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Title: MYCORRHIZAL FUNGI AND THEIR RELATIONSHIP TO PLANT SUCCESSION IN SUBALPINE HABITATS

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These studies were conducted primarily in the Lyman glacier area in the subalpine zone of the North Cascade Mountains of Washington. The aim was to determine relationships between mycotrophy of plant species and availability of mycorrhizal propagules that may affect plant community patterns in recently exposed substrates such as glacier forefronts. Four groups of plant species are considered: (1) mycorrhiza independent or facultatively mycorrhizal, (2) ectomycorrhiza, and ericoid mycorrhiza-dependent, with mycobiont propagules dispersed by air, (3) vesicular-arbuscular mycorrhiza-dependent with mycobiont propagules dispersed mostly by soil movement, and (4) dark septate endophyte hosts, means of dispersal of the mycobionts are not well understood. The plant communities on the glacier forefront are patchy because of environmental constraints. Mycorrhizal colonization was determined for 67 species representing 43 genera and 19 families established in communities along a chronosequence on the glacier forefront as well in adjacent communities for comparison. Nonmycorrhizal plant species represented the largest proportion of the different mycotrophic habits along the central chronosequence on the forefront, followed by facutatively mycorrhizal and mycorrhiza dependent plants Dark septate endophytes were present in all plant families except the

Polypodiaceae. The soil propagule content was poor as indicated by soil sievings and soil bioassays.

Vesicular-arbuscular mycorrhizae (VAM) are reported in the Pinaceae. Seedlings of *Abies lasiocarpa*, *Pseudotsuga mensiezii*, *Tsuga heterophylla* and *T. mertensiana* growing in their natural habitats were commonly found colonized by VAM. The ecological role VAM play in the Pinaceae is not well understood.

Mycophagy was determined by the examination of fecal pellets of diverse animals inhabiting the Lyman glacier area as well some adjacent meadows. Hypogeous mycorrhizal fungi such as *Elaphomyces* and *Rhizopogon* spores were commonly present in pika and marmot fecal pellets. Mammals thus play a role in dispersal of spores onto the glacier forefront.

Two species of hypogeous mycorrhizal fungi were described from the Lyman glacier area: *Hymenogaster glacialis* associated with *Salix* roots and *Macowanites lymanensis* with *Abies amabilis-A. lasiocarpa* roots. A new combination, *Gastroboletus ruber*, is made from *Truncocolumella rubra*, a hypogeous fungus in the Lyman Lake area.

Mycorrhizal Fungi and their Relationship to Plant Succession in Subalpine Habitats

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MYCORRHIZAL FUNGI AND THEIR RELATIONSHIP TO PLANT SUCCESSION IN SUBALPINE HABITATS

INTRODUCTION

Mycorrhizae, intimate associations between most land plant roots and fungal hyphae, are the driving force of many terrestrial ecosystems (Harley and Smith, 1983; Malloch, *et al.*,1980). About 95% of vascular plant species in the world belong to families which are typically mycorrhizal (Trappe, 1987). Two kinds of mycorrhizae are generally recognized: endomycorrhize and ectomycorrhizae, depending upon whether or not the hyphae penetrates the root cells. However, mycorrhizae types can be better distinguished by structures formed in the roots. Vesicular-arbuscular mycorrhizae (VAM) are formed by aseptate fungi belonging to the Glomaceae (Zygomycotina). They generally form either vesicules, arbuscules or hyphal coils or all of these inside root cells. Ericoid mycorrhizae (ERM) are formed by septate fungi, Ascomycotina or Basidiomycotina and distinguished by coils of hyphae inside root cells of most Ericaceae. Ectomycorrhizae (EM) are formed by Ascomycotina, Basidiomycotina and Zygomycotina (*Endogone*) and characterized by forming a Hartig net between the root cells without penetrating them and a hyphal mantle on the surface of colonized roots.

Mycorrhizal associations are symbioses in which the plants and the fungi benefit each other. Photosynthate (C source) produced by the plant symbiont is transferred to the mycorrhizal fungi in exchange for soil minerals, especially phosphorus. Other benefits of this symbiosis are increased water uptake and physical and biochemical protection against root pathogens. The results is

improved growth and survival of plant hosts, most particulary in adverse habitats.

The importance of mycorrhizae in terrestrial ecosystems is undisputed. Our research is the beginning of long term studies on relationships between mycotrophy and plant succession in subalpine and alpine zones. The initial hypothesis to be tested was that availability of mycorrhizal propagules determines which plant species can successfully colonize new substrates under natural conditions of plant succession. Four major groups of plant species can be differentiated in terms of mycorrhizal ecology of plant succession in our study: (1) mycorrhiza independent or facultatively mycorrhizal, (2) ectomycorrhiza (EM) and ericoid (ERM) mycorrhiza dependent hosts with aerially dispersed mycobionts, (3) vesicular-arbuscular mycorrhiza (VAM) dependent hosts, i.e., with mycobionts dispersed by soil movement, and (4) hosts with dark septate (DS) endophytes of unknown dispersal modes.

Mycotrophy of plant species may play a major role in plant community patterns in naturally evolved ecosystems such as Lyman glacier forefront.

