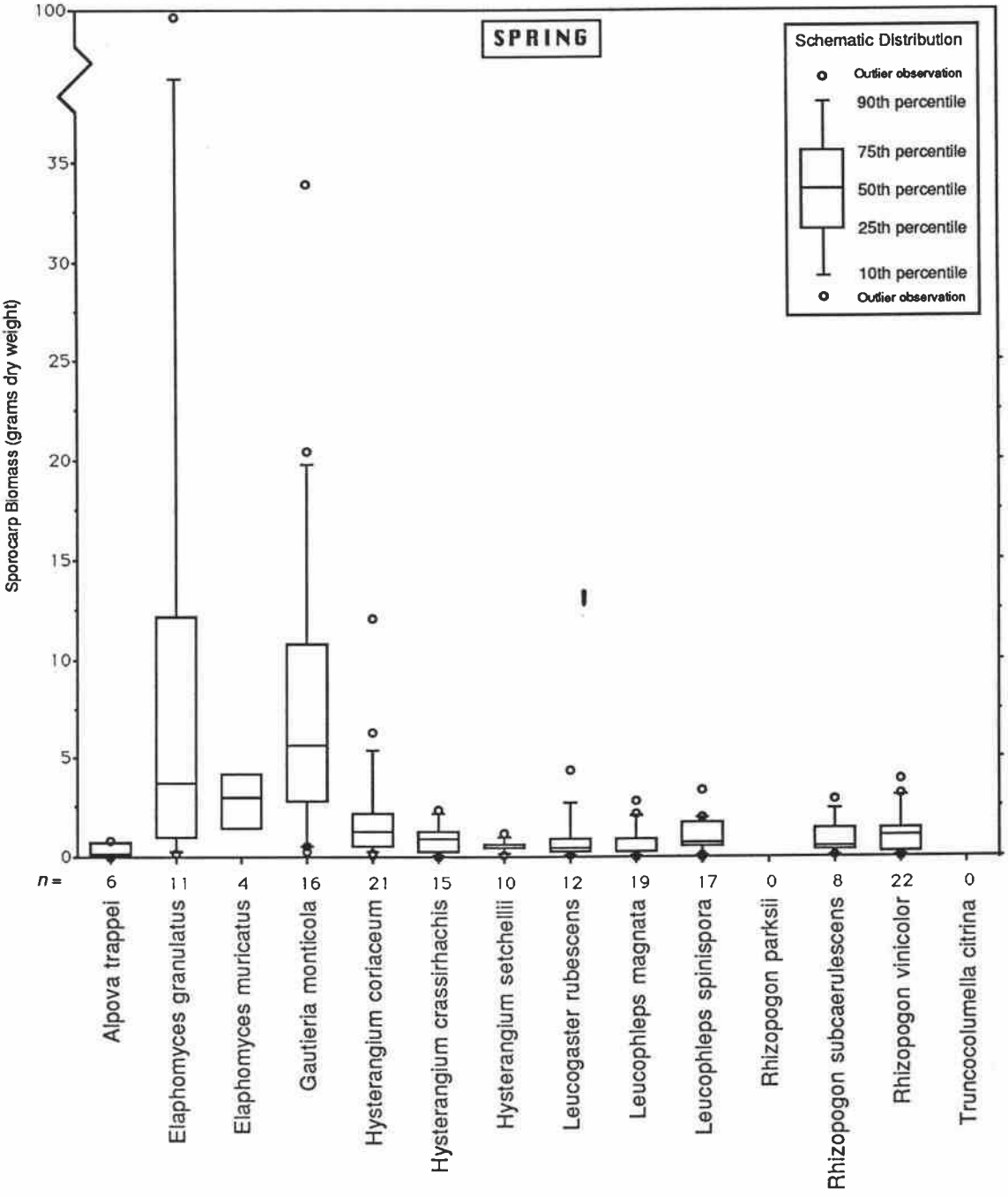


Figure 1.5. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for spring stand samples (total $N = 28$) from a 2,800 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The caution and limits imposed on interpretations by the small number of observations (*n*) for most species' summer biomass values is apparent (Figure 1.6). However, none of the summer sample values for species with low (1-2) *n*'s are extreme in comparison with the other seasonal values, so interpretative comparisons can be made, keeping in mind the small total sample size (500 m^2).

The pattern of summer fruiting is both transitional and distinctive (Figure 1.6). Biomass is more equably distributed among the dominant species. Seven species each contribute 5% or more to the total seasonal biomass (Table 1.4). *Leucogaster rubescens*, with 100% frequency (Table 1.5), dominates summer biomass. *Elaphomyces granulatus* and *Gautieria monticola*, spring codominants, are summer co– and subdominant, respectively. *Rhizopogon parksii* is a biomass subdominant, but its biomass is attributable to a single stand sample collected in the last week of summer. That same stand sample also contained the only summer occurrence of *Truncocolumella citrina*. Both species are harbingers of the fall fruiting season. *Alpova trappei*, *Hysterangium setchellii*, and *Rhizopogon subcaerulescens* reach subdominant status only in summer. In terms of frequency, *Rhizopogon subcaerulescens* and *R. vinicolor* were commonly encountered (Table 1.5).

Total summer biomass is 1.6 kg/ha but an adjusted summer total biomass of 1.4 kg/ha is obtained by more appropriately including *Rhizopogon parksii* biomass in the fall total.

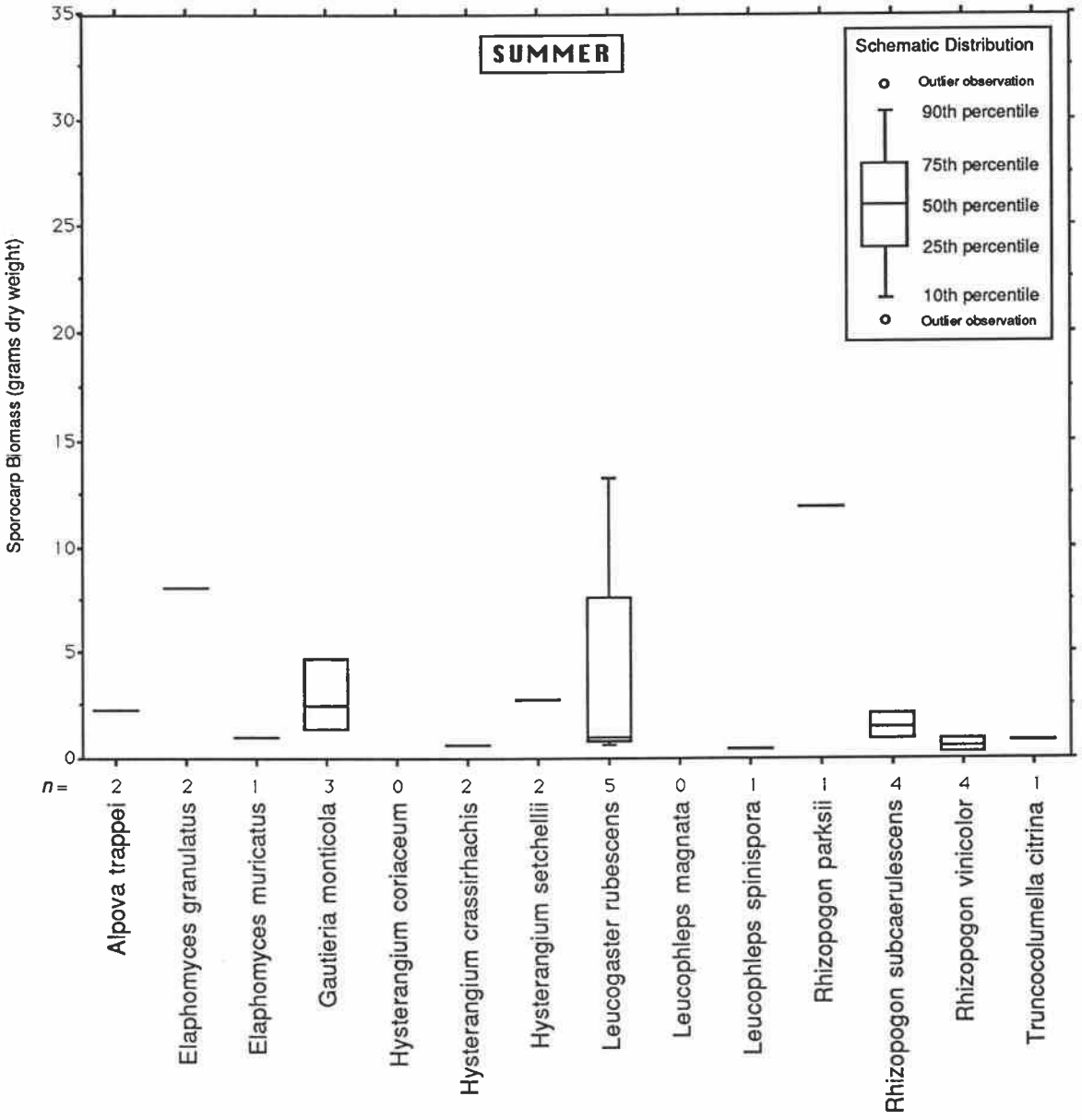


Figure 1.6. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for summer stand samples (total $N = 5$) from a 500 m^2 total sample in three Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The adjusted value is more meaningful because total summer sample area is small. The occurrence and dominance of both spring and fall fruiting species during the summer can be expected to vary with weather conditions from year to year (Fogel, 1981). Conversely, the distinctive summer dominant/subdominant species (e.g., *Leucogaster rubescens* and *Alpova trappei*) could be expected to retain their importance from year to year.

Fall sporocarp production is dominated by *Rhizopogon parksii* with >50% of the total biomass (Table 1.4) and an 88% frequency (Table 1.5). Two samples (Figure 1.7) contributed 25% of *R. parksii*'s fall biomass. The spring dominant, *Elaphomyces granulatus*, is a fall subdominant. *Truncocolumella citrina* is a characteristic fall species although it had one late summer occurrence coincidental with *Rhizopogon parksii*. *Leucogaster rubescens* is another fall subdominant. *Hysterangium crassirhachis* and *Rhizopogon subcaerulescens* show moderate importance with respect to frequency.

Total fall seasonal biomass was equivalent to 0.8 kg/ha. In contrast to Fogel and Hunt's (1979) marked fall peak biomass, this is only half the value of the spring or summer seasonal biomass values. Adding the *Rhizopogon parksii* summer sample to the fall category adjusts the fall total to 0.9 kg/ha. Because of the smaller total sample area for the summer period, the *Rhizopogon parksii* sample contributes relatively little to the fall equivalent kg/ha total.

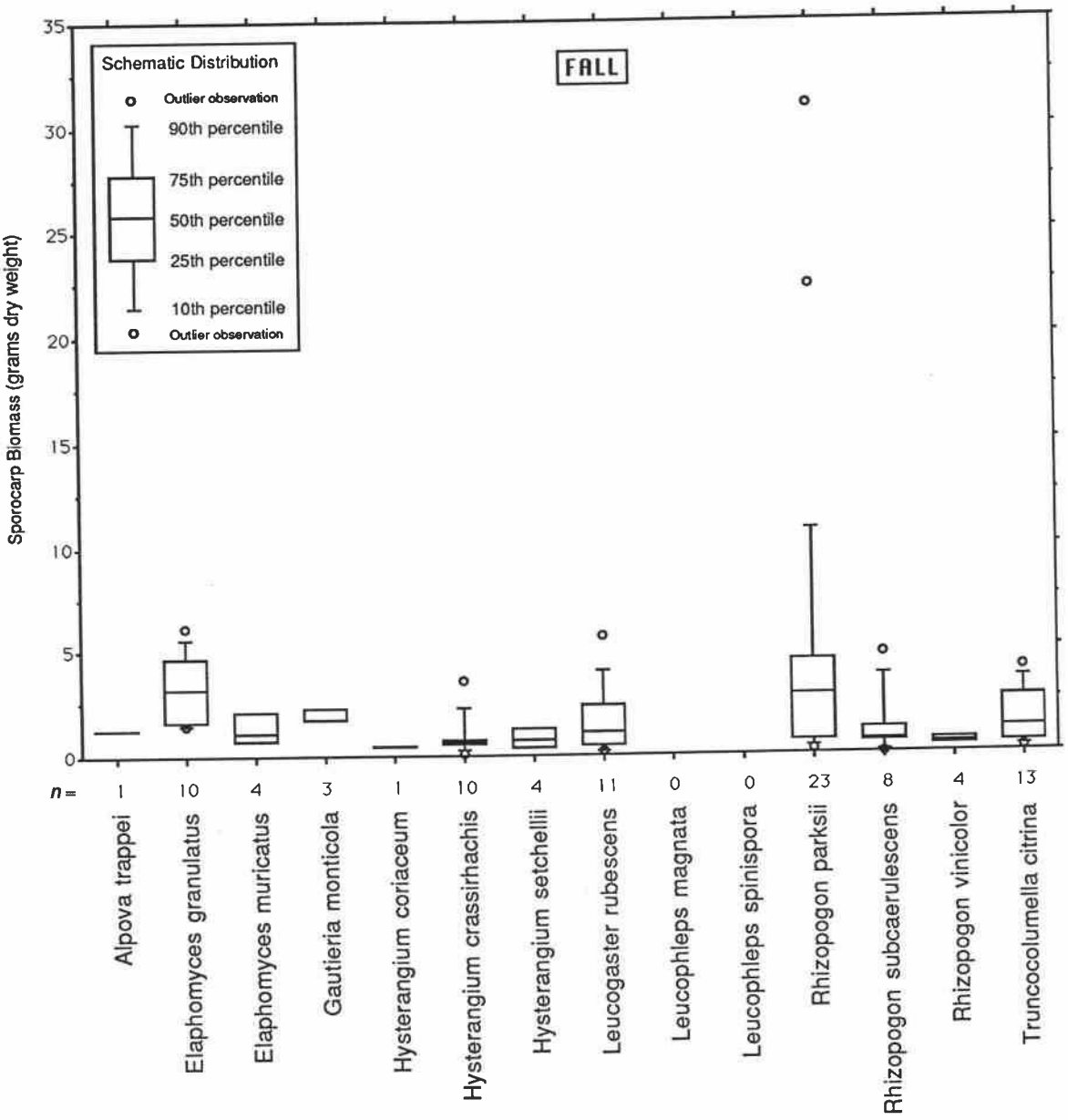


Figure 1.7. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for fall stand samples (total $N = 26$) from a 2,600 m^2 total sample in ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Sporocarp production by habitat

Comparisons between species biomass in a particular habitat and comparisons of biomass for a particular species between habitats are shown in Table 1.6 and Figures 1.8 –1.12. Changes in the relative importance (as measured by biomass) of a species between habitats can also be seen by examining the percentage data in Table 1.6. In order to fully interpret the equivalent g/ha biomass values for each species it is necessary to consider individual stand sample values in relation to the overall range and frequency of values and the total sample area for each habitat. The percentile diagrams show which biomass values are associated with strongly skewed distributions.

The wet old–growth (WOG) habitat is codominated by *Elaphomyces granulatus* and *Rhizopogon parksii* (Table 1.6). Nearly 90% of *R. parksii*'s total biomass is attributable to its highest single stand sample value (Figure 1.4, Figure 1.8). However, in relation to total habitat sample area and overall biomass value distribution, the value is judged not so extreme as to justify an "adjusted" value as was done with the seasonal data. The biomass total for *E. granulatus* is based on a more normal distribution of values, hence, *E. granulatus* may be the typical dominant based on sporocarp biomass. *Elaphomyces muricatus, Gautieria monticola, Hysterangium coriaceum,* and *Rhizopogon subcaerulescens* are subdominants, each with >5% of the total biomass. *R. vinicolor* has the highest frequency at 62% (Table 1.5). Total standing equivalent biomass is 0.9 kg/ha for the WOG habitat.

Table 1.6. Species sporocarp biomass (equivalent g/ha) and percent (%) of total biomass by habitat, for the 14 most important species in a 5,900 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

	Habitat[1]									
Species	WOG		MOG		DOG		MM		MY	
Acronym	g/ha	%	g/ha	%	g/ha	%	g/ha	%	g/ha	%
ALTR	2	<1	8	<1	25	3	35	2	3	<1
ELGR	**278**[2]	**29**	**993**	**63**	6	<1	**384**	**18**	**122**	**10**
ELMU	**63**	**7**	19	1	—	—	85	4	—	—
GAMO	**78**	**8**	50	3	**168**	**22**	**768**	**35**	**378**	**32**
HYCO	**69**	**7**	65	4	24	3	55	3	**178**	**15**
HYCR	8	<1	54	3	**84**	**11**	60	3	—	—
HYSE	13	1	60	4	21	3	18	<1	5	<1
LERU	25	3	18	1	**204**	**27**	81	4	**71**	**6**
LEMA	7	<1	11	<1	4	<1	74	3	43	4
LESP	5	<1	46	3	**44**	**6**	58	3	18	2
RHPA	**278**	**29**	**155**	**10**	**101**	**13**	**404**	**18**	**179**	**15**
RHSU	48	5	49	3	24	3	65	3	17	1
RHVI	52	5	29	2	38	5	65	3	65	5
TRCI	22	2	23	1	—	—	35	2	**110**	**9**
Total	948		1580		743		2187		1189	

[1] WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

[2] Values for dominant and subdominant species (sporocarp biomass > 5%) are shown in bold type.

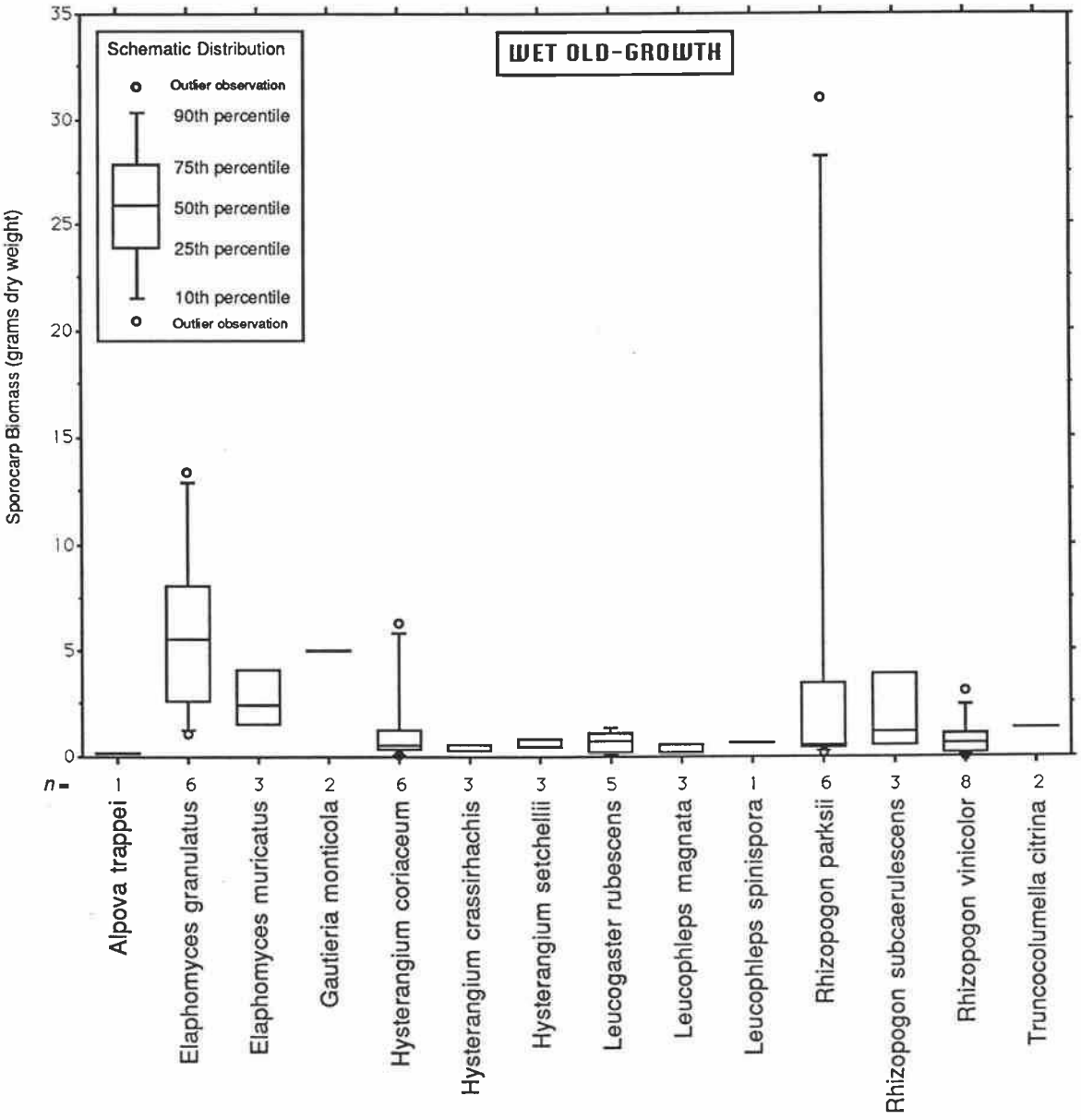


Figure 1.8. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for wet old-growth stand samples (total $N = 13$) from a 1,300 m^2 total sample in two Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Elaphomyces granulatus is the major biomass dominant of the mesic old-growth (MOG) habitat (Table 1.6). As discussed earlier, the extreme 99 g stand sample value is involved (Figure 1.9). Substituting a 35 g value (based on comparison with the distribution of biomass values from all stand samples and total habitat sample area) gives a biomass value of 455 g/ha equivalent which would represent 44% of the MOG habitat total. *Elaphomyces granulatus* retains dominant status and *Hysterangium coriaceum, H. crassirhachis,* and *H. setchellii* then join *Rhizopogon parksii* as biomass subdominants. *Hysterangium crassirhachis* is the most frequent species, occurring in 67% of the stand samples (Table 1.5). The equivalent biomass total for the MOG habitat is 1.6 kg/ha with an adjusted value of 1.0 kg/ha.

The dry old-growth habitat (DOG) is codominated by *Leucogaster rubescens* and *Gautieria monticola* (Table 1.6). *Rhizopogon parksii* and *Hysterangium crassirhachis* are the most important subdominants. *Leucophleps spinispora* also contributes >5% to the DOG habitat biomass total. *H. crassirhachis* has the highest frequency (79%). *R. vinicolor* and *Leucophleps spinispora* are the second most frequent species at 50% (Table 1.6). There are no extreme stand sample biomass values from this habitat (Figure 1.10). The equivalent biomass total for the type is 0.7 kg/ha, the lowest of the habitats.

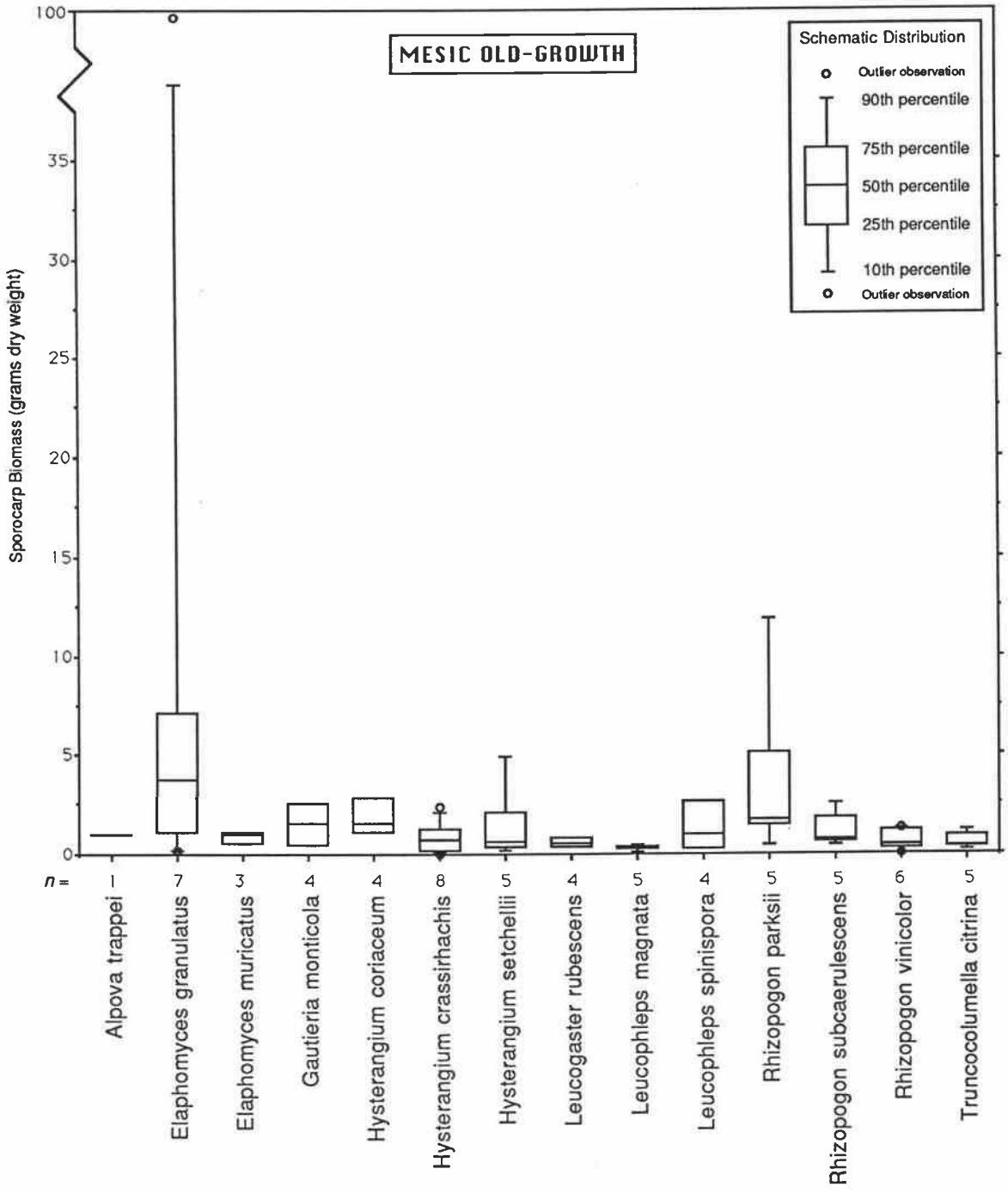


Figure 1.9. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for mesic old-growth stand samples (total $N = 12$) from a 1,200 m^2 total sample in two Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

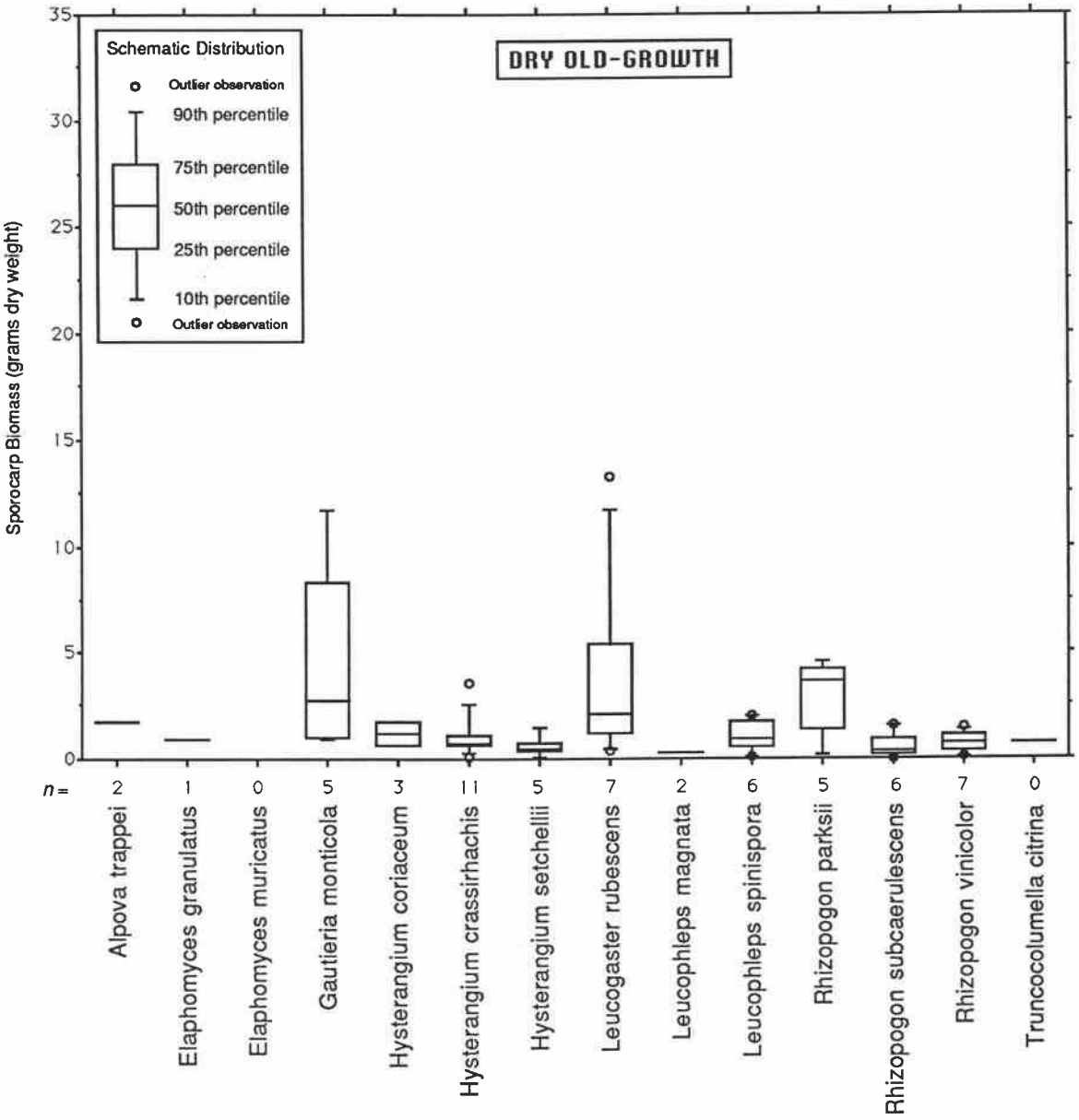


Figure 1.10. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for dry old-growth stand samples (total $N = 14$) from a 1,400 m^2 total sample in two Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Even though the mesic mature (MM) habitat has fewer stand samples (*N*=8) than the other habitats, the least frequent species (*Hysterangium setchellii, Truncocolumella citrina*) each have two occurrences suggesting that the sample size is adequate if not ideal (Figure 1.11). *Gautieria monticola* dominates with 35% of the total sporocarp biomass (Table 1.6); however, its single highest stand sample value (Figure 1.4) contributed 55% of the species biomass. The cautions imposed by the smaller total sample area (800 m^2) from which mesic-mature habitat data were obtained must be considered. The equivalent g/ha biomass for *Gautieria monticola* in the mesic-mature habitat might have been less, had the total sample area in the habitat been larger. Discounting this single extreme sample, *Rhizopogon parksii* and *Elaphomyces granulatus* would achieve codominant status in this habitat. The codominants also share a wide range of values from the 25th to the 75th percentile. *Leucogaster rubescens* and *Hysterangium crassirhachis* along with *Gautieria monticola* have the highest frequency (63%), as seen in Table 1.5. With an equivalent biomass of 2.2 kg/ha, the mesic mature habitat has the highest standing biomass of any habitat (Table 1.6).

