Chapter 2

MYCOLOGICAL INPUTS TO ECOSYSTEMS ANALYSIS

George C. Carroll
University of Oregon
Eugene, Oregon

I. INTRODUCTION

In considering the ecology of fungi, various contributors to the present volume have noted the dearth of studies in which fungi have been employed to develop or test some fundamental ecological concept. In short, as a discipline, mycology has made little contribution to the development of ecological theory, and general ecologists have adopted a take-it-or-leave-it attitude toward the fungi when considering possible organisms for testing such theory. In contrast, studies initiated under the International Biological Program (IBP) have repeatedly demonstrated the centrality of fungi in the functioning of ecosystems, and as a consequence an attitude of indifference toward fungi is less prominent among practitioners of ecosystems analysis than among professional ecologists as a whole. The question for large, integrated studies of ecosystems has become not whether microorganisms in general and fungi in particular will be considered but whether essentially mycological investigations will be undertaken by workers with backgrounds in classical mycology or by investigators from other disciplines forced by necessity to confront the fungi and their activities.

In the following pages I hope to demonstrate that the mycologist can make unique contributions to programs in ecosystems analysis and that such collaborative efforts can provide information about the biology of fungi unobtainable in any other fashion. For this discussion I have relied heavily on my own experiences with the Coniferous Forest Biome (US/IBP) and on consultation with Drs. James Trappe and William C. Denison, who were involved with the Coniferous Forest Biome research effort from its inception. This work has also benefited from useful conversations with several colleagues at Oregon State University and the University of Oregon who have also been heavily involved with research in coniferous forests. (See the Acknowledgments at the end of this chapter.)

In summary, then, I wish to address two questions within the historical context of IBP ecosystems research in western coniferous forests: (1) Which lines of productive inquiry have been initiated on the advice of mycologists, and how might the program have faltered without such mycological expertise? (2) What have mycologists learned about fungi in the process of collaborating in ecosystems research?

II. FUNGAL TAXONOMY AND ECOSYSTEMS ANALYSIS

Since its inception the organizers of biome projects under the IBP have demonstrated justifiable concern that research not become bogged down with interminable census studies and species lists. Rather, it was hoped that from the beginning efforts could be focused on process studies and computer modeling. It was recognized, however, that vastly different amounts of floristic and faunistic information existed for various groups of organisms, with rather complete species lists available for flowering plants and mammals, and almost nothing known about the composition of microbial and microfaunal communities. Since process studies frequently involve laboratory research with organisms prevalent in the field or organisms chosen to represent functional groupings, preliminary census studies often proved a necessity.

Within the Coniferous Forest Biome, mycological opinion dictated that preliminary species lists be prepared for a number of groups of fungi, including hypogeous fungi (Fogel, 1976), mycorrhizal and litter-decomposing fleshy fungi (Rhoades, 1972), microfungi (Sherwood, 1973; Sherwood and Carroll, 1974; Bernstein and Carroll, 1977a, b), and lichens (Pike, 1972; Pike et al., 1975). As a result of such studies, the dominance of just a few taxa in each of the habitats surveyed has been recognized, and more focused investigations using these species have been initiated. Examples are cited below.

The degree to which temperate zone ectomycorrhizal fungi degrade litter has long been debated in the mycological literature, with recent papers suggesting that such fungi have negligible capacities for litter decomposition (Hacskaylo, 1973). In view of the enormous standing crops and rather short turnover times reported for mycorrhizal fungi in the forest floor of a Douglas fir stand in Oregon (Fogel and Hunt, 1979), this question appears of considerable importance for modeling carbon fluxes in coniferous forests. Current work with *Laccaria laccata* (Fr.) Berk. and Br. and *Cenococcum geophilis* Fr., species found to be prevalent in early census studies, has shown these fungi to degrade coniferous litter to a significant extent in two-membered cultures with Douglas fir seedlings (A. Todd, personal communication).