Chapter 1

Mycorrhizae as Determinants of Plant Colonization Patterns on a Subalpine Glacier Forefront

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SUMMARY

Lyman glacier (48°10'N, 120°54'W) is located in the North Cascades Mountains of Washington. Its subalpine forefront (elev. 1900 m) is characterized by well developed moraines, fluting, and outwash. These deposits were initially devoid of symbiotic fungi but were colonized by them over time as the glacier receded. Availability of mycorrhizal propagules determines which of three major groups of plant species can colonize new substrates in naturally evolved ecosystems. The four major groups of plant

species are (1) mycorrhiza independent or facultatively mycotrophic, (2) ectomycorrhiza (EM) and ericoid mycorrhiza (ERM) dependent plant hosts with mycobionts disseminated by air, (3) vesicular-arbuscular mycorrhiza (VAM) dependent plants with mycobionts disseminated by soil movement, and (4) hosts with dark septate (DS) endophytes. Both EM and VAM fungi can also be disseminated by animal mycophagy. Root samples of 67 plant species were examined for mycorrhizal colonization. Mycotrophy of the plant communities on the glacier forefront (from south to north) was determined by a chronosequence sampling plan: center, east and west boundaries. Also, two well established communities adjacent to the glacier forefront were sampled for comparison. Dark-walled septate endophytes (DS) were commonly present in most of the plant species colonizing the forefront. VAM was present, mostly at low levels and nearly absent in two sites of the forefront. ERM were present in all Ericaceae. EM were present in all the Pinaceae and Salicaceae sampled. The proportion of mycorrhizal plants increased with increased time of exposure of the chronosequence site from under the ice. This trend did not occur in either east or west chronosequences.

INTRODUCTION

Lyman glacier (48°10'N, 120°54'W) is in the North Cascades Mountains of Washington within the Glacier Peak Wilderness Area of the Wenatchee National Forest. It is the origin of Railroad Creek, a tributary of Lake Chelan. This glacier now terminates at ca 1900 m elev. The ice front of Lyman Glacier receded 533 m from 1895 to 1940, an average of about 12 m per year (Freeman, 1941). By 1988, Lyman Glacier had receded about 1065 m from a Washington Water Power Company bench mark established in 1930 (W. A.

Long pers. comm.). The glacier forefront is characterized by well-defined moraines, fluting, and outwash plains. Precipitation at a nearby snow survey station averages 2750 mm per year, mostly as snow, and the growing season is only about 3 months between disappearance of snowpack in early to mid July to onset of fall frost and snow in early October.

Plant succession studies on new substrates traditionally focus on aboveground biotic observations coupled with climatic, topographic and non-biological edaphic factors. However, mycotrophic patterns of colonizing plants correlate strongly with successional stages of the plant community in disturbed and nondisturbed habitats (Allen & Allen,1984; Allen *et al.,* 1987; Reeves *et al.*,1979; Trappe, 1987).

Timberline and alpine habitats are under constant environmental stress and disturbance in which fungi and plants have evolved together. At Lyman Glacier, man-induced disturbance is negligible and introduced plants scarce or absent. In this naturally stressed and disturbed setting, we can interpret results of evolution in terms of broader considerations such as mycorrhiza dependence and independence by both fungus and host and the role of mycotrophy in successional patterns.

Four major groups of plant species can be differentiated in terms of mycorrhizal ecology of plant succession in our study: (1) mycorrhiza independent or facultatively mycorrhizal, (2) ectomycorrhiza (EM) and ericoid (ERM) mycorrhiza dependent hosts with aerially dispersed mycobionts, (3) vesicular-arbuscular mycorrhiza (VAM) dependent hosts, i.e., with mycobionts dispersed by soil movement, and (4) hosts with dark septate (DS) endophytes The first group can establish in the absence of mycobionts. The second requires the mycobiont, but mycobiont propagules are dispersed by air to the substrate surface. The third group depends on dispersal of mycobiont

containing soil onto the new substrate, a relatively slow and undependable process in alpine zones. Neither the nature of the association of the fourth nor the dispersal mechanisms of the DS endophytes is well understood, but at least they show no symptoms of pathogenicity.

Alpine zones in general are characterized by a higher proportion of mycorrhiza independent species (group 1) than other populations (Read & Haselwandter,1981; Currah & Van Dyk,1986; Trappe,1987, 1988). These plus EM and ERM species (group 2, with aerially dispersed mycobionts) are common early colonizers, whereas VAM hosts (group 3, with mycobionts dispersed with soil movement), such as most perennial forbs, are infrequent as such (Trappe, Cazarés, Luoma & O'Dell, unpublished data). DS endphytes (group 4) are common root colonizers in many plant species of diverse habitats (Stoyke & Currah, 1991; Kohn & Stasovski, 1990; Sengupta *et al.*, 1988; Read & Haselwandter, 1981).

These groupings lead to the hypothesis that availability of mycorrhizal propagules determines which plant species can successfully colonize new substrates under natural conditions of plant succession (Trappe, 1988).

The studies reported here are part of a program to test that hypothesis.

MATERIALS AND METHODS

Chronosequence sampling plan

Three sampling lines leading away from the glacier terminus were established for examining the chronosequential development of mycorrhizae on the forefront which runs South to North: (1) along the east boundary of the forefront, (2) down the center, and (3) along the west boundary.

The east chronosequence included a series of small lateral morainal rises and ran along the lake in which the active flow of the glacier now terminates. Cliffs, including vegetated benches, rise from talus above the east chronosequence, which is also followed by an unmaintained trail to Spider Pass used by wildlife and hikers.

The central sampling line started at the glacier terminus and followed a penninsula between the terminus lake to the East and mud flats to the West. Because the penninsula dead-ends at the glacier, only occasional mountain goats use the penninsula as a through route. However, deer and elk tracks were occasionally seen on the penninsula.

The west sampling line ran from the glacier terminus between the mud flats noted above and talus, cliffs and benches of the main North-South ridge extending north from Chiwawa Mountain, the originating peak of Lyman Glacier. This ridge, the crest of the North Cascades, was the source of avalanche debris, including soil, roots and trunks of trees, that was scattered along the west sampling line. No signs of animal traffic were noted along this sampling line.

