

Ectomycorrhizal fungi in Lyman Lake Basin: a comparison between primary and secondary successional sites

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Abstract: The results of eight years of study of the ectomycorrhizal macrofungi at the subalpine Lyman Lake Basin (Glacier Peak Wilderness area in the North Cascade Mountains, Washington, USA) are reported. The basin was divided into three sites: the primary successional glacier forefront vs two secondary successional habitats (subalpine parkland and old-growth montane *Tsuga mertensiana*-*Abies amabilis*). The 145 collections of ectomycorrhizal fungi obtained represented 68 species, 25 genera, 14 families and 7 orders. The Cortinariaceae was the most species-rich family with 25 species. *Cortinarius* was the most species-rich genus with 17 species. The two secondary successional sites shared 12.1% of the species; while the primary successional site shared only 2 and 5.1%, respectively, with the two secondary successional sites. No ectomycorrhizal species occurred on all three sites. The secondary successional sites shared 7 species (*Boletus edulis*, *Elaphomyces granulatus*, *Hydnотrya variiformis*, *Rhizopogon subsalmoneus*, *Rh. vulgaris*, *Russula silvicola* and *Thaxterogaster pingue*) while the primary successional site shared two species with the parkland (*Suillus aeruginascens* and *Su. cavipes*) and only one with the montane site (*Inocybe lacera*). Fifty-eight species occurred at only one site. These data show that the communities of ectomycorrhizal fungi differ between the primary and secondary successional sites. We hypothesize that fungal life history strategies and habitat characteristics are more important determinants of succession of mycorrhizal fungi than host age or physiology as suggested by the relatively simple early- and late-stage model.

Key Words: alpine mycology, early/late stage model, ecology, ectomycorrhizae, fungal communities, succession

INTRODUCTION

Communities of macrofungi have been only infrequently studied in arctic and alpine environments (e.g., Favre 1955, Graf 1994, Kernaghan and Currah 1998, Lange 1946, 1949, Lange and Skifte 1967, Laursen and Ammirati 1982, Laursen et al 1987, Petersen 1977, Petrini and Laursen 1993, Senn-Irlet 1987, Trappe 1988, Watling 1988). Consequently, the fungal flora in these environments is well known for only a few sites, and discovery of new species is not uncommon (Cázares and Trappe 1990, 1991a, b, Graf and Horak 1993, Jumpponen et al 1997).

Glacier forefronts have special importance for several reasons. They represent a new, primary successional parent material distinctively different from the immediate surroundings. Primary succession is defined as vegetation development on newly formed or exposed substrate. It proceeds on raw parent material, rather than on developed or modified soil and is usually characterized by low nitrogen and organic matter (Glenn-Lewin et al 1992, Matthews 1992). Furthermore, glacier forefronts provide a unique habitat for ruderal organisms absent from adjacent secondary successional sites. Secondary succession is defined as replacement of preexisting vegetation following disturbance (Glenn-Lewin et al 1992) on developed soil with an organic component and a biological legacy of at least a propagule bank. Hence secondary succession can range from new communities on burns or fields to ancient forests that over time replaced previous communities destroyed by fire or other natural catastrophe.

Adjacent primary and secondary successional ecosystems supply ecologists with experimental field laboratories for studying similarities and differences between the two, ultimately allowing inferences on successional patterns. Mycologists have rarely utilized the research opportunities provided by primary successional ecosystems created by glacier forefronts (see Alfredsen 1997, Horak 1960, Matthews 1992, and references therein). Mycorrhizal associations and mycorrhizal flora of these primary successional ecosystems are even more rarely studied (Cázares 1992, Helm et al 1996, Rossow et al 1997). One model of ectomycorrhizal fungus succession is based on studies at the Institute of Terrestrial Ecology (ITE) in Scotland (Deacon et al 1983, Dighton et al 1986, Fleming

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1983, Fleming et al 1984, Last et al 1987, Mason et al 1982, 1983). This "early-" and "late-stage" model has found support (Helm et al 1996, Jansen 1991, Visser 1995) as well as criticism (Keizer and Arnolds 1994, Termorshuizen 1991) but has not been addressed by a comparison of true primary to secondary successional systems.