For the lichens the foliose cyanophycophilous species *Lobaria oregana* (Tuck.) Müll. Arg. was early identified as predominant in Douglas fir canopies in low-elevation stands (Pike et al., 1975). Because of its capacity for nitrogen fixation, investigations on growth rates (Rhoades, 1977, 1978), litterfall (Rhoades, 1978; Pike and Carroll, unpublished data) and rates of nitrogen fixation (W. Denison, M. Roose, and L. Pike, personal communication) have been carried out (discussed later).

Estimation of microbial biomass from visual measurements of cell volume requires that dry weight/volume ratios be calculated for the cells which are measured. In attempting to estimate standing crops of needle microepiphytes in a Douglas fir canopy, Carroll (1979) determined these ratios for cultures of *Atichia glomerulosa* (Ach. *ex* Mann.) Stein, *Aureobasidium pullulans* (De Bary) Arn., and *Cladosporium* spp., fungi which had previously been identified as prevalent on needles and twigs in the Douglas

fir canopy (Sherwood and Carroll, 1974). In all of these cases the recognition of the preeminence of just a few characteristic fungi in any given habitat was first revealed through taxonomic surveys which required mycological expertise and which necessarily preceded field and laboratory process studies.

In several cases, the mycologist's familiarity with fungal taxa has led to the recognition of certain fungi in unexpected places, revealing clues about habitats and processes. While carrying out a preliminary census of microepiphytes in the canopy of Douglas fir, I attempted to culture several of the more common species. One of these, *A. glomerulosa*, typically forms a nonmycelial pseudoparenchymatous thallus on needles and twigs (Sherwood and Carroll, 1974; Meeker, 1975). When grown on agar media, however, the fungus produces pigmented yeastlike cells in the film of water on the agar surface. *A. pullulans*, another prevalent canopy fungus, produces similar yeastlike cells in liquid films. These observations suggested an aquatic dispersal of vegetative fungal cells and prompted me to look for additional evidence of aquatic spore dispersal in canopy fungi. Samples of throughfall from an old-growth Douglas fir stand were collected within several hours of rainstorms intermittently over a 2-year period. The water samples were brought back to the laboratory and filtered through Nuclepore filters (0.2 µm pore size). Microscopic examination of the filters revealed numerous triradiate and tetraradiate spores including representatives of *Tripospermum*, *Tridentaria*, *Ceratosporium*, and many other genera (see also Bandoni, Chap. 37). Conidia from needle endophytes from such forests typically occur in gloeoid masses and are either known or presumed to be also water dispersed (Carroll and Carroll, 1978). Low elevation Douglas fir forests in the Pacific Northwest normally receive 200–250 cm of rain a year, 70–80% of which may fall from November through March. Canopy fungi clearly respond to such seasonal inundation as if they existed in an aquatic habitat; many, like *Seuratia* (= perfect state of *Atichia*), probably produce aerially dispersed ascospores during the dry season and aquatically dispersed conidia or vegetative cells during the wet season.

Such fungi, then, constitute a guild of arboreal aquatic hyphomycetes which may function in canopies much as classical Ingoldian aquatic hyphomycetes function in streams (see Part VIII). Investigators should expect to find such fungi implicated in the decomposition of litter lodged in the canopy and in the processing of such litter for consumption by canopy arthropods. The litter may be smaller than the allochthonous materials degraded by stream fungi, as with pollen attacked by *Retiarius* in the phyllosphere of evergreen forests in South Africa (Olivier, 1978). The arthropods will also prove to be smaller than those in streams; D. Voegtlin in our laboratory has found fungivorous mites and collembolans to be the most abundant grazers in the Douglas fir canopy. Further, the absorption and concentration of dilute organic substrates from canopy leachates by fungi, while of little significance in streams, appears to be an important process in the canopy subsystem (discussed later). Although set apart by such superficial distinctions, the fundamental role of the arboreal aquatic fungi appears similar to that of aquatic hyphomycetes in streams; they

serve as ecological transducers, converting and concentrating recalcitrant and/or dilute substrates to available food sources which serve as the base for arthropod food chains.