The time that each site on a sampling line had been exposed from the receding ice was estimated from old photographs and conifer sampling ages (on the older sites). On the central sampling line, site 0 was within 4 m of the glacier terminus and had been exposed about 15 years; site 1 was exposed about 25 years, site 2 about 35 years, site 3 about 45 years and site 4 about 60 years. On the east and west sample lines only sites 2 and 3, representing equivalent exposure times as the same numbered sites in the central line, were sampled.

Plants were also collected from well established communities adjacent to the Lyman forefront on a low ridge that we designated "Glacier View Ridge" and

well above timberline near the higher limits of plant survival on nearby Cloudy Peak at an elev. of ca. 2,600 m for comparison.

Plant community description

Colonizer communities on glacial forefronts present sampling problems because of wide spacing of plants and nonrandom distributions (slumping, frost heaving, stream washing, and snow deposition can locally prevent plant establishment). Communities selected to represent a variety of habitats presented in the Lyman forefront were sampled for mycorrhiza characteristics of component species. At each sample site, 10 to 15 1-m^2 quadrats clustered in a 4 x 4 grid were laid out as described by Matthews (1979 a & b) for studies of forefields. Species frequencies were numbered within each 1-m^2 quadrats in which any aerial part of a species occured.(Matthews, 1979 a). This single measure combines number, size, shape and pattern, is easily measured for species of diverse life-form, is sensitive where cover and density are low, and varies relatively little as the phenological aspect of the vegetation fluctuates through the short growing season (Matthews, 1979 a).

Plant species cover dominance and frequency were determined for all sample sites except 3-West, which experienced late snow cover and frequent disturbance by rocks falling from cliffs.

Soil sampling

Soils were analysed from sites C0, C2, E2, W2 and GVR. The data included pH, total C (%), total N (mg/l), total P (mg/l). Analyses of Al, Ca, Mg, Na, K, Cu, and Fe were conducted for total cations by the perchloric acid method and for extractable cations by the ammonium acetate method.

A second set of samples was obtained from soil collected where no vegetation was growing (NR) compared to soil around the root zone (RZ) of random plants in the central chronosequence.

Soil was randomly sampled from the study sites to determine the presence of VAM spores by wet sieving and decanting.

A bioassay for presence of viable root fungal propagules was conducted with soil sampled from sites C0, C2, E2, W2, and GVR. Seeds of *Anemone occidentalis*, *Aster alpigenum*, *Epilobium latifolium*, *Petasites frigidus* and *Vaccinium deliciosum* were germinated and planted to a 200 cc Ray Leach tubes with a mix 1:1 soil and "leca" (expanded clay). Control treatments consisted of the same mixture for each soil site autoclaved. No fertilizer was applied to the soil. All treatments were replicated five times.

Root sampling

Representative samples of plant species within each site were excavated wholly or in part to provide roots and surrounding soil for determination of mycorrhizal colonization and presence of spores. We restricted root sampling in site 1-central because only a few individuals had become established.

Determination of mycorrhizal colonization

Fine root samples were cut into segments that would fit handily in small containers used for clearing and staining to determine mycorrhizal colonization in a modification of the method of Phillips and Hayman (1970). Roots were cleared in 10% KOH solution, steamed for 30 min, rinsed with tap water and transferred to 1% HCL solution for 30 min, rinsed with tap water. Cleared samples were transferred into a staining solution of 0.5% trypan-blue in lactoglycerol, steamed for 30 min, rinsed with tap water and stored in cold water

or lactoglycerol solution until microscopic examination. Colonization was confirmed by use of a compound microscope but quantified as proportion of root length colonized by scanning with a stereomicroscope in a modification of the method described by Kormanik and McGraw (1982). Proportions of root lengths colonized were by five categories: (NM), lacking endophytes; trace levels: (+), 1-25%; (++), 26-50%; high levels: (+++), 51-75%; (++++), 76-100%.

DS colonizations were characterized by their dark brown, thick-walled septate hyphae, commonly forming clumps or chains of cells (microsclerotia) within the root cells or simply colonizing the root cells with meandering hyphae (Fig. 1.1a). VAM were considered present if vesicles, arbuscules and/or broad, aseptate hyphae were present in root cells. Vesicles and aseptate hyphae were more common than arbuscules. Occasional examples of VAM formed by the "fine endophyte", *Glomus tenue* (Grenall) Hall, were noted and recorded separately from the other VAM. ERM were distinguished as brown thin-walled septate hyphae which form coils or clumps of hyphae inside outer root cells (Fig. 1.1b). EM were judged to be present if a Hartig net was evident or if feeder rootlets were mantled with hyphae and hypertrophied.

RESULTS

The plant communities

In all, 504 plants representing 19 families, 43 genera and 67 species were evaluated for mycorrhizal colonization (Table 1.1). Communities are described below by the three chronosequence sampling lines: central (C), east (E), and west (W).

Central chronosequence

Site C0, closest to the base of the glacier, was free of ice ca 15 years and lacked vegetation.

Site C1 (Table 1.2), exposed ca. 25 years, had a widely and erratically spaced plant community with cover co-dominant species being *Juncus mertensianus*, *J. drummondii*, and *Saxifraga ferruginea*. Other species included *Arenaria rubella*, *Epilobium alpinum*, *Luzula hitchcockii*, *Saxifraga tolmiei*, and *Carex nigricans*. Three individual members of the Pinaceae were also present as new seedlings in the first year of sampling: *Abies lasiocarpa*, *Picea engelmannii*, and *Pinus contorta*. Because sampling these would have eradicated the conifer component of this pioneering community, we left them undisturbed. They persisted through the third year of the study, growing about 1 cm in height in both the second and third growing seasons. The *P. contorta* seedling was the only representative of that species seen in the entire Lyman Glacier basin.