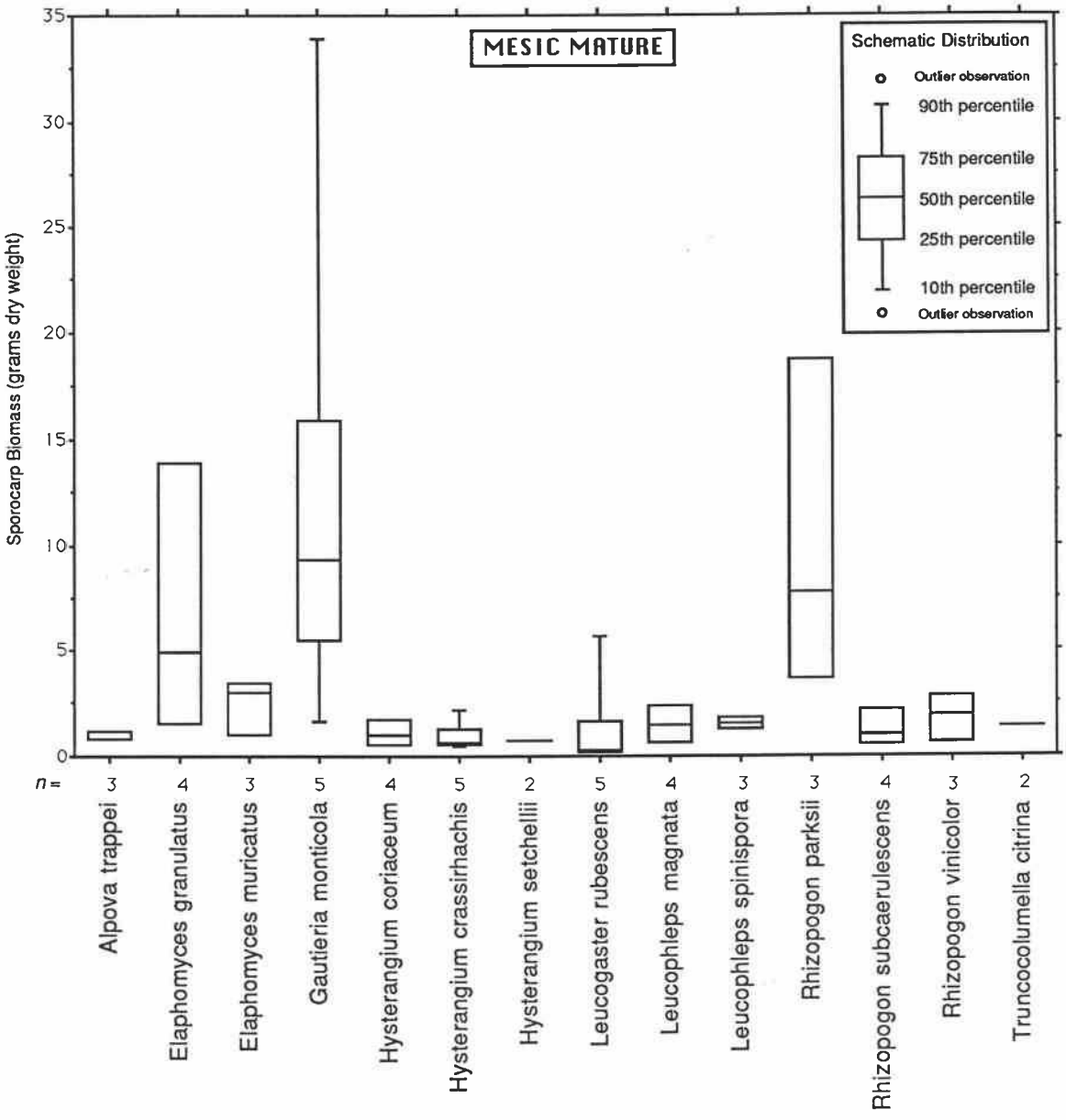


Figure 1.11. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for mesic mature stand samples (total $N = 8$) from an 800 m^2 total sample in two Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The mesic young (MY) habitat is also dominated by *Gautieria monticola* (Table 1.6). *Hysterangium coriaceum* and *Rhizopogon parksii* are subdominants. Again, the dominant species have wide ranges in the 2nd and 3rd quartiles (Figure 1.12). Other species contributing >5% to the biomass total for the MY habitat are *Elaphomyces granulatus, Truncocolumella citrina,* and *Leucogaster rubescens. Leucogaster rubescens* is the most frequent species at 58% (Table 1.5). Equivalent biomass total for the MY habitat (1.2 kg/ha) is half that of the MM habitat (Table 1.6).

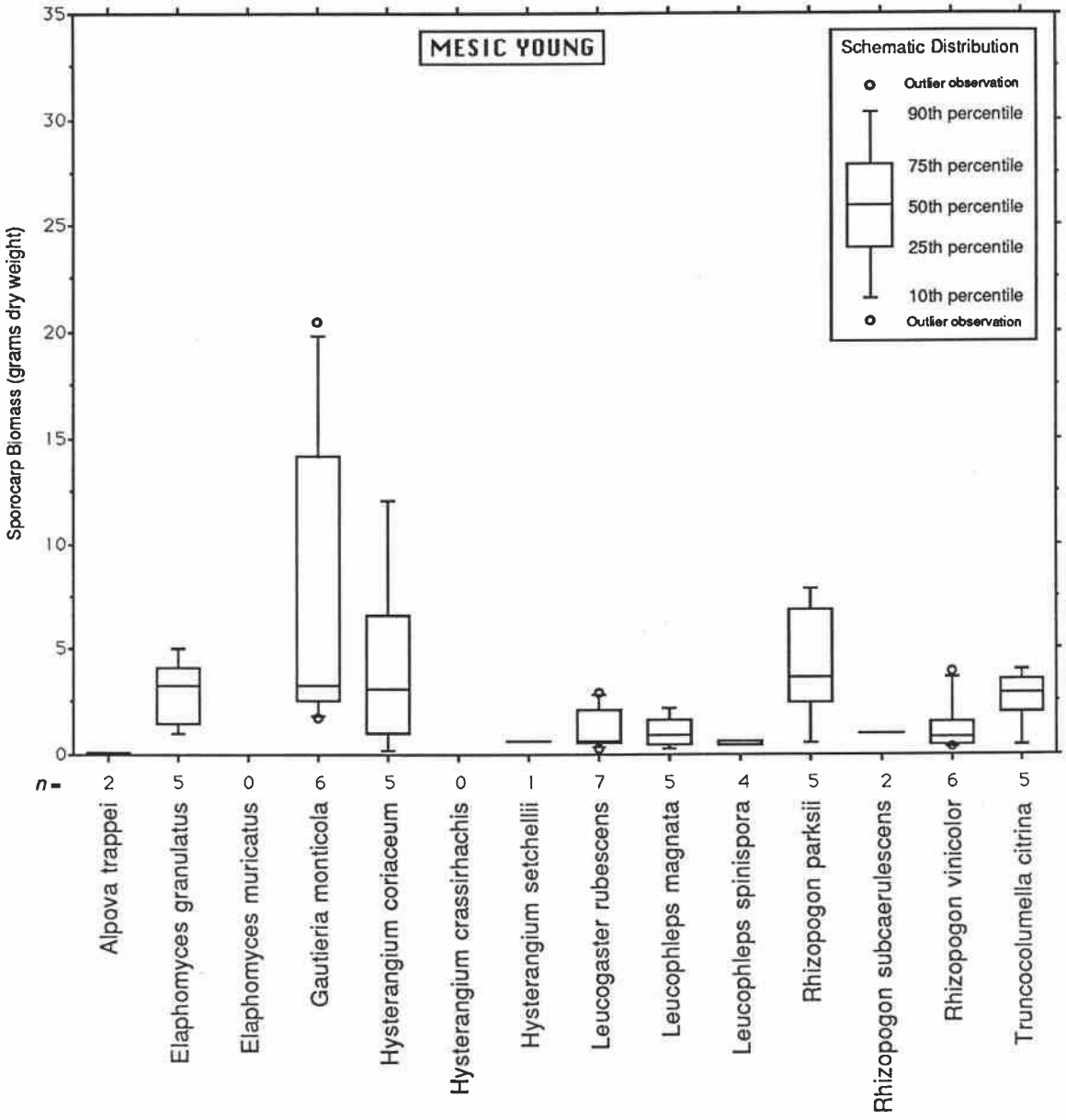


Figure 1.12. Percentile distribution of species stand sample biomass values and number of stand samples (*n*) in which each species occurred for the 14 most important species for mesic young stand samples (total $N = 12$) from a 1,200 m^2 total sample in two Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

DISCUSSION

Interpretations of ecological importance

Interpretations of ecological "importance" based on sporocarp formation are limited. Sporocarp biomass is a direct measure of importance when considering sporocarps as a food source for animals (Fogel and Trappe, 1978). The usefulness of sporocarp biomass as an index to ecological and physiological functioning of the mycelial "body" of a fungal organism can only be inferred or assumed. The correlation between sporocarp formation and symbiotic "importance" in areas such as efficiency of nutrient uptake and translocation or competitive interactions for root space is unknown. Furthermore, Kropp and Fortin (1988) report that isolates from different mycelia of the same species of mycorrhizal fungus vary in their colonization density on root systems of seedlings grown in test tubes.

Fogel (1976) and Hunt and Trappe (1987) have shown that sporocarp biomass production of a single species varies from year to year. Similar variation was noted in this study. Weather patterns likely account for much year to year variation (Fogel, 1981). Although it is ecologically meaningful in the context of 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. In this study, that constraint was overcome by combining data from all four sample years. The use of numbers of sporocarps as a measure of importance was not pursued because the

overall correlation between number of sporocarps for an individual species in a plot and its total sporocarp dry weight in a plot was poor.

Frequency provides another means of evaluating the data, both for interpreting the biomass data and as a measure of "commonness" itself. Sporocarp biomass values may not always be the best measure of the importance of a species. Since, the relationship between sporocarp biomass, the abundance of a fungus in the soil, the extent of mycorrhizal symbiosis, and the physiological "importance" of a species is unknown, the high frequency of a species in seasons or habitats can give another perspective on the potential "importance" of a species which otherwise has relatively less "important" biomass values for a particular season or habitat. Traditionally, in studies of vascular plant communities, frequency is concerned with the regularity of a species distribution throughout a community (homogeneity) and has been interpreted with caution because variations in plot size, number, and vegetation structure produce different results (Cain and Castro, 1959; Mueller–Dombios and Ellenberg, 1974). Moreover, this study uses frequency as a measure of abundance to convey importance by presence or absence in stand samples. Species which fruit predominantly in spring or fall are restricted to fewer potential samples (on a habitat basis) compared to species which fruit in both seasons.

Interpretations of importance (as measured by sporocarp biomass dominance) are restricted to comparisons among ectomycorrhizal fungi producing hypogeous sporocarps. Epigeous sporocarps of mycorrhizal fungi

were excluded due the amount of sampling necessary in relation to available resources, but potential corollary interpretations should be kept in mind. Fogel and Hunt (1979) found epigeous sporocarps had nearly twice the standing crop of hypogeous sporocarps in a young Douglas-fir stand. Vogt et al. (1981) found only one hypogeous fungus species compared to six epigeous species in a study of mycorrhizal dynamics in an *Abies* stand. Separate consideration of ectomycorrhizal fungi which produce hypogeous sporocarps is valid because they can be considered a guild (community sub-group) of organisms united by mode of nutrition and specially adapted reproductive biology.

Cooke (1955) measured epigeous sporocarp dominance by estimating fruit 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 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.

Sporocarp production by species

Each major hypogeous ectomycorrhizal species sporocarp production is discussed in relation to its seasonal and habitat distribution. If one assumes that sporocarp production provides some rough measure of ecological influence, then inferences about each species functional optimum by season and habitat can cautiously be made. Distribution of species biomass (calculated in equivalent g/ha for each category and not "adjusted" as in Table 1.4) is shown as a percentage of a species total biomass for all seasons or habitat types (Figures 1.13a–1.13e). This procedure allows for relative within– and between–species comparisons. This section serves to integrate, summarize, and interpret the analysis on a species by species basis.

***Alpova trappei* Fogel** has a distinct summer seasonal peak in relative biomass (Figure 1.13a). However, this peak is attributable to its maximum stand sample value (see Figure 1.4). Since the high value for this species occurred in the season with substantially fewer samples and because the distribution of biomass is skewed towards few relatively large values, the apparent summer peak in relative biomass could be an artifact of a small total sample area. With increased total sample area given more stand samples in summer, the few high stand sample values would have less proportional effect and a smaller equivalent biomass value would be expected. *Alpova trappei*, never a frequent species, also had its greatest frequency in the summer.

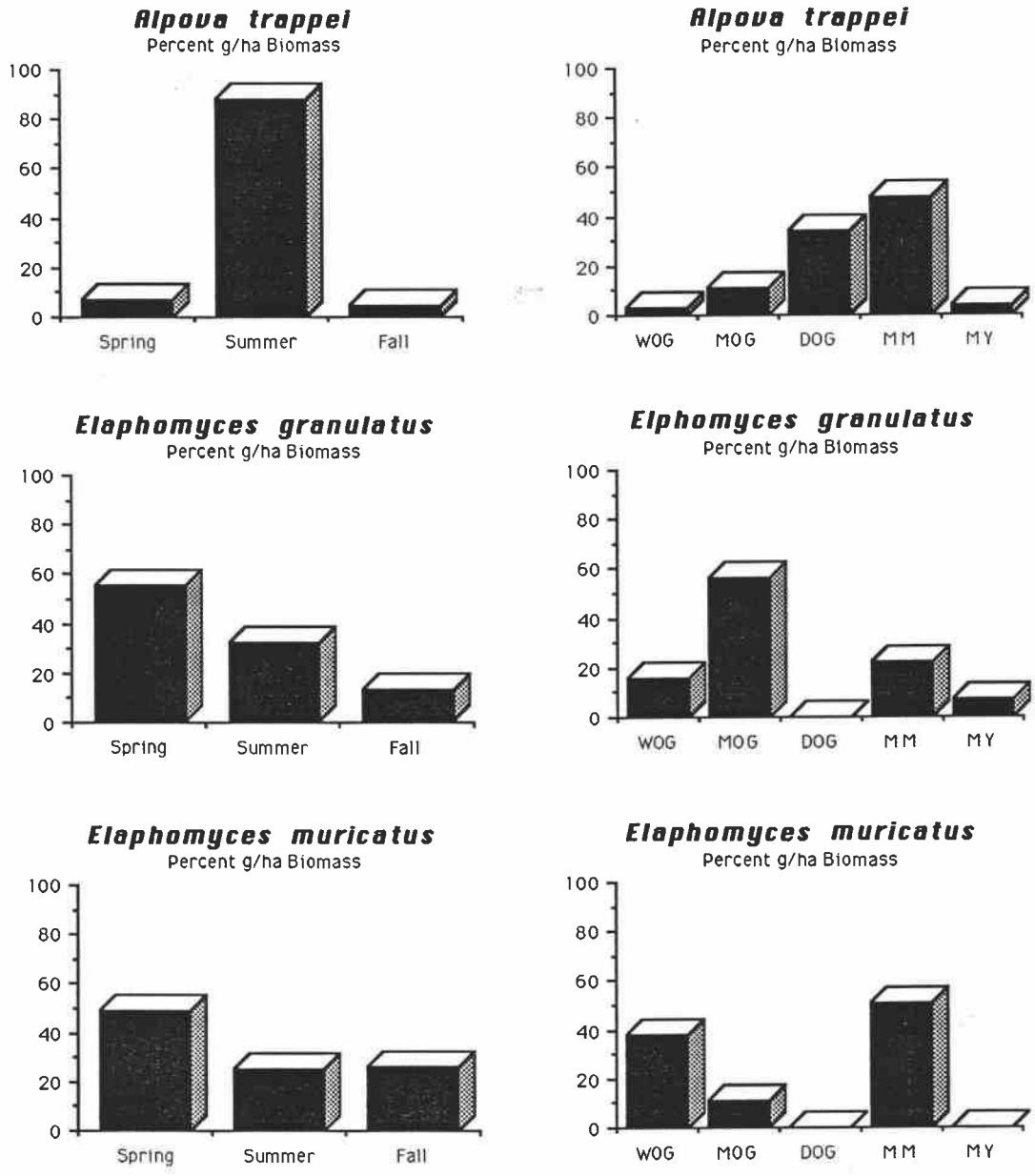


Figure 1.13a. Percent of each species total sporocarp biomass (equivalent g/ha) by season and habitat, for the 14 most important species in a 5,900 m^2 sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

Of all the habitats, the mesic-mature habitat supported the largest proportion of the sporocarp biomass of *A trappei* on a g/ha basis (Figure 1.13a). This is partly a function of greater frequency in that habitat (Table 1.5). Its maximum stand sample biomass value (see Figure 1.4) occurred in the dry old-growth but because of the greater number of stand samples (larger total sample area) in that habitat the equivalent g/ha value is not inflated. An apparent gradient of increasing relative biomass from wet old-growth to dry old-growth exists though the frequency in mesic and wet old-growth habitats is the same.

***Elaphomyces granulatus* Fr.** shows a gradual decline in relative biomass from spring to fall (Figure 1.13a). Over 50% of its relative sporocarp biomass occurred in spring. Frequency was essentially the same in each season. The largest biomass values were in the spring including the 99 g value (Figure 1.5). *E. granulatus* had the highest biomass overall, which supports the observation of Smith et al. (1981) that it may be the most common hypogeous fungus in North America.

Biomass increases markedly from younger to older mesic habitats (Figure 1.13a). Adjusting for the occurrence of the single 99 g stand sample value in the mesic old-growth habitat would lower its proportion of the biomass to 40% which, however, would remain the largest share of biomass. *E. granulatus* shows a minimum of biomass and frequency in the dry old-growth habitat, though frequency variation is not marked between habitats (Table 1.5).

***Elaphomyces muricatus* Fr.** is relatively constant in sporocarp biomass production throughout the fruiting seasons with peak production in spring (Figure 1.13a). Colonies of *E. muricatus* are moderately productive (Figure 1.4) but highly dispersed (Table 1.2) Frequency shows a slight peak in summer (Table 1.5).

Within the old-growth categories, an increase from the dry to wet habitat is apparent. *E. muricatus* has peak production in biomass and highest frequency in the mesic mature habitat. Both *Elaphomyces* species show minimal sporocarp production in the dry and young habitats.

***Gautieria monticola* Harkn.** is predominantly a spring fruiter with moderate relative biomass production in summer and minor production in fall (Figure 1.13b). Spring and summer frequencies are about equal while fall frequency is strongly diminished (Table 1.5).

Gautieria monticola sporocarp biomass production predominates in the young to mature habitats but is markedly lower in the old-growth habitats (Figure 1.13b). Again, because its highest stand sample value (Figure 1.11) occurred in the least sampled habitat, the strength of its presence in this habitat is subject to overestimation. Although the within–species biomass allocation of *G. monticola* is relatively low in the dry old-growth habitat, it is a co-dominant in sporocarp biomass production in that habitat (Table 1.6). The trends in frequency (Table 1.5) generally reflect those of relative biomass with the exception of the mesic old-growth habitat (with minimum biomass) in which the frequency of *G. monticola* approximates that in the dry old-growth.

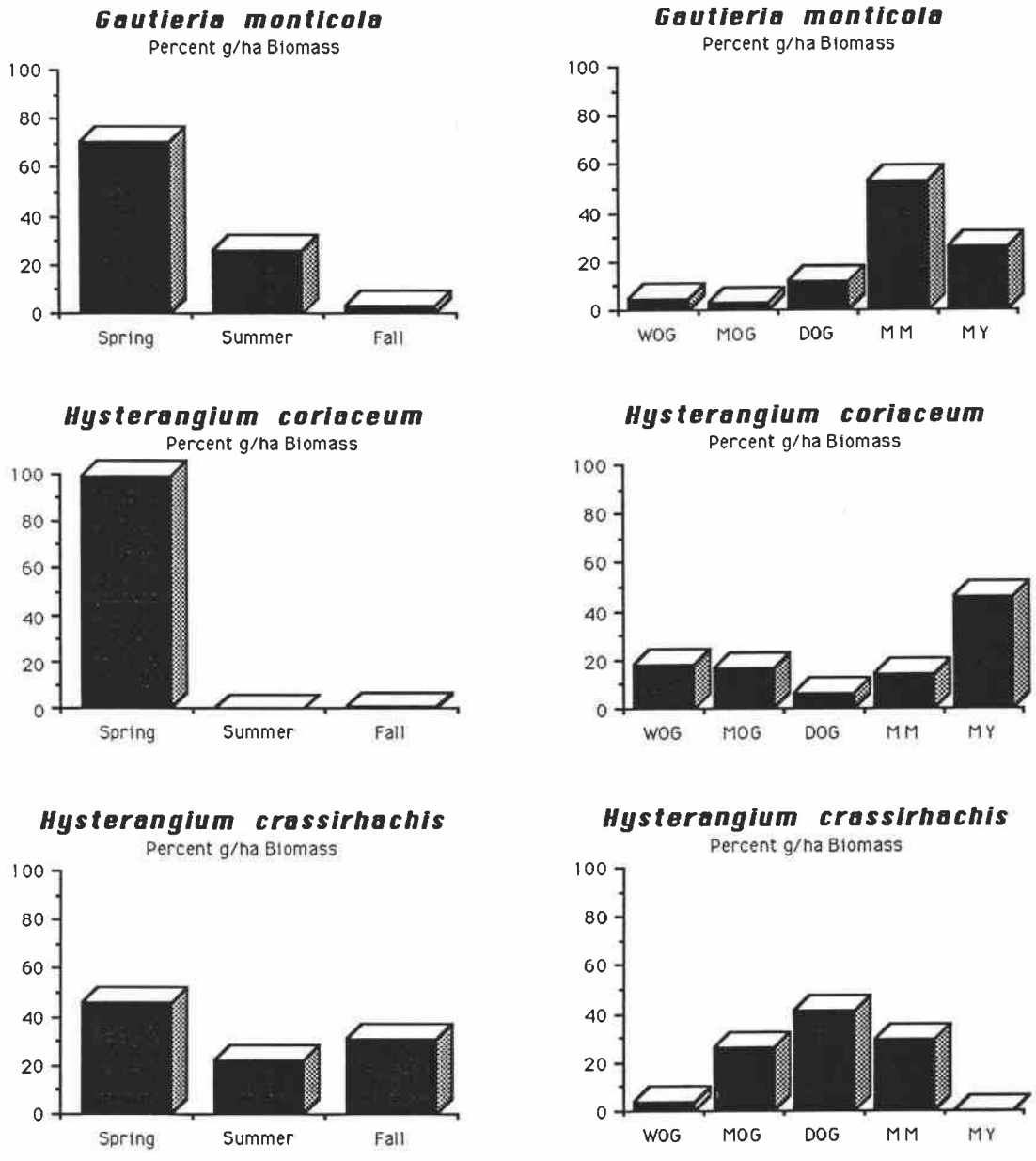


Figure 1.13b. Percent of each species total sporocarp biomass (equivalent g/ha) by season and habitat, for the 14 most important species in a 5,900 m^2 sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

***Hysterangium coriaceum* Hesse** fruits in spring with little exception (Figure 1.13b). The mesic young habitat has the highest proportion of sporocarp biomass. The relative biomass is rather evenly distributed through the other habitats with the least amount found in the dry old-growth habitat. This is a marked contrast to a related species with similar macromorphology, *H. crassirhachis,* which has its maximum relative biomass in the dry old–growth. *H. coriaceum* has its highest frequency in the mesic mature habitat (50%) and only half that in the dry old–growth (Table 1.5).

***Hysterangium crassirhachis* Zeller & Dodge** relative biomass is rather evenly distributed through the seasons (Figure 1.13b). There is a slight spring maximum followed by a summer minimum of relative sporocarp biomass production for this species. Spring also has the highest frequency (50%, Table 1.5) while summer and fall frequencies are nearly equal.

Biomass distribution among the habitats shows an increase along the moisture gradient from wet to dry old-growth. The mesic mature habitat is about equal to the mesic old-growth habitat in relative biomass production for this species. *H. crassirhachis* was not found in the mesic young habitat. The frequency data show a similar pattern to that of relative biomass production.

***Hysterangium setchellii* Fischer** shows a distinct summer peak in relative sporocarp biomass (Figure 1.13c). However, due to the occurrence of the highest stand sample value for this species in the summer sampling, the equivalent g/ha biomass value may be substantially inflated (based on the

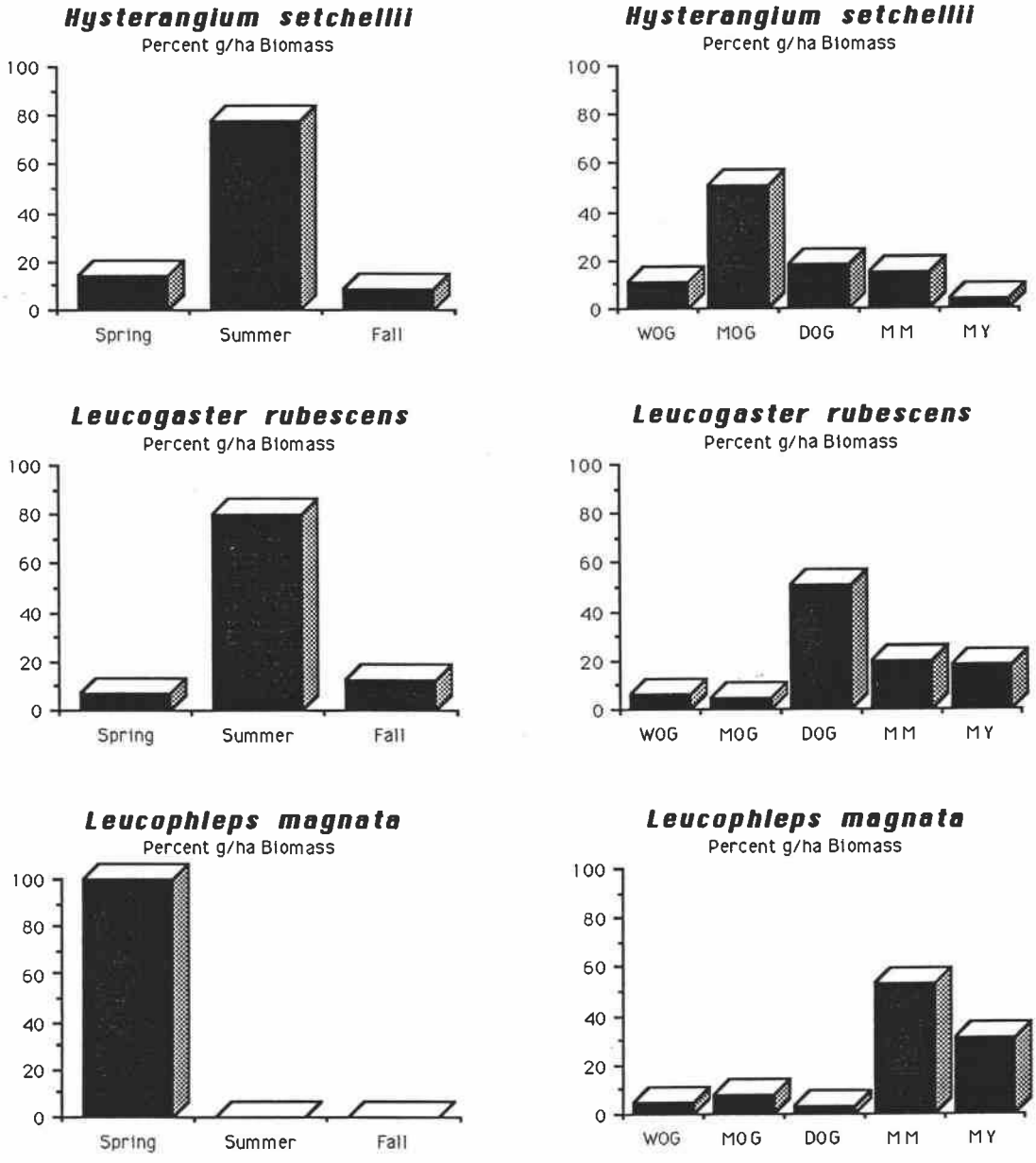


Figure 1.13c. Percent of each species total sporocarp biomass (equivalent g/ha) by season and habitat, for the 14 most important species in a 5,900 m^2 sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

distribution of sample values from larger samples) over the value that might be expected with a larger total summer sample area. Frequency in spring and summer samples is about equal but is reduced by more than half in fall (15%, Table 1.5).