This conclusion is further supported by another set of mycological clues. During the warmer months of the year microfrass (<1 mm diameter) becomes very abundant in the Douglas fir canopy. Examination of such frass under the microscope reveals the presence of abundant cell wall fragments from algal and fungal cells, largely *Protococcus viridis* Agh., *Atichia* sp., and various metacapnodiaceous taxa; apparently the resident microarthropods graze almost exclusively on canopy microorganisms.

The recent recognition of spores from hypogeous fungi in the gut contents of small forest mammals constitutes a second situation in which expertise on fungal taxonomy has yielded important information about processes in ecosystems. Maser et al. (1978) have shown that such fungi constitute a major food source for many rodents in the Pacific Northwest and that certain species (northern flying squirrel and red-backed vole) may subsist almost exclusively on hypogeous fungi. They have further demonstrated that habitat preferences of *Clethrionomys californicus*, the California red-backed vole, appear to be tied to the availability of sporocarps from obligate mycorrhizal hypogeous fungi; when a tract of forest is clear-cut, populations of this species vanish within a year, presumably because the fungi upon which they are known to feed have disappeared with the trees.

Aside from the obvious applicability of such information to models of carbon cycling and secondary productivity in forest ecosystems, these discoveries have further implications for an understanding of forest succession and for practical aspects of forest management. Animal species such as the Oregon vole (*Microtus oregoni*), which feed on fungal sporocarps in the forest and on grasses in adjacent clear-cuts are strongly suspected to serve as agents of dispersal for the fungi on which they feed, depositing viable spores in fecal pellets over the entire area where they range. Such pellets may well serve as the inoculum for mycorrhizal fungi during the natural afforestation of denuded areas. Since mycorrhizal associations are an essential requirement for the survival and growth of coniferous stands, the mycophagous activities of small mammals assume considerable importance for forest regeneration. These findings also cast doubt on the wisdom of scattering poison baits in clear-cuts as a tactic for protecting young seedlings from rodent grazing pressures (Maser et al., 1978).

III. THE MYCOLOGIST AS COMMENTATOR ON FUNGAL PROCESSES IN ECOSYSTEMS

While few classically trained mycologists would consider themselves fungal physiologists, most have grown fungi in laboratory culture and have an intuitive appreciation for fundamental aspects of fungal metabolism. In culture fungi are seen to be capable of rapid growth in even dilute liquid medium, a process which may bring impressive absorptive and translocational capacities into play. On solid medium fungi may also grow rapidly, decomposing recalcitrant substrates such as filter paper or crystalline cellulose. Repeated pure culture work from a variety of natural substrates reveals that the fungi are truly ubiquitous. Thus, in viewing processes in ecosystems, the mycologist looks for the insidious but consequential fungi at every turn.

Rapid growth responses and short turnover times are frequently stated attributes of microbial populations. The implications of these characteristics for ecosystems analysis have often been explicitly set forth (e.g., by Odum, 1971): comparisons of standing crops in an ecosystem overemphasizes the importance of larger organisms; energy flow or biomass production provide the only really suitable index for comparing all components in an ecosystem. The above notwithstanding, general forest ecologists have frequently been reluctant to give fungi serious consideration in ecosystems analysis because their standing crops are dwarfed by those of the trees themselves. Nowhere is this situation more pronounced than in the coniferous forests in the Pacific Northwest where the aboveground biomass of trees in old-growth stands may range from 500-1000 t/ha* (Grier and Logan, 1977).

In spite of this disparity in standing crops, mycologists associated with the Coniferous Forest Biome and subsequent research programs have recognized the possibility for the rapid microbial turnover times alluded to earlier. Standing crops and turnover times have been investigated for three different guilds of fungi: mycorrhizal and saprophytic fungi in the forest floor (Fogel and Hunt, 1979); *L. oregana*, an arboreal epiphytic lichen (Rhoades, 1978); and epiphytic fungi associated with needles and twigs in the Douglas fir canopy (Carroll, 1979; Carroll et al., 1980). Perhaps the most impressive data emerge from a study by Fogel and Hunt (1978) on fungal biomass and turnover in the forest floor in a young second-growth Douglas fir stand in the Oregon Coast Range. In this stand total tree biomass accounted for approximately 320 t/ha while total fungal biomass in the forest floor was estimated at 20 t/ha, half of which was localized in mycorrhizal mantles. However, when turnover times and annual throughput were considered, the fungi accounted for 50% of the total stand throughput of 30 t/ha. Clearly fungi in the forest floor must be considered for any models of carbon cycling in forest ecosystems.

