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Occurrence of ectomycorrhizal fungi on the forefront of retreating Lyman Glacier (Washington, USA) in relation to time since deglaciation

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Abstract Glacier forefronts provide a unique system for studying primary succession of plants and fungi. We constructed a chronosequence of ectomycorrhizal fungus occurrence on the forefront of Lyman Glacier in the North Cascades mountain range in Washington, USA. The plant communities established on non-vegetated substrate as patchily distributed plant individuals and developed towards complex vegetation with a variety of ectomycorrhizal hosts, including *Salix commutata*, *S. phylicifolia*, *Abies lasiocarpa*, *Larix lyallii*, *Pinus contorta*, *Tsuga mertensiana* and additional infrequent taxa. A most probable number assay of non-vegetated substrates over the chronosequence indicated that ectomycorrhizal propagules were few or absent in the non-vegetated areas adjacent to the glacier terminus but increased with time since deglaciation. Ectomycorrhizal fungus sporocarps occurred as soon as the first host plants of substantial size were present. However, none were observed with the most recently established hosts – small *A. lasiocarpa* seedlings. Only four species (*Cortinarius decipiens*, *C. tenebricus*, *Inocybe lacera*, and *Laccaria cf. montana*) occurred on substrate deglaciated for less than 40 years. Three of these species (*C. tenebricus*, *I. lacera*, and *L. cf. montana*) occurred along the chronosequence to the terminal moraine on substrate deglaciated for 70–100 years. An additional five species (one unidentified species each of *Cortinarius* and *Lactarius*, *Cortinarius mutabilis*, *Lactarius uvidus* var. *montanus*, and *Suillus cavipes*) occurred only on the oldest substrate. Our results support the current “early- and late-stage” model of ectomycorrhizal fungus succession in that additional species enter the community over time. However, we hypothesize that diversification of the my-

corrhizal fungus community in this primary successional habitat resulted from an increasing diversity of host plants along with changing habitat attributes.

Keywords Chronosequence · Establishment · Revegetation · Succession

Introduction

Succession is regarded by many ecologists as the most important ecological concept after that of the ecosystem itself (Cherrett 1989). Glacier forefronts provide a unique system for studying primary succession whereby non-vegetated terrain exposed from beneath glacial ice develops toward a complex plant community. The first such time series (chronosequence) of plant community development was described over a 100 years ago at the Rhonegletscher in the European Alps; subsequent descriptions have emerged for numerous additional sites over the past century (Matthews 1992).

Plants with mycorrhizal associations predominate in most natural terrestrial ecosystems. However, the supply of inoculum, i.e., propagules, may be limited in primary successional ecosystems such as the forefronts of retreating glaciers. Compatible fungal associates are vital for successful establishment and long-term persistence of mycorrhiza-dependent plants in environments with no prior vegetation cover.

Presence of mycorrhizal fungi can be assessed in various ways. One is to collect data on occurrence of mycorrhizal fungus fruiting bodies. Presence of a sporocarp indicates presence of that taxon at the study site, whereas the opposite may not be true: absence of a taxon in the fruiting fungus community may merely mean that the environmental conditions have not been suitable to initiate fruiting. The infrequent and unpredictable fruiting of fungi combined with the usually difficult access to glacier forefronts have prevented fungal ecologists from utilizing these primary successional sites in their studies. Consequently, studies on fungi and their successional dynamics

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on glacier forefronts are rare, although chronosequences of macromycetes (Alfredsen 1997; Horak 1960; Sprague and Lawrence 1959a, b, c), soil microfungi (Baxter and Middleton 1961; Cooke and Lawrence 1959) and mycorrhizal morphotypes (Helm et al. 1996) have been reported.