Among mesic habitats, relative sporocarp biomass of *H. setchellii* apparently increases with increasing stand age. A majority of its biomass is produced in the mesic old-growth habitat. The wet old-growth, dry old-growth, and mesic mature habitats have moderate biomass production. The mesic young habitat is strongly depressed in relative biomass. The pattern of frequency generally reflects that of biomass except that the difference between mesic old-growth (42%) and dry old-growth (36%) is relatively smaller (Table 1.5).

***Leucogaster rubescens* Zeller & Dodge** also has a strong summer maximum of relative sporocarp biomass (Figure 1.13c). Like *Hysterangium setchellii,* the equivalent g/ha biomass value may be inflated over the value that might be expected with a larger number of summer samples due to the maximum sample value occurring in summer (Figure 1.6). Although summer was sampled least, *L. rubescens* occurred at 100% frequency in summer samples (Table 1.5). This is more than twice the spring or fall frequencies, reinforcing the interpretation of summer as its optimum fruiting season.

Much more confidence can be placed in the maximum relative biomass of this species in the dry old-growth because that habitat was the most intensively sampled (N=14). The mesic mature and mesic young habitats have

moderate amounts of biomass, unfortunately, corresponding dry habitats were not sampled. In terms of frequency, the mesic mature and mesic young habitats have values of about 60% compared to 50% for dry old-growth (Table 1.5).

***Leucophleps magnata* Harkn.** fruited exclusively in the spring (Figure 1.13c). Its spring frequency is 68% (Table 1.5). Eighty-five percent of the relative sporocarp biomass is distributed between the mesic young and mesic mature habitats. The relatively low biomass in old-growth habitats implies that this species is sensitive to changes in habitat associated with vegetation change in a chronosequence (succession) and could reflect a similar response within the fungal community. Its frequencies among the mesic habitats are similar and are about double those of wet and dry old-growth.

***Leucophleps spinispora* Fogel** produced sporocarp biomass predominantly in spring (Figure 1.13d). Fruiting continued (or carried over) slightly into summer but no fruiting occurred in fall. The frequency data reflect the same trend (Table 1.5). Relative sporocarp biomass is rather evenly distributed between the mesic old-growth, dry old-growth, and mesic mature types, and a minor proportion of the biomass is accounted for in the young or wet forests. Frequency data show a strong minimum in the wet old-growth and increase through the mesic, to a dry old-growth maximum. *L. spinispora* has similar frequencies in the three mesic habitats (≈35%).

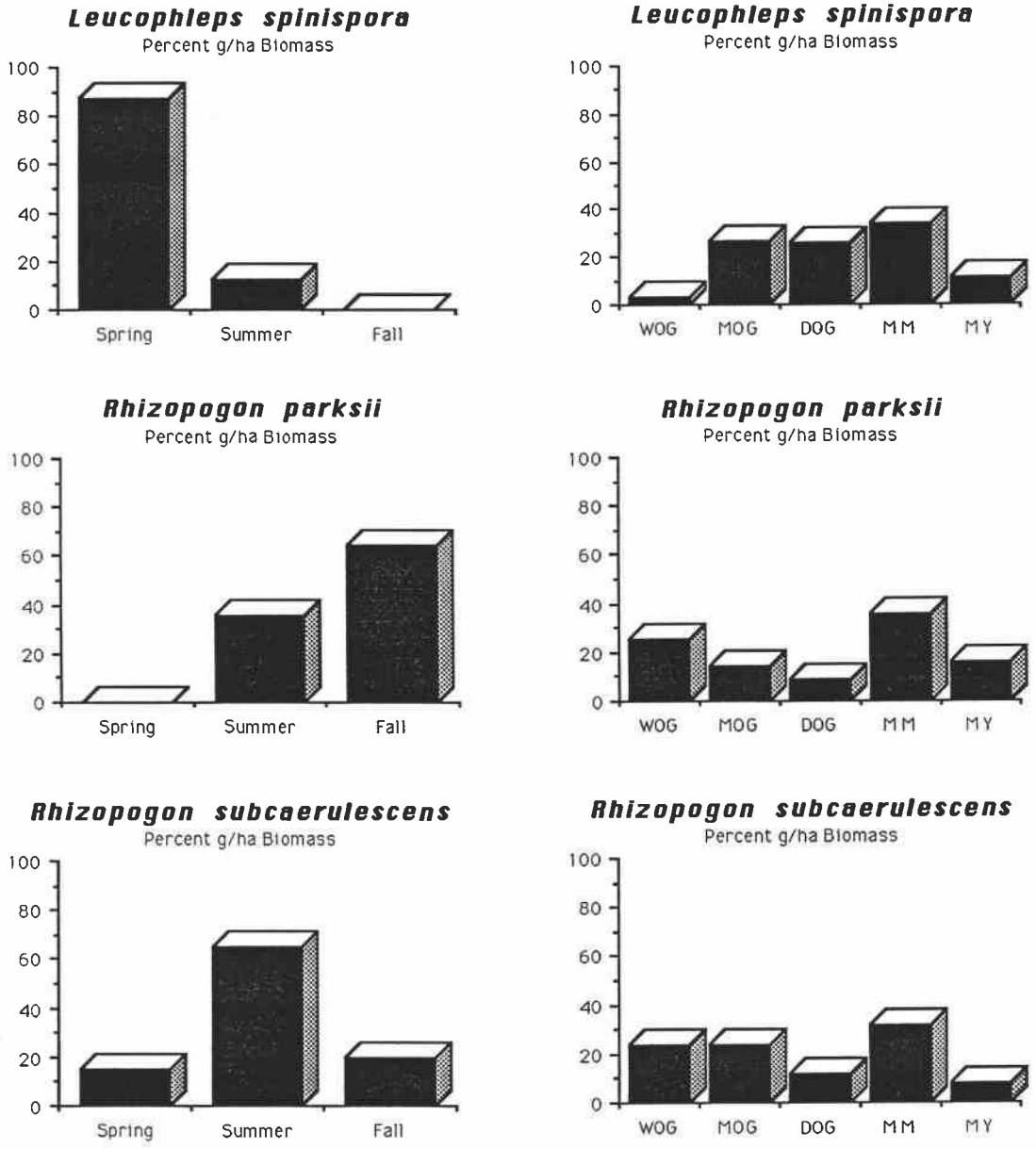


Figure 1.13d. Percent of each species total sporocarp biomass (equivalent g/ha) by season and habitat, for the 14 most important species in a 5,900 m^2 sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

***Rhizopogon parksii* Smith** is characteristic of the fall fruiting season (Figure 1.13d). *R. parksii* did not fruit in the spring. The summer value is attributable to a single late season stand sample which was the third largest biomass value for the species. It was found in 88% of the fall stand samples (Table 1.5), the highest frequency value other than the summer value for *Leucogaster rubescens.*

Relative sporocarp biomass decreased slightly along the moisture gradient from wet to dry old-growth (Figure 1.13d). The mesic mature habitat has the largest relative biomass production, about double that of the other mesic types. Frequency among the habitats is relatively even, ranging from 36% to 46%.

***Rhizopogon subcaerulescens* Smith** has a marked summer peak in relative sporocarp biomass production (Figure 1.13d). In this case however, the maximum stand sample value occurred in fall, so more confidence may be placed in the summer peak despite the small summer sample size. Further evidence that *R. subcaerulescens* is predominantly a summer fruiting species is provided by its frequency which is 60%, double that of spring or fall (Table 1.5).

Rhizopogon subcaerulescens' relative biomass and frequency are strongly depressed in the mesic young habitat. The mesic mature habitat has a slight maximum in both biomass and frequency. Frequencies are lowest in the wet old-growth and mesic young habitats.

***Rhizopogon vinicolor* Smith** predominantly fruited in the spring, declining through the summer to a pronounced fall minimum (Figure 1.13e). Frequency data reflect this same trend (Table 1.5).

Biomass was rather evenly distributed among the habitats. Although the mesic mature habitat shares (with mesic young) the highest biomass proportion (26%), *R. vinicolor* had its lowest frequency (38%) there. The second highest (but not extreme) stand sample biomass value occurred in the mesic mature habitat. Due to the smaller sample size the equivalent biomass value for the mesic mature habitat may be slightly inflated compared to what it would have been with a larger total sample area. The wet old-growth had the highest frequency (62%). Although Castellano and Trappe (1985) found that seedlings inoculated with *R vinicolor* had increased growth and survival on harsh sites in SW Oregon, the widespread distribution of *R. vinicolor* across all habitats in this study is evidence that *R. vinicolor* is not specifically adapted to warm dry sites.

***Truncocolumella citrina* Zeller** did not fruit in spring (Figure 1.13e). Limited fruiting began in late summer, but the preponderance of sporocarp production occurred in the fall. Biomass and frequency (Table 1.5) reflect this trend.

Truncocolumella citrina did not occur in the dry old-growth. The highest proportion of sporocarp biomass is found in the mesic young habitat. Although not high in biomass production, the mesic old-growth shares the high frequency (42%) with the mesic young habitat.

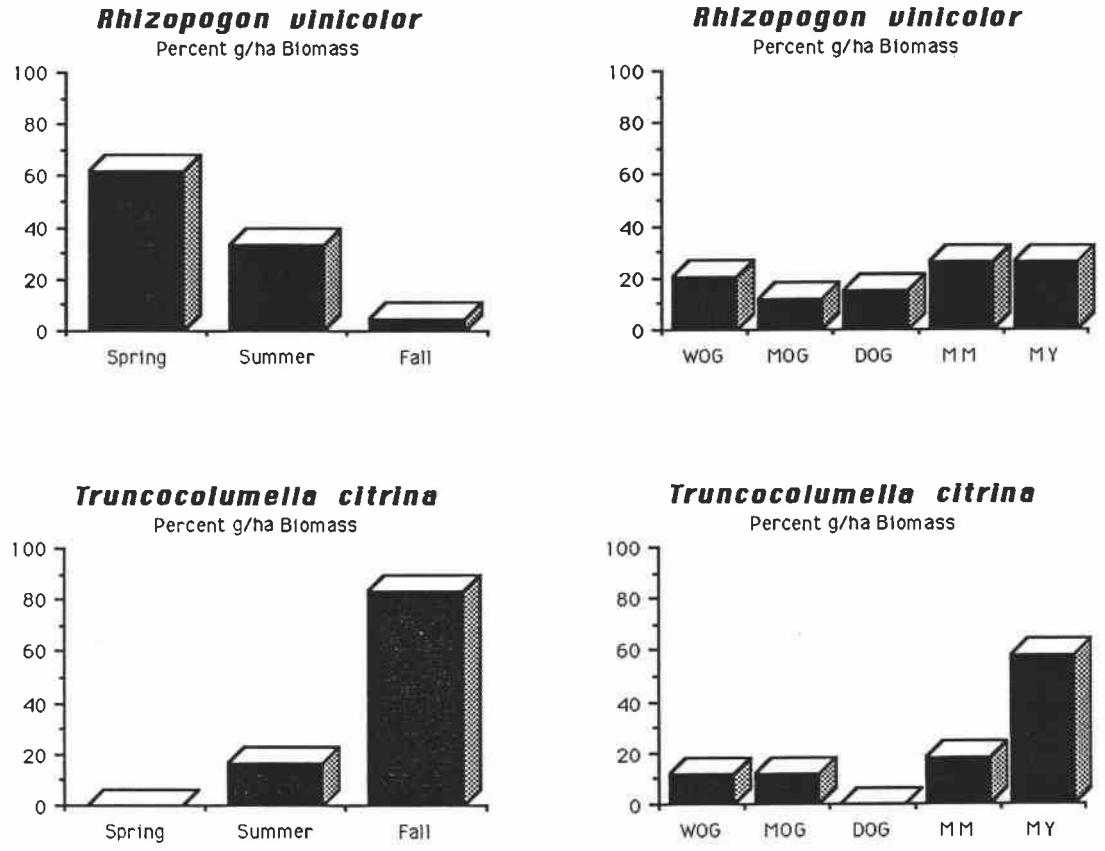


Figure 1.13e. Percent of each species total sporocarp biomass (equivalent g/ha) by season and habitat, for the 14 most important species in a 5,900 m^2 sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

***Endogone lactiflua* Berk. & Br.** has not yet been discussed because low total biomass (1.0 g) precludes its consideration as a "major" species, but it nonetheless has higher overall frequency than the least frequent "major" species. For that reason a brief discussion of frequency is worthwhile. It occurred in 12 of the 59 stand samples for an overall frequency of 20%. Seasonal distribution was bimodal, with 29% frequency in spring, no occurrences in summer, and 15% frequency in fall. *Endogone lactiflua* was found with 31% frequency in wet old-growth, 33% in mesic old-growth, 25% in the mesic mature habitat, these are comparable to the higher mid-range values of the "major" species (Table 1.5). It occurred only once each in the dry and young habitats.

Estimation of annual production

This study was not specifically designed to provide estimates of annual sporocarp biomass production (productivity), but the data can be used to examine assumptions used in other studies which attempted to ascertain annual biomass production. In Fogel's (1976) pioneering study, hypogeous sporocarps were collected from a 50 m^2 total sample area monthly for three years in a Douglas-fir stand in the Oregon Coast Range. His single-sample maximum standing biomass was equivalent to 9.6 kg/ha (comparable to the 9.9 kg/ha value from the current study) and annual standing crop ranged from 2.3 to 5.4 kg/ha. Hunt and Trappe (1987) calculated Fogel's (1976 annual productivity (by summing monthly equivalent values) to be 43.9 kg/ha. Fogel

(1976) concluded that his small sample area might have underestimated biomass because the species/area curve indicated a desirable minimum area of 100 m^2. However, the species/area curve is concerned with assessment of species richness (Cain and Castro, 1959). Examination of the distribution of sample biomass values provides a sounder basis for judging over- or underestimation of sporocarp production.

Analysis of biomass sample values in this study (covering ten stands, replicating five habitats, by three seasons, and over parts of four calendar years) consistently shows that most species exhibit strong skewing towards high values. This fact leads to the conclusion that small sample sizes tend to overestimate biomass because the smaller the total area sampled, the stronger the overestimate caused when high sample values are encountered. It is reasonable to conclude that the smaller stand sample area used in Fogel's (1976) study (located 100 km to the northwest of the current study), would more likely overestimate sporocarp production. At present, the degree to which predation (mycophagy) causes underestimation in studies of hypogeous sporocarp production is unknown.

Extraordinary sporocarp biomass production by mycelial colonies is an occasional but consistent characteristic of many hypogeous ectomycorrhizal fungi, both in this study and elsewhere (J. M. Trappe, personal communication). The goal is to interpret biomass production with consideration given to the overall range of values in relation to total sample area and the areal extent over which the samples are located.

Fogel (1976) used randomly located quadrats. This study used systematically placed quadrats. In ecological field work, Hurlbert (1984) discusses of the need for well–dispersed samples within a landscape segment that is to be characterized (interspersion vs. randomization of samples). In attempting to estimate annual sporocarp biomass production, the areal extent of the objective and spatial pattern of fungal fruiting must be kept in mind. The implication is that we are typifying sporocarp biomass for a forest stand of a given geographic extent which is relatively homogeneous in its vascular plant composition. Random placement of a relatively small number (with respect to the total area of the representative stand) of quadrats is particularly prone to sample clustering Hurlbert (1984). Sporocarp production is relatively clustered (Fogel, 1976; 1981; States, 1985). If quadrats happen to fall in an area of sporocarp clustering, biomass may be overestimated. As an alternative to an impracticably large number of random quadrats (of a given size) necessary to achieve a well dispersed sample pattern, interspersion of fewer quadrats will reduce the coincidence of quadrats with localized concentrations of biomass and lessen the tendency for overestimation.

Vogt et al. (1981) report on hypogeous sporocarp biomass production in two *Abies amabilis* stands. The stands were 23 and 180 years-old. Each stand was sampled once a month for six months by 12 randomly chosen 4 m^2 quadrats yielding a total sampled area of 288 m^2. The areal extent over which the quadrats were distributed is not given. Hypogeous sporocarp

production was given as 1 kg/ha/yr in the young stand. They calculated annual biomass production of *Elaphomyces* sp. in the 180 year old stand as 380 kg/ha/yr by summing the monthly equivalent biomass values. This is particularly prone to overestimate sporocarp productivity for *Elaphomyces* spp. because of their long maturation time (Hunt and Trappe, 1987). Several of the monthly samples may represent a single production event. Additionally, the small total sample area used by Vogt, et al. (1981) further increases the likelihood of overestimation at the stand level. Their average monthly standing biomass was equivalent to 64 kg/ha.

Because rates of sporocarp maturation, decay, and predation are largely unknown, any estimates of productivity are highly speculative. Even so, the biomass values found by Vogt, et al. (1981) considerably exceed those of the current study. For example, if the highest sample value from the current study – 99 g (coincidentally from a collection of *Elaphomyces granulatus*), were used in the context of their study; the resulting equivalent biomass would be 21 kg/ha — equal to the lowest sample equivalent biomass in their study.

Hunt and Trappe (1987) also address many of the difficulties mentioned here. Estimations of annual sporocarp productivity (35.4 kg/ha) and single sample maximum (17.5 kg/ha) are contrasted with annual average standing biomass which ranged from 2.0 to 3.2 kg/ha. Underestimation of species richness due to small stand samples and the infrequent fruiting of some species is also noted.

CONCLUSION

Previous workers have not used analysis of the distribution of sample values to adequately address the issues of sampling strategy and areal extrapolation. Stand sample sporocarp biomass values were found to be strongly skewed towards high values. Traditional analysis of variance for the comparison of means is difficult to interpret because mean values of normalized (transformed) variables mask the contribution of the few high biomass values to production estimates. Rather than relying on means for standardized comparisons, the actual values obtained need to be totaled for any particular sample category (or species) and converted to equivalent g/ha values. The geographically infrequent occurrence of a relatively large amount of sporocarp biomass is an observed stand characteristic that needs to be accurately reflected in production estimates. Counting sporocarps is less labor intensive than obtaining biomass values but such counts are shown to be poorly correlated with biomass.

When the total area sampled is small and includes one or more high to extreme biomass values, the derived sporocarp production in equivalent g/ha biomass is greatly overestimated. In the converse situation (given strong positive skewing), when only median to low values occur in a small total sample area, the degree of underestimation is not great because the low values are not greatly less than the median. This study allowed the comparison of sample values from a range of total sample areas: 5,900,

2,800, 1,400, 800, and 500 m^2. Determination of an adequate total sample area depends somewhat on the distribution of sample values after the fact. Both the 500 and 800 m^2 sample areas were inadequate in this study because some species had their extreme sample values of the entire 5,900 m^2 area in these smallest sub-samples. The sample areas in the range of 1,400 m^2 were generally adequate, but even the combined total sample area of 5,900 m^2 contained one value so extreme as to require considerable "adjustment".

Relatively few species (five) accounted for a dominant proportion of the total biomass (73%). Many species showed strong seasonal variation in relative biomass production and the spring had a higher equivalent biomass production in g/ha than fall. Similarly, many species seemed to exhibit changes in relative biomass production in response to habitat gradients, particularly in the old-growth forests. In addition their being united by mode of nutrition and specialized reproductive biology, the recurrence of the same dominant (as measured by sporocarp biomass) species of hypogeous ectomycorrhizal fungi in habitats over a period of years suggests that hypogeous ectomycorrhizal fungi form a cohesive guild and that study of these organisms from a mycocoenological perspective (Cooke, 1972; Arnolds, 1981) would be fruitful.

Chapter 2

Community Structure of Hypogeous Sporocarps Along Douglas-fir Forest Gradients in the Central Western Cascades of Oregon

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SUMMARY

Hypogeous ectomycorrhizal fungi were assessed through use of sporocarp biomass in ten stands of Douglas-fir forests representing wet–to–dry and young–to–old-growth gradients in and near the H. J. Andrews Experimental forest. Forty-seven species of hypogeous fungi were recorded during the study. Ascomycotina are represented by six families and 13 species, Basidiomycotina by seven families and 32 species, Zygomycotina by two families and two species.

Multivariate techniques are used to relate fungal community structure to vascular plant communities and their habitats. Detrended correspondence analysis (DCA) ordination of sporocarp biomass data for all 59 stand samples shows strong seasonal separation of the samples along the DCA 1 axis. The seasonal aspect of species sporocarp production overwhelmed the ordination and classification making fungal community responses habitat gradients impossible to detect.

By combining yearly spring and fall samples into a composite sample representative of the annual fungal aspect (within each stand) and ordinating these composite samples, the dry old-growth habitat is generally seen in the ordination as segregated from wet old-growth. In the center of the ordination, composite samples from mesic habitats overlap both dry and wet habitat samples. Yearly variation in weather patterns causes variation in sporocarp production that tends to obscure community structure responses to environmental gradients

Ordination of composite samples of the sporocarp biomass data integrated for each of the ten Douglas-fir forest stands shows that the dry and wet old-growth stands are strongly segregated along the DCA 1 axis and that the mesic stands occupy a central position along the axis without overlapping the wet or dry stands. Fungal community structure is interpreted as responding strongly to the moisture (DCA 1) gradient. Ordination of the mesic subset of these stands suggests a separation of old-growth from younger stands along the DCA 2 axis.

The compositional data was classified by two–way indicator species analysis (TWINSPAN). Classification of the hypogeous ectomycorrhizal fungus community, by employing sporocarp biomass data, corresponds closely to classification of forest habitats based on vascular plant composition. Additionally, a fungal community guild structure was delineated that reflected subtle variation in the habitats along an effective moisture gradient. The subterranean dominant counterpart to *Pseudotsuga* is *Rhizopogon parksii*; *Gautieria monticola* is nearly as wide spread and abundant. The results indicate that moist and dry Douglas-fir forest communities in the study area contain distinct communities of hypogeous ectomycorrhizal fungi.

INTRODUCTION

Most of the dominant forest trees in the Pacific Northwest (*Pseudotsuga, Tsuga, Abies, Pinus, Picea, Larix, Quercus, Castanopsis, Lithocarpus,* and *Alnus* species) form ectomycorrhizae with fungi that reproduce from epigeous sporocarps (above ground mushrooms) or from hypogeous sporocarps (below ground truffles) (Trappe, 1962; 1971). Ectomycorrhizal fungi develop mutually beneficial associations in the exterior layers of the feeder roots of forest trees and act as extensions of the root system (Trappe and Fogel, 1978). Without mycorrhizal fungi, trees cannot absorb enough water and minerals from soil to sustain life.

The distribution of hypogeous sporocarps with respect to forest types and environmental gradients has received limited investigation. Maser et al. (1978a), focused on sporocarps as food for small mammals associated with specific forest types. The most extensive previous studies of hypogeous sporocarp production are those of Fogel (1976), Fogel and Hunt (1979), and Hunt and Trappe (1987). Their major goals were to quantitatively estimate sporocarp production, determine phenology of production, and characterize the hypogeous fungal species community composition. Additionally, Hunt and Trappe (1987) calculated the mycofloristic similarity between their stand and the stands of Fogel (1976) and Fogel and Hunt (1979). Those studies were confined to single stands of Douglas-fir located on Marys Peak, Oregon and are from similar, relatively young (35-65 years) second-growth developed after clear-cut logging and

burning. Although these studies fall within the realm of Arnold's (1981) "myco-coenological approach", their major focus is on characterization of the hypogeous mycoflora of the particular plant community and not the association between fungal communities and vascular plant communities.

The current study is an out-growth of research initiated by Hunt and Trappe (1984). Their initial objectives addressed fungi in the diet of small mammals, sporocarp production, and fungal species composition in forest types of varying age and moisture status. This paper extends that approach to analysis of vegetational/fungal community relationships and presents the first use of multivariate analyses (Gauch, 1982) of hypogeous sporocarp production. A major goal is to explore whether sporocarp biomass reveals an intrinsic fungal community structure. Rather than merely characterizing and comparing the mycoflora of plant communities or habitats, the multivariate approach considers each fungal species abundance across all habitats and the relative proportion of species within each habitat. The attractiveness of this approach to mycocoenologists is that the resulting ordination and classification (determined solely by individual species sporocarp biomass) permit independent interpretation of the fungal community with reference to the preexisting classification of the vascular plant habitats. Nevertheless, even recent ecological studies of ectomycorrhizal fungi have made little use of multivariate techniques (Bills et al., 1986) to relate fungal community structure to vascular plant communities and their habitats.

In general, multivariate ordination and classification allow the interpretation of community composition in relation to a wide variety of complex gradients. Samples of vascular plant communities are frequently related to their relative position along moisture and temperature gradients (Whittaker, 1967; Dyrness et al., 1974; Gauch, 1982; Luoma, 1987), but placement with respect to gradients of successional change and spatial variation in disturbance intensity have also been noted (Curtis and McIntosh, 1951; van der Maarel, 1969; Halpern, 1987). It is reasonable to expect that the interpretation of fungal communities would benefit from this type of analysis.

Multivariate ordination is a two-way iterative process that permits the inherent complexity in the data set (individual species sporocarp biomass in samples) to be reduced to a few values for each sample. The samples can then be ordinated (ranked) on independent axes on the basis of these multivariate scores. When the results of this ordination are displayed with reference to two independent axes forming a plane, samples are said to be positioned on a community plane defined by complex environmental gradients (Gauch, 1982). As a companion to ordination, divisive multivariate classification involves a similar process that orders and progressively splits the entire set of samples (and species) into smaller groups at each level of the hierarchy. The technique used in this paper splits sets of samples (and species) based on the presence of indicator species. The resulting classification developed from fungal data can be compared with an independently derived classification based on vascular plant species.

This study applies established plant community field and multivariate analysis techniques (ordination and classification) to hypogeous sporocarp biomass data with the following objectives: (1) to inventory species of hypogeous mycorrhizal fungi found in Douglas–fir stands of various age and moisture classes by identification of sporocarps and measurement of sporocarp biomass; (2) to determine if sporocarp biomass reveals a fungal community composition and structure; and, (3) if fungal communities are identifiable, to determine if communities occur: (a) co-extensively with associated vascular plant habitats, (b) more narrowly within vascular plant habitats, or (c) broadly, over more than one vascular plant habitat.

METHODS

Study area

The H. J. Andrews Experimental Forest occupies the 6,000 ha drainage of Lookout Creek, a tributary of the McKenzie River, in Lane Co., Oregon The area is considered typical of the western slopes of the central Cascade Range in Oregon (Dyrness et al, 1974; Zobel et al., 1976). The forest has been administered by the U. S. Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948. The location of the study stands in the experimental forest and vicinity is presented in Figure 2.1..

The regional climate is classified as Temperate Oceanic by Trewartha and Horn (1980) or Csb (cool–summer Mediterranean) by Köppen (1936). Average annual precipitation varies from about 2,300 to 2,800 mm, depending on topography. About 90% of the precipitation occurs from October through April. Above 900 m elevation, winter snowpacks accumulate to a depth of one meter or more. Summers are dry. Temperatures are moderate with a range from -3° (mean January minima) to 29° C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Franklin and Dyrness, 1971).