In this study we tested the hypothesis that communities of ectomycorrhizal fungi fruiting in the primary successional forefront of the receding Lyman Glacier in the northern Cascade Mountains, Washington, differ from those of two secondary successional systems: (i) a subalpine parkland adjacent to the terminal moraine of the glacier and (ii) a nearby, old-growth montane forest. The results can be interpreted in respect to the early- and late-stage hypothesis on succession of ectomycorrhizal fungi. The site is ideal for such research except that it is 15 km from the nearest road in a designated wilderness area. All equipment and supplies must be carried in by backpacking or horses. Inclement mountain weather often interferes with collecting and drying specimens and recording field data. In compensation for these obstacles, the site is relatively undisturbed because of its remoteness. No introduced plants or fungi have been found there (Jumpponen et al 1998), so the system is naturally evolved rather than anthropogenically created as are most of the previous studies of the early- and late-stage concept of ectomycorrhizal fungal succession. The study reported here was limited in scope because it was incidental to research funded to define relationships of mycorrhiza formation to plant succession on the glacier forefront.

MATERIALS AND METHODS

Lyman Lake Basin, located between Spider Pass (48° 10' 52" N, 120° 53' 87" W) and Cloudy Pass (48° 12' 13" N, 120° 55' 56" W) in the Glacier Peak Wilderness Area, Wenatchee National Forest, Washington, USA, contains distinctively different, primary and secondary successional habitats. The primary successional habitat, Lyman Glacier Forefront, has been deglaciated over the past century. The glacier has not exceeded its terminal moraine of the late 1890s for the past ca 7000 yr, as beyond that moraine is an undisturbed deposit of volcanic ash from the Mount Mazama eruption that formed Crater Lake in Oregon (W. Long pers comm). The glacier has been receding steadily since the 1890s, vacating an 1100-m forefront for establishment of pioneering colonizers.

The terminal moraine distinctly separates the primary successional glacier forefront from the secondary successional habitats, which have been exposed to fire and localized recreational disturbance. Periodic photographs between 1898 and 1915 (Lindsley photographs at Special Collections Division, University of Washington, Seattle) show

that most of the eastern Lyman Lake Basin was burned at the turn of the century. However, old growth stands of montane forest by Lyman Lake escaped these fires. Recreation has produced small scale disturbance on trails and at camp sites in the popular Lyman Lake Basin, but these were not given special study because of their very limited size.

Study sites.—We divided Lyman Lake Basin into three sites differing in ecological (primary vs secondary successional ecosystem) and geological history (young soils of newly exposed parent material vs developed soils with a strong litter and humus accumulation), flora of ectomycorrhizal hosts, and habitat type.

Lyman Glacier Forefront, ca 50 ha and 1800 m above sea level, supports a naturally evolved primary successional community: no exotic weeds have been detected (Jumpponen et al 1998). Vegetation is developing in a chronosequence from earliest colonization of barren parent material to a plant community resembling that at Glacier View Ridge beyond the terminal moraine. Domination by Saxifragaceae at the initial successional stage changes to the century-old stage of a community resembling an alpine parkland with patches of conifers and Ericaceae, including *Vaccinium* spp., *Phyllodoce* spp., *Cassiope mertensiana* intermingled with *Luetkea pectinata* and forbs (Jumpponen et al 1998). Ectomycorrhizal hosts include *Abies lasiocarpa*, *Alnus sinuata*, *Larix lyallii*, *Picea engelmannii*, *Pinus contorta*, *Polygonum bistortoides*, *Populus trichocarpa*, *Salix commutata*, *S. nivalis*, *S. phyllifolia*, and *Tsuga mertensiana*.

Glacier View Ridge, ca 70 ha and 1800–2100 m, has secondary successional communities developed after fire in the 1890s. It is adjacent to the Lyman Glacier forefront, from which it is clearly demarcated by the terminal moraine. The vegetation ranges from subalpine parkland with patches of conifers ranging from seedlings to >100 yr old to krummholz *Abies lasiocarpa* and *Pinus albicaulis* on the higher, exposed ridges. Plant communities include heath shrub, lush herb, and dwarf sedge (Franklin and Dyrness 1973), resembling the ecotone between the upper parkland subzones of the *Abies lasiocarpa* Zone and the *Tsuga mertensiana* Zone of the North Cascade Range (Franklin and Dyrness 1973) and extending above timberline to krummholz as defined by Art (1993). Ectomycorrhizal hosts include *Abies amabilis*, *Ab. lasiocarpa*, *Larix lyallii*, *Pinus albicaulis*, *Polygonum bistortoides*, *Salix* spp., *Sorbus sitchensis*, and *Tsuga mertensiana*.