Our primary goal in this study was to determine the presence of ectomycorrhizal fungus propagules and the order of appearance of ectomycorrhizal fungus sporocarps over the chronosequence of a glacier forefront. One model of ectomycorrhizal fungus succession is derived from studies at the Institute of Terrestrial Ecology in Scotland (Deacon et al. 1983; Dighton et al. 1986; Fleming 1983; Fleming et al. 1984, 1986; Last et al. 1987; Mason et al. 1982, 1983). This model suggests that early ectomycorrhizal communities are composed of a narrow selection of non-host-specific (early stage) fungi which colonize young seedlings or younger regions of the root systems (Deacon and Fleming 1992). These fungus communities are then joined by additional, potentially more host-specific (late stage) fungi in older regions of root systems. The successional changes in the ectomycorrhizal fungus communities are often hypothesized to be associated with changing soil conditions as measured by organic matter, pH, or nitrogen (Deacon and Fleming 1992; Jumpponen et al. 1999a; Last et al. 1987; van der Heijden et al. 1999). Similarly, changes in quality and quantity of root exudates as a result of aging of root systems may also play an essential role in determining the ectomycorrhizal community structure during succession (Deacon and Fleming 1992; Gibson and Deacon 1988; Gibson and Deacon 1990). Although the mechanisms driving the successional change in ectomycorrhizal fungal communities may still remain unclear, the "early" and "late-stage" model has found both support (Helm et al. 1996; Jansen 1991; Jumpponen et al. 1999a; Visser 1995) and criticism (Keizer and Arnolds 1994; Termorshuizen and Schaffers 1989). To address the general patterns and concepts of succession among mycorrhizal fungi in a true primary successional system and on the level of an ecosystem, we utilized our earlier published work (Jumpponen et al. 1998a, 1999a, b) plus additional data to explore the occurrence of ectomycorrhizal fungi in relation to plant succession.

Materials and methods

Study site

Lyman Glacier (48°10'52"N, 120°53'87"W) is located in the Glacier Peak wilderness area in the North Cascade Mountains (Washington, USA). The elevation of the present terminus is about 1,800 m. The deglaciated forefront is approximately 1,000 m long over an elevational drop of only about 60 m with no distinctive recessional moraines (Cázares 1992; Jumpponen et al. 1998a). The glacier has been receding steadily since the 1890s opening the forefront for pioneering colonizers. Periodic photographs taken between 1898 and 1915 by Lindsley (available at Special Collections Division, University of Washington, Seattle), snow survey data recorded between the late 1920s and 1930s, photographs taken between the 1940s and 1980s by the United States Geological Survey, and photographs taken by the authors between the late 1980s and 1990s have allowed reconstruction of the glacier retreat (Jumpponen et al. 1998a).

Vegetation chronosequence

The vegetation on ridges and benches adjacent to the forefront is in the ecotone between the upper parkland subzones of the *Abies lasiocarpa* zone and *Tsuga mertensiana* zone of the North Cascades (Franklin and Dyrness 1973). The primary tree species near the forefront are *A. lasiocarpa* (Hook.) Nutt., *Larix lyallii* Parl., and *T. mertensiana* (Bong.) Carr. Patches of trees are separated by open meadows dominated by various herbs and small ericaceous shrubs. Plant communities adjacent to the forefront include heath shrub, lush herb, and dwarf sedge according to Franklin and Dyrness (1973).

We characterized the vegetation on the glacier forefront with four parallel transects placed approximately 20 m apart, starting from the present glacier terminus and ending at the century-old terminal moraine. On each transect presence/absence of plant species was recorded on four 0.25-m² subplots comprising a 1-m² plot located every 20 m along the transects; 768 subplots were recorded in all. From these data we estimated frequencies of the common vascular plants along the glacier forefront.

Most probable number of propagules

The most probable number (MPN) method was employed to estimate the number of effective ectomycorrhizal propagules over the deglaciated forefront (Alexander 1965; Daniels and Skipper 1982). The topsoil (0–5 cm) was sampled within non-vegetated areas (stage 1; see Results) in the areas deglaciated for 20, 40, 60, and 80 years. Five different non-vegetated patches were selected on the east and west sides of the central transect. Soils were sieved through a 6-mm soil sieve and the large fraction discarded. Approximately 200 ml of the sieved soil from each of the five non-vegetated patches was pooled into one sample representing either the east or west side of each of the four different age zones. Samples were then stored in coolers with ice and transported to the laboratory for the MPN assay.

A tenfold dilution (undiluted, 10⁻¹, 10⁻², and 10⁻³) series was prepared by thorough mixing and dilution of the inoculum soil with pasteurized Willamette Valley sandy loam. Five replicate 200-cc Ray Leach (Corvallis, Ore.) tubes were prepared for each dilution of each individual sample. The soil served as substrate and the source of the ectomycorrhizal propagules. Potential contamination was monitored by 20 control tubes containing only the pasteurized substrate. None of the control tubes showed any ectomycorrhizal colonization at harvest.