Site C2 (Table 1.3), exposed ca 35 years had *Salix planifolia* and *Juncus drummondii* as cover co-dominants. Other common species were *Arenaria rubella*., *Luzula hitchcokii*, *Saxifraga ferruginea*, *Epilobium latifolium*, *Phyllodoce empetriformis*, and *Vaccinium deliciosum*. The *Phyllodoce* and *Vaccinium* tended to establish under the low crowns of the *Salix* to form patches of vegetation. The other species, in contrast, established in the open or in the protection of stones. Scattered gymnosperms, especially *Abies lasiocarpa* and *Tsuga mertensiana*, occured on raised ground.

Site C3 (Table 1.4), exposed ca 45 years, had *Epilobium latifolium*, *Salix planifolia* and *Phyllodoce empetriformis* as cover co-dominants. Other common species included *Saxifraga ferruginea*, *Luzula hitchcokii*, *Juncus drummondii*, *Luetkea pectinata* and *Carex nigricans*. Plant spacing was still open, with much

bare ground between plants of plant patches. Scattered gymnosperms were present as in C2.

Site C4 (Table 1.5), exposed ca 60 years had *Salix planifolia*, *Phyllodoce empetriformis* and *Juncus drummondii* as cover co-dominants. Other common species were *Epilobium latifolium*, *Saxifraga ferruginea*, *Luzula hitchcokii*, *Cassiope mertensiana* and *Tsuga mertensiana*. This site still had much open ground on which few or no plants had established.

East chronosequence

Site E2 (Table 1.6), exposed ca 35 years, had *Phyllodoce empetriformis* and *Cassiope mertensiana* as cover co-dominant species. Other common species included *Juncus drummondii*, *J. mertensianus*, *V. deliciosum*, *Luetkea pectinata* and *Tsuga mertensiana*. In contrast to site C2, the *Phyllodoce* and *Cassiope* at E2 established in open to protected niches rather than under *Salix* crowns.

Site E3 (Table 1.7), exposed ca 45 years was wet and had *Luetkea pectinata*, *Juncus drummondii* and *Phyllodoce empetriformis* as cover co-dominants. Other common species were *Vaccinium deliciosum*, *Luzula hitchcockii* and *Poa cusickii*. The site bordered on a wet area that contained a wetland-adapted species such as *Carex spectabilis* and *Juncus mertensianus*.

West chronosequence

Site W2 (Table 1.8), exposed approx. 35 years, had *Juncus drummondii* and *Mimulus tilingii* as cover co-dominants. Other common species were *Juncus mertensianus*, *Epilobium alpinum*, *Arenaria rubella*, and *Saxifraga tolmiei*. This site was perenially wet from runoff from cliffs above and from melting of snow that persisted well into summer.

Site W3 (Table 1.9), exposed ca 45 years, was characterized by sparse vegetation. Being in the shade of cliffs and subject to snow and rock avalanches, it was perennially wet and under snow cover into midsummer. Some plant species established in this site were *Arenaria rubella*, *Epilobium alpinum, E. latifolium*, *Juncus mertensianus*, *Saxifraga tolmiei* and *Mimulus tilingii.* The latter species is especially abundant in wet habitats.

Glacier View Ridge

Rising gently from the 1890 terminal moraine of Lyman Glacier, this area includes heathlands, wet and dry meadows, and conifer parkland. The soil has not been glaciated for at least 6,900 years, judging from its undisturbed layer of Mount Mazama ash (W. Long, personal communication). The plant communities are major seed sources for the glacier forefront of grasses, conifers, Ericaceae, and species such as *Anaphalis margaritacea, Anemone occidentalis, Epilobium angustifolium, Potentilla flabellifolia, Sorbus sitchensis, Veratrum viride* and *Veronica cusickii* (Table 1.10).

Cloudy Peak

This exposed ridge, about 400 m. above timberline, represents a pioneering situation with only widely scattered plants. Of the seven species found there, three also occurred on Lyman Glacier forefront: *Anemone occidentalis, Luetkea pectinata, Phyllodoce empetriformis* (Table 1.11). The other four are more typical of the alpine habitat than of the subalpine habitat of the glacier forefront.

Soil characteristics

The pH ranged from 4.49 to 7.02 within the forefront sites. The latter corresponds to C0, the youngest site which lacks vegetation. Total carbon and nitrogen levels within the forefront sites were extremely low compared to GVR, which supports well established plant communities. Total phosphorus levels differed little between the forefront sites and GVR (Table 1.12). Total contents of Al, Ca, Mg, Fe, K, and Cu were considerable higher in the forefront sites than those in the GVR site. Total Na content differed little between the forefront sites and the GVR site (Table 1.13). Extractable cations such as Ca, Mg, K, Cu were higher in the forefront than in the GVR. Extractable Al was lower in the forefront sites than in GVR. Extractable Na was about twice as high in site C0 (the youngest site) than the other sites. Extractable Fe was about the same in all the sites (Table 1.14).