Rhoades (1978) has carried out similar investigations for one of the most abundant lichens in the Douglas fir canopy, *L. oregana*. Sampling of *Lobaria* on a number of individual old-growth Douglas fir trees has led to estimates of 500-600 kg/ha for standing crops. Photographic measurements of thallus growth rates have yielded estimates for annual production of 150-200 kg/ha. Since *Lobaria* and similar cyanophycophilous canopy lichens fix nitrogen and, indeed, appear to be the principal source of newly fixed nitrogen in old-growth Douglas fir forests, this production

*Tonnes (i.e., metric tons) per hectare.

assumes an importance larger than that suggested by simple comparison with annual primary productivity of the trees themselves. *Lobaria* thalli typically contain about 2% nitrogen; thus, annual *Lobaria* production should account for 3-4 kg of fixed nitrogen per hectare, a substantial contribution to the nitrogen economy of the forest. Epiphytic lichens may also play a significant role in the cycling of other minerals such as phosphorus and potassium (Pike, 1978).

Needle and twig surfaces in mature Douglas fir trees represent a third habitat in the Pacific Northwest for which the estimation of fungal standing crops has been attempted (Carroll, 1979; Carroll et al., 1980). Here standing crops of algal and fungal microepiphytes appear to be on the order of 40-50 kg/ha when sampled at the end of the summer dry season. Data on annual production are completely lacking. However, annual turnover rates are unlikely to be less than 100%, as with fungi in the forest floor (Fogel and Hunt, 1979), or more than 1000%, as with microorganisms in several other phyllosphere habitats (see references in Carroll, 1979). Thus, annual secondary production of microbial cells in this habitat probably amounts to 50-500 kg/ha, a total small by comparison with total primary production in the forest, but large by comparison with the substrates available for growth of heterotrophic microepiphytes in the canopy. Clearly such organisms must be important in influencing throughfall chemistry.

Recognition of the abilities of microorganisms to absorb and utilize organic substances from dilute solutions has led to investigations of interactions between epiphytic microorganisms and nutrients leached from the coniferous canopy in rainstorms (G. C. Carroll, unpublished data). Various canopy components, notably thalli from *L. oregana*, moss bolsters, chlorophycophilous lichens such as *Alectoria* spp., Douglas fir needles of several age classes, and living twigs have been brought into the laboratory, picked clean of extraneous materials, and misted with rainwater previously collected for the purpose. Leachates collected in bottles beneath the funnels containing the samples were then analyzed routinely for total nitrogen, total suspended particulates, and total dissolved solids; occasionally samples were analyzed for total phosphorus, total polyols, total protein, and various cations (Na^+, K^+, Ca^{2+}, Mg^{2+}).

When concentrations of these substances in the leachates are compared with concentrations in the incident rainwater, net fluxes of substances during the misting episode can be easily computed. Consideration of lumped data from 20 one-hour leaching episodes on samples collected over a 17-month period (Sept. 20, 1976, through Feb. 12, 1978) reveals the following trends: (1) All components show initial losses of dissolved solids. (2) Nitrogen is taken up by mosses and chlorophycophilous lichens but is lost by cyanophycophilous lichens and the various tree components; such losses are particularly pronounced after periods of dry weather. (3) Release of suspended solids is high, particularly for the epiphytes and particularly when the samples have been exposed to prolonged periods of wet weather in the field prior to collection and misting in the laboratory. These trends become more explicable

when filters bearing the released particulates are examined under the microscope. Filterable solids from *Lobaria* leachates consist almost exclusively of bacterial cells from populations resident on the surface of the lichen; those from needles and twigs are composed largely of fungal and algal cells from populations resident on those surfaces. When prolonged leaching experiments are carried out in the laboratory, it is found that all components eventually begin to take up dissolved nitrogen from the incident rainfall while continuing to export particulates in the leachates. Analysis of the nitrogen content of such particulates reveals that they largely account for this nitrogen uptake. The point at which uptake begins appears to be correlated with the growth rates of the responsible microorganisms. Thus, for *Lobaria*, nitrogen uptake (by bacteria) begins after several hours; microbial responses to moisture and nutrients on foliage (by algae and fungi) require several days.