Each tube was watered and sown with lodgepole pine seed (*Pinus contorta* Dougl.). *P. contorta* was chosen as a test plant because: (1) it naturally occurs at the study site; (2) it and *A. lasiocarpa* are among the first ectomycorrhizal hosts to establish in areas with no previous, visible vegetation; (3) its seeds were more readily available than seeds of the other ectomycorrhizal hosts at the study site (*A. lasiocarpa*, *L. lyallii*, *Picea engelmannii* Parry, *Pinus albicaulis* Engelm., *Polygonum bistortoides* Pursh, *Salix* spp., and *T. mertensiana*); and (4) *P. contorta* seeds germinate reliably and are easy to manipulate in the laboratory. Seeds had been surface sterilized and scarified by soaking in 30% H₂O₂ for 50 min. The substrate surface was covered with a ca. 1-cm layer of sterilized quartz sand after sowing. The seedlings were grown in a growth chamber at constant 25°C temperature and a 16/8-h day/night cycle with light intensity of approximately 270 μmol s⁻¹ m⁻². Plants were watered every third day.

Seedlings were harvested 10 weeks after seed germination, thoroughly washed and assessed under a dissecting microscope for the presence of ectomycorrhizal colonization.

Fungus chronosequence

Macromycetes were collected during 17 separate expeditions to the Lyman Basin spread over the period of 1988 through 1999, with the exception of 1991 when the site was not visited. Sporocarps were collected as encountered and their location and habitat re-

MPN of propagules

Results of the MPN assay are summarized in Table 1. The estimated number of propagules was generally low throughout the whole chronosequence. No or only a few ectomycorrhizal propagules were present in the 20-year-old substrate. Areas deglaciated longer contained more ectomycorrhizal propagules; the ectomycorrhizal propagule bank seemed to establish in areas deglaciated for at least 40 years. The strikingly high number of propagules on the west side of the 40-year-old region indicates stochastic variation possibly because of minor fall of soil and plants from the ridge

Table 1 Most probable number (MPN; Alexander 1965) of ectomycorrhizal propagules on the receding forefront of Lyman glacier. *Sample codes* indicate the time since deglaciation (20, 40, 60, and 80 years since deglaciation) and location (east vs. west side of the central transect). The 95% confidence intervals are in parentheses

Sample	MPN of ectomycorrhizal propagules
20 West	0.20 (0.06–0.66)
20 East	0
40 West	54.0 (12.36–178.20)
40 East	1.10 (0.33–3.63)
60 West	0.40 (0.12–1.32)
60 East	— ^a
80 West	7.00 (2.12–23.10)
80 East	2.10 (0.64–6.93)

^a Sample was not processed

above; no other samples contained comparable propagule numbers.

Fungus chronosequence

No ectomycorrhizal sporocarps were observed with the earliest, scattered, small *A. lasiocarpa* seedlings occurring on substrate deglaciated for 20 years. The first sporocarps (*Laccaria* cf. *montana*) were collected with the first mycorrhizal hosts of substantial size (*Salix commutata* and *S. phylicifolia*) occurring in areas deglaciated for 30 years (Fig. 1). Within a short distance further, representing a few years of additional time since deglaciation, small, seemingly ruderal, species of Cortinariaceae (*Cortinarius decipiens*, *C. tenebricus* and *Inocybe lacera*) were observed. Adjacent to the terminal moraine, *C. tenebricus*, *I. lacera*, and *L.* cf. *montana* were observed to fruit in association with *Salix* spp. (Table 2). An additional five taxa were also observed within 100 m of the terminal moraine (one unidentified species each of *Cortinarius* and *Lactarius*, *Cortinarius mutabilis*, *Lactarius uvidus* var. *montanus*, and *Suillus cavipes*).

Several species were encountered only once during this survey (Fig. 1; Table 2). These included *Hymenogaster glacialis*, the only hypogeous taxon recorded on the glacier forefront, and two *Larix*-associated species of Gomphidiaceae, *Suillus aeruginascens* and *S. cavipes*. *S. cavipes* and *C. mutabilis* were recorded only once and then only in the immediate vicinity of *Larix lyallii* next to the *Alnus sinuata* shrub.