Soil pH in the central chronosequence for the NR ranged 4.81 to 6.58 and for the RZ, 5.8 to 6.34. Total carbon for the NR ranged 0.060 to 0.077% and for RZ, 0.077 to 0.115%. Total N for NR was 22.1 to 53.6 mg/kg and for RZ, 31.7 to 73.7 mg/kg. Total P for NR ranged 225 to 282 mg/kg and for RZ, 211 to 293 mg/kg (Table 1.15). Total cation content differed little between the sites or between NR and RZ (Table 1.16)

Extractable Al differed little between sites or between NR and RZ, except in RZ from the site C1 which was quite low. Extractable Ca, Mg and Na differed little between sites or between NR and RZ. Extractable K of NR soils decreased with increasing time of exposure of the site. Extractable Cu was lower in the C1 from the RZ than the rest of the samples. Extractable Fe was higher in the C1 from the RZ than the rest of the samples (Table 1.17)

Soil propagule content

No VAM spores could be detected in soils from forefront sites. However, spores of*Glomus fasciculatum* (Thaxter) Gerd. & Trappe *sensu stricto* were present among roots of occasional sampled plants. Usually the host plant had at least some VAM development, but a curious exception to this was with an *Oxyria digyna* from site West-2. That plant was several meters from the nearest other plant and showed no trace of VAM colonization. Yet, an abundant mycelium with several dozen apparently healthy spores was associated with its roots.

The survival rate of seedlings in the soil bioassay was low except for those growing in the GVR soil. Only *V. deliciosum* showed mycorrhizae colonization when grown in C0, C2, E2, W2. *V. deliciosum* showed ERM colonization when growing in soils from C2 (two seedlings), E2 (three seedlings), W2 (one seedling). Apparently sterilization of the GVR soil (Control) did not affect the ERM propagules due to the fact that ERM was observed in *V. deliciosum* (four seedlings). High levels of VAM colonization were observed in all plant species when growing in GVR soil, but *V. deliciosum* of which only one seedling showed traces of colonization. Also, DS colonization was observed in at least one seedling of all five plant species.

Mycotrophy of the plant communities

Proportions of the plants that were nonmycorrhizal or that had DS, VAM, EM or ERM are shown for all sampling sites on the three chronosequences in Table 1.18. DS occurred at moderate rates in all chronosequence sites (24-46%) except C1, which had only 13% of the sample plants colonized. DS occurred in all plants in the long established communities of Glacier View Ridge and Cloudy Peak. VAM were generally low (less than 30%) in all but site W2

(49%) and nearly or altogether absent in sites C1 and W3. EM were present in all the PInaceae and Salicaceae sampled, and ERM were present in all the Ericaceae. In the central chronosequence, the proportion of mycorrhizal plants increased with increased time of exposure of the site from under the ice. In both east and west chronosequences, that trend did not occur.

Central chronosequence

Site C1, exposed ca 25 years, 11 species (Table 1.2): 26 of the 31 sampled plants (84%) were NM, four (13%) had low levels of DS, one *Mimulus lewisii* had a low level of VAM and one *Salix planifolia* had a high level of EM along with some DS.

Site C2, exposed ca 35 years, 28 species (Table 1.3): 45 of the 105 sampled plants (43%) were NM, 37 (35%) had low to high levels of DS, 29 (28%) had low to high levels of VAM, 12 (11%) had EM, and nine (9%) had ERM. One *Salix planifolia* specimen had DS, EM and VAM.

Site C3, exposed ca 45 years, 15 species (Table 1.4): 20 of the 46 plants sampled (43%) were NM, 21 (46%) had low to high levels of DS, two (4%) had low levels of VAM, ten (22%) had low to high levels of ERM and six (13%) had low to high levels of EM.

Site C4, exposed ca 60 years, 18 species (Table 1.5): 26 of the 69 plants sampled (38%) were NM, 29 (42%) had low to high levels of DS, 11 (16%) had low to high levels of VAM , 13 (19%) had low to high levels of ERM and fifteen (22%) had low to high levels of EM. One *Salix planifolia* plant had DS, VAM and ER.

East chronosequence

Site E2, exposed ca 35 years, 26 species (Table 1.6): 25 of the 85 plants sampled (29%) were NM, 30 (35%) had low to high levels of DS, 23 (27%) had low to high levels of VAM , 20 (23%) had low to high levels of ERM and 12 (14%) had EM.

Site E3, exposed ca 45 years, 21 species (Table 1.7): 21 of the 47 plants sampled (45%) were nonmycorrhizal, 15 (32%) had low to high levels of DS, six (13%) had low to high levels of VAM, five (11%) had hyphae and vesicles that resembled VAM, 14 (30%) had low to high levels of ERM and six (13%) had high levels of EM. One plant of *Salix commutata* had DS, VAM and EM.

West chronosequence

Site W2, exposed ca 35 years, 23 species (Table 1.8): 17 of the 76 plants sampled (22%) were NM, 31 (41%) had low to high levels of DS, 37 (49%) had low to high levels of VAM, ten (13%) had low to high levels of ERM and four (5%) had low to high levels of EM. One plant of *Salix nivalis* had DS, VAM and EM.

Site W3, exposed ca 45 years, eight species (Table 1.9): 13 of the 17 plants sampled (76%) were NR and four (24%) had low levels of DS. VAM, ERM and EM were not present. Facultative mycorrhizal hosts such as *E. alpinum, E. latifolium, O. dygina* and *P. davidsonii* were all nonmycorrhizal here. Ericaceous and EM hosts were absent in this site.

Glacier View Ridge

On this area, evidently bearing plants for several millenia, we selected 21 species for sampling (Table 1.10). All 21 were mycorrhizal and all had low to high levels of DS, 11 (52%) had low to high levels of VAM, three (14%) had low

to high levels of ERM, and three (14%) had low levels of EM. The specimen of *Potentilla flabellifolia* had DS, VAM and EM. Facultative species such as *Luzula hitchcockii* were mycorrhizal in the well developed communities of this area.

Cloudy Peak

All of the seven species sampled had low to high levels of DS, four (57%) had low to higl levels of VA, and one (14%) had ER (Table 1.11). Since the site was well above timberline, no conifers or other EM hosts were present.