These results have implications not only for models of nutrient cycling within canopies. They also relate to studies on inputs to the forest floor in rain and throughfall, suggesting that the standard technology for throughfall collection may be inadequate. When recently collected throughfall is subjected to microbiological filtration and the filters are examined under a microscope, they are found to be coated with assorted microbial cells; in view of the microbiological uptake of organic materials from canopy leachates already described, it should come as no surprise to find that throughfall enters ground-level collectors laden with actively metabolizing microbial cells which are probably adapted to growth over a wide range of temperatures. Such microbial cells persist and grow in slimy layers on the inner surfaces of the containers in which the throughfall is collected, sequestering nutrients from the throughfall during the time the cumulative sample is taken and altering their concentrations prior to analysis. These slimy layers cannot be dislodged by simple mechanical agitation; their buildup can be restricted only partially through the use of metabolic poisons in the collectors. Impregnation of plastic containers with iodine (Heron, 1962) prevents the buildup of slimes but may alter the water chemistry (e.g., pH) of samples to an unacceptable degree. Frequent collection of samples and the replacement of dirty containers or liners with each collection may ameliorate the situation, the integrity of the samples improving with the frequency of collection (Carlisle et al., 1966; G. C. Carroll and J. Perkins, unpublished data). While metabolic poisons are widely used in collectors for throughfall studies, other precautions to minimize microbial growth during the sampling interval are less frequently seen. Consequently, results from published throughfall studies should be evaluated with respect to methods used to preserve the integrity of the samples; they should be regarded with caution if they fail to address the possibility of microbial growth in the samplers.

Although several studies have been carried out on decomposition in the coniferous forest biome, all of them have relied chiefly on weight loss data from litter bags and thus have not required any special mycological expertise (e.g., see Fogel and Cromack, 1977). However, results from at least one such study can be more eas-

ily interpreted if the remarkable absorptive and translocational abilities of fungi are kept in mind. Pike and colleagues (unpubl.) have shown an actual increase in the total Ca^{2+} capital during decomposition of several classes of litter (*Lobaria*, *Alectoria*, and Douglas fir needles) over a 14-month period. Temporary increases in the total K^{+} capital were also demonstrated for these litter types following bud burst of the trees the second season the litter bags were in place. The probable absorption and mobilization of Ca^{2+} and K^{+} by fungi into the rotting substrates provides a ready explanation for these otherwise inexplicable effects.

IV. ECOSYSTEMS ANALYSIS AS A CATALYST FOR MYCOLOGICAL DISCOVERIES

If integrated studies of ecosystem function have gained from the involvement of professional mycologists, what has mycology, the study of fungi for their own sake, gained from entanglement in ecosystems analysis? Several obvious benefits have accrued to the discipline. Because of the possible direct applicability of results from ecosystems research to problems in the management of natural resources, programs in ecosystems analysis have been liberally funded in recent years. In a less mercenary, more scholarly vein, mycologists have been forced to deal with the fungi beyond the confines of the laboratory, in habitats where they really grow and function. In the process, mycologists have acquired skills and adopted techniques previously little in evidence in the mycological literature. Most notably we have seen an increased competence for experimental design and the statistical analysis of data on the part of mycoecologists (for instance, see Pike, Chap. 27, and Fogel, Chap. 28). In many instances sampling of fungal populations in the field has proved so laborious that mycologists have sought more sophisticated and efficient sampling schemes than those normally used (Pike et al., 1977; Carroll et al., 1980; Pike, Chap. 27). Because mycological data sets seldom meet the assumptions for standard parametric statistical procedures, mycologists can be expected to rely increasingly on nonparametric tests (e.g., see Carroll, 1979).