The Lyman Lake site, ca 100 ha and 1650–1800 m, is a secondary successional, old growth forest that escaped recent fire but, as evidenced by abundant charcoal in the soil, established on a burn some centuries ago. Vegetation consists of closed stands of mixed conifers. The plant community represents a transition between the mature phase of *Tsuga mertensiana*—*Abies amabilis* (Douglas 1972) and *Abies lasiocarpa* dominated krummholz stands (Douglas 1971, Douglas and Bliss 1977) both characteristic of the Western North Cascades region (Douglas 1971, 1972, Douglas and Bliss 1977). Ectomycorrhizal hosts include *Abies amabilis*, *A. lasiocarpa*, *Alnus sinuata*, *Picea engelmannii*, *Pinus monticola*, *Salix* spp., *Sorbus sitchensis*, and *Tsuga mertensiana*. *Larix lyallii* is absent. Limited disturbance from camping

occurs near the lake shore, but this was not a major factor in our collecting except for one species, *Macowanites lymanensis*, known only from the type locality, a campsite with severely compacted soil.

Collections.—Ectomycorrhizal macromycetes were collected during 15 expeditions to Lyman Lake Basin in the summers of 1988 through 1996 (except for 1991, when the sites were not visited). Sporocarps were collected as encountered incidentally to studies of mycorrhizal development over the Lyman Glacier forefront chronosequence. Because the primary successional community of the forefront was the target of the funded research project, it received more attention than the surrounding secondary successional communities. We nonetheless collected in the secondary successional communities as thoroughly as time and circumstances permitted. Some years witnessed poor fruiting because of warm, dry summers and autumns followed by early frost. For example, a thorough search revealed no mycorrhizal species at the glacier forefront in 1996. No epigeous sporocarps were observed at the secondary successional sites either, although several hypogeous species were collected.

Macroscopic characters of fresh specimens were recorded at the sites, then specimens were dried in a propane-fueled field drier. Satisfactory drying was difficult when rainstorms passed, as happened fairly often in this mountain environment. Microscopic features were later described from dried material mounted in 5% KOH, cotton blue in lactic acid and/or Melzer's reagent. Nomenclature follows Hansen and Knudsen (1992, 1997) and Moser (1983) for Agaricales, Boletales, Gautieriales, Russulales, and Thelephorales with a few exceptions: the family Elasmomycetaceae and the genus *Boletinus*, for example, are not recognized. Species of Cortinariaceae were identified in part with assistance by Dr Joseph Ammirati. The collections are deposited in the Cryptogamic Herbarium of the Department of Botany and Plant Pathology, Oregon State University (OSC).

Similarities and differences in the ectomycorrhizal fungi between the three sites were estimated by a pairwise Jaccardian similarity matrix; the presence/absence data describing the flora at the three sites were calculated using CORR procedure (SYSTAT 1992). The pairwise matrix of similarities indicates the proportion of shared taxa when only the taxa present on either or both of two compared sites are considered. This approach should not be considered as a statistical analysis. Rather, the correlation matrix (see TABLE II) provides an efficient tool for visualizing and summarizing similarities and differences between the sites. Our goal was comparison of mycorrhizal fungal communities between the primary and secondary successional communities. Gathering quantitative data on numbers or biomass of sporocarps was precluded by the difficult access of the sites, lack of time for studies adjunct to the main goals of the funded research, and often severe weather conditions.

RESULTS

During the 8 yr of field survey, 145 collections of ectomycorrhizal fungi were obtained: 68 species rep-

resenting 25 genera, 14 families, and 7 orders (TABLE I). The Lyman Lake site had 37 species recorded. Lyman Glacier Forefront and Glacier View Ridge sites had 13 and 28 species, respectively.

No ectomycorrhizal fungi were common to all three sites. Ten of the 68 species were common to two sites. Glacier View Ridge and Lyman Lake shared seven species (*Boletus edulis*, *Elaphomyces granulatus*, *Hydnotrya variiformis*, *Rhizopogon subsalmoneus*, *Rh. vulgaris*, *Russula silvatica* and *Thaxterogaster pingue*) while Lyman Glacier Forefront shared two species with Glacier View Ridge (*Suillus aeruginascens* and *Suillus cavipes*) and only one with Lyman Lake (*Inocybe lacera*). Fifty-eight species were unique to one of the three sites: 10 to Lyman Glacier Forefront, 19 to Glacier View Ridge, and 29 to Lyman Lake.