Three general soil types are characteristic of the experimental forest (Berntsen and Rothacher, 1959; Franklin and Dyrness, 1973; Dyrness et al., 1974). Steeper slopes and ridgetops often support a residual Brown Podzolic

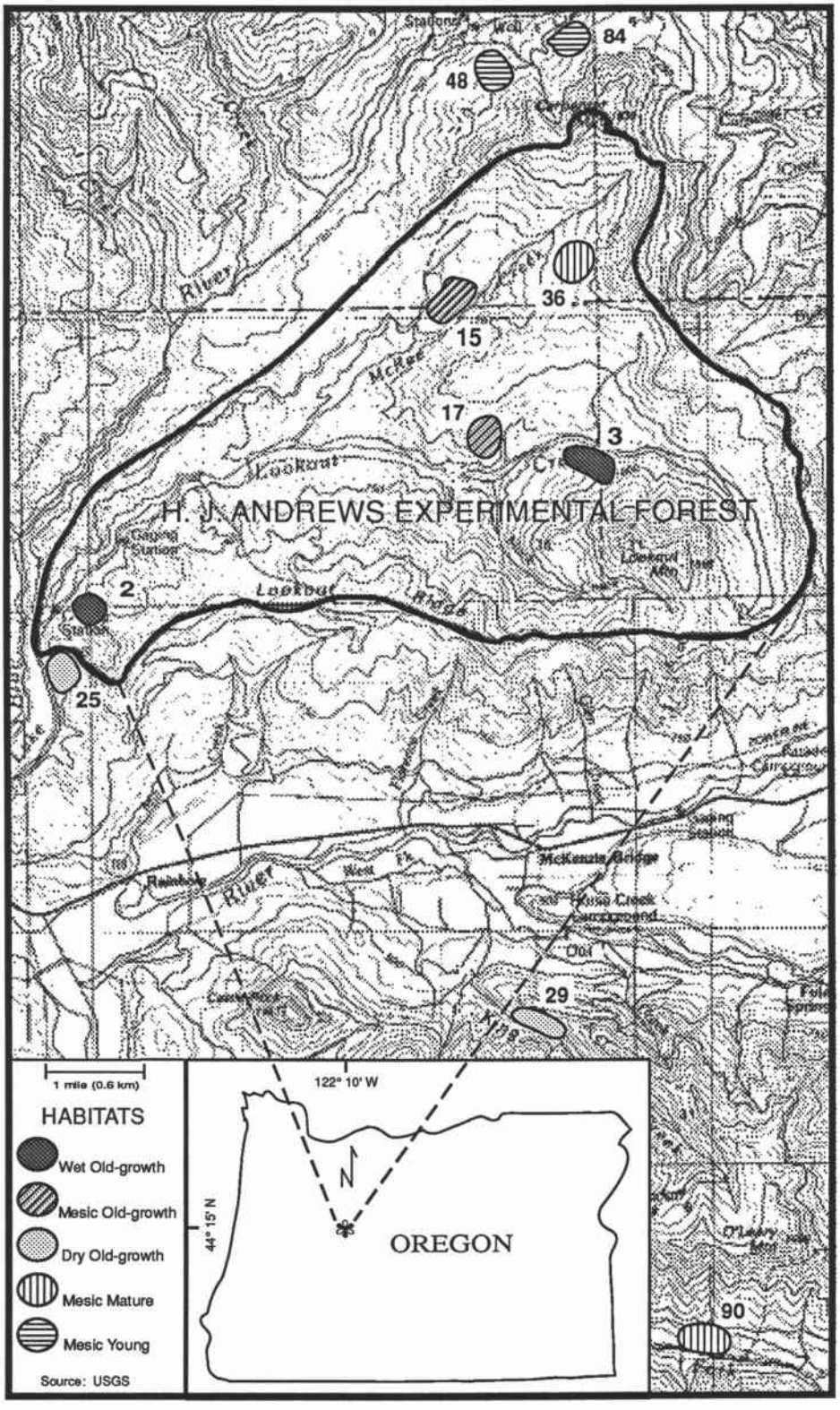


Figure 2.1. Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

gravelly clay loam formed from andesite or basalt (usually classified as Haplorthods or Xerumbrepts). Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams (generally classified as Haploxerults and 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 *Tsuga heterophylla* Zone of Franklin and Dyrness (1973). Studies of forest communities within the *Tsuga heterophylla* Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Franklin and Dyrness, 1973; Dyrness et al., 1974; Zobel et al., 1976). Characteristic understory species are used to describe the community types. *Lysichitum americanum* indicates extremely wet forest sites with the water table near or seasonally above the surface. Abundant *Polystichum munitum* and *Oxalis oregana* typify moist sites. Mesic sites may be occupied by *Berberis nervosa* and/or *Rhododendron macrophyllum*. Towards the dry end of the scale, *Gaultheria shallon* increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities belonging to the *Pseudotsuga menziesii* series. In these communities Douglas-fir is often considered climax and *Holodiscus discolor* is an important shrub (Hemstrom et al., 1987). A temperature gradient reflecting elevation has also been noted (Zobel et al., 1976). The coolest extreme is represented by the *Tsuga–Abies amabilis/Linnaea borealis* association, transitional to associations in the *Abies amabilis* Zone.

Dyrness et al. (1974) found classification of communities to be challenging because of the wide geographic and ecologic distribution of most plant species. In modal (with respect to moisture and temperature gradients) communities, the difference in relative abundance of shared species was the basis for community recognition. Zobel et al. (1976) studied the relationships of environment to forest composition in a subset of those stands investigated by Dyrness et al. (1974). The measurements of Zobel et al. (1976) enable firmer decisions to be made as to the appropriate selection of forest plant communities to represent environmental gradients.

Sampling

Ten Douglas-fir forest stands were selected for sampling on the basis of age and moisture status. Age classes were 75, 150, and 300+ years of age and are referred to respectively in this paper 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 et al. (1988):

Pseudotsuga menziesii / Polystichum munitum / Oxalis oregana (**wet**)

Pseudotsuga / Acer circinatum / Berberis nervosa (**mesic**)

Pseudotsuga / Gaultheria shallon–Rhus diversiloba (**dry**)

Five habitats were selected for study: wet old-growth, mesic old-growth, dry old-growth, mesic mature and mesic young. Two stands each of the five habitats shaded in the matrix (Figure 2.2) were sampled. Consisting of approximately five hectares of relatively homogeneous forest, the chosen stands represent a subset of typical stands originally located and classified with respect to vascular plant composition by other researchers as part of a regional forest characterization (Spies et al., 1988). Selected descriptive characteristics of each stand are presented in Table 2.1.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps, because fruiting varies so much by species and abundance in time and space. Fogel (1976, 1981) and States (1985) also report the clustered distribution of sporocarps produced by simultaneous fruiting of individual mycelial colonies. Given the clumped distribution of sporocarps, the sampling strategy in this study was to employ well–distributed small plots to obtain a representative stand sample. Random sampling requires many more plots than does systematic, interspersed sampling to achieve this goal (Hurlbert, 1984). Ideally, with more resources, random sampling stratified by microsite would have been employed.

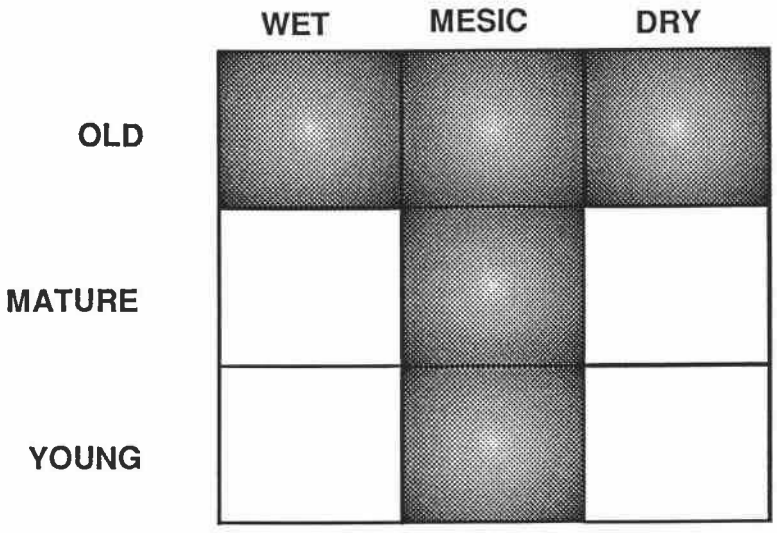


Figure 2.2. Sampling matrix for five chosen Douglas-fir habitats, H. J. Andrews Experimental Forest, Oregon.

Table 2.1. Selected stand characteristics by habitat from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Habitat[1]	Stand (#)	Basal[2] Area (m^2/ha)	Stem[2] Density (#/ha)	Coarse[2,3] Soil (% vol.)	Median Elevation (m)	Aspect	Slope[4] (°)
WOG	2	81	280	47	550	NNE	30-35
	3	101	526	19	800	N	0-35
MOG	15	146	392	8	800	SW	0-15
	17	108	670	13	770	SSE	10-30
DOG	25	49	443	55	550	W	30-35
	29	47	463	52	700	SW	30-40
MM	36	71	408	33	1160	W	15-30
	90	38	433	25	930	SSW	10-30
MY	48	58	1410	48	1050	NW	20-30
	86	52	1535	59	930	NW	20-30

[1]WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

[2]T. Spies, personal communication.

[3]Fragments > 2mm.

[4]Stand 3 occupied a series of slumps causing high slope variability.

Seasonal sampling occurred over a period of four years from spring of 1983 through spring of 1986. Stand sampling in each season occurred over a period of six to seven weeks. For spring and summer samples, stands on lower elevation south slopes were sampled first, and those on higher elevation north slopes sampled last. This procedure allowed the sample period to be condensed relative to the temperature and moisture controlled fruiting phenology. The fall sampling strategy was reversed with stands on higher, northerly slopes sampled first. Because personnel were limited in summer, only old–growth stands were sampled.

For each stand sample, sporocarps were harvested from 25 circular four-square-meter plots for a total sample area of 100 m^2. Plots were placed systematically approximately every 25 m along three transects spaced equidistantly (about 75 m) and arranged parallel to the slope contour. New transects were established for each stand sample; no plots were reraked. In the conifer forests of western Oregon, most hypogeous sporocarps are produced at or above the mineral/organic soil interface (personal observations, J. Trappe, G. Hunt, D. Luoma, M. Castellano). In each plot, the forest floor was raked back to a 5 to 10 cm depth, exposing sporocarps in the upper layers of the soil. The number of sporocarps of each species in a plot was recorded. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain < 15% relative humidity, and weighed to the nearest 0.01 g to determine biomass.

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. Over four years, data were collected from 59 stand samples in all. Twenty-eight were taken in spring, five in summer, and 26 in fall. Seasons were defined by equinox and solstice calendar dates. Thirteen stand samples were taken in wet old-growth (WOG), 12 in mesic old-growth (MOG), 14 in dry-old growth (DOG), 8 in mesic mature (MM), and 12 in mesic young (MY) habitats.

Analysis

Community analysis techniques (ordination and classification) were used to assess within- or between-stand variation in the fungal component of the habitats.

Ordination is defined as "an arrangement of units in a uni- or multidimensional order" (Goodall, 1954). Sample units are arranged by individual values rather than by group values. Ordination exposes relative continuity or discontinuity among stands (Mueller-Dombois and Ellenberg, 1974). Ordination was conducted in this study using the Cornell Ecology Series program DECORANA, a FORTRAN program.

DECORANA stands for detrended correspondence analysis (DCA), and defines each sample score as a weighted mean related to the scores of all the species that occur in the sample. Successive two-way iterations of reciprocal averaging are repeated until scores stabilize to a final result which

is independent of the initial species scores (Hill, 1979a). DECORANA is a modification of basic reciprocal averaging and uses a procedure designed to remove any relation between second and higher ordination axes to the first axis. "Detrending" removes the tendency for within-sample standard deviation to be smaller at the ends of a gradient than in the middle (Hill, 1979a). The resulting ordination is a geometrically more accurate portrayal of the relative positions of samples with respect to the DCA axes. The interpretation of the axes, which represent complex environmental gradients, is thereby improved.

Classification of the samples (and species) was obtained by use of a companion Cornell program TWINSPAN, for two–way indicator species analysis (Hill, 1979b). Samples are first ordinated by reciprocal averaging, then grouped by species composition into ordinally hierarchical clusters. By convention, TWINSPAN assigns the whole data set to the "*" group. Subsequent divisions form *1, *0; *01, *00, etc. groups at the various levels of the hierarchy. The technique is polythetic by use of quantitative measures of entity (sample) resemblance over all attributes (species scores) and divisive by progressively splitting the entire set of samples (and species) into smaller groups at each level of the hierarchy (Boesch, 1977).

For ordination and classification analysis, species biomass data (dry weight in grams or standardized to equivalent g/ha) were transformed to an octave (log base 2) scale to provide the initial scores. This transformation reveals community structure that otherwise would be overwhelmed by the

dominant species biomass (Gauch, 1982) and normalizes the distribution of biomass values [Chapter 3]. Octave values are shown in TWINSPAN ordered two-way tables. Fifty-nine stand samples containing 48 species were entered in the first data set. A second data set was derived by eliminating four summer samples, converting one summer sample to the fall category, eliminating one "orphan" spring sample, and by then combining spring/fall pairs of samples to characterize each stand on a yearly basis. This synthesis of seasonal data created new composite samples that represent species sporocarp biomass in each stand on an annual basis. The second data set contained 27 composite samples and 46 species. A third data set was obtained by excluding summer samples, converting species raw dry weight biomass values to equivalent grams per hectare values (standardized due to unequal number of stand samples from each stand), and obtaining each species total biomass for each of the ten stands. This synthesis of yearly data created composite samples that represent species sporocarp biomass in each stand for the four–year study period The third data set contained ten samples and 45 species. The three–tiered approach to analysis of the data in this study allows interpretation and successive integration of seasonal and year–to–year variation in sporocarp production. Use of the terms "dominant" and "subdominant" within categories refers to sporocarp biomass as an indicator of a species importance relative to other species.

RESULTS

Forty-seven species of hypogeous fungi were recorded during the study (although a few collections are of uncertain taxonomic affinity and some taxa are of uncertain status). The species collected and their acronyms are given in Table 2.2. Ascomycotina are represented by six families and 13 species, Basidiomycotina by seven families and 32 species, Zygomycotina by two families and two species (family determinations follow Trappe et al., 1989).

Ordination

In DECORANA,within-sample variance is set to a constant value 1, to achieve standard scaling of the axes. This results in the species-abundance curve having unit standard deviation and axis length is expressed in units of standard deviation (Hill and Gauch, 1980). With two ordination dimensions, the bivariate normal distribution of species abundance values define gradients of variation said to form a "coenoplane", that is, the DCA axes form a "community plane". Along a DCA axis gradient, a species distribution should be within ± two standard deviations in abundance from its mode (Hill and Gauch, 1980.) In other words, samples four or more standard deviations apart should have few or no shared species.

Table 2.2. Species of hypogeous fungi (with acronyms) occuring in a 5,900 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Alpova trappei Fogel	ALTR
Destuntzia fusca Fogel & Trappe	DEFU
Elaphomyces granulatus Fries	ELGR
Elaphomyces mruicatus Fries	ELMU
Endogone lactiflua Berkeley & Broome	ENLA
Gautieria monticola Harkness	GAMO
Gautieria gautierioides (Lloyd) Zeller & Dodge	GAGA
Genabea cerebriformis (Harkness) Trappe	GECE
Genea intermedia Gilkey	GEIN
Geopora cooperi Harkness	GECO
Hydnotrya variiformis Gilkey	HYDV A
Hymenogaster gilkeyae Zeller & Dodge	HYMG I
Hymenogaster parksii Zeller & Dodge	HYMP A
Hymenogaster sublilacinus Smith	HYMS U
Hysterangium coriaceum Hesse	HYSC O
Hysterangium crassirhachis Zeller & Dodge	HYSC R
Hysterangium setchelii Fischer	HYSS E
Leucogaster gelatinosus Fogel	LEGE
Leucogaster rubescens Zeller & Dodge	LERU
Leucophleps magnata Harkness	LEMA
Leucophleps spinispora Fogel	LESP
Martellia brunnescens Singer & Smith	MABR
Martellia ellipsospora (Zeller) Singer & Smith	MAEL

Table 2.2 (cont.)

Martellia fallax Singer & Smith	MAFA
Martellia oregonensis (Zeller) Singer & Smith	MAOR
Martellia parksii Singer & Smith	MAPA
Martellia vesiculosa Singer & Smith	MAVE
Modicella malleola (Harkness) Gerderman & Trappe	MOMA
Picoa carthusiana Tulasne & Tulasne	PICA
Radiigera atrogleba Zeller	RAAT
Radiigera taylori (Lloyd) Zeller	RATA
Rhizopogon atroviolaceus Smith	RHAT
Rhizopogon clavitisporus Smith	RHCL
Rhizopogon parksii Smith	RHPA
Rhizopogon subcaerulescens Smith	RHSU
Rhizopogon truncatus Linder	RHTR
Rhizopogon villosulus Zeller	RHVI L
Rhizopogon vinicolor Smith	RHVI N
Thaxterogaster pingue (Zeller) Singer & Smith	THPI
Truncocolumella citrina Zeller	TRCI
Truncocolumella sp. nov.	TRSP
Tuber asa Tulasne & Tulasne	TUAS
Tuber californicum Harkness	TUCA
Tuber gibbosum Harkness	TUGI
Tuber monticola Harkness	TUMO
Tuber rufum Pico ex Fries	TURU
Tuber shearii Harkness in Murrill	TUSH

A detrended correspondence analysis (DCA) ordination of sporocarp biomass data for all 59 stand samples is presented on two axes in Figure 2.3. The x axis (DCA axis 1) has an eigenvalue of 0.59 and represents 3.9 standard deviation units by the length of the gradient. The y axis (DCA axis 2) has an eigenvalue of 0.38 and represents 3.4 standard deviation units by the length of the gradient. Strong seasonal separation of the samples is evident along the DCA 1 axis.

Ordination of the yearly spring and fall composite stand samples is shown in Figure 2. 4. The x axis (DCA axis 1) has an eigenvalue of 0.35 and represents 3.0 standard deviation units by the length of the gradient. The y axis (DCA axis 2) has an eigenvalue of 0.20 and represents 1.9 standard deviation units by the length of the gradient. Dry old-growth samples are generally segregated on the left from wet old-growth samples on the right of the ordination. In the middle of the ordination, samples from mesic habitats overlap both dry and wet habitat samples.

An ordination of the total composite stand samples classified by habitat is depicted in Figure 2.5. The x axis (DCA axis 1) has an eigenvalue of 0.28 and represents 2 standard deviation units by the length of the gradient. The y axis (DCA axis 2) has an eigenvalue of 0.15 and represents 1.5 standard deviation units by the length of the gradient. Dry and wet old-growth stands are strongly segregated along the x axis and the mesic stands occupy the middle of the axis without overlapping the wet or dry stands.

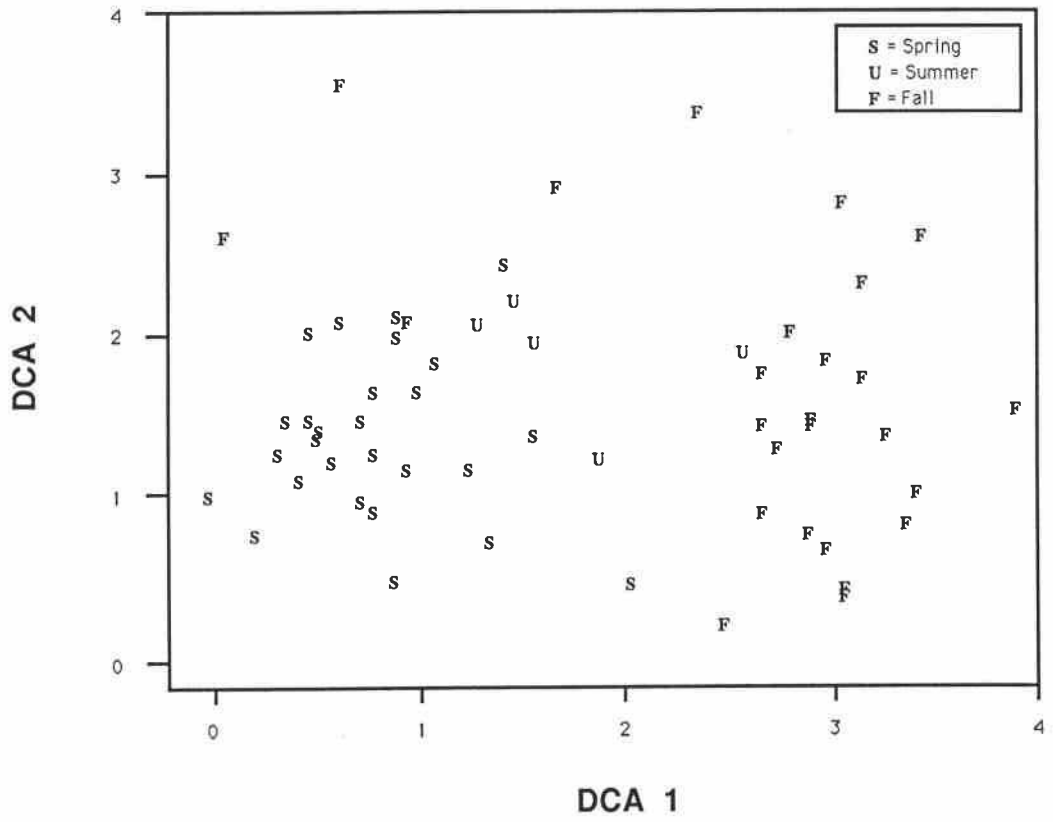


Figure 2.3. DECORANA ordination of stand samples, classified by season, in a 5,900 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Axes scaled in standard deviation units.

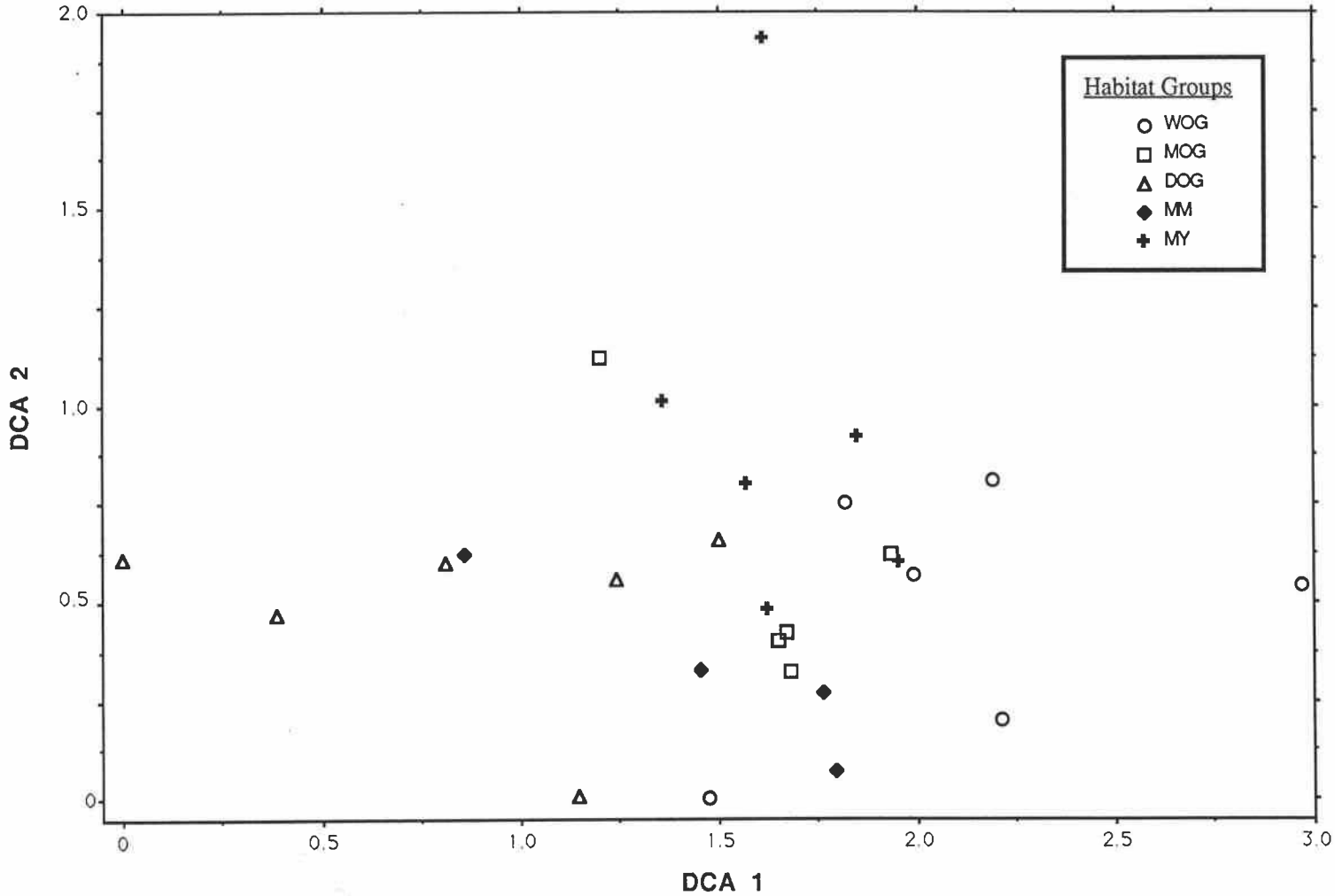


Figure 2.4. DECORANA ordination of composite spring/fall annual stand samples classified by habitat, in a 5,400 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Stand habitat code: WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young. Axes scaled in standard deviation units.

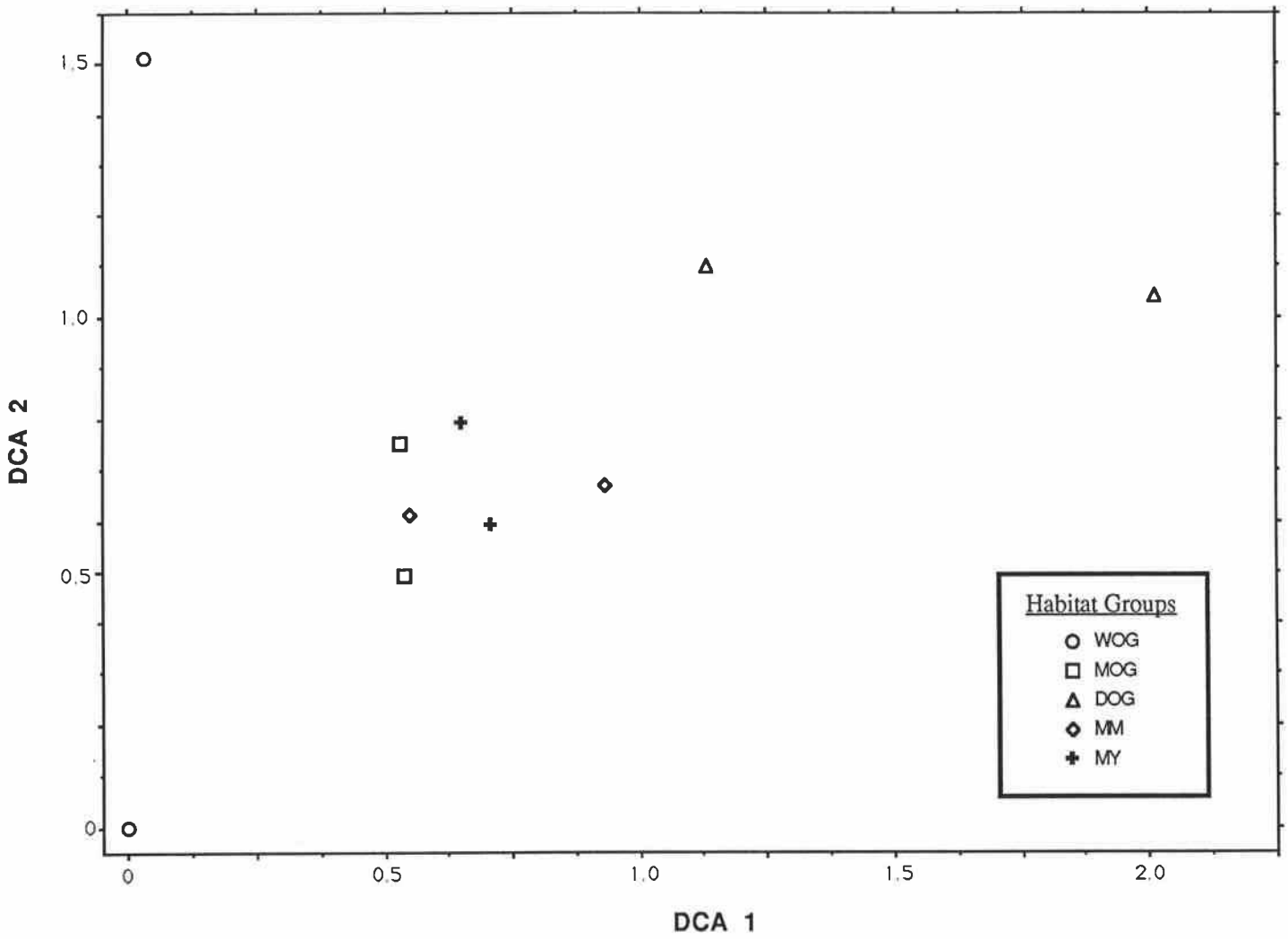


Figure 2.5. DECORANA ordination of total composite stand samples classified by habitat, in a 5,500 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Stand habitat code: WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young. Axes scaled in standard deviation units.

Ordination of the mesic subset of these stands is shown in Figure 2.6. The x axis (DCA axis 1) has an eigenvalue of 0.19 and represents 1.8 standard deviation units by the length of the gradient. The y axis (DCA axis 2) has an eigenvalue of 0.16 and represents 1.3 standard deviation units by the length of the gradient. The y axis suggests a separation of old-growth from younger stands.

Classification

Two–way indicator species (TWINSPAN) classification of all 59 stand samples (Table 2.3) reveals the general dichotomy between the spring and fall aspects of fruiting. Ninety-six percent of the stands to the right of the first division (the *1 group) are fall samples. Seventy-eight percent of the plots to the left side of the first division (the *0 group) are spring samples. Summer samples are more closely allied with spring samples than with fall; four of the five summer stand samples are contained within the *00 group. The *01 group is the core spring group. Division of the fall (*1) group is based on the general dichotomy in the occurrence of *Elaphomyces granulatus* and *Leucogaster rubescens* but no significant interpretation is evident.

Table 2.4 shows the TWINSPAN ordered two-way table produced with the 27 composite spring/fall stand samples. A general segregation of wet and dry stands is exhibited but with an admixture of mesic stands. The left–to–right arrangement can be interpreted as a dry-mesic to mesic to mesic-wet ordering.