Beyond these generalities, programs in ecosystems analysis have yielded discoveries about the fungi that deserve widespread recognition among professional mycologists and mention in any introductory mycology textbook. Among these I would count the detection of extensive calcium oxalate production by soil fungi and the elucidation of its role in the inorganic nutrition of higher plants and fungi (cf. Sollins et al., Chap. 31; also Cromack et al., 1979). A second, more diffuse discovery has involved recognition of animals as a significant selective force in fungal habitats. Thus, standing crops of arboreal microepiphytes appear to be grazed extensively by canopy microarthropods, and the intensity of the grazing pressure may be a major factor in regulating microbial standing crops (Carroll, 1979). Much of the structure of the fungal thallus becomes explicable in light of such pressures. A coenocytic organization in which individual compartments can be sealed off quickly

by an elaborate septal pore apparatus has obviously evolved in an environment in which injury to the thallus is a common event; grazing activities of small arthropods would appear to be the most frequent source of such injury. Many other attributes of phyllosphere fungi such as thick, heavily melanized cell walls, gelatinous or slimy coverings, and very large cells (as in the Metacapnodiaceae) may also constitute highly evolved responses to grazing pressures. The discovery of hypogeous sporocarps as a major constituent in the diets of a number of small mammals (Maser et al., 1978) has explained the rank or fragrant odors associated with these subterranean fruiting bodies as well as the widespread distribution of the fungi that produce them. Further observations of animals gorging on hypogeous sporocarps plainly reveal aerial dispersal of spores from certain species (*Elaphomyces* spp.) and explain the anatomical features which ensure such dispersal: a powdery spore mass and resilient capillitium (J. Trappe, personal communication).

The aforementioned examples are striking and known to me. Mycologists working in biomes other than the coniferous forest biome could surely cite numerous other equally relevant case histories. In summary, I wish to urge the professional mycologist toward involvement with ecosystems studies. Individuals with formal training in the taxonomy and biology of fungi can frequently posit the crucial questions and interpret the important clues with regard to the roles of fungi in ecosystems as no one else can. The collaborating mycologist may be rewarded with financial support for his research and with the opportunity, even necessity, for scholarly growth. With any imagination he or she will certainly be rewarded with new insights about the behavior of fungi in real habitats.

ACKNOWLEDGMENTS

Various people have provided valuable suggestions for this paper. I particularly wish to acknowledge the input of Dr. William C. Denison (Dept. of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon) and Dr. James Trappe (U.S. Dept. of Agriculture Forest Service, Corvallis, Oregon), whose early efforts in the Coniferous Forest Biome served to catalyze much of the research described herein. I also wish to acknowledge useful conversations with Drs. Kermit Cromack, Kenneth Cummins, and Phillip Sollins (Oregon State University) and Dr. Lawrence Pike (University of Oregon). Much of this work was initiated with funding from the National Science Foundation to the Coniferous Forest Biome (IBP). Subsequent work has been funded with separate research grants from the National Science Foundation to Drs. George C. Carroll, Kermit Cromack, William Denison, Robert Fogel, Charles Grier, Lawrence Pike, Phillip Sollins, and James Trappe. This paper is contribution number 303 from the Coniferous Forest Biome (NSF Grant GB 20963 to the Coniferous Forest Biome, Ecosystems Analysis Studies, US/IBP).

REFERENCES

Bernstein, M. E., and Carroll, G. C. (1977a). Internal fungi in old-growth Douglas fir foliage. *Can. J. Bot. 55*: 644-653.

Bernstein, M. E. , and Carroll, G. C. (1977b). Microbial populations of Douglas fir needle surfaces. *Microbial Ecol. 4*: 41-52.

Carlisle, A., Brown, A. H. F., and White, E. J. (1966). The organic matter of nutrient elements in the precipitation beneath a sessile oak canopy. *J. Ecol. 54*: 87-98.

Carroll, G. C. (1979). Needle microepiphytes in a Douglas fir canopy: biomass and distribution patterns. *Can. J. Bot. 57*: 1000-1007.