Mycotrophy of plant species by family and genus

Asteraceae

Anaphalis margaritacea, sampled only once but common in the Glacier View Ridge meadows, had both DS and VAM (Table 1.10). Allen *et al.* (1984) recorded this species as sometimes VAM, sometimes NM at Mount St. Helens in the southern Washington Cascades.

Aster alpigenum had moderate to high levels of DS and low to moderate levels of VAM (Table 1.3). Other *Aster* spp. have been recorded as VAM or NM (Currah & Van Dyk, 1986 Dominik *et al.,* 1954); ours is the first report of DS for the genus.

Of the *Crepis nana* samples, one had a low level of DS and five had low to high levels of VAM, including one with *G. tenue* (Tables 1.7, 1.8). Other *Crepis* spp. have been observed to be either NM, DS, VAM or EM (Read & Haselwandter, 1981; Selivanov & Shkaraba, 1970).

The single sample of *Senecio cymbalarioides* had a low level of DS colonization and a high level of VAM (Table 1.7). Four *Senecio fremontii* were

NM, whereas three had low to high levels of VAM. Other species of *Senecio* have been recorded as NM, VAM or DS (Saif *et al.* 1977; Read & Haselwandter, 1981).

Brassicaceae

The only sample of this family, a *Draba oligosperma* from above timberline had a low level of DS (Table 1.11). This species has been reported as NM by Currah & Van Dyk (1986) and Lesica & Antibus (1986). Ours is the first report of DS for the genus.

Caryophyllaceae

Arenaria rubella was found common throughout the forefront. Of the 21 samples examined, 17 were NM, three had low to moderate levels of DS, and one had a moderate level of *Glomus tenue*. VAM (Tables 1.2 — 1.5,1.8,1.9). This species has been recorded as NM (Daubenimre, 1941; Katenin, 1964; Stutz, 1972) or occasionally VAM (Tikhomirov & Strelkova, 1954). Ours is the first record of DS for the genus.

Cyperaceae

C. nigricans, Carex scopulorum, C. spectabilis, and Carex sp. #1 samples were largely NM (Tables 1.2 — 1.8).samples were largely NM (Tables 1.2 — 1.8). A few samples of *C. nigricans* , *C. scopulorum* and *Carex* sp. #2 had low to moderate levels of DS and VAM, either singly or both on the same plant (Tables 1.3, 1.4, 1.6, 1.8, 1.10). *Carex* spp. are generally reported to be NM, but occasional DS and VAM have been observed (Dominik *et al.*, 1954; Katenin, 1964; Mejstrik,1972; Read & Haselwandter 1981; Selivanov &

Shkaraba, 1970; Stutz, 1972). Haselwandter & Read (1982) demonstrated a positive response of one *Carex* sp. to colonization by a DS endophyte.

Equisetaceae

A low level of VAM was found in the one sample of *Equisetum arvense* (Table 1.6). This species has been reported as usually NM but sometimes as having DS or VAM (Berch & Kendrick, 1982; Boullard 1957; Currah & Van Dyk, 1986; Katenin, 1964; Leferriere & Koske, 1981; Stutz, 1972).

Ericaceae

Of the 83 ericaceous plants sampled only three lacked ERM: a *Phyllodoce empetriformis* (Table 1.5) and a *Vaccinium deliciosum* (Table 1.3) were NM on the forefront and a *V. caespitosum* had only a low level of DS on Cloudy Peak (Table 1.11).

Of the 17 samples of *Cassiope mertensiana* (Tables 1.3-1.8, 1.10), five showed low to high levels of DS. Largent *et al.* (1980) reported ERM on this species, but ours is the first observation of DS for the genus.

Of five samples of *Ledum glandulosum* three had low levels of DS and one had VAM (Tables 1.5, 1.7). Largent *et al.* (1980) reported this species to be sometimes NM, ERM or EM, but ours is the first report of DS or VAM.

Of 25 samples of *Phyllodoce empetriformis*, 14 samples had low levels to high levels of DS along with ERM and four had VAM (Tables 1.3-1.8, 1.10, 1.11). Largent *et al.* (1980) reported ERM on this species. Of the 12 samples of *P. glanduliflora,* eight had low to high DS and one had VAM. Ours is the first report of mycorrhizae in *P. glanduliflora* and the first of DS or VAM in the genus.

One sample of *Vaccinium deliciosum* was NM; the other 22 had ERM from low to high levels (Tables 1.3-1.8, 1.10). *Vaccinium* spp. are usually

reported to be ERM (Haselwandter & Read, 1981; Katenin, 1964; Largent *et al.* , 1980; Selivanov & Shkaraba, 1970). Ten also had low to high levels of DS, and two also had low levels of VAM. Koske & Gemma (1990) reported VAM on other *Vaccinium* spp. The one sample of *V. caespitosum,* from Cloudy Peak, had only DS at a low level (Table 1.11). These are the first reports of mycorrhizae in these species and the first of DS for the genus.

Fabaceae

No legumes occurred on the forefront, but *Lupinus lepideus* was scattered in various communities of Glacier View Ridge (Table 1.10). The one sample examined had a moderate level of DS and low level of VAM. DS are common on legumes in the Pacific Northwest (T. O'Dell, unpublished data), and *Lupinus* spp. may be either NM or VAM (Lusnikova, 1970; Trinick, 1977; T. O'Dell, unpublished data).

Juncaceae

Twenty of the 27 samples of *J. drummondii* var. *subtriflorus*, were NM, seven had low to high levels of DS, one had a high level of VAM, and two had high levels of hyaline hyphae with clamp connections inside root cortical cells (Tables 1.2-.1.4, 1.7-1.9). Of the 18 samples of *J. mertensianus* , 14 were NM, four had low levels of DS, and one had a low level of VAM (Tables 1.2-1.4, 1.6, 1.8, 1.9). *Juncus* spp. are generally reported as NM (Dominik, 1951; Katenin, 1964; Mejstrik, 1972; Stutz, 1972) but have occasionally been found to be VAM (Dominik, 1951; Saif, Ali & Zaidi, 1977). Ours are the first reports for these two species and the first records of DS for the genus.