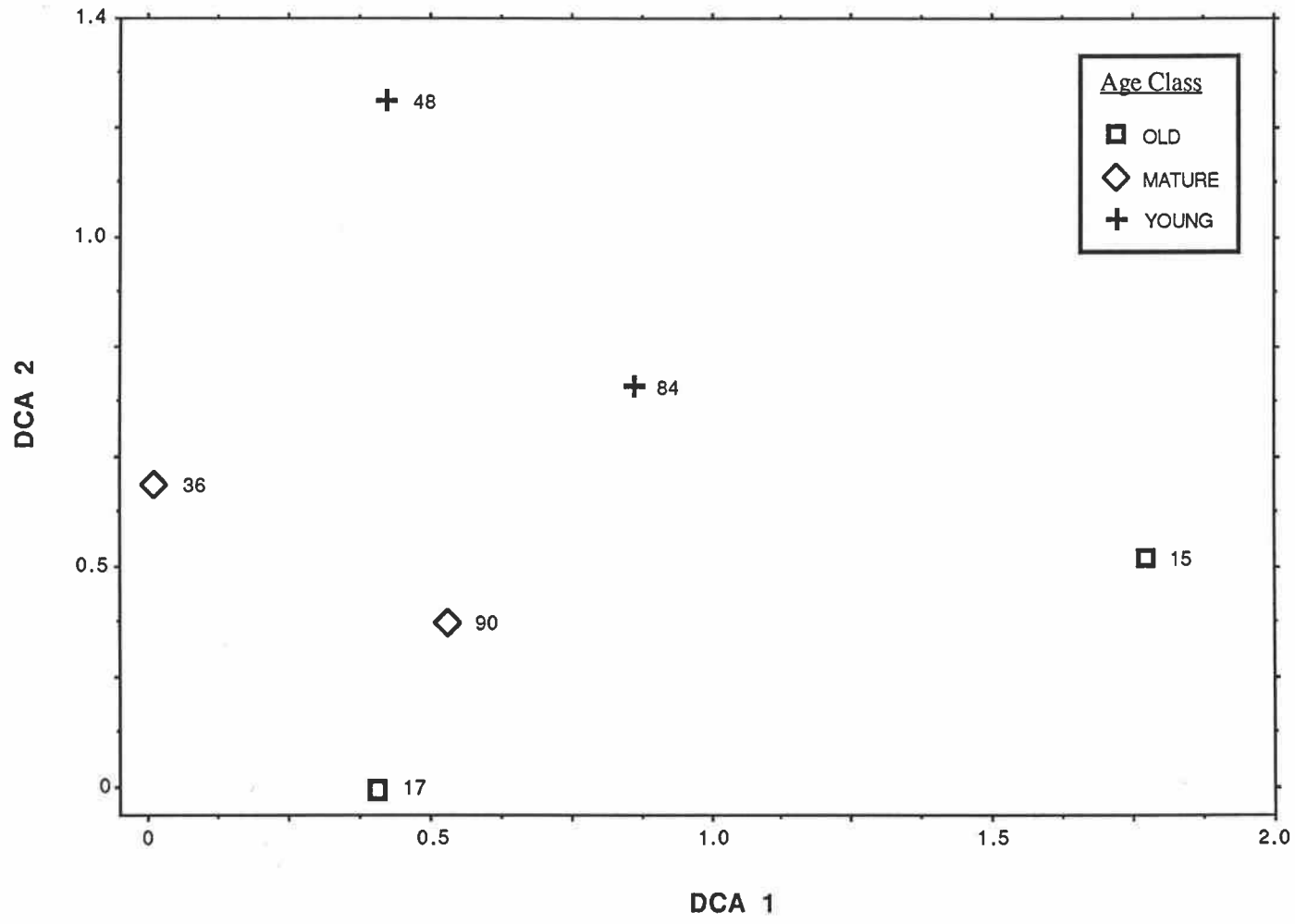


Figure 2.6. DECORANA ordination of total composite stand samples classified by age in a 2,000 m^2 total sample from six mesic Douglas-fir stands (numbered), H. J. Andrews Experimental Forest, Oregon. Axes scaled in standard deviation units.

Table 2.3. TWINSPAN ordered two-way classification of all stand samples (coded by season and habitat of occurence) in a 5,900 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Species acronyms are given in Table 2.2.

	[a]SUFUSUUSF DDMDWWMMM OOMOOOOYY	SSSSSSSSSSSSSSSSSSSSSSFSSF WWWMMMMMMMMDDMMDMMWWMDMDMDD OOOOMYMYYOOOOMOOYMOOOOYOOOO	FFFFFFUFFFFFFFF WWMMWMMMMDMDWWD OOOYOOOMOOMOOOO	FFFFFFFF MMMMMWDM YYYOYOOM	
GEIN	----------	----------1---1----------	----------	--------	00
HYMG I	----------	----------1----------	----------	--------	00
LESP	22--------	---133-214544411242--3-----	----------	--------	00
MAOR	----------	----------1----------	----------	--------	00
MOMA	----------	----------1----------	----------	--------	00
RHAT	----------	----------16---------2-	----------	--------	00
TUCA	----------	----------1----------	----------	--------	00
TUMO	----------	----------1	----------	--------	00
GAGA	----------	-2----------	----------	--------	00
HYDV A	----1-----	2-1---1-------2----11------	----------	--------	00
HYMS U	----------	-----1----------	----------	--------	00
HYSC O	2---1--1-	312-2345525-3-44-4164-7----	-------2-------	--------	00
LEMA	-------3-	--2-3-4311---11-4411212-11-	1----------	--------	00
RAAT	----------	-------1----------	----------	--------	00
GAMO	6--3-5454	5---6785--46462376------1--	----------	4------4	00
RHVI L	--------2	----------5---	----------	--------	00
RHVI N	33-3-121-	3131455421331-3-3151----221	-2----------	----1---	00
ALTR	-53---31-	--1-31-------2-1----------	----------	--------	00
GECE	1---------	-----1----------	----------	--------	00
MAPA	-----1----	----------	----------	--------	00
TUSH	---1------	----------	----------	--------	00
HYSS E	2-32------	-32------3-1--11-1----232--	-1----5-1------	--------	01
MAEL	-2---1----	----------	-1----------	--------	01
RATA	1---1-----	-------1----------	------1--------	--------	01
ENLA	1-1-------	1-1------11--11-1----------	-1--1----------	---1----	01
HYMP A	----------	----------1--------1-------	1----------	--------	01
HYSC R	---2------	---1--4--1123-44-31133-5332	------32222--21	------32	01
ELGR	-----6----	7-3975635--3--1-----1------	465555645-3----	4-------	10
ELMU	----------	54--5---------1----------	------313------	-----3-5	10
GECO	----------	---------11----------	----1-------1--	--------	10
DEFU	----------	----------	----1----------	--------	10
MAFA	----------	------1----------	2----------	--------	10
MAVE	----------	----------	-------2-------	--------	10
PICA	----------	----------	-1----------	--------	10
RHCL	----------	----------	----------2-	--------	10
RHPA	----------	----------	684624644564155	56-24217	10
THPI	----------	----------	-------1--------	--------	10
TRCI	----------	----------	2425-1333-2--1-	45412--4	10
TRSP	----------	----------	1--------3------	--------	10
TUGI	----------	----------1----------	----------3-2-	1-------	10
TURU	-2--------	----------	------3-----22-	--------	10
LEGE	----------	----------	----------	----3---	10
MABR	----------	----------	---2---------3-	3--35---	10
RHTR	----------	----------1	----------	------2-	10
LERU	57-53222-	-1-----2--11-1-411---3-----	------31--1----	24423345	11
RHSU	4--2134--	----4-13-2----21-------1--3	------4-2-2--51	2------3	11
TUAS	-----3----	----------	---2----------	--------	11
	[b]000000000 000000000	000000000000000000000000000 111111111111111111111111111	111111111111111 000000000000000	11111111 11111111	

[a] Stand sample code (vertical): S = spring, U = summer, F = fall, WO = wet old-growth, MO = mesic old-growth, DO = dry old-growth, MM = mesic mature, MY = mesic young.

[b] TWINSPAN division group code, i.e. *0, *01 (vertical).

Table 2.4. TWINSPAN ordered two-way classification for composite spring/fall annual stand samples (coded by habitat of occurence) in a 5,400 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Species acronyms are given in Table 2.2.

	[a]DMDD OMOO	DWMD OOOO	WMDMMWMMMMM OOOYYOOMYYM	WMMM OOMY	WWMM OOOY	
ELMU	----	----	53---535--5	-11-	----	000
GAGA	----	----	-----2-----	----	----	000
GECE	----	----	--1-----1--	----	----	000
HYMS U	----	----	--------1--	----	----	000
MOMA	----	1---	----------	----	----	000
PICA	----	----	1----------	----	----	000
RAAT	----	----	---1-------	----	----	000
TRCI	----	-11-	43-45-32544	-2--	--12	000
TRSP	----	3---	----------	----	----	000
TUAS	----	----	--------2--	----	----	000
TUCA	----	----	------1----	----	----	000
TUGI	----	12--	--31-------	----	----	000
ALTR	13--	----	-------3112	----	1---	001
GEIN	1---	1---	----------	----	----	001
LERU	414-	1-23	-3535311-55	3-1-	---3	001
LESP	144-	42-3	-4222-533-4	-1-1	----	001
RHAT	6--2	----	----------	-1--	----	001
RHSU	2--3	-5-1	-444--25--3	121-	----	001
RHTR	--21	----	----------	----	----	001
TUMO	---1	----	----------	----	----	001
ENLA	-1--	--1-	111-1-1---1	-1--	11--	010
GAMO	364-	6-1-	5-657-46756	-284	----	010
HYSS E	43--	1-2-	162--31----	-1--	2--2	010
RATA	----	----	-111-------	1---	----	010
RHPA	--1-	5525	864562466-7	244-	1244	010
RHVI N	-112	352-	4134313451-	2352	31-1	010
TURU	----	-2--	-3---------	----	2---	010
HYSC R	5343	3333	-3----32--2	-44-	-13-	011
RHVI L	5---	----	----------	---2	----	011
LEMA	-4-1	-111	-1-34-13-31	-141	2122	10
MABR	----	-33-	---3----2--	----	---5	10
ELGR	----	3---	76-4--576--	4565	355-	110
GECO	----	----	-1---------	----	11--	110
HYMP A	----	----	------1----	----	-1--	110
HYSC O	443-	-1--	3225-15231-	1445	2647	110
DEFU	----	----	----------	----	-1--	111
HYDV A	----	----	2---------	121-	111-	111
HYMG I	----	----	----------	11--	----	111
LEGE	----	----	----------	----	---3	111
MAEL	----	----	1---------	2---	----	111
MAFA	----	----	----------	--1-	----	111
MAOR	----	----	----------	-1--	----	111
MAVE	----	----	----------	--2-	----	111
RHCL	----	-2--	----------	6---	----	111
THPI	----	----	----------	1-1-	----	111
	[b]0000 0000	0000 1111 0000	00000000000 11111111111 11111111111	1111 0000	1111 1111	

[a] Stand habitat code (vertical): WO = wet old-growth, MO = mesic old-growth, DO = dry old-growth, MM = mesic mature, MY = mesic young.

[b] TWINSPAN division group code, i.e. *0, *01 (vertical).

Classification of the ten stands based on the total composite sporocarp biomass standardized to equivalent grams per hectare is presented in Table 2.5. The first division splits off one dry stand (#29) from the others. By the third division one wet stand (#2) and the other dry stand (#25) are identified as separate "groups". The other wet stand (#3) is retained with a mesic group. A general left-to-right order in the arrangement of samples separates wet stands from dry stands with mesic stands between.

A final classification was made using a data subset consisting of the total composite samples for the six mesic stands (Table 2.6). The young stands separate out as a group to the right of the first division, however, each old-growth stand was grouped with a mature stand.

Table 2.5. TWINSPAN ordered two-way classification of ten composite Douglas-fir stand samples (coded by habitat, with stand number) from a 5,400 m^2 total sample, H. J. Andrews Experimental Forest, Oregon. Species acronyms are given in Table 2.2.

		[a]W WMMM MMM D D	
		O OOOM YYM O O	
		• •113 489 2 2	
		2 3576 840 5 9	
DEFU		- 1--- --- - -	000
ELGR		3 7657 6-- 2 -	000
ELMU		4 4134 --4 - -	000
GAGA		1 ---- --- - -	000
GECO		- 1-1- --- - -	000
HYDV	A	1 22-1 --- - -	000
HYMG	I	1 -1-- --- - -	000
HYMP	A	- 1-1- --- - -	000
MAEL		1 1--- --- - -	000
MAFA		- ---1 --- - -	000
MAOR		- -1-- --- - -	000
MAVE		- ---2 --- - -	000
PICA		- 1--- --- - -	000
RHCL		5 ---- --- - -	000
THPI		1 ---1 --- - -	000
TUCA		- --1- --- - -	000
TURU		2 2-2- --- - -	000
ALTR		- 1--3 114 - 1	001
ENLA		- 111- -11 1 -	001
GECE		- ---- 1-- 1 -	001
HYMS	U	- ---- 1-- - -	001
LEGE		- ---- -2- - -	001
LEMA		1 2224 344 1 1	001
MABR		2 --3- 34- - -	001
MOMA		- ---- --- 1 -	001
RAAT		- ---- 1-- - -	001
RATA		1 --1- 1-- 1 -	001
RHPA		4 7466 557 5 1	001
TRCI		1 3232 554 - -	001
TRSP		- ---- --- 2 -	001
TUAS		- ---- 1-- - -	001
TUGI		2 ---- 1-- 3 -	001
GAMO		- 4238 767 6 4	010
HYSC	O	2 5444 563 1 4	010
HYSS	E	2 225- -23 2 3	010
RHSU		4 -234 3-3 3 3	010
RHVI	N	4 3335 431 3 2	010
LERU		3 --32 355 4 4	011
LESP		2 -143 314 4 3	011
HYSC	R	2 1434 --3 3 5	10
GEIN		- ---- --- 1 1	110
RHAT		- -1-- --- - 5	111
RHTR		- ---- --- - 2	111
RHVI	L	- ---- 2-- - 4	111
TUMO		- ---- --- - 1	111
		[b]0 0000 000 0 1	
		0 0000 111 1	
		0 1111 000 1	

[a] Stand habitat code and number (vertical): WO = wet old-growth, MO = mesic old-growth, DO = dry old-growth, MM = mesic mature, MY = mesic young.

[b] TWINSPAN division group code, i.e. *0, *01 (vertical).

Table 2.6. TWINSPAN ordered two-way classification of composite stand samples (coded by relative age and stand number) in a 2,000 m^2 total sample from six mesic Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Species acronyms are given in Table 2.2.

		[a]OMOM YY	
		1319 48	
		5670 84	
HYDV	A	21-- --	00
HYMG	I	1--- --	00
HYSC	R	4433 --	00
MAFA		-1-- --	00
MAOR		1--- --	00
MAVE		-2-- --	00
RHAT		1--- --	00
THPI		-1-- --	00
ELMU		1434 --	00
GECO		--1- --	00
HYMP	A	--1- --	00
HYSS	E	2-53 -2	00
TUCA		--1- --	00
TURU		--2- --	00
ELGR		675- 6-	01
ALTR		-3-4 11	01
ENLA		1-11 -1	01
LEMA		2424 34	01
LESP		1344 31	01
RHPA		4667 55	01
RHSU		2433 3-	01
RHVI	N	3531 43	01
GAMO		2837 76	10
HYSC	O	4443 56	10
LERU		-235 35	10
TRCI		2234 55	10
MABR		--3- 34	11
RATA		--1- 1-	11
GECE		---- 1-	11
HYMS	U	---- 1-	11
LEGE		---- -2	11
RAAT		---- 1-	11
RHVI	L	---- 2-	11
TUAS		---- 1-	11
TUGI		---- 1-	11
		[b]0000 11	
		0011 01	

[a] Stand habitat code and number (vertical): O = mesic old-growth, M = mesic mature, Y = mesic young.
[b] TWINSPAN division group code, i.e. *0, *01 (vertical).

DISCUSSION

The attractiveness to mycocoenologists of multivariate approaches is that the resulting ordination and classification (determined solely by individual fungal species sporocarp biomass) allow for independent interpretation of the fungal community with reference to the preexisting habitat classification based on vascular plant species. This approach offers a chance to present empirical evidence that addresses long standing theoretical concerns (Cooke, 1979; Arnolds, 1981). Namely, what are the spatial, functional, and classification relations between fungi and plant communities?

The discussion illustrates how the strong seasonal aspect of species sporocarp production at first overwhelms any attempt to relate fungal community structure to environmental gradients. These constraints to elucidating fungal community structure and those imposed by year to year variation in sporocarp production, are overcome by DECORANA ordinations of successively integrated data sets. Each ordination is discussed in relation to the external (season or habitat) classification and the intrinsic TWINSPAN classification which is based on fungal composition, expressed as sporocarp biomass. The relative degree to which samples are compositionally similar can be ascertained because equal distances in a DCA ordination correspond to equal differences in species composition. For example, along a DCA axis, a 50% change in sample composition occurs in about one standard deviation unit of species turnover (Gauch, 1982).

Ordination and classification of all stand samples

The degree to which the stand samples share environmental space is approximated in Figure 2.3. Stand samples are arranged along the first ordination axis (DCA 1) from spring to fall. Although four autumn samples are grouped with the spring samples in relation to the first axis, only one of those four remains so grouped in relation to the second axis, therefore, the spring and fall stands share little environmental space on the coenoplane. Along the DCA 1 axis there is an approximately 75% change in sample composition from spring to fall. Summer samples are mostly grouped with those from spring and occupy a transitional position in the ordination between spring and fall samples.

The TWINSPAN classification (Table 2.3) closely matches the seasonal classification of the 59 stand samples. The spring fruiting aspect is characterized by *Gautieria monticola, Hydnotrya variiformis, Hysterangium coriaceum, Leucophleps magnata, Leucophleps spinispora,* and *Rhizopogon vinicolor* (*01 group, Table 2.3). The summer aspect (*00 group) is not strongly differentiated from the spring, but is characterized by an increase in the importance of *Leucogaster rubescens* and declining importance of *Hysterangium coriaceum* and *Leucophleps* spp.

TWINSPAN identified *Rhizopogon parksii* and *Truncocolumella citrina* as indicators of the *1 (fall) group. Two of the fall stand samples are classified in the *0 group and lack *Rhizopogon parksii*, both samples contained sporocarps which were assigned to *R. villosulus*, a species argu-

ably distinct from *R. parksii.* The data from this study reinforce the tenuous nature of the species distinction. Although not abundant, *Martellia brunnescens* is also part of the fall fruiting aspect. Important species found throughout the fruiting period are: *Hysterangium crassirhachis, Elaphomyces granulatus, Leucogaster rubescens,* and *Rhizopogon subcaerulescens.*

Ordination and classification of yearly spring/fall composited stand samples

The strong seasonal aspect inherent in the structure of the stand sample data set is removed through ordination and classification of the composite spring/fall yearly sample data set. Superimposing the classification of the 27 composite spring/fall stand samples (Table 2.4) on the same ordination that was classified by habitat in Figure 2.4 allows a reexamination of that ordination.

In Figure 2.4, the dry old-growth and wet old-growth habitat samples are ordered along the first axis with only two composite stand samples occupying approximately the same DCA 1 axis position. Mesic stand samples occupy the center of the first axis (DCA 1) overlapping about half of the dry and wet stand samples. Wet old-growth are on the right. The ordination of the first axis can be interpreted as a classic dry–to–wet effective moisture gradient when the stands are classified by habitat. When the TWINSPAN classification (Table 2.4) is superimposed on stands in that same ordination (Figure 2.7) comparisons with the ordination as classified by habitat (Figure 2.4) can be made.

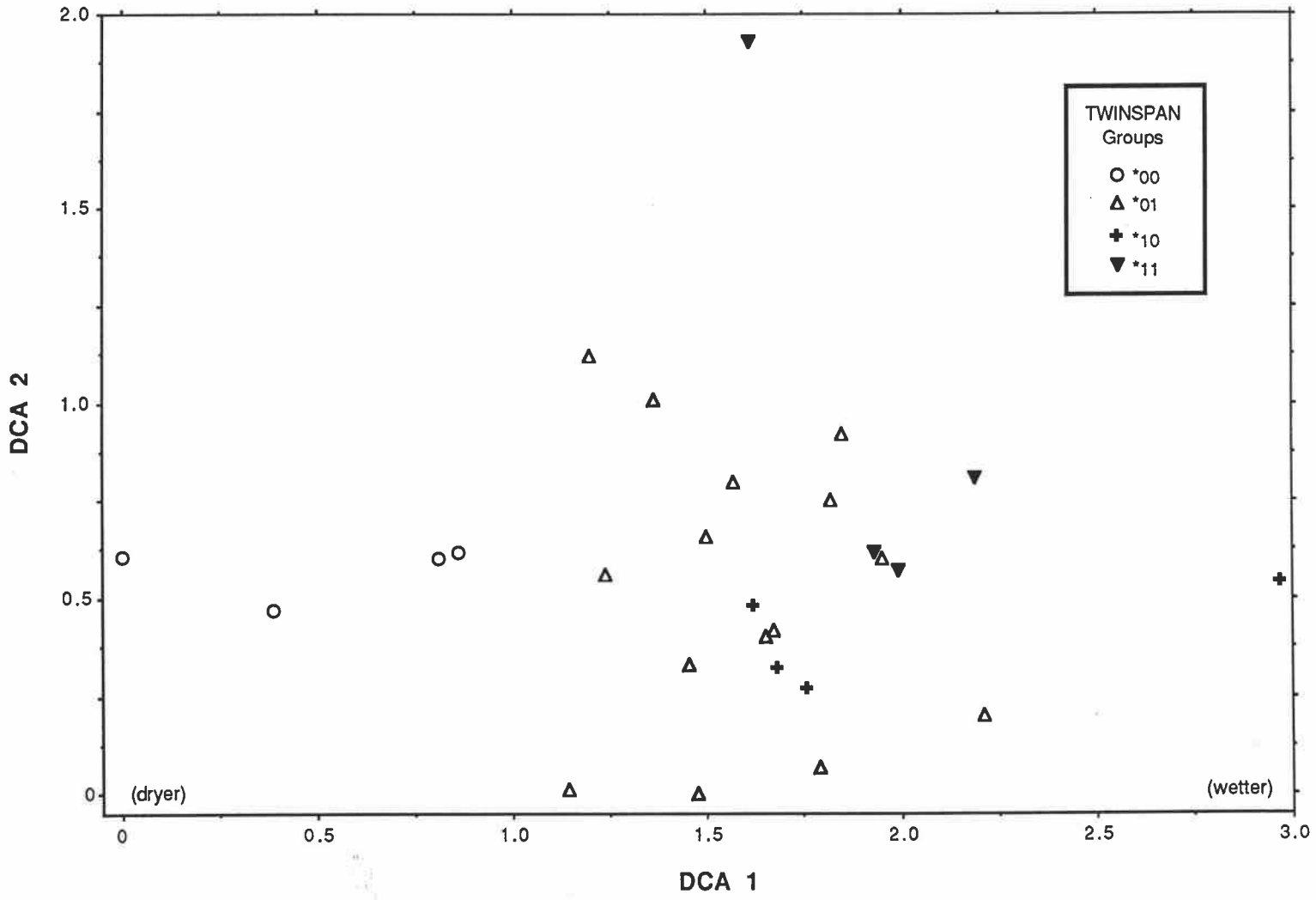


Figure 2.7. DECORANA ordination of composite spring/fall annual stand samples classified by TWINSPAN, in a 5,400 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. Axes scaled in standard deviation units.

Classification of the 27 composite spring/fall stand samples by use of the fungal TWINSPAN output presents a less clear interpretation. In Figure 2.7, only stands at the dry end of the gradient retain a distinct identity in the *00 group. This group is marked by the absence of *Truncocolumella citrina* and absence to minor importance of *Rhizopogon parksii* (Table 2.4). On an annual basis, fungal community structure is maintained to the greatest degree by dry habitat stand samples. TWINSPAN is meant to objectively optimize the homogeneity of the groups it forms based on the structure of the data set. The wet habitat has lost its separate identity with stand samples divided between the *01, *10, and *11 TWINSPAN groups. This suggests that, on a year–to–year basis, the fungal component of the wet stands is not strongly differentiated from that of the mesic stands and/or that there was some misclassification (to which a divisive technique like TWINSPAN is prone, Boesch, 1977). Of course, the yearly nature of the data introduces a further confounding factor, namely that imposed by annual vagaries of weather. In order to properly interpret the community structure of the hypogeous ectomycorrhizal fungi, a more stable basis for comparison is needed than provided by annual data.

Ordination and classification of total composited stand samples

Integrating four years' data for each stand produces a data set that synthesizes the yearly variation in fungal fruiting. One negative consequence in the present study is that the data set is reduced to ten composite samples

with only two samples representative of each habitat. When the habitat classification is superimposed on the ordination, the dry to wet ordering of stands along the first axis is without overlap (Figure 2.5).

The TWINSPAN classification (Table 2.5) is superimposed on the ordination in Figure 2.8, dry old-growth stand #29 is identified as sufficiently distinct from the others to warrant its own category (*1) at the first division level. The second level division separates wetter from dryer stands. Wet old-growth stand #2 is separated from the *00 group and dry old-growth stand #25 is separated from the *01 group in the third level divisions. The resulting classification could be interpreted as: Wet (*000), Wet-mesic (*001), Dry-mesic (*010), Dry (*011), and Very dry (*1)

Subtle habitat differences are reflected in the TWINSPAN classification. The ordination placed the wet stands very near each other on the first axis, but they occupy extremes on the second axis. Because wet-mesic old-growth stand #3 covers a series of slumps, much of the landform it occupies reflects a mesic mid-slope to raised bench topographic position. Wet-mesic old-growth stands #15 and #17 occupy mostly gentle to moderate lower mid-slopes with low amounts of coarse fragments in the soil in contrast to dry-mesic young stands #48 and # 84, which occupy moderate to steep upper slopes and have high amounts of coarse fragments in the soil (Table 2.1). Another wetter mesic vs. drier mesic contrast is found between the mature stands #36 and #90. Wet-mesic stand #36 is the highest elevation stand and has a west aspect while dry-mesic stand #90 occupies a steep site

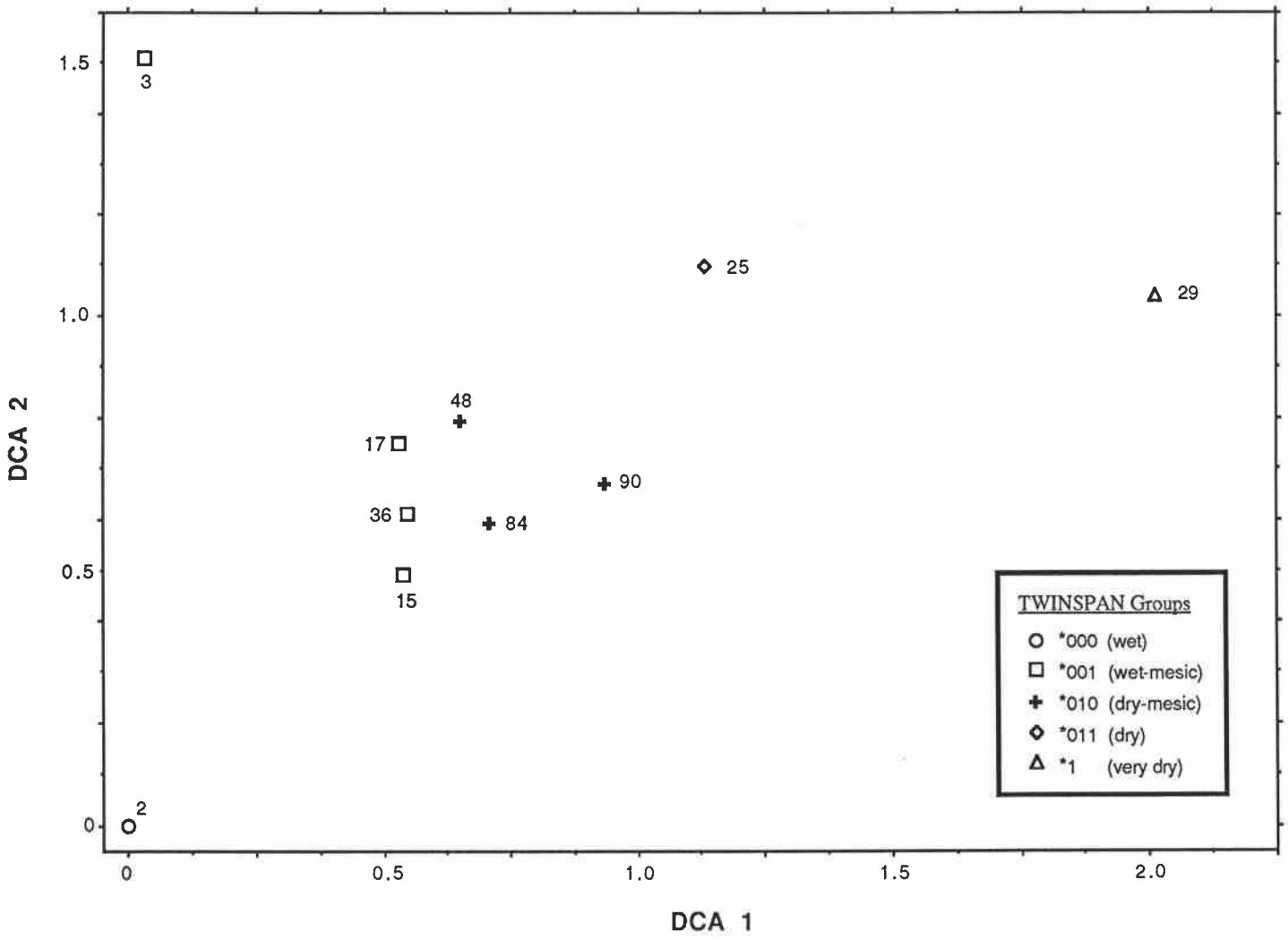


Figure 2.8. DECORANA ordination of total composite stand samples classified by TWINSPAN, in a 5,500 m^2 total sample from ten Douglas-fir stands (numbered), H. J. Andrews Experimental Forest, Oregon. Axes scaled in standard deviation units.

with a warm SSW aspect. Many of the habitat aspects of very dry stand #29 are substantially distinct from the other stands. It is the only stand where *Pinus lambertiana* shares dominance with *Pseudotsuga menziesii*. The slopes are steep to very steep with a SW aspect and soils have a high (52%) volume of coarse fragments (Table 2.1).