Table 2 Ectomycorrhizal fungi on the Lyman Glacier forefront and a brief description of their habitats. *Collection numbers* refer to original collections now deposited in the Oregon State University Herbarium

Fungus species	Habitat	Collection number
<i>Cortinarius decipiens</i> (Pers.: Fr.) Fr.	Under <i>Salix</i> spp.	Trappe 10,679
<i>Cortinarius mutabilis</i> A. H. Smith	Under <i>Abies lasiocarpa</i> , <i>Larix lyallii</i> , <i>Alnus sinuata</i>	Trappe 10,712
<i>Cortinarius tenebricus</i> Favre	Under <i>Salix</i> spp.	Trappe 10,433; 10,434; 10,488; 10,681; 10,541; 10,891; 10,903; 10,962
<i>Cortinarius</i> sp. 1	Under <i>Salix commutata</i>	Trappe 10,673; 10,553
<i>Cortinarius</i> sp. 2	Under <i>Salix commutata</i>	Trappe 10,667
<i>Fuscoboletinus aeruginascens</i> (Secr.) Snell	Under <i>Larix lyallii</i>	Trappe 10,709
<i>Hymenogaster glacialis</i> Cázares & Trappe	Under stones in wet area among <i>Salix</i> sp. roots in raw moraine	Trappe 10,418
<i>Inocybe lacera</i> (Fr.: Fr.) Kumm.	Under <i>Salix</i> spp.	Trappe 10,390; 10,405; 10,427; 10,466; 10,537; 10,489; 10,490; 10,710
<i>Laccaria</i> cf. <i>montana</i> ^a	Under <i>Salix phylicifolia</i> and <i>S. commutata</i>	Trappe 10,400; 10,478; 10,481; 10,561; 10,660; 10,686; 10,870; 10,871; 10,872; 10,892; 10,904; 10,956
<i>Lactarius uvidus</i> var. <i>montanus</i> Hesler & Smith	Under <i>Salix phylicifolia</i>	Trappe 10,669
<i>Lactarius</i> sp. 1	Under <i>Salix</i> sp.	Trappe 10,687; 10,911
<i>Russula fragilis</i> var. <i>fragilis</i> (Pers.: Fr.) Fr.	Among <i>Salix</i> spp. and conifers	Trappe 10,567
<i>Suillus cavipes</i> (Opat.) Smith & Thiers	Under <i>Abies lasiocarpa</i> , <i>Larix lyallii</i> , <i>Alnus sinuata</i>	Trappe 10,711

^a We could not dependably distinguish between *Laccaria laccata* var. *pallidifolia* (Peck) Peck and *L. montana* Singer. These taxa are mainly separated by: (1) *L. montana* being strongly striate and *L. laccata* var. *pallidifolia* being striate or not; (2) *L. montana* having spores 8.5–14×8–12 μm vs. *L. laccata* var. *pallidifolia*

7.5–10(–13)×7–10(–11.5) μm. We frequently observed spores >11 μm, and in some collections up to 15 μm, but in most cases the larger spores fell within the upper range of *L. laccata* var. *pallidifolia* and median range of *L. montana*

Discussion

We report here the occurrence of ectomycorrhizal fungi in relation to plant community development over a chronosequence on a retreating glacier forefront. Based on the MPN assay with *P. contorta*, ectomycorrhizal propagules were few or non-existent near the glacier terminus but seemed to appear in greater abundance with increasing time since deglaciation. Using just one host species may underestimate the true propagule numbers in a system with several ectomycorrhizal hosts with various specific fungal associates. The observed patterns are, however, intuitively expected: the propagule bank from either airborne or vegetative sources can be expected to increase with time since deglaciation. The observed variation in the MPN data suggests that stochastic patterns are important in propagule accumulation. Instead of a linear increase in propagule numbers with increasing time since deglaciation resulting from steady propagule rain, we obtained a large propagule number in one sample collected at an intermediate distance from the glacier terminus.

Our sporocarp records include 13 species, most recorded only on the glacier forefront, not in the adjacent plant communities (Jumpponen et al. 1999a). Generally, the few common species early in the chronosequence were joined by several infrequently fruiting taxa with increasing distance from the glacier terminus (i.e., increasing time since deglaciation). Only four species were observed to fruit on substrate deglaciated <40 years ago. Three of these also occurred among the eight species that fruited near the terminal moraine on substrate deglaciated 70–100 years ago.

No sporocarps were observed in areas with the first small *Abies lasiocarpa* seedlings. These young seedlings may not have provided a carbon supply adequate to support fruiting of ectomycorrhizal fungi. However, saprotrophic fungi, *Omphalina* sp. and *Galerina terrestris* Wells & Kempton, were observed on the Lyman glacier forefront on substrates of comparable age, indicating that a carbon supply adequate for saprophytic fungus fruiting was present with pioneering vascular and non-vascular plants as an important carbon source.