Eight of the 22 samples of *L. hitchcockii* were NM, 12 had low levels of DS, and three had low levels of VAM (Tables 1.2-1.6, 1.8, 1.10). The two

samples of *L. parviflora* were NM (Table 1.7). Katenin (1964) also reported this species as NM. Other *Luzula* spp. are most often recorded as NM (Dominik *et al,* 1954; Katenin, 1964; Selivanov & Shkaraba, 1970; Stutz, 1972; Tikhomirov & Strelkova, 1954). However, both DS and VAM have been occasionally reported (Read & Haselwandter, 1981; Stutz, 1982).

Liliaceae

The one sample of *Erythronium grandiflorum*, from Glacier View Ridge, had moderate levels of both DS and VAM. Currah and Van Dyk (1986) reported both types on this species.

The one sample of *Tofieldia glutinosa* had a low level of DS (Table 1.7). The only other species of this genus examined to date was found to have both DS (Currah & Van Dyk, 1986) and VAM (Sycheva, 1955).

The one sample of *Veratrum viride,* from Glacier View Ridge, had moderate levels of both DS and VAM. Other species in the genus have been reported to have VAM (Dominik *et al.,* 1954; Katenin, 1964; Selivanov & Shkaraba, 1970) and DS (Peyronel, 1924).

Onagraceae

Nine of the 17 samples of *E. alpina* were NM, seven had from low to high levels of DS and seven had low to high levels of VAM (Tables 1.2, 1.3, 1.6, 1.8, 1.9). Peyronel (1924) reported both types on this species. The one sample of *E. angustifolium* also had low levels of both DS and VAM (Table 1.10), as earlier reported by Currah and Van Dyk (1986). Of the 15 samples of *E. latifolium*, eight were NM, four had low levels of DS and six had low to high levels of VAM (Tables 1.3, 1.5, 1.6, 1.8, 1.9). Katenin (1964) and Stutz (1972) earlier recorded NM and Currah and Van Dyk (1986) recorded DS for *E. latifolium;* ours is the first VAM record. The two samples of *E. watsonii* were NM (Tables 1.6, 1.7). Gerdemann and Trappe (1974) reported VAM on this species.

Pinaceae.

All ten samples of *Abies lasiocarpa* had EM, four had low levels of DS, one had a few VAM hyphae and vesicles (Tables 1.4-1.6). EM have been reported on this species (McDougall & Jacobs, 1927; Trappe 1961, 1964). Other *Abies* spp. have been recorded as having DS (Blaschke, 1981) and VAM (Golubinskaya, 1967; Khan, 1972; Malloch & Malloch, 1981), but ours is the first report of these types on *A. lasiocarpa.*

The two samples of *Larix lyalli* had low to high EM (Table 1.6), as reported earlier by Trappe (1964). VAM has been recorded for two other *Larix* spp. (Golubinskaya, 1967; Malloch & Malloch, 1981), but DS have yet to be reported for the genus.

The two samples of *Picea engelmanii* had moderate levels of EM (Table 1.6). MacDougal and Jacobs (1927), Trappe (1964) and others have reported EM on this species. Other *Picea* spp. are normally EM (Dominik *et al.* 1954; Frank, 1885; Malloch & Malloch, 1981; Trappe, 1964). VAM have been

discovered on two species (Golubinskaya, 1967; Henry, 1933), but as yet DS has not been reported for the genus.

Of the samples of *Tsuga mertensiana*, one was NM and 12 had low to high levels of EM (Tables 1.3, 1.5-1.7). Ten had low to high levels of DS, and one had VAM. *T. mertensiana* and other *Tsuga* spp. have been reported as EM (Noelle, 1910; Trappe, 1964); ours is the first report of DS and VAM for the genus.

Poaceae

The two samples of *Agrostis variabilis* were NM (Table 1.7). This is the first record of root examination of this species. Other *Agrostis* spp. have been reported as NM, VAM, or DS (Dominik, 1951; Mejstrik, 1972; Read & Haselwandter, 1981; Selivanov & Utemova, 1968).

Of the three samples of *Deschampsia caespitosa*, one was NM, one had a low level of DS and two had low levels of VAM by *Glomus tenue*. (Table 1.6). This species has been previously recorded as being NM or having VAM (E. B. Allen *et al.*,1987; Katenin, 1964; Selivanov & Shkaraba, 1970; Selivanov & Utemova, 1968). Other *Deschampsia* spp. have been reported as having DS (Read & Haselwandter, 1981). Of the four samples of *Poa cusickii* , two were NM, one had a low level of DS and one had a high level of VAM (Table 1.6). E. B. Allen *et al.* (1987) reported this species as VAM. Ours is the first report of it being NM or having DS, but other species of the genus have been observed as being NM or having VAM or DS (Dominik, 1951; Katenin, 1964; Read & Haselwandter, 1981; Selivanov & Utemova, 1968). The seven samples of *P. nevadensis* included one NM, four with low levels of DS, and four with low to high levels of VAM (Table 1.3). Ours is the first examination of this species. Of

the four samples of *Poa* sp. , one was NM, three had low to high levels of DS and two showed from low to high levels of VAM (Table 1.8).

Two unidentified grasses from Glacier View Ridge both had low to moderate levels both of DS and VAM.