In Table 2.5, the moister stands (*00 group) are characterized by *Hydnotrya variiformis*. They are distinguished from the dryer stands (*01 group) by the greater frequency and abundance of *Elaphomyces* spp. and the coincidental presence of a number of minor species, particularly *Hymenogaster* and *Martellia* spp. Wet old-growth stand #2 (*000 group) is split from the *00 group by its lack of *Gautieria monticola*. *G. gautierioides* is found only in stand #2, potentially a case of ecological replacement. Wet old-growth stand #2 is further distinguished by the large (and only) collection of *Rhizopogon clavitisporus* and low biomass of *Hysterangium coriaceum*.

Herbarium records also indicate that *Genea intermedia* is usually found in dryer forests (as indicated by vegetation, i.e., *Pseudotsuga-Quercus*). In the present study, *G. intermedia* is restricted to the two dry stands (*1 and *011 groups, Table 2.5). The two dry stands share the absence of *Truncocolumella citrina*, an otherwise common and abundant species in Douglas-fir forests of western Oregon (J. Trappe, unpublished data). *Rhizopogon truncatus,* which herbarium records show is often associated with *Pinus lambertiana* in western Oregon and northern California, is the indicator species for very dry old-growth stand #29 (*1 group), but this has somewhat

limited value for a "group" of one. The stand is better marked by the maximum importance for *Hysterangium crassirhachis* and *Rhizopogon atroviolaceus* and a lack of many species found in other stands.

Fungal community guild structure

The guild concept was developed by Root (1967) to group species by their similarity in exploitation of the same class of environmental resources. Guilds are based on known patterns of resource use (Landers, 1983). Ectomycorrhizal fungi form a guild by the commonality of their nutritional symbiosis with the roots of vascular plants. Hypogeous ectomycorrhizal fungi are further delimited by specialized reproductive biology in which spore dispersal is dependent upon the sporocarps functioning as a nutritional resource for animals. The guild concept has been employed with respect to higher fungi in a study of the food habits of Douglas tree squirrels (Sanders, 1983).

The data are too limited to propose broad regional community guild types for hypogeous ectomycorrhizal fungi associated with all Western Cascades Douglas-fir forests; however, a local fungal guild structure can be delineated which is related to TWINSPAN groups. Figure 2.9 presents a diagrammatic representation of the hypogeous ectomycorrhizal fungal guild structure.

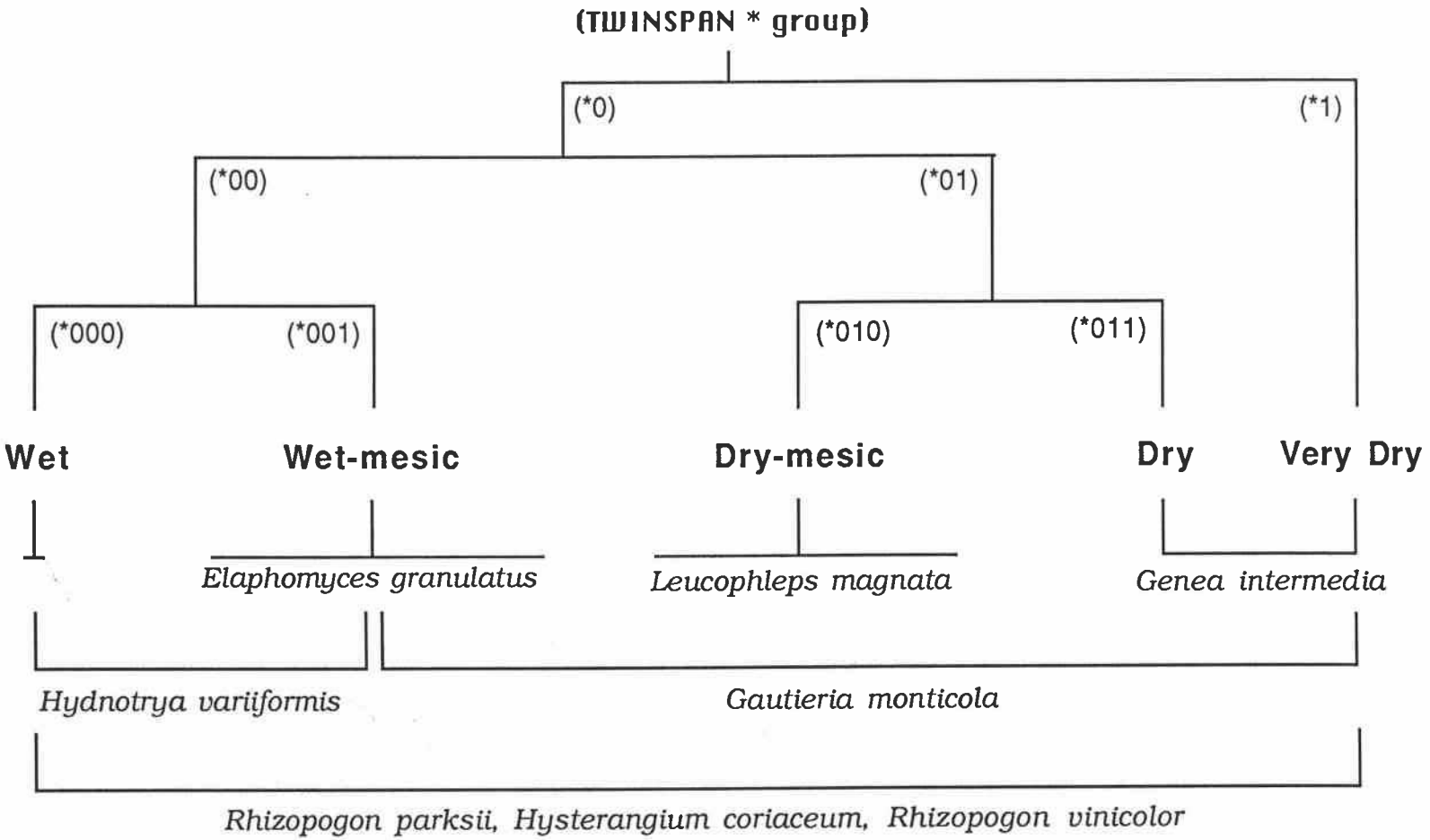


Figure 2.9. Hierarchy of hypogeous fungi useful for delineating changes in guild structure (related to TWINSPAN groups, numbered) along a moisture gradient, in a 5,500 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon. TWINSPAN groups are shown in Table 2.5.

Over all stands (Figure 2.9), *Rhizopogon parksii*, *Hysterangium coriaceum*, and *Rhizopogon vinicolor* are constant (> 80%) and important species (the * group, Table 2.5). *Hydnotrya variiformis* is a constant species for the wetter stands (*00 group) and *Gautieria monticola* is important in all stands but the wet old-growth stand (*000 group). Ultimately, *Elaphomyces granulatus* is an important and constant species for the wet-mesic (*001) group, *Leucophleps magnata* for the dry-mesic (*010) group, and *Genea intermedia* as a constant species for the dry stands (*011 and *1 groups). Since they are represented by single stands, the *000, *011, and *1 groups can not be individually typified in a meaningful way.

Ordination and classification of composite mesic stand samples

Investigation of a potential successional gradient in fungal community composition within the mesic stands is pursued with the final ordination and classification. Figure 2.6 shows the ordination with the composite stand samples classified by age class. DCA axis 2 can be interpreted as an age gradient although stands #15 and #90 overlap. TWINSPAN classification of the stands is presented in Table 2.6. The young stands form a distinct group (*1). Stands #17 and #90 were meaningfully grouped (*01) in Table 2.6 and in the ordination but that left an improbable combination of stands (#15 and #36) positioned at opposite ends of the DCA 1 axis grouped together (*00) and the reciprocal averaging process was left with a residual an order of magnitude above its tolerance (.003).

The young stands share the absence of *Hysterangium coriaceum* and *Elaphomyces muricatus*. Several minor species are found exclusively in the young stands and *Truncocolumella citrina* reaches its maximum importance in these stands. One mesic old-growth stand (#17) and one mesic mature stand (#90) form the *01 group united by the abundances of *Leucogaster rubescens*, *Leucophleps spinispora* and *Truncocolumella citrina* and by the absence of *Hydnotrya variformis* which is an indicator for the *00 group (stands #15 and #36).

As noted, the divisive technique used in TWINSPAN finished with two rather different stands classified together and a resulting high residual for the *00 group. An alternative case for classifying both mature stands together based on species abundances can be made. A clear young–to–old ordering of the mesic stands is presented in Table 2.7. *Gautieria monticola* and *Alpova trappei* biomass are strongly maximized in the mature stands with *A. trappei* achieving indicator status for differentiating mature from old stands. Additionally, *Elaphomyces muricatus* and *Leucophleps magnata* abundances are maximized in the mature stands.

Table 2.7. Ordered two-way classification of composite stand samples (coded by relative age and stand number) in a 2,000 m^2 total sample from six mesic Douglas-fir stands , H. J. Andrews Experimental Forest, Oregon. Species acronyms are given in Table 2.2.

	[a]YY	MM	OO
	48	39	11
	84	60	57
GECO	--	--	-1
HYMP A	--	--	-1
TUCA	--	--	-1
TURU	--	--	-2
HYMG I	--	--	1-
MAOR	--	--	1-
RHAT	--	--	1-
HYDV A	--	1-	2-
HYSC R	--	43	43
HYSS E	-2	-3	25
ELGR	6-	7-	65
ENLA	-1	-1	11
ELMU	--	44	13
MAFA	--	1-	--
MAVE	--	2-	--
THPI	--	1-	--
ALTR	11	34	--
LEMA	34	44	22
LESP	31	34	14
RHPA	55	67	46
RHSU	3-	43	23
RHVI N	43	51	33
HYSC O	56	43	44
GAMO	76	87	23
LERU	35	25	-3
TRCI	55	24	23
MABR	34	--	-3
RATA	1-	--	-1
LEGE	-2	--	--
GECE	1-	--	--
HYMS U	1-	--	--
RAAT	1-	--	--
RHVI L	2-	--	--
TUAS	1-	--	--
TUGI	1-	--	--

[a] Stand habitat code and number (vertical): Y = mesic young, M = mesic mature, O = mesic old-growth.

CONCLUSION

Vegetation studies have shown that for vascular plants, similar species combinations recur under similar habitat conditions. Also, species abundance and composition changes more or less continuously over the landscape (Mueller-Dombois and Ellenberg, 1974). Necessarily classification of communities is not absolutely objective. Objective procedures are used as a starting point, but final classifications are "fine tuned" based on the investigator's experience and judgment. This study found communities of hypogeous ectomycorrhizal fungi to be co-extensive with associated vascular plant communities and sensitive to variation within habitats.

A profound dichotomy in seasonal fruiting pattern between spring and fall precludes the use of single season sampling to reveal fungal community structure. Yearly variation in weather patterns causes variation in sporocarp production that tends to obscure community structure responses to environmental gradients. When stand data collected over the entire fruiting period for a number of years are integrated, subsequent ordination and classification of the hypogeous ectomycorrhizal fungi community by use of sporocarp biomass closely reflect classification of habitats as determined by vascular plant communities. Furthermore, a fungal community guild structure was delineated that seemed to accurately reflect subtle variation in the habitats along an effective moisture gradient. The subterranean dominant counterpart to *Pseudotsuga* is *Rhizopogon parksii*, and *Gautieria monticola* is

nearly as wide spread and abundant. Changes in fungal community structure with seral stage of the stands are tentatively noted but the sampling of six stands in the present study is small.

Chapter 3

Variation in Sporocarp Production by Hypogeous Ectomycorrhizal Fungi within Three Douglas-fir Stands in the Central Western Cascades, Oregon

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SUMMARY

Coarse woody debris and associated forest floor characteristics are hypothesized to contribute structurally and functionally to the formation and development of hypogeous sporocarps. Although sporocarp production is potentially important to the reforestation of disturbed sites, the role of fallen trees and decaying woody debris with regard to the production of hypogeous sporocarps has not been previously investigated.

Sporocarp biomass and numbers of hypogeous sporocarps are assessed with relation to each other, to coarse woody debris cover, to forest floor litter, and to other selected forest floor parameters in three old-growth Douglas-fir stands ranging from wet to dry habitats. It was necessary to transform the numerical values of sporocarp biomass and number to achieve normality required for subsequent linear regression models. The $\log_2$ transformation was particularly effective in normalizing the distribution of sporocarp biomass values.

This paper shows that there is a weak but significant relationship between increasing sporocarp biomass and increasing number of sporocarps. The weakness of the relationship brings into question the use of numbers of sporocarps as a substitute for biomass when making between–species comparisons of "importance". Examination of the relationship between sporocarp biomass and numbers of sporocarps in a sample on an individual species basis shows that variation in mean sporocarp weight (for each collection of *n* sporocarps) is low for *Hysterangium coriaceum* while *Rhizopogon vinicolor*

shows greater variation in mean sporocarp weight.

Significant regression relationships between sporocarp biomass and forest floor parameters are confined to a single forest floor variable in each stand. In the wet old-growth stand, sporocarp biomass decreased with increasing forest floor depth. Sporocarp biomass increased with increasing moss cover in the mesic stand, but decreased with increasing moss cover in the dry stand. Over all stands, there is a slight tendency for forest floor depth to increase with the amount of coarse woody debris cover.

All stands sampled were in old-growth Douglas-fir forests aged at greater than 300 years. Centuries of development of the structural aspects of the forest floor may have reduced within–stand variation in the chosen forest floor variables to the point where trends in the relationships between sporocarp production and forest floor parameters are difficult to detect. Future studies should be designed to include stands that vary appreciably in old-growth characteristics and in the amount of "carry over" of old-growth structural attributes (such as forest floor parameters) into second growth stands.

INTRODUCTION

Trees cannot absorb enough water and minerals from soil to sustain life without mycorrhizal fungi. Most of the dominant forest trees in the Pacific Northwest (*Pseudotsuga, Tsuga, Abies, Pinus, Picea, Larix, Quercus, Castanopsis, Lithocarpus*, and *Alnus* species) form ectomycorrhizae with fungi that reproduce from epigeous sporocarps (above ground mushrooms) or from below ground (hypogeous) sporocarps (broadly referred to as truffles)(Trappe, 1962; 1971). Spores of hypogeous fungi are often dispersed via consumption by animals (mycophagy). The overwhelming importance of these sporocarps in the diet of small mammals has been documented by investigators in different regions of the world (Maser et al., 1978a, 1978b; Ure and Maser, 1982; Durrieu et al., 1984; Hunt and Trappe, 1984; Kotter and Farentinos, 1984; Lamont et al., 1985; Hayes et al., 1986; Malajczuk et al., 1987; Maser and Maser, 1987; Maser et al., 1988). Even though Tevis (1952) recognized the importance of small mammals to spore dispersal more than three decades ago, the attributes of coarse woody debris critical to the life history of many small mammals are just beginning to be understood (Maser and Trappe, 1984). Mycophagous small mammals are particularly active around coarse woody debris. Their movement between micro-habitats has been hypothesized as a mechanism for spore dispersal into logged habitats (Hayes et al., 1986).

Well decayed fallen tree boles are rich in mycorrhizal roots and hyphae of the associated fungi (Harvey et al., 1976, J. Trappe unpublished data).

Deposition of spore–rich fecal pellets by small mammals in and around coarse woody debris is thought to play an important role in the establishment of tree seedlings on such substrates (Maser et al., 1978b; Trappe and Maser, 1978). "Nurse logs" are particularly important to *Picea, Tsuga,* and *Abies* seedlings (Franklin, 1966; Thornburgh, 1969; LaRoi and Franklin, 1979). All *Tsuga heterophylla* seedlings older than one year on coarse woody debris were found to be mycorrhizal by Christy et al., (1982). *Rhizopogon vinicolor* is common (vegetatively) in decaying wood (Zak, 1971) and is adapted to increasing drought resistance in its associated host (Parke et al., 1983). Coarse woody debris has been found to be the most frequent (or only) site of active ectomycorrhizae on dry and disturbed sites (Harvey et al., 1979; Amaranthus et al., 1989)

Given this complex of interdependent biological symbioses, coarse woody debris and associated forest floor characteristics can be generally hypothesized to contribute structurally and functionally to the formation and development of hypogeous sporocarps. Although sporocarp production has been recognized as potentially important to the reforestation of disturbed sites (Perry et al., 1987; Maser et al., 1978b), the role of fallen trees and decaying woody debris with regard to the production of hypogeous sporocarps has not been investigated previously. The only quantitative analysis of the relation of hypogeous sporocarp production to environmental factors is by Fogel (1981) who found significant correlations between biomass and temperature and precipitation parameters.

During the studies of hypogeous ectomycorrhizal fungi described in Chapters 1 and 2, readily obtainable data were collected from individual plots on

selected forest floor parameters that are potentially important to the production of sporocarps. In this study, old-growth Douglas-fir forest stands representing a range in moisture status were chosen to intensively assess within–stand relations of biomass and numbers of hypogeous sporocarps with respect to coarse woody debris, forest floor litter, and other selected forest floor parameters. This assessment permits the following questions to be addressed: (1) What is the relationship between sporocarp numbers and biomass of sporocarps? (2) Are the forest floor variables of coarse woody debris, forest floor depth and other selected parameters significantly related to biomass or number of sporocarps? (3) Do these forest floor variables relate significantly as independent or dependent variables to each other? (4) Are significant relationships the same or different between the selected stands?

METHODS

Study area

The H. J. Andrews Experimental Forest occupies the 6,000 ha drainage of Lookout Creek, a tributary of the McKenzie River, in Lane Co., Oregon. The prevailing Douglas-fir dominated forests are considered typical of the western slopes of the central Cascade Range in Oregon. The forest has been administered by the U. S. Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948. The location of the study stands and the Experimental Forest is presented in Figure 3.1.

The regional climate is classified as Temperate Oceanic by Trewartha and Horn (1980) or Csb (cool–summer Mediterranean) by Köppen (1936). Average annual precipitation varies from about 2,300 to 2,800 mm, depending on topography. About 90% of the precipitation occurs from October through April. Above 900 m elevation, winter snowpacks accumulate to a depth of one meter or more. Summers are dry. Temperatures are moderate with a range from -3° C (mean January minima) to 29° C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Franklin and Dyrness, 1971).

Three general soil types are characteristic of the Experimental Forest (Berntsen and Rothacher, 1959; Franklin and Dyrness, 1973; Dyrness et al.,

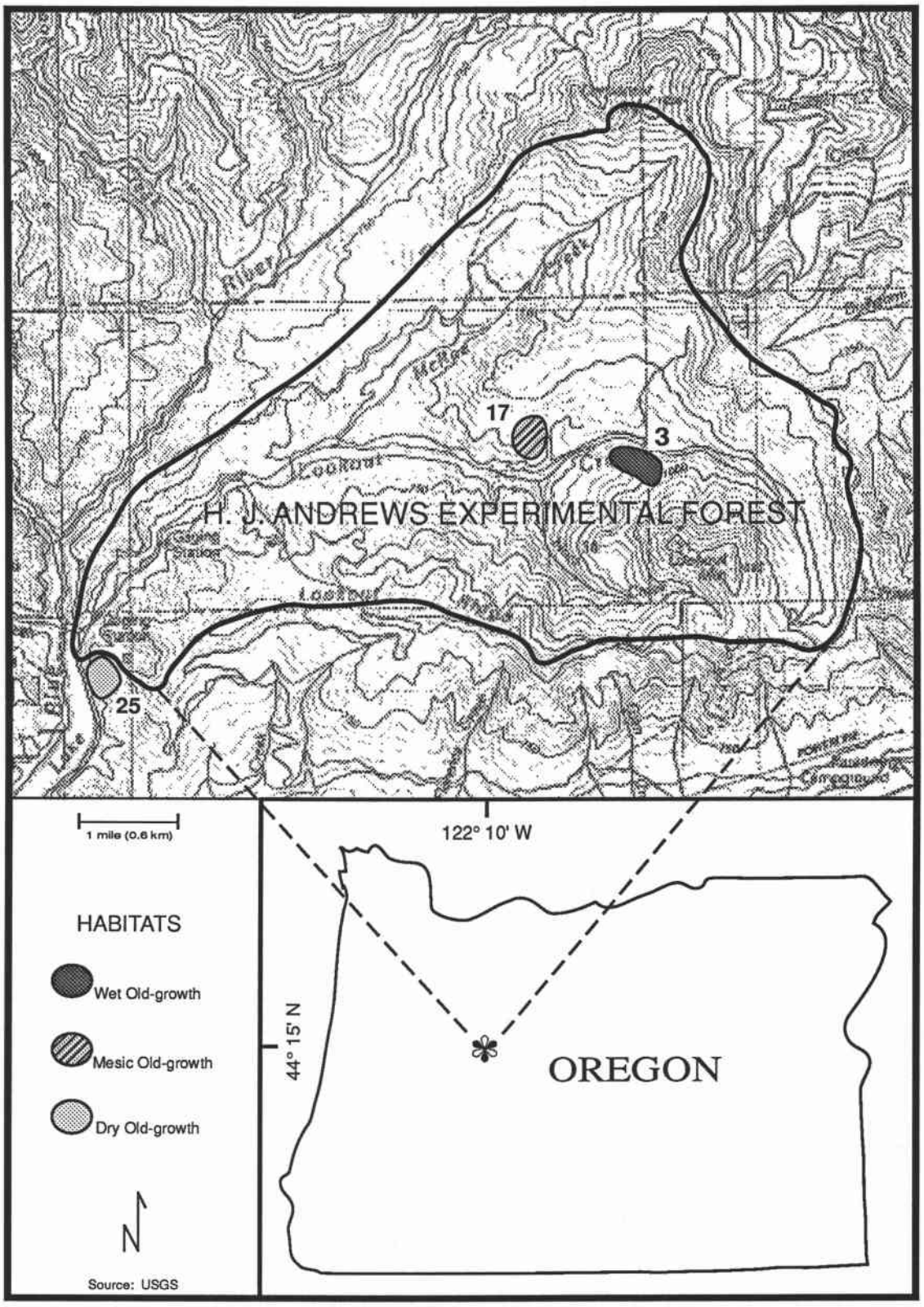


Figure 3.1. Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

1974). Steeper slopes and ridgetops often support a residual Brown Podzolic gravelly clay loam formed from andesite or basalt (usually classified as Haplorthods). Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams (generally classified as Haploxerults and associated with breccia and tuff parent material) are commonly found on midslopes. Gentle slopes and benches are often occupied by a colluvial clay loam.

Studies of forest communities within the *Tsuga heterophylla* Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Franklin and Dyrness, 1973; Dyrness et al., 1974; Zobel et al., 1976). Characteristic understory species are used to describe the community types. *Lysichitum americanum* indicates extremely wet forest sites with the water table near or seasonally above the surface. Abundant *Polystichum munitum* and *Oxalis oregana* typify moist sites. Mesic sites may be occupied by *Berberis nervosa* and/or *Rhododendron macrophyllum*. Towards the dry end of the scale, *Gaultheria shallon* increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities belonging to the *Pseudotsuga menziesii* series. In these communities Douglas-fir is often considered climax and *Holodiscus discolor* is an important shrub (Hemstrom et al., 1987).

Field sampling

Because a primary interaction of mycorrhizal fungi with coarse woody debris relates to the wood's water holding capacity (Maser and Trappe, 1984), three old-growth Douglas-fir forest stands were selected for sampling on the basis of moisture status. Sites were chosen with old-growth stands greater than 300 years of age from a range of plant communities representing a moisture gradient. Relative moisture classes prevailing at these sites were identified by generalized vascular plant habitat or community types by Spies et al. (1988):

Pseudotsuga menziesii / Polystichum munitum / Oxalis oregana (**wet**)

Pseudotsuga / Acer circinatum / Berberis nervosa (**mesic**)

Pseudotsuga / Gaultheria shallon–Rhus diversiloba (**dry**)

One stand in each forest type moisture class was intensively sampled. Consisting of approximately five hectares of relatively homogeneous forest, the stands represent a subset of sample stands originally located by other researchers as part of a regional forest characterization (Spies et al., 1988). Selected descriptive characteristics of each stand are presented in Table 1.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps, because

Table 3.1. Selected stand characteristics by habitat, from three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Habitat[1]	Stand (#)	Basal[2] Area (m^2/ha)	Stem[2] Density (#/ha)	Coarse[2,3] Soil (% vol.)	Median Elevation (m)	Aspect	Slope[4] (°)
WOG	3	101	526	19	800	N	0-35
MOG	17	108	670	13	770	SSE	10-30
DOG	25	49	443	55	550	W	30-35

[1] WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth.

[2] T. Spies, personal communication.

[3] Fragments > 2mm.

[4] Wet old-growth stand 3 occupied a series of slumps causing high slope variability.

fruiting varies so much by species and abundance in time and space (see also pp. 66 in Chapter 1). Fogel (1976, 1981) and States (1985) also report the clustered distribution of fruitbodies. Given the clumped distribution of sporocarps, the sampling strategy in this study was to use well–distributed small plots to obtain a representative stand sample. Random sampling requires many more plots than does systematic sampling to achieve this goal (Hurlbert, 1984). Ideally, with more resources, random sampling stratified by microsite would have been employed.

Hypogeous sporocarps were harvested in each stand three times (spring, summer, fall) yearly over two consecutive years except that one summer sample was missed in the wet stand and, due to an unusually early and heavy snowfall, one fall sample was missed in the mesic stand. Sampling in each season occurred over a six to seven week period. For spring and summer samples, stands on lower elevation south slopes were sampled first, those on higher elevation north slopes last. This procedure allowed the sample period to be shortened relative to the temperature and moisture controlled fruiting phenology. The fall sampling strategy was reversed with the higher, northerly slopes sampled first. Overall, data were collected from 16 stand samples totaling 1,600 m^2

For each stand sample, sporocarps were harvested from 25 circular four-square-meter plots for a total sample area of 100 m^2. Plots were placed systematically approximately every 25 m along transects spaced equidistantly (about 25 m) and arranged parallel to the slope contour. In each plot, the forest

floor was raked back to a depth of 5 to 10 cm in order to collect the sporocarps. The following data were recorded for each sample plot:

a. slope and aspect

b. percent cover of coarse woody debris by decay class and total

c. percent moss cover

d. thickness of forest floor horizons: undecomposed organics (O1), partially decomposed organics (O2), and humic (H)

e. total number of sporocarps

Slope and aspect were measured in degrees with a clinometer and compass, respectively. Coarse woody debris ground cover was estimated visually before and during the collection process. For the purposes of this study, pieces of woody material greater than 2.5 cm diameter (Harmon et al., 1986) in aggregations that exceeded approximately 250 cm^3 were considered coarse woody debris with potential influence on sporocarp production. Coarse woody debris decay classes were determined after Fogel et al. (1973). Percent cover of moss over the plot before collecting sporocarps was estimated visually. Thickness of the forest floor horizons was measured during the collection process and included the undecomposed organic material (O1), partially decomposed organic material (O2), and humic material (H) horizons. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain < 15% relative humidity, and weighed to the nearest 0.01 g to determine biomass.

Analytical Methods

Transformation. For each plot in which sporocarps occurred the following forest habitat parameters were used as variables in the analysis:

Coarse woody debris in percent cover by:

Decay class 4 (DC4)

Decay class 5 (DC5)

Total of decay classes 1-5 (TDC)

Slope in degrees (SLOPE)

Moss in percent cover (MOSS)

Forest floor depth, total O1, O2, and H horizons, in centimeters (FFD)

Total dry sporocarp biomass in grams (TBIO)

Number of sporocarps (CARPS)

Coarse woody debris decay classes 1-3 were not included in the analysis separately because they were not encountered often enough to provide meaningful information as variables.

The Shapiro–Wilk statistic, skewness, and Kurtosis were obtained for all variables to measure of the normality of the distribution of observed values (Snedecor and Cochran, 1980). Transformations were made to normalize the distributions of the data for all variables except slope. The percent data of DC4, DC5, TDC, and MOSS were transformed by X' = ARCSIN(SQRT(.01*X)). The count data CARPS and integer data FFD were given a $X' = \sqrt{X}$ transformation. TBIO was transformed by $X' = \log_2 X$ as recommended by Gauch (1982) for values ranging from 0 to 100 that show a distribution of high values for few

entries and low values for many entries.

The percentile distribution of the data was graphically presented to visually inspect comparisons of raw vs. transformed data. Data transformation improved the normality of the distributions in most cases. Table 3.2 shows that DC4, SLOPE, and MOSS are little changed. DC4 departs most from normality and transformation did little to normalize its distribution. SLOPE is nearly normal initially and shows only slight improvement with transformation. MOSS was not improved by transformation.