Cortinariaceae was the most species-rich family in all the sites, with 25 taxa, some of which remained unidentified due to inadequate collections or lack of generic monographs for the region. *Cortinarius* was the most species-rich genus with 17 recorded. Fourteen species of hypogeous fungi were collected: 13 in the secondary successional sites and one in the primary successional site, (*Hymenogaster glacialis*). *Hymenogaster glacialis* is endemic to this area and known only from two collections from Lyman Glacier Forefront. Five of the hypogeous taxa occurred on both secondary successional sites; 2 were unique to Glacier View Ridge and 6 to Lyman Lake.

The Jaccardian similarity coefficients calculated from the binary (presence/absence) data indicated that the species composition at Glacier View Ridge and Lyman Lake were most alike (TABLE II). They shared 7 of the 58 species occurring at the two sites (12.1%). The primary successional site at the glacier forefront shared only 2% and 5.1% of the species with Lyman Lake and Glacier View Ridge, respectively. This represents only one shared species of the 49 at Lyman Lake and the forefront and 2 of the 39 at Glacier View Ridge and the forefront (TABLE I).

DISCUSSION

Most species (58 out of 68) collected were unique to one site. The fungal communities clearly differed between sites, despite overlapping ectomycorrhizal host species and close physical proximity. Only 13 fungal species were encountered at the primary successional site at the glacier forefront, which shared only three species with the secondary successional sites (*Inocybe lacera* with Lyman Lake, *Suillus aeruginascens* and *Su. cavipes* with Glacier View Ridge). Disturbance generally decreases numbers of species and individuals of ectomycorrhizal fungi (Zak 1992). Primary successional ecosystems are extreme examples of distur-

TABLE I. Ectomycorrhizal fungal species obtained on 3 sites in Lyman Lake Basin during 8-yr field survey

Ectomycorrhizal taxa ^a	Site ^b
ASCOMYCOTA (4)	
Elaphomycetales (2)	
Elaphomyceteaceae (2)	
<i>Elaphomyces granulatus</i> Fr.	GVR, LL
<i>E. muricatus</i> Fr.	LL
Pezizales (2)	
Discinaceae (2)	
<i>Hydnotrya cerebriformis</i> Harkness	LL
<i>H. variiformis</i> Gilkey	GVR, LL
BASIDIOMYCOTA (64)	
Agaricales (40)	
Amanitaceae (4)	
<i>Amanita muscaria</i> (L.:Fr.) Hooker	LL
<i>A. pantherina</i> (D.C.:Fr.) Schumacher	LL
<i>A. fulva</i> (Schaeff.) Pers.	LL
<i>A. vaginata</i> (Bull.:Fr.) Vittad. var. <i>vaginata</i>	GVR
Cortinariaceae (25)	
<i>Cortinarius cinnamomeus</i> (L.:Fr.) Fr.	LL
<i>C. croceus</i> (Schaeff.) Bigeard & Guillemin	GVR
<i>C. decipiens</i> (Pers.:Fr.) Fr.	LGF
<i>C. duracinus</i> Fr.	LL
<i>C. fulvoohrascens</i> Henry	GVR
<i>C. idahoensis</i> (Ammirati & A. H. Smith) Ammirati	LL
<i>C. montanus</i> Kauffm.	LL
<i>C. mutabilis</i> A. H. Smith	LGF
<i>C. semisanguineus</i> (Fr.) Gill.	GVR
<i>C. tenebricus</i> Favre	LGF
<i>C. violaceus</i> (Fr.) Fr.	LL
<i>Cortinarius</i> sp. 1	LGF
<i>Cortinarius</i> sp. 2	GVR
<i>Cortinarius</i> sp. 3	GVR
<i>Cortinarius</i> sp. 4	GVR
<i>Cortinarius</i> sp. 5	LL
<i>Cortinarius</i> sp. 6	LGF
<i>Hebeloma strophosum</i> (Fr.) Sacc.	LL
<i>Hebeloma</i> sp. 1	GVR
<i>Hymenogaster glacialis</i> Cázares & Trappe	LGF
<i>Inocybe lacera</i> (Fr.:Fr.) Kumm.	LGF, LL
<i>I. lanuginosa</i> (Bull.:Fr.) Kumm.	GVR
<i>Inocybe</i> sp. 1	GVR
<i>Rozites caperata</i> (Pers.:Fr.) Karst.	LL
<i>Thaxterogaster pingue</i> (Zeller) Singer & A. H. Smith	GVR, LL
Hygrophoraceae (5)	
<i>Hygrocybe ceracea</i> (Wulf.:Fr.) Karst.	GVR
<i>H. miniata</i> (Fr.) Kumm.	LL
<i>Hygrophorus pudorinus</i> (Fr.) Fr.	LL
<i>H. purpurascens</i> (Fr.) Fr.	GVR
<i>H. subalpinus</i> A. H. Smith	LL