Carroll, G. C., and Carroll, F. E. (1978). Studies on the incidence of coniferous needle endophytes in the Pacific Northwest. *Can. J. Bot. 56*: 3034-3043.

Carroll, G. C., Pike, L., Perkins, J., and Sherwood, M. (1980). Biomass and distribution patterns of conifer twig microepiphytes in a Douglas fir forest. *Can. J. Bot. 58*: 624-630.

Cromack, K., Sollins, P., Graustein, W. C., Speidel, K., Todd, A., Spycher, G., Li, C., and Todd, R. L. (1979). Calcium oxalate accumulation and soil weathering in mats of the hypogeous fungus *Hysterangium crassum*. *Soil Biol. Biochem. 11*: 463-468.

Fogel, R. (1976). Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas fir stand. *Can. J. Bot. 54*: 1152-1162.

Fogel, R., and Cromack, K. (1977). Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. *Can. J. Bot. 55*: 1632-1640.

Fogel, R., and Hunt, G. (1979). Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. *Can. J. Forest Res. 9*: 245-256.

Grier, C. C., and Logan, R. S. (1977). Organic matter distribution and net production in plant communities of a 450-year-old Douglas-fir ecosystem. *Ecol. Monogr. 47*: 213-300.

Hacskaylo, E. (1973). Carbohydrate physiology of ectomycorrhizae. In *Ectomycorrhizae*, G. C. Marks and T. T. Kozlowski (Eds.). Academic Press, New York, pp. 207-230.

Heron, J. (1962). Determination of PO_4^{3-} in water after storage in polyethylene. *Limnol. Oceanogr. 7*: 316-321.

Maser, C., Trappe, J. M., and Nussbaum, R. A. (1978). Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. *Ecol. 59*: 799-809.

Meeker, J. A. (1975). Revision of the Seuratiaceae. I. Morphology of *Seuratia*. *Can. J. Bot. 53*: 2462-2482.

Odum, E. P. (1971). *Fundamentals of Ecology*, 3rd ed. Saunders, Philadelphia.

Olivier, D. L. (1978). *Retiarius* gen. nov.: phyllosphere fungi which capture wind-borne pollen grains. *Trans. Brit. Mycol. Soc. 71*: 193-201.

Pike, L. H. (1972). *Lichens of the H. J. Andrews Experimental Forest: Preliminary Checklist*. Coniferous Forest Biome Internal Report No. 46. Biome Central Office, Univ. of Washington, Seattle, 13 pp.

Pike, L. H. (1978). The importance of epiphytic lichens in mineral cycling. *Bryologist 81*: 247-257.

Pike, L. H., Denison, W. C., Tracy, D. M., Sherwood, M. A., and Rhoades, F. M. (1975). Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. *Bryologist 78*: 389-402.

Pike, L. H., Rydell, R. A., and Denison, W. C. (1977). A 400-year-old Douglas fir tree and its epiphytes: biomass, surface area, and their distributions. *Can. J. Forest Res. 7*: 680-699.

Rhoades, F. M. (1972). *Fleshy Fungi Fruiting in the H. J. Andrews Experimental Forest: A Partial List of Collections from Fall 1970 to Spring 1972*. Coniferous Forest Biome Internal Report No. 45. Biome Central Office, Univ. of Washington, Seattle, 16 pp.

Rhoades, F. M. (1977). Growth-rates of the lichen *Lobaria oregana* as determined from sequential photographs. *Can. J. Bot. 55*: 2226-2233.

Rhoades, F. M. (1978). *Growth, Production, Litterfall, and Structure in Populations of the Lichen Lobaria oregana (Tuck.) Müll. Arg. in Canopies of Old-growth Douglas Fir*. Ph.D. dissertation, Univ. of Oregon, Eugene, 139 pp.

Sherwood, M. A. (1973). *Microfungi of the H. J. Andrews Experimental Forest: A Preliminary Checklist*. Coniferous Forest Biome Internal Report No. 58. Biome Central Office, Univ. of Washington, Seattle, 12 pp.

Sherwood, M. A., and Carroll, G. C. (1974). Fungal succession on needles and young twigs of old-growth Douglas fir. *Mycologia 66*: 499-506.