Total sporocarp biomass (TBIO) showed a pronounced improvement to a nearly ideal normal distribution from the $\log_2$ transformation (Figure 3.2). This is particularly important since total sporocarp biomass is used exclusively as a dependent variable and may be a parameter of interest to other investigators. Number of sporocarps (CARPS) is used as a dependent and an independent variable. There was improvement in the skewing that resulted from high values, but an abundance of single occurrences of sporocarps limited the degree to which normality could be achieved for its use as an dependent variable (Figure 3.3).

Table 3.2. Comparison of the Shapiro–Wilk statistic (W), skewness (S), and Kurtosis (K) before and after (') transformation of parameter values, from an 1,600 m^2 sample from three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Parameter[1]	W	W'	S	S'	K	K'
DC4	.50	.54	6.02	2.71	44.80	9.00
DC5	.69	.87	3.20	1.71	12.12	3.46
TDC	.71	.87	2.68	1.56	7.85	3.20
SLOPE	.89	—	-0.16	—	-1.47	—
MOSS	.85	.94	-0.01	-0.01	-1.47	-1.17
FFD	.66	.76	3.75	2.19	19.96	8.30
TBIO	.65	.95	2.92	-0.38	9.60	-0.14
CARPS	.52	.70	3.63	1.69	19.72	4.10

[1] DC4 = Decay class 4 coarse woody debris cover.
DC5 = Decay class 5 coarse woody debris cover.
TDC = Total cover all classes coarse woody debris.
SLOPE = Slope at the plot sample.
MOSS = Moss cover.
FFD = Forest floor depth total .
TBIO = Total dry sporocarp biomass.
CARPS = Number of sporocarps.

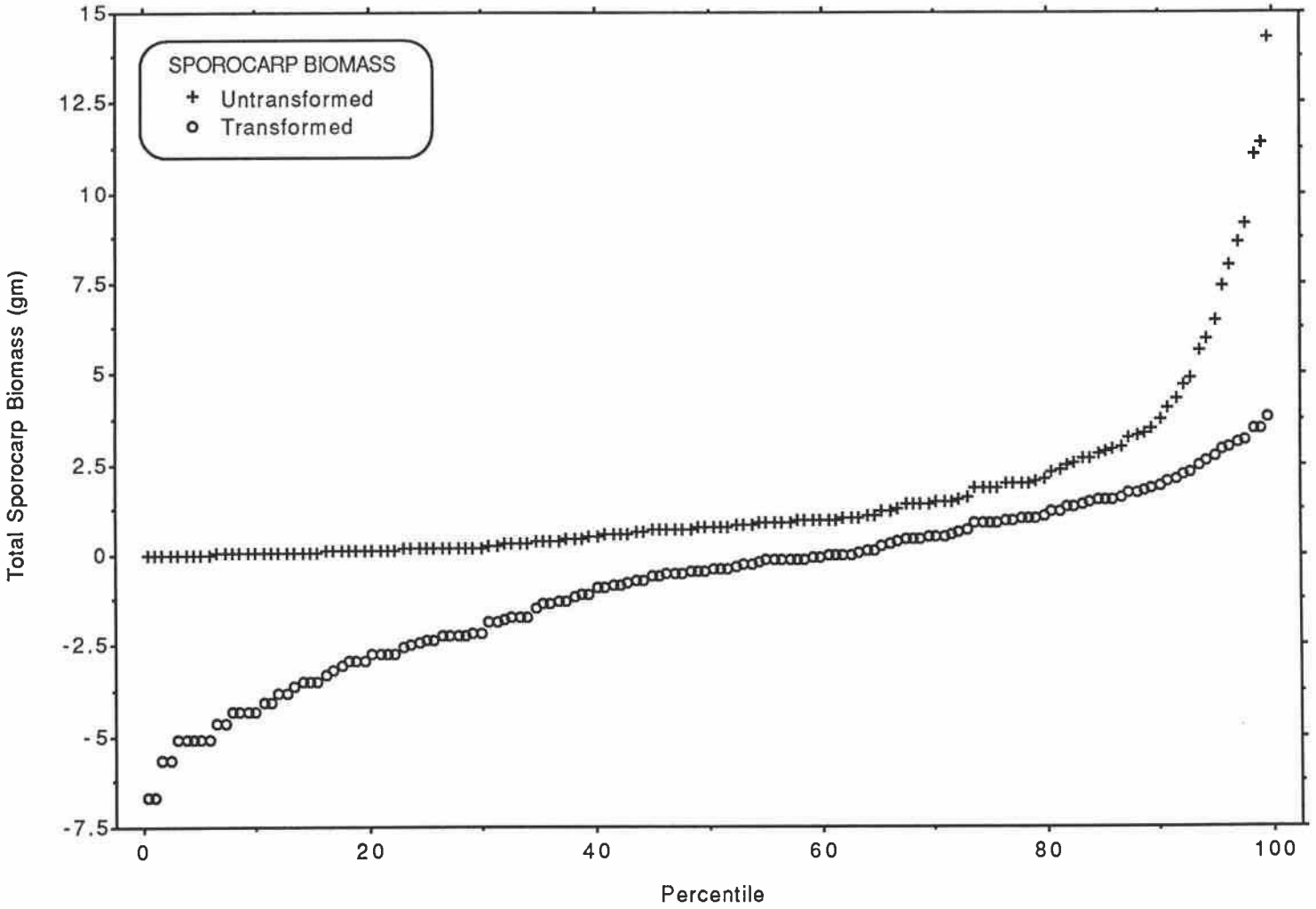


Figure 3.2. Percentile distribution of total sporocarp biomass (TBIO) and transformed values (TBIOT) from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

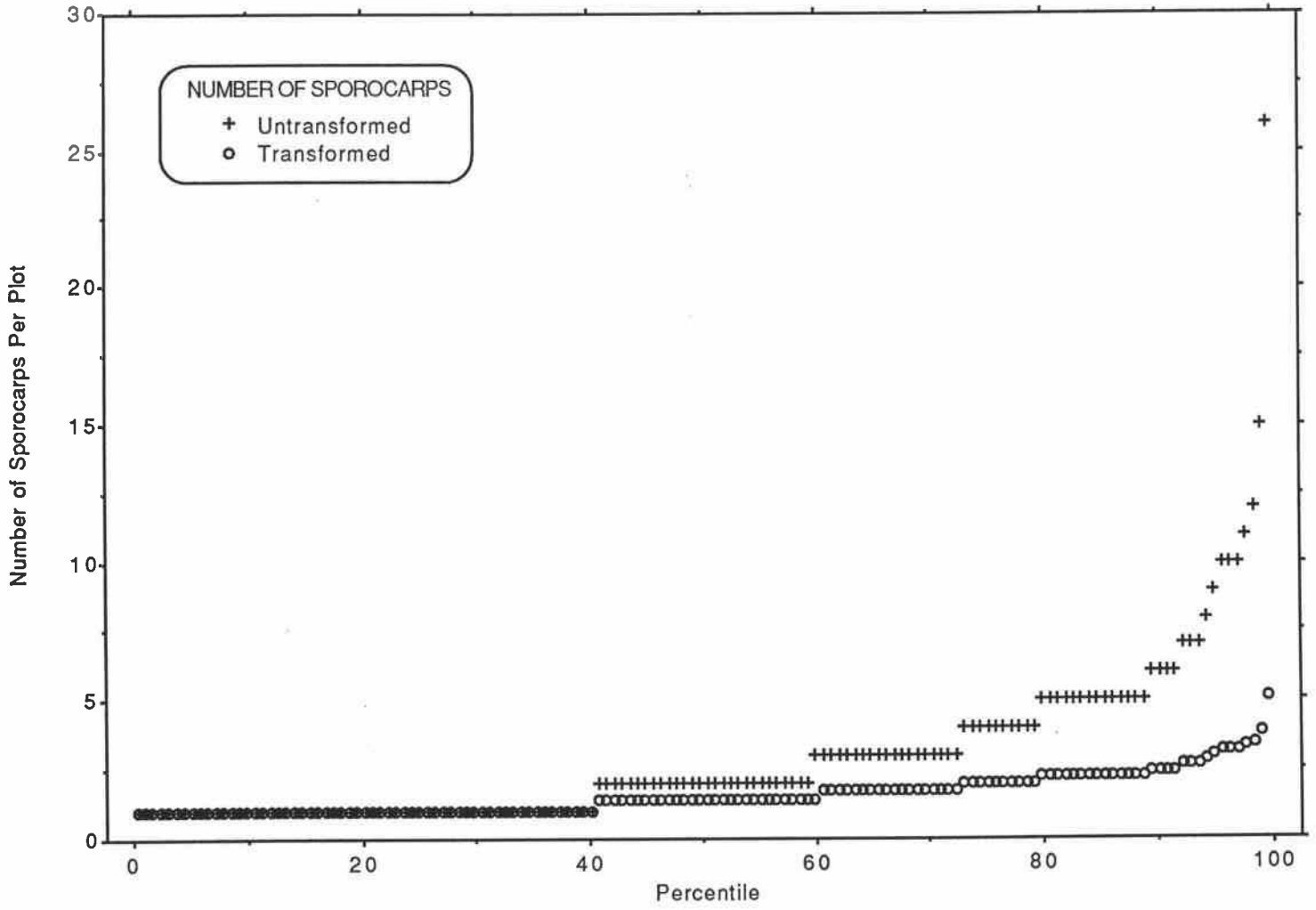


Figure 3.3. Percentile distribution of number of sporocarps (CARPS) and transformed values (CARPST) from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

Regression. A commercial software package was used to perform the linear regression analysis. Covariances and correlations are computed using provisional means. The program uses the Sweep Operator procedure to invert matrices (Hocking, 1985, cited in Feldman, 1987). Calculations were executed on a Macintosh II microcomputer.

The data set (including transformed parameters) was analyzed across all stands and separately for each stand. Total plot sporocarp biomass was regressed against total plot sporocarp number for all three stands together and individually. Using data from all 59 stand samples [Chapter 1] for the six most abundant fungal species, regressions of stand sample sporocarp biomass *vs.* stand sample sporocarp number were made for each species individually. Candidate forest floor parameters serving as variables for regression analysis were chosen from a correlation matrix of all parameters based on statistical significance ($p \leq 0.05$). For regression, raw data values were used for independent variables and transformed data for dependent variables when transformation was necessary to improve the normality of the variable (Neter and Wasserman, 1974). Because the coarse woody debris parameters DC4 and DC5 are interdependent with total coarse woody debris (TDC), the variable with highest regression value among them is used as an example in the results and discussion.

RESULTS

Two relationships are emphasized, those between sporocarp biomass and sporocarp number and those between sporocarp production and selected forest floor parameters. Major relationships between forest floor parameters are also presented. Data are analyzed for three combined stands and for three individual stands spanning a wet to dry gradient. Because most of the raw data exhibited non-normal distributions, various transformations were made as discussed in "Methods". Table 3.3 shows a correlation matrix for 11 transformed and untransformed forest floor variables and 4 transformed and untransformed sporocarp variables. This table presents a composite of all three forest stands. Correlations significant at $p \leq 0.05$ are underlined and in bold type. Except for trivial relationships between each variable and its transformed counterpart, most correlations are weak.

Sporocarp biomass and number

Significant relationships exist between all sporocarp variables (Table 3.3). Disregarding the trivial relationships, there are moderate positive correlations between total sporocarp biomass and number of sporocarps. Regression of the dependent variable total sporocarp biomass transformed *vs.* the independent variable number of sporocarps (TBIOT = CARPS) is shown in Figure 3.4. Although the relationship is significant ($p = .0001$), the predictive power of the model is poor ($r^2 = 0.20$).

Table 3.3. Correlation matrix of sporocarp variables and selected forest floor variables from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest , Oregon[a].

Variable	Forest Floor Variables											Sporocarp Variables			
Name[b]	DC4	DC4T	DC5	DC5T	TDC	TDCT	SLOPE	MOSS	MOSST	FFD	FFDT	TBIO	TBIOT	CARPS	CARPST
DC4	—														
DC4T	.906	—													
DC5	-.017	-.001	—												
DC5T	-.032	-.024	.950	—											
TDC	.357	.299	.862	.792	—										
TDCT	.350	.319	.823	.805	.964	—									
SLOPE	.120	.087	**-.215**	**-.292**	**-.177**	**-.238**	—								
MOSS	-.072	-.028	-.136	**-.180**	-.154	-.157	**.184**	—							
MOSST	-.056	-.017	-.131	**-.174**	-.143	-.147	**.176**	.994	—						
FFD	**.601**	**.487**	**.238**	**.263**	**.494**	**.503**	-.147	**-.207**	**-.200**	—					
FFDT	**.528**	**.443**	**.266**	**.304**	**.483**	**.517**	**-.198**	**-.214**	**-.209**	.980	—				
TBIO	-.032	.002	-.060	-.083	-.075	-.064	-.065	.024	.039	-.092	-.087	—			
TBIOT	-.024	-.009	-.073	-.111	-.093	-.122	.060	.004	.018	-.139	-.159	.727	—		
CARPS	-.050	-.007	-.081	-.115	-.066	-.053	-.040	.056	.063	-.080	-.068	**.509**	**.443**	—	
CARPST	-.051	.009	-.101	-.137	-.094	-.088	.014	.048	.053	-.115	-.107	**.506**	**.513**	.960	—

a Significant ($p \leq .05$) correlations (r values) are bold and underlined, DC4 and DC5 are each interdependent with TDC, so those correlations are ignored as are trivial correlations between a variable and its transformed value.

Table 3. continued.

[b] DC4 = Decay class 4 coarse woody debris cover, DC4T = transformed value.

DC5 = Decay class 5 coarse woody debris cover, DC5T = transformed value.

TDC = Total cover all classes coarse woody debris, TDCT = transformed value.

SLOPE = Slope at plot sample.

MOSS = Moss cover, MOSST = transformed value.

FFD = Forest floor depth total, FFDT = transformed value.

TBIO = Total dry sporocarp biomass, TBIOT = transformed value.

CARPS = Number of sporocarps, CARPST = transformed value.

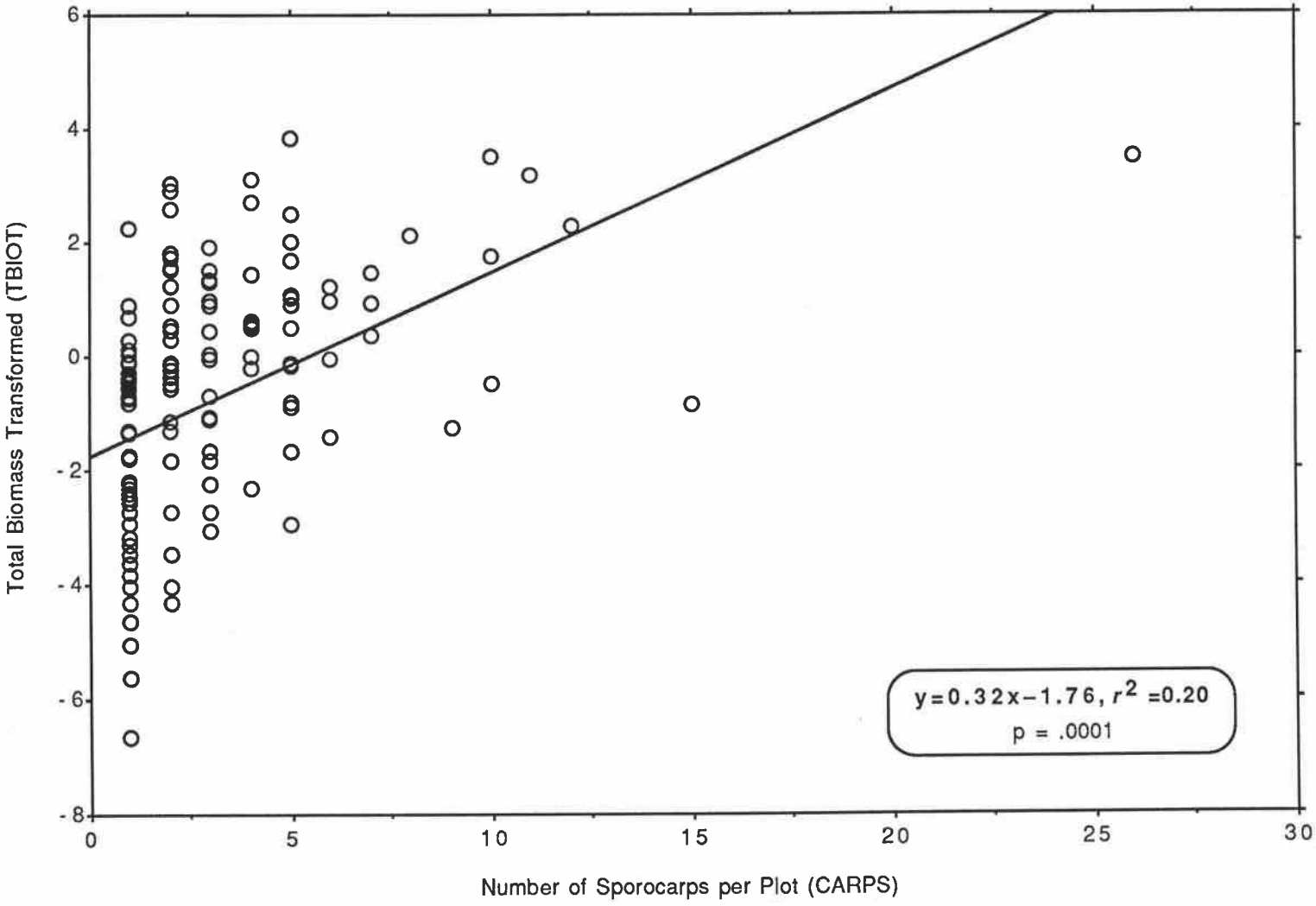


Figure 3.4. Regression of the model: TBIOT = CARPS (total sporocarp biomass, transformed values = number of sporocarps), from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The regression relationship was similar on a stand by stand basis as exhibited for the mesic old–growth stand (Figure 3.5) where $r^2 = 0.25$, $p = .0004$. Removal of the single highest outlier values from the number of sporocarps variable in the wet old-growth and dry old-growth results in the r^2 values being lowered to 0.15 and to 0.14 respectively.

Figures 3.6 and 3.7 illustrate the range of regression responses from the six most abundant fungal species when each species total stand sample sporocarp biomass *vs* total stand sample sporocarp number is considered. The high correlation expressed for *Hysterangium coriaceum* (Figure 3.6) shows that the amount of variation in mean sporocarp weight for each sample of *n* sporocarps is small while *Rhizopogon vinicolor* shows greater variation in the mean sporocarp weight for each sample (Figure 3.7).

Sporocarp production and forest floor parameters

Six forest floor parameters are considered: decay class 4 woody debris, decay class 5 woody debris, total woody debris, slope, moss, and forest floor organic soil depth. Since these are independent variables, non-transformed values may be considered, whereas transformed values of sporocarp biomass and number are entered as dependent variables into regressions. For the three stands combined, there were no significant relationships between transformed sporocarp biomass or transformed number of sporocarps and forest floor variables at $p \leq .05$ (Table 3.3). The best correlation was between sporocarp biomass and forest floor depth transformed, but the predictive power of the

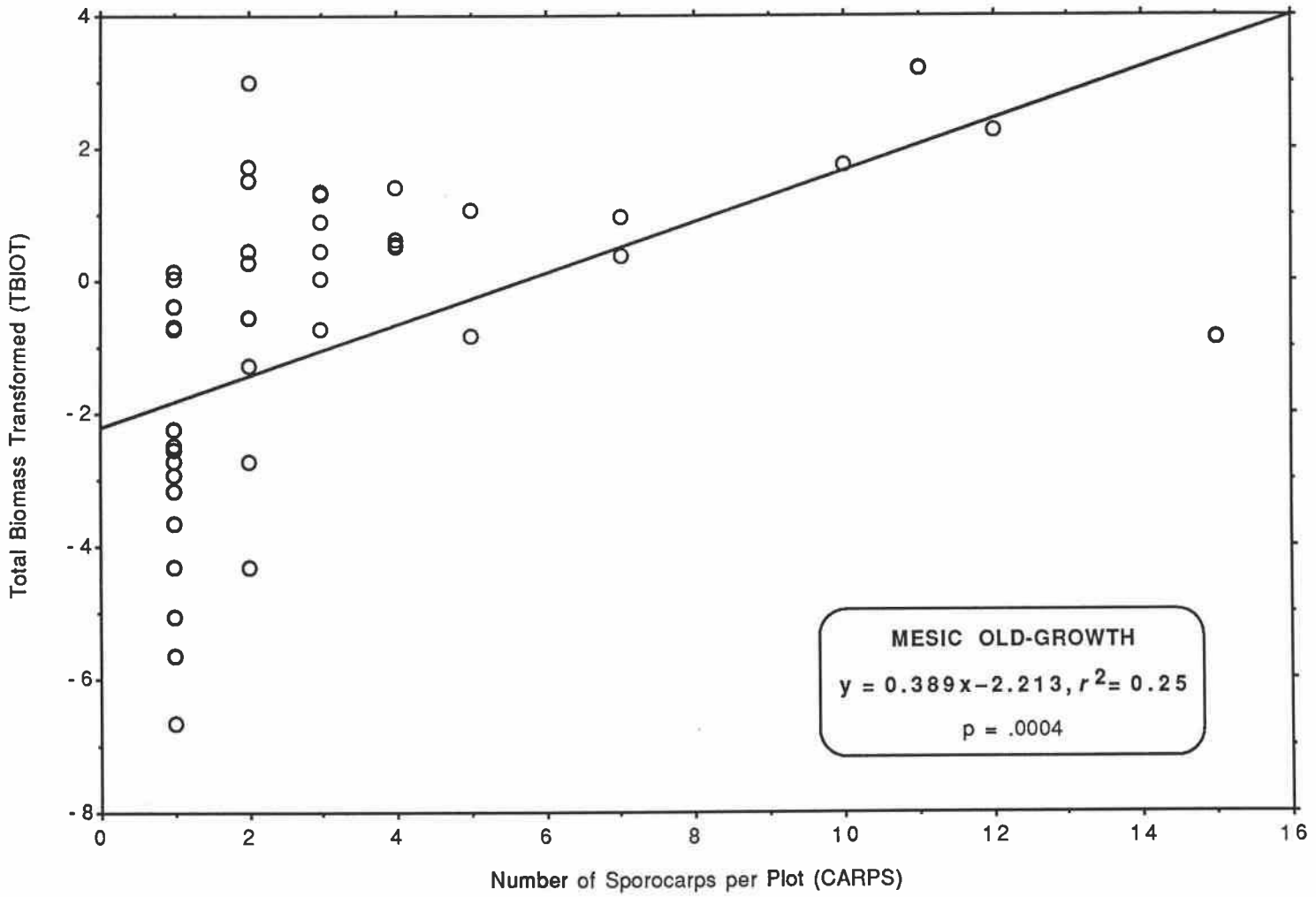


Figure 3.5. Regression of the model: TBIOT = CARPS (total sporocarp biomass, transformed values = number of sporocarps), from a 500 m^2 total sample in a mesic old-growth Douglas-fir stand, H. J. Andrews Experimental Forest, Oregon.

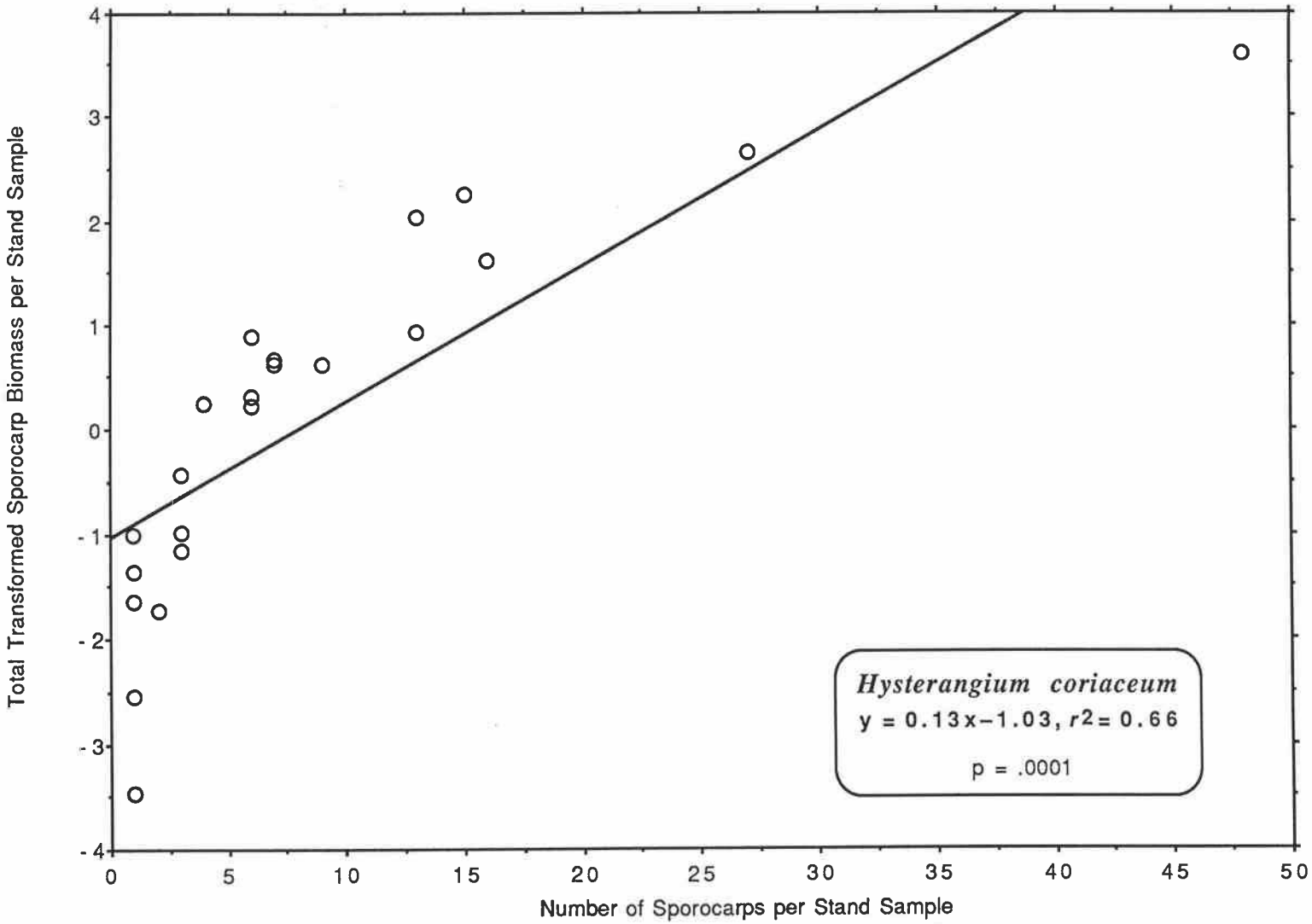


Figure 3.6. Regression of the model: TBIOT = CARPS (total sporocarp biomass transformed = number of sporocarps) for ***Hysterangium coriaceum***, from a 5,900 m^2 total sample in ten Douglas-fir forest stands, H. J. Andrews Experimental Forest, Oregon.

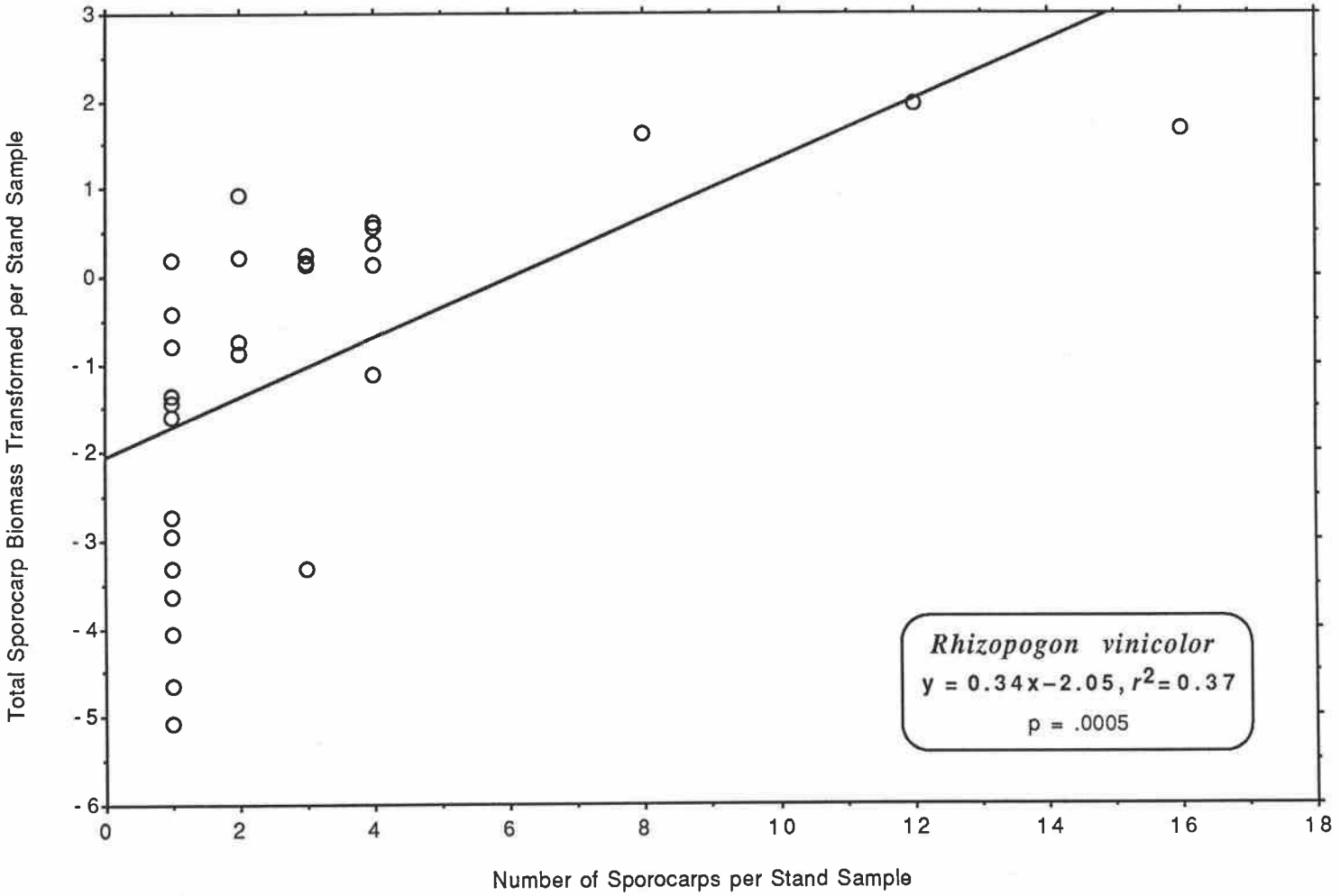


Figure 3.7. Regression of the model: TBIOT = CARPST (total sporocarp biomass transformed = number of sporocarps for ***Rhizopogon vinicolor***, from a 5,900 m^2 total sample in ten Douglas-fir forest stands, H. J. Andrews Experimental Forest, Oregon.

model TBIOT = FFDT is poor (r^2 = 0.03) and the p value is marginally significant (.056).