TABLE I. Continued

Ectomycorrhizal taxa ^a	Site ^b
Tricholomataceae (6)	
<i>Catathelasma ventricosum</i> (Peck) Singer	LL
<i>Laccaria bicolor</i> (Maire) Orton	LL
<i>L. laccata</i> (Scop.:Fr.) Berkeley & Broome	LL
<i>L. montana</i> Singer	LGF
<i>L. nobilis</i> A. H. Smith	GVR
<i>Tricholoma focale</i> (Fr.) Rick.	LL
Boletales (13)	
Boletaceae (7)	
<i>Boletus calopus</i> Fr.	LL
<i>B. edulis</i> Bull.:Fr.	GVR, LL
<i>B. rubripes</i> Thiers	LL
<i>B. smithii</i> Thiers	LL
<i>Chalciporus piperatus</i> (Bull.:Fr.) Bat.	GVR
<i>Gastroboletus ruber</i> (Zeller) Cázares & Trappe	LL
<i>G. turbinatus</i> (Snell) A. H. Smith & Singer	LL
Gomphidiaceae (3)	
<i>Fuscoboletinus ochraceoroseus</i> (Snell) Pom. & A. H. Smith	GVR
<i>Suillus aeruginascens</i> (Opat.) Snell	LGF, GVR
<i>S. cavipes</i> (Opat.) A. H. Smith & Thiers	LGF, GVR
Rhizopogonaceae (3)	
<i>Rhizopogon subcaerulescens</i> A. H. Smith	GVR
<i>R. subsalmoneus</i> A. H. Smith	GVR, LL
<i>R. vulgaris</i> (Vittad.) M. Lange	GVR, LL
Gautieriales (1)	
Gauteriaceae (1)	
<i>Gautieria monticola</i> Harkness	GVR
Russulales (9)	
Russulaceae (9)	
<i>Lactarius deterrimus</i> Gröger	GVR
<i>L. pseudomucidus</i> A. H. Smith	GVR
<i>L. uvidus</i> var. <i>montanus</i> Hesler & A. H. Smith	LGF
<i>Lactarius</i> sp. 1	LGF
<i>Macowanites lymanensis</i> Cázares & Trappe	LL
<i>Gymnomyces</i> sp. ined.	LL
<i>Russula silvicola</i> Shaffer	GVR, LL
<i>Russula fragilis</i> var. <i>fragilis</i> (Pers.:Fr.) Fr.	LGF
<i>Russula olivacea</i> (Schaeff.) Fr.	LL
Thelephorales (1)	
Thelephoraceae (1)	
<i>Bankera violascens</i> (A. & S.) Pouz.	LL

^a Numbers in parentheses indicate the number of recorded species within taxa above the genus level.

^b LGF, Lyman Glacier Forefront, GVR, Glacier View Ridge; LL, Lyman Lake.

TABLE II. The Jaccardian pairwise correlation matrix calculated for the three sites

Jaccardian correlation matrix ^a			
	LGF ^b	GVR	LL
LGF	—	2/39	1/49
GVR	0.051	—	7/58
LL	0.020	0.121	—

^a Jaccardian pairwise correlations are below the diagonal; actual values of the proportion of shared taxa of those present at one or both compared sites are above the diagonal.

^b LGF = Lyman Glacier Forefront, GVR = Glacier View Ridge, LL = Lyman Lake.

bance where the biotic component is initially nearly absent (Glenn-Lewin et al 1992, Matthews 1992). The harsh environment selects for ruderal species able to colonize newly exposed niches. In general, most taxa observed on the glacier forefront produced small fruit bodies, indicating a ruderal life strategy.