Our data on fungus fruiting suggest that the early communities of mycorrhizal fungi comprise a few ruderal species later supplemented with additional species in areas of litter accumulation. The “early-” and “late-stage” model states that a narrow selection of ruderal fungi with a wide host range colonizes young regions of root systems and with time is joined and replaced by additional, increasingly host-specific species as a result of changes in soil conditions or the quantity or quality of carbon supply (Deacon and Fleming 1992; Last et al. 1987). The ectomycorrhizal fungi dominating the early chronosequence (*C. tenebricus*, *I. lacera*, *L.* cf. *montana*) were present on the older substrates adjacent to the terminal moraine. None of these three species have been reported to be host specific. They may be able to colonize all ectomycorrhizal hosts present on the forefront and fa-

cilitate the successful establishment of the hosts. These fungi were later joined by other species, some of which are known to be host specific (e.g., *Suillus aeruginascens* and *S. cavipes* with *Larix* spp.). In general, our data on fungus fruiting on a glacier forefront support the early/late-stage hypothesis in that the older parts of the chronosequence have additional species. However, for over a century the initial fungal colonizers remain prominent and have been joined, but not replaced, in this primary successional site. Although the average age and species diversity of host plants increases with time since deglaciation, hosts ranging in age from 1 to more than 40 years are present even in the oldest areas adjacent to the terminal moraine. This heterogeneity in the host age distribution may allow the greatly overlapping occurrence of both early and late-stage fungi at the glacier forefront site. Similarly, as indicated by our vegetation transect data open, patchy plant communities with scattered early successional plants mixed with non-vegetated substrate occur throughout the entire glacier forefront chronosequence, including areas adjacent to the terminal moraine. Taken together, this primary successional chronosequence contains both hosts of various ages as well as substrates with differing soil conditions characterized by a range of organic matter and soil nitrogen contents (see Jumpponen et al. 1998a), thus facilitating the presence of early, ruderal ectomycorrhizal fungi in the oldest parts of the chronosequence.

As a result of the correlation between the increasing host age and changes in the soil conditions along the successional gradient on the Lyman glacier forefront, the mechanisms behind our observations on the development of the ectomycorrhizal fungus communities remain unresolved. However, we hypothesize that several factors contribute to the observed increase in the diversity of ectomycorrhizal fungi with increasing time since deglaciation. The number of host species and the range of their ages increased, which in turn increased the diversity of available habitats as well as the diversity of different host age classes. In the stages most recently colonized by ectomycorrhizal hosts, little or no litter has accumulated under the seedlings. In contrast, litter built up over time in the older parts of the chronosequence, especially under willows. The *Larix*-specific fungi (*S. aeruginascens* and *S. cavipes*) clearly cannot occur prior to the establishment of their hosts. Finally, habitat diversification is also likely to be of major importance. For example, the only collections of *S. cavipes* and *C. mutabilis* were collected adjacent to the single *Alnus* shrub present on the glacier forefront. Neither of the two fungi is specifically associated with *Alnus* and *S. cavipes* is specific to genus *Larix*. However, nitrogen is a strong limiting factor for plant growth in this substrate (Cázares 1992; Jumpponen et al. 1998b). The nitrogen limitation likely affects fungus fruiting because mycelium development requires nitrogen. Therefore, nitrogen availability is linked to the quantity of fungal biomass (Colpaert et al. 1992) and observed fruiting. The ruderal fungi close to the glacier terminus evidently have adapted to a rela-

tively low nitrogen supply. Recent nitrogen deposition studies have clearly shown that nitrogen additions on the ecosystem level alter ectomycorrhizal fungus fruiting patterns and shift ectomycorrhizal community composition as assessed by sporocarp production (Peter et al. 2001; Wallenda and Kottke 1998).

In summary, our MPN data estimating the propagule numbers in the glacier forefront substrate indicate that ectomycorrhizal propagules are sparse in this recently deglaciated area. The early fungus community, as inferred from sporocarp occurrence, is composed of a narrow selection of assumed ruderal species. These few ectomycorrhizal fungi present on the recently deglaciated substrate are joined by additional, sometimes host-specific species later in succession. Our sporocarp observations are in concert with the early and late-stage model of ectomycorrhiza succession (Deacon and Fleming 1992; Last et al. 1987), which largely attributes successional phenomena to changes in soil organic matter quantity and quality over time since host establishment, or to quality and quantity of host metabolites as determined by the age of the root region. At the Lyman Glacier primary successional site, however, these changes are slow and the host-age distribution and habitat heterogeneous, so that the “early” stage extends over almost a century.

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