The significant regression between total sporocarp biomass transformed (TBIOT) and forest floor depth (FFD) was confined to the mesic old-growth stand (Figure 3.8) which showed that sporocarp biomass decreased with increasing forest floor depth, but the predictive power of the model was poor (r^2 = 0.17)

In the wet old-growth stand, total biomass transformed was correlated with moss cover, however the relationship fell outside the 95% confidence level. Examination of the residuals plotted against the fitted values showed three strong residuals with absolute values greater than five. All other residuals have absolute values less than four. When the strong residuals are removed, the model TBIOT = MOSS, total biomass transformed = moss cover, becomes significant (Figure 3.9). Again, the predictive power of the model is poor (r^2 = 0.19).

In the dry old-growth stand, moss cover was negatively correlated with total biomass transformed (TBIOT) but not significantly (p = .06). Examination of the regression showed a stronger correlation might exist for higher values of total biomass transformed. Removal of the values from the lowest 20 percentile of the distribution had little effect on the normality of the distribution of total biomass transformed. The subsequent regression of total sporocarp biomass transformed (after removal of the lowest 20 percentile) with percent moss cover was significant but with low predictive power (r^2 = 0.14, Figure 3.10).

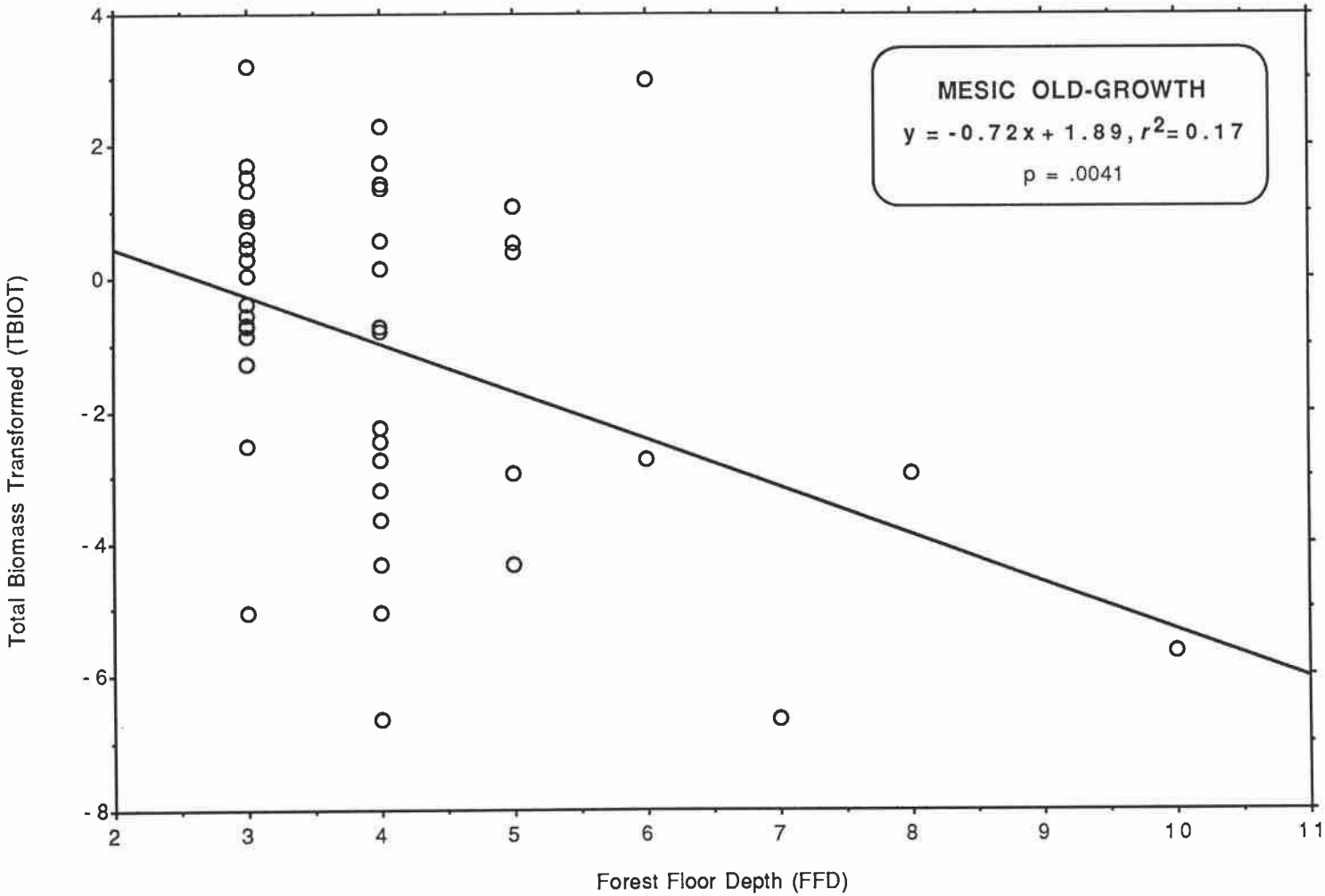


Figure 3.8. Regression of the model: TBIOT = FFD (total sporocarp biomass, transformed values = forest floor depth), from a 500 m^2 total sample in a mesic old-growth Douglas-fir stand, H. J. Andrews Experimental Forest, Oregon.

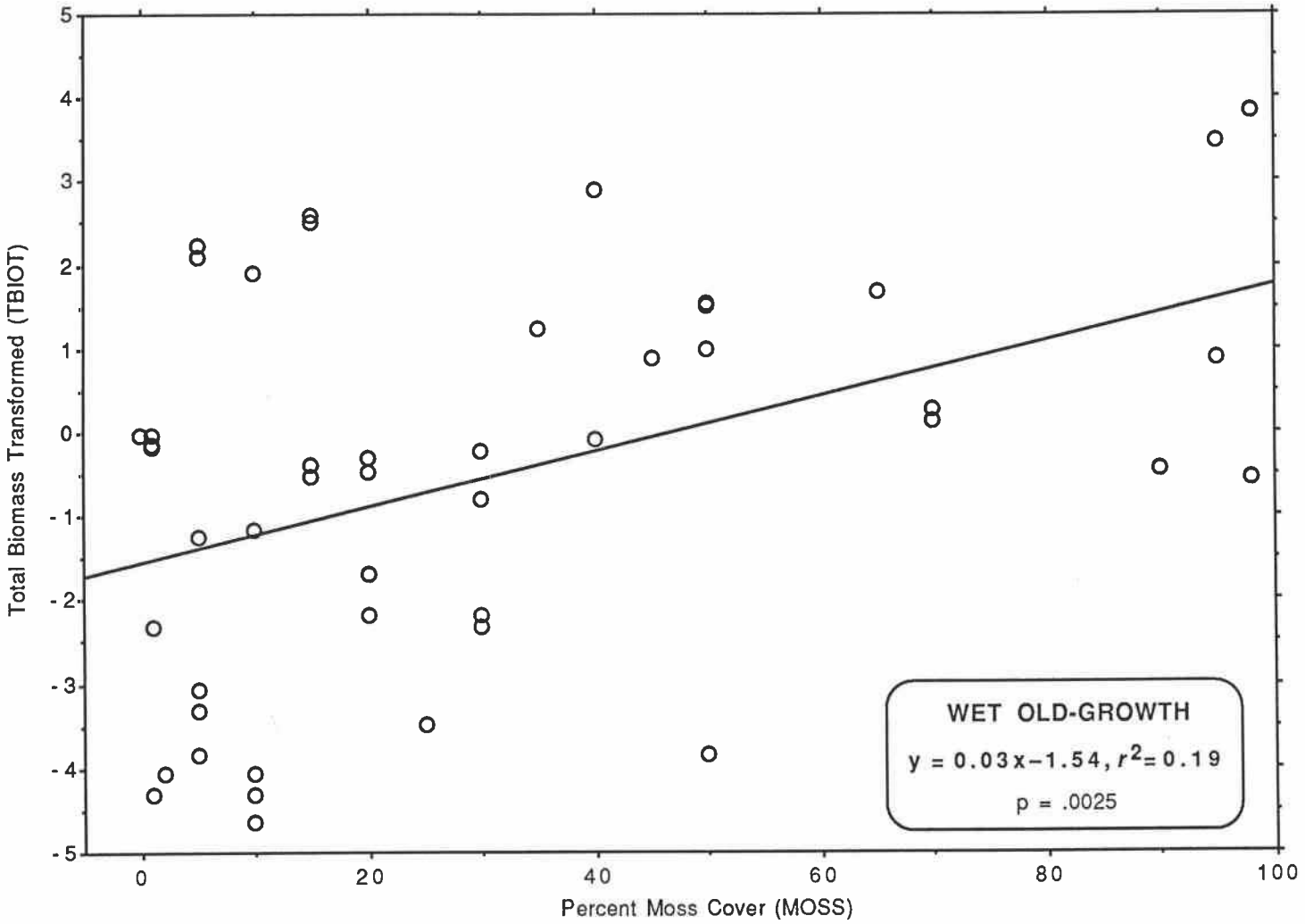


Figure 3.9. Regression of the model: TBIOT = MOSS (total sporocarp biomass, transformed values = percent moss cover) with the three strongest residuals removed, from a 500 m^2 total sample in a wet old-growth Douglas-fir stand, H. J. Andrews Experimental Forest, Oregon.

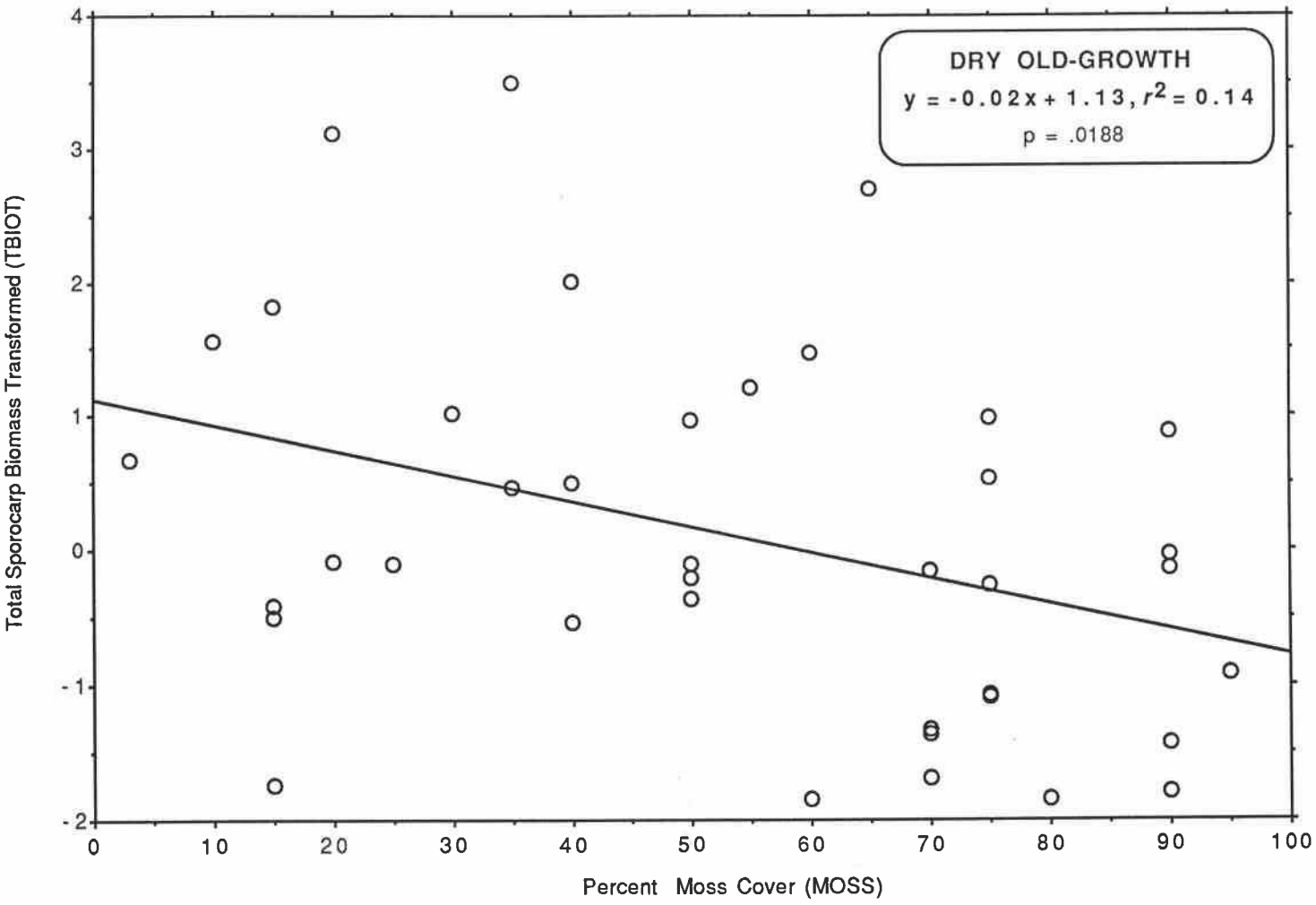


Figure 3.10. Regression of the model: TBIOT = MOSS (total sporocarp biomass, transformed values with the first 20 percentile removed = percent moss cover), from a 600 m^2 total sample in a dry old-growth Douglas-fir stand, H. J. Andrews Experimental Forest, Oregon.

Other variables producing significant ($p \leq 0.05$) regression relationships are of only incidental interest; however, the correlations between forest floor depth (FFD) and coarse woody debris variables are a prominent feature of Table 3.3. As representative examples, the highest correlation across all stands and the highest single stand correlation were regressed. Over all three stands, a moderate positive correlation was found between decay class 4 coarse woody debris cover and forest floor depth transformed (Figure 3.11). However, the low r^2 value (0.28) gives the regression model FFDT = DC4 low predictive power. The dry old-growth stand shows a good positive correlation ($r = 0.70$) between increasing coarse woody debris decay class 4 cover and forest floor depth transformed (Figure 3.12). While the predictive value of the model FFDT = DC4 for this stand is still not high ($r^2 = 0.49$), it is the best relationship in the entire data set.

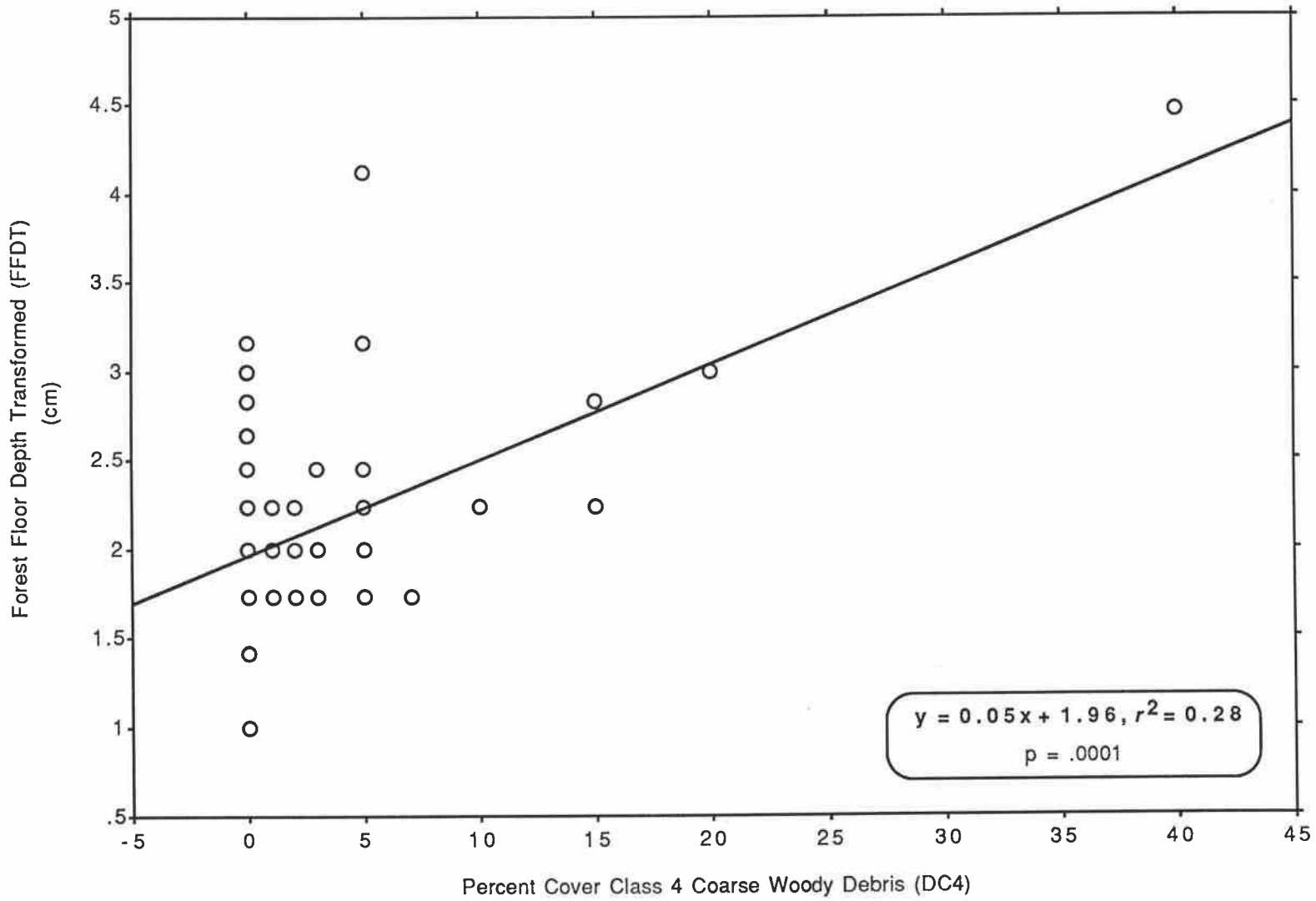


Figure 3.11. Regression of the model: FFDT = DC4 (forest floor depth, transformed values = class 4 coarse woody debris percent cover), from a 1,600 m^2 total sample in three old-growth Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

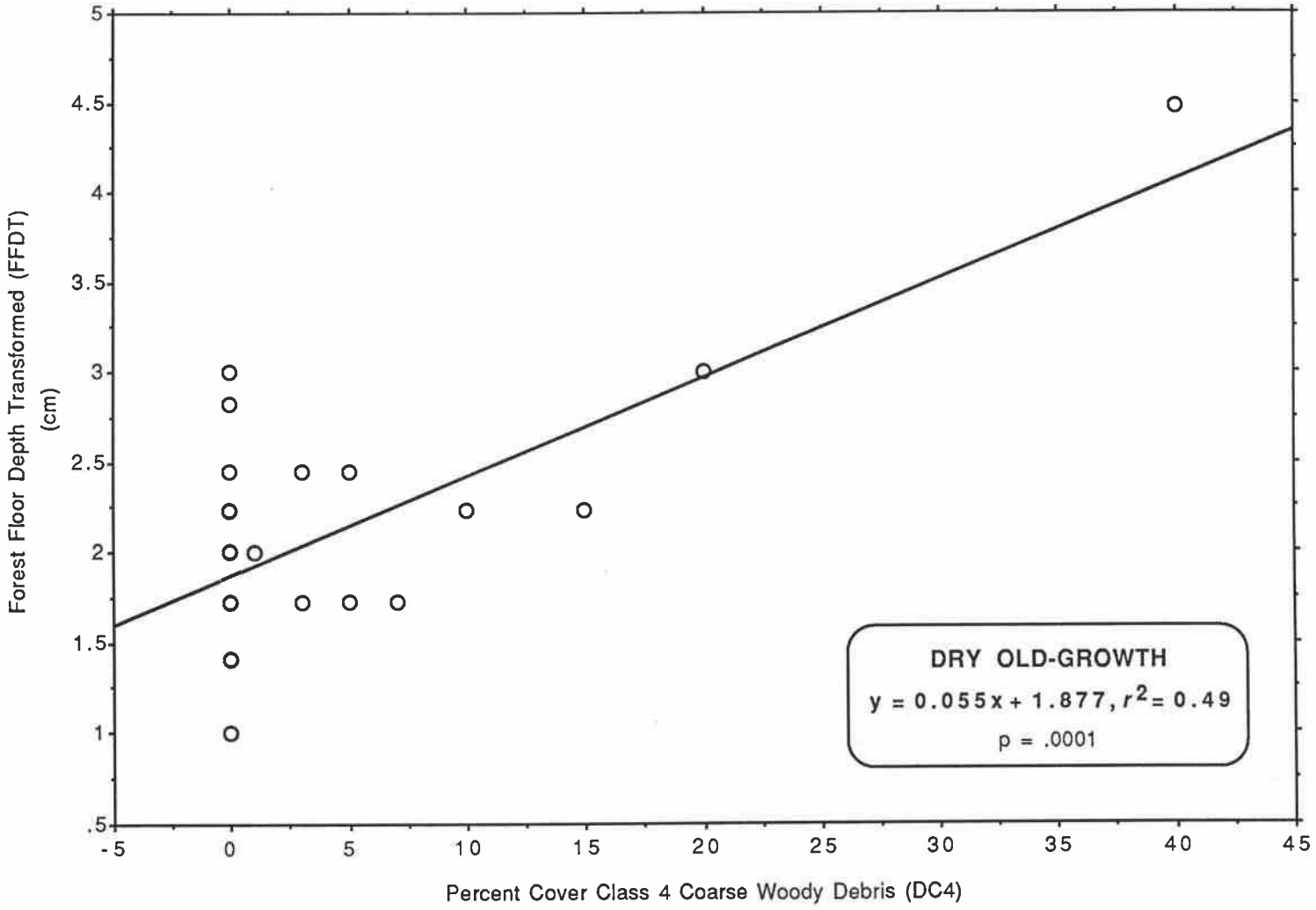


Figure 3.12. Regression of the model: FFDT = DC4 (forest floor depth, transformed values = class 4 coarse woody debris percent cover), from a 600 m^2 total sample in a dry old-growth Douglas-fir stand, H. J. Andrews Experimental Forest, Oregon.

DISCUSSION and CONCLUSIONS

Previous workers have often quantified fungi solely on the basis of sporocarp number (Orłoś, 1966; Winterhoff, 1984; Bills et al., 1986; Cibula and Ovrebo, 1988) or have used sporocarp number in addition to sporocarp weight (Fogel, 1976, 1981; Hunt and Trappe, 1987). The sole use of sporocarp number has been perfunctory and without critical evaluation of the implicit assumptions as related to objectives. Hunt and Trappe (1987) noted a discrepancy in the average weight of sporocarps between species and a significant change in average sporocarp weight in different seasons within some species. This paper shows that a significant relationship exists between increasing sporocarp biomass and increasing number of sporocarps. The regression of sporocarp biomass with number is not strong however, and brings into question the usefulness of numbers of sporocarps as predictors of biomass. Hunt and Trappe (1987) found a similarly poor relationship between biomass and numbers of sporocarps($r^2 = 0.15$) The present study looked at the relationship of biomass and number of sporocarps for all species in a plot combined. For the quantification of plot data, the use of numbers of sporocarps as a substitute for biomass is not recommended. Different species would be expected to have different mean biomass per sporocarp and different variances.

The qualification above, does not mean that the correlation of sporocarp biomass with number of sporocarps in a sample for a single species can not be high, as for example with *Hysterangium coriaceum* (Figure 3.6) nor that the

regression relationship for one species does or does not differ from that of another species. This is shown by comparison of the relation for *Hysterangium coriaceum* with that for *Rhizopogon vinicolor* (Figure 3.7). These variable results suggest that for between species comparison of "importance", measurement of reproductive potential, or assessment as a food source, sporocarp numbers will provide less reliable information for developing interpretations and conclusions than will biomass.

Of the variables studied combining data from all stands, only forest floor depth is even marginally significant when related to sporocarp biomass transformed. The predictive power of the model is poor. However, the strength of the relationship as expressed by r^2 is not the only interest. The regression relationship is not the same for the three old-growth stands taken individually. The model total sporocarp biomass transformed = forest floor depth (TBIOT = FFD, Figure 3.8) is significant only for the mesic stand. In particular, forest floor depths greater than six centimeters were related to lower biomass values. Since spore dispersal is dependent on the sporocarps being detected by their odor and consumed (Fogel and Trappe, 1978; Kotter and Farentinos, 1984), sporocarp formation under deep accumulations of litter and coarse woody debris could be selected against in the course of evolution. The level of CO_2 in a substrate can affect sporocarp development (Alexopoulos and Mims, 1979) and is hypothesized as a potential selective mechanism for limiting sporocarp development under deep accumulations of litter. If reproductive fitness is reduced when sporocarps develop under heavy accumulations of litter,

ectomycorrhizal fungi which produce hypogeous sporocarps may have developed adaptations which limit allocation of resources to sporocarp formation when litter depth restricts CO_2 dispersal. In the mesic old-growth stand that may occur when coarse woody debris exceeds six centimeters in depth (Figure 3.8).

In the dry and wet stands, total biomass transformed correlates significantly with moss cover only after some modification of the data. The correlation is positive in the wet old-growth stand and reinforces the hypothesis that moss cover can provide an appropriate casing (regulating humidity and CO_2 exchange) for the development of sporocarps. An explanation for the negative correlation between total biomass transformed and moss cover in the dry old-growth stand (and only for the highest 80 percentile TBIOT values) is difficult to postulate. Possibilities are that high moss cover could increase moisture stress or be associated with the shade of a non-ectomycorrhizal host species such as *Acer circinatum*.

Over all stands, the only major trend in comparisons between forest floor parameters was for forest floor depth to increase with coarse woody debris cover (Table 3.3). As an example, the model forest floor depth transformed = decay class 4 cover (FFDT = DC4, Figure 3.12) was presented because this regression has the highest r^2 value of any model using forest floor parameters. As coarse woody debris decays to the class 4 stage and beyond, it breaks up, gets spread around, and is incorporated into the forest floor. In the individual stands, the only other significant correlation between forest floor parameters was in the wet stand

where forest floor depth transformed had a negative relationship to slope. The wet stand had the greatest within–stand variation in slope and the relationship could be related to the rate of land slumping in the stand.

In this study, significant regression relationships between sporocarp biomass and forest floor parameters are highly individualistic by stand (Figures 3.8–3.10). Since most of the significant correlations did vary in the strength of the relationship from stand to stand, and since the stand types were not replicated, generalizations can not be inferred which encompass Douglas-fir forests of the study area or other stands of the same types sampled. The strength of the relationships in this study can be compared to those of Fogel (1981) who found significant correlations between sporocarp biomass production and temperature and precipitation parameters using single and multiple regression models (r^2 values ranged from 0.17 to 0.67 and R^2 ranged from 0.42 to 0.68). Fogel's (1981) values are based on untransformed biomass, therefore his values have a somewhat different basis, but do range higher than those found in this study ($r^2 = 0.14$ to 0.19).

This study was confined to old-growth stands. Abundant coarse woody debris is a common characteristic of all old-growth stands (Franklin et al., 1981). Perhaps, due to centuries of development without catastrophic disturbance, within–stand variation in the parameters measured has been reduced to the point that strong correlations with sporocarp production are difficult to detect. The disparate nature of the relationships between the stands provides a clue that functions of forest floor parameters in the production of sporocarps are complex

and likely to change in different habitats.

The methodology used in this study was necessarily of a reconnaissance nature (e.g., Franklin et al., 1971) and may not have been sensitive enough to detect strong trends in the relations between the selected parameters. In designing future research, it would be advisable among other things, to consider a full range of stand ages and habitats, the amount of "carry over" of coarse woody debris into second growth stands, changes in the moisture holding capacity of coarse woody debris relative to that of the soil with season, and patterns of small mammal mycophagy in relation to coarse woody debris. Furthermore, an approach specifically designed to consider the spatial aspects of sporocarp production and consumption in the forest floor and the location and type of coarse woody debris should provide more sensitive data for the detection of associations. The current study has provided information that should be helpful in the selection of parameters for the design of a study stratified by microsite considerations The sporocarp mapping approach of Fogel (1981) could serve as a starting point in study design.

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