Organic matter, decaying woody debris in particular, is an essential characteristic of mature forests in the Pacific Northwestern United States. Lack of such organic matter in the primary successional forefront is among the more likely explanations for the differences observed between it and the secondary successional systems. Species such as *Hydnotrya cerebriformis*, *Hyd. variiformis*, *Hygrocybe miniata*, and *Inocybe lanuginosa*, fruiting in microhabitats rich in such debris, were present only at the secondary successional sites.

Glacier View Ridge, a close secondary successional counterpart for Lyman Glacier Forefront, had twice as many species (28) as the forefront. The two are separated by less than 50 m but are demarcated by the outermost terminal moraine. Glacier View Ridge has well-developed litter and humus layers that are absent at Lyman Glacier Forefront. Despite their immediate proximity and similarity in ectomycorrhizal host species, these two sites shared only two ectomycorrhizal fungal species: the *Larix*-associated *Suillus aeruginascens* and *Su. cavipes*. Moreover, they occurred only in the oldest part of the forefront adjacent to the subalpine parkland of Glacier View Ridge.

The largest number of ectomycorrhizal species (39) was collected at the secondary successional Lyman Lake old-growth forest. More than half of all species recorded were present here, most being unique to the site. Several factors may account for the larger ectomycorrhizal fungus diversity at the old-growth forest. Closed-canopy structure broken by mortality-caused openings with uneven host ages and sizes and abundant coarse woody debris provide a wide variety of habitats.

The ectomycorrhizal fungal communities also differed substantially between the two secondary successional sites; only 7 species were common to these sites as well as absent from the glacier forefront. Five of the shared taxa were hypogeous: *Elaphomyces granulatus*, *Hyd. variiformis*, *Rh. subsalmoneus*, *Rh. vulgaris*, and *Thaxterogaster pingue*. Hypogeous fungi depend on animal vectors for their spore dispersal (Cázares and Trappe 1994, Trappe and Maser 1977). Several species of potentially mycophagous mammals frequently visit the primary successional site as indicated by tracks, sightings, or fecal deposits: mule deer (*Odocoileus hemionus*), mountain goats (*Oreamnos americanus*), hoary marmots (*Marmota caligata*), and pikas (*Ochotona princeps*). Cázares and Trappe (1994) identified spores of *Elaphomyces* sp., *Rhizopogon* sp., and *Thaxterogaster pingue* in samples of mammal feces from the forefront site. Hence, the propagules are distributed to the primary successional site. We hypothesize that the main reason for the absence of these five species on the forefront is the lack of legacies of mature forests, especially soil development (organic matter content, well-developed litter and humus layers). Amaranthus et al (1994) showed that most hypogeous species in their study occurred in mature *Pseudotsuga menziesii* stands rather than in adjacent, young reforested stands. More than a third of those were present only in or under coarse woody debris at various stages of decay. This indicates the importance of mature stand structure and associated legacies in modifying fungal communities.

Some species appear to require the decayed wood habitat (e.g., *Hydnotrya variiformis* and *Inocybe lanuginosa*). Glacier View Ridge has less coarse woody debris than does Lyman Lake; it burned more recently than did the Lyman Lake old growth, and its clumps of trees are dispersed in meadows and heathlands. This may have resulted in a lower frequency of fungal species associated with decaying wood. Additionally, large-scale disturbances such as intensive fire may have homogenized an otherwise patchy distribution of different microhabitats within the tree clumps (see Zak 1992, and references therein). This may have additionally limited the species diversity observed at the Glacier View Ridge. Alternatively, shade and complete canopy cover may be essential to the fruiting of some species. The subalpine parkland habitat that dominates Glacier View Ridge provides such conditions only patchily and the open primary successional habitat not at all.

The early- and late-stage model introduces the succession of ectomycorrhizal fungi in terms of age of the plant community or age of the dominant overstorey vegetation. Furthermore, the model proposes that the community structure of fruiting ectomycorrhizal

fungi is regulated by changes in host physiology, photosynthate allocation in particular, as a result of aging (Danielson and Visser 1989). Some of the species we recorded only at the secondary successional sites are considered late successional, e.g., *Amanita muscaria*, *Cort. semisanguineus*, *Hyg. purpurascens*, and *Rozites caperata* (Fleming et al 1984, Hintikka 1988, Jansen 1991, Visser 1995). Because no barrier to mycorrhiza formation with tree seedlings by some of these species exists in experimental conditions (e.g., Hintikka 1974, Kropp and Trappe 1982, Molina and Trappe 1982) we infer their presence at our secondary successional sites is the product of differences between characteristics of primary and secondary successional sites.

The early- and late-stage model further states that a narrow selection of ectomycorrhizal fungi with a wide host range colonizes the root systems in young trees and is later joined and replaced by other species (see Last et al 1987). Similarly, the species richness and diversity increase at least until canopy closure (Dighton et al 1986, Last et al 1987). The few ectomycorrhizal fungi dominating our primary successional site were mostly absent at the older, secondary successional sites; only *Inocybe lacera* was common to Lyman Lake and Lyman Glacier Forefront; *Su. aeruginascens* and *Su. cavipes* were common to Glacier View Ridge and the forefront. Our data, however, merely indicate that differences exist. It is unclear to what degree the differences can be attributed to the different life history strategies of the ectomycorrhizal fungi, age of the ectomycorrhizal hosts, successional stage of the habitat, or greater diversity of habitats available at the secondary successional sites.

It is clear, however, that on the glacier forefront the first species to fruit under young willows persists into the 80–100 yr forefront plant communities. *Laccaria montana* fruited abundantly from the youngest willow communities to the 80–100 yr-old communities. *Cortinarius tenebricus* did not show up at the earliest stage of the chronosequence but appeared soon thereafter. As neither of these was found in the secondary successional communities and fruited only in very low organic substrates, they could in a sense be considered early stage. Under the forefront conditions, then, the early stage may last the better part of a century, ending abruptly at the relatively high-organic secondary successional subalpine parkland habitat even though young trees are present. Succession here seems to relate to soil characteristics and probably fungal competition rather than an early stage governed by tree age, canopy cover, host physiology or photosynthate allocation.

A vast body of evidence leaves no doubt as to the presence of different life strategies of ectomycorri-

zal fungi (see references in Frankland 1992, Last et al 1987, Visser 1995). Some patterns revealed by our data in addition to those noted above lead to hypotheses on the adaptation of other species of ectomycorrhizal fungi to early successional habitats. Several species (e.g., *Boletus rubripes*, *Laccaria bicolor*, *Hydnотrya cerebriformis*, and *Macowanites lymanensis*) were observed only at disturbed areas within the secondary successional sites: campsites and trails. These species may be ruderal or merely tolerant of frequent disturbance. Nonetheless, their absence at the primary successional site permits the hypothesis they depend on legacies of late successional communities, such as abundant soil organic matter. Other disturbance-adapted species may hypothetically depend on efficient dispersal and colonization of vacated niches, but not on the legacies associated with mature plant communities: *Inocybe lacera*, for example, was collected both at a campsite in the secondary successional site at Lyman Lake and at the glacier forefront.

Relevance of the early- and late-stage model may be questionable in primary successional sites, as it was derived from secondary successional systems. The glacier forefront is a relatively homogeneous open habitat lacking the moist microsites rich in organic matter and coarse woody debris abundant at Lyman Lake. Keizer and Arnolds (1994) concluded that the early- and late-stage model fails to acknowledge changes in the physical and chemical characteristics of soil as well as stand architecture. They propose an alternative model based on six phases of stand rotation that relate to both canopy closure and stand age. However, their alternative model does not address other successional changes (e.g., in species composition) taking place in natural ecosystems. As Keizer and Arnolds (1994) concluded, the succession of ectomycorrhizal fungi appears much more complicated than the relatively simple model of early- and late-stage fungi. The different factors, including host species composition, host age, and stand and soil characteristics all likely contribute to the ectomycorrhizal fungal flora present in a stand at a given time. The separate effects of the factors are difficult to isolate. More data are needed to better understand how successional changes in belowground systems relate to aboveground fruiting (see e.g., Gardes and Bruns 1996). Data such as we report here can be a first step for generating testable hypotheses.

Fungal succession along natural successional gradients requires further study, preferably with true replication. Appropriate sites for conducting such studies are rare. Glacier forelands and their immediate surrounding communities may prove invaluable as field laboratories for studying these successional

phenomena and researching the dynamics of fungal communities on landscape and ecosystem levels.

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