Polygonaceae

Oxyria digyna is common in the older moraines and adjacent cliffs in protected areas. It has a long, fragile tap root difficult to sample. Of 15 plants sampled, nine were NM, five had low to high levels of DS and three had low levels of VAM (Tables 1.2, 1.3, 1.5, 1.8, 1.9). One nonmycorrhizal sample had a clump of *G. fasciculatum* spores on the root surface. This species has been found to be either NR or VAM by others (Dominik *et al.,* 1954, Katenin, 1964; Stutz, 1972); ours is the first record of DS and EM for the genus.

Polygonum bistortoides is a common on Glacier View Ridge but rare in the glacier forefront. The one sample from the forefront had a low level of EM (Table 1.3). A sample from Glacier View Ridge.had a low level of EM but also a moderate level of DS (Table 1.10). Lesica and Antibus (1986) reported VAM on this species; ours is the first report of EM or DS. Other species of *Polygonum* have been variously found to be NM or have DS, EM or VAM (Daubenmire, 1941; Dominik, *et al.,* 1954; Katenin, 1964; Lesica & Antibus, 1986; Peyronel, 1924; Read & Haselwandter, 1981; Saif *et al.,* 1977; Selivanov & Shkaraba, 1970).

Polypodiaceae

The four samples of *Cryptogramma crispa* all had low to moderate levels of VAM (Table 1.8). Fontana (1959) and Hepden (1960) also found VAM on this species. Boullard (1957) reported it to be nonmycorrhizal.

The three samples of *Cystopteris fragilis* had low to high levels of VAM (Table 1.3). This species has been earlier reported to be either NM (Berch & Kendrick, 1982; Boullard, 1957; Fontana, 1959) or VAM (Berch & Kendrick, 1972; Dominik, *et al.,* 1982).

Rosaceae

Of 15 samples of *Luetkea pectinata*, a common mat-forming species, one was NM, seven had low to high levels of DS and 12 had low to high levels of VAM (Tables 1.3-1.6, 1.10, 1.11). This is the first report on the mycorrhizal status of this genus.

The one plant of *Potentilla flabellifolia* sampled, from Glacier View Ridge, had high levels of DS and VAM and a few EM (Table 1.10). This is the first report for this species, but others have been variously reported to be NM or to have DS, VAM or EM (E. B. Allen *et al.*, 1987; Currah & Van Dyk, 1986; Daubenmire 1941; Dominik, 1951, Dominik *et al.*, 1954; Katenin, 1964; Lesica & Antibus, 1986; Mejstrik, 1972; Peyronel, 1924; Read & Haselwandter, 1981, Selivanov & Shkaraba, 1970; Stutz, 1972).

The one plant of *Surbus sitchensis* sampled, from Glacier View Ridge, had high levels of VAM and low levels of DS and EM (Table 1.10). Trappe (1964) reported EM for this species, but ours is the first record of VAM and DS. Other *Sorbus* spp. have been recorded as sometimes NM but usually having DS, VAM or EM (Dominik, 1951; Dominik *et al.,* 1954; Dominik & Pachlewski, 1955; Golubinskaya, 1967; Malloch & Malloch, 1981; Selivanov & Shkaraba, 1970).

Salicaceae

Of 11 plants of *S. commutata* sampled, nine had low to high levels of DS, three had low levels of VAM, and all had low to high levels of EM (Tables 1.3, 1.5, 1.7). The two samples of *S. nivalis* had low levels of DS and low to high levels of EM; one additionally had low levels of VAM (Table 1.8). Of the 18 samples of *S. planifolia*, one had only young, NM root tips, 14 had low to high levels of DS, one had a low level of VAM and 16 had low to high levels of EM (Tables 1.2-1.5, 1.7, 1.9). Ours are the first reports for these species, but other *Salix* spp. have been reported variously as NM, VAM, DS or EM (Dominik, 1951; Dominik *et al.*, 1954; Fontana, 1962; Harris & Jurgensen, 1977; Katenin, 1964; Selivanov & Shkaraba, 1970; Stutz, 1972; Tikhomirov & Strelkova, 1954; Trappe, 1964)

Saxifragaceae

Of the 27 plants of *Saxifraga ferruginea* sampled, 22 were NM, four had low levels of DS and one had a low level of VAM (Tables 1.2-1.7). Ours is the first study of mycotrophy in this species. The one sample of *S. punctata* had low levels of both DS and VAM (Table 1.6). This species had been reported as having VAM (Tikhomirov & Strelkova, 1954), but this is the first report of DS for it. Of the 26 samples of *S. tolmei* 24 were NM and two had low levels of DS colonization (Tables 1.2-1.6, 1.9). Other *Saxifraga* spp. have been reported as NM, DS, VAM or EM (Currah & Van Dyk, 1986; Dominik, *et al.*, 1954; Katenin, 1964; Read & Haselwandter, 1981; Stutz, 1972; Tikhomirov & Strelkova, 1954).

Scrophulariaceae

All three samples of *Castilleja parviflora* had VAM, one of them formed with *Glomus tenue* (Table 1.3). Ours is the first report of VAM for the genus.

DS has been found on another species (Trappe, unpublished data), and Katenin (1964) reported yet another to be NM.

Of the 12 plants of *Mimulus lewisii* sampled, four were NM, one had a low level of DS and seven had low to high levels of VAM, including one colonized by *G. intraradices* Schenck & Smith (Tables 1.2, 1.3, 1.6, 1.7). Of the 15 samples of*M. tilingii*, nine were NM, two had low levels of DS and four had low levels of VAM (Tables 1.3-1.6, 1.8, 1.9). These are the first reports of mycotrophy for this genus.

All six plants of *Pedicularis attollens* sampled were NM (Tables 1.6, 1.7). Ours was the first examination of this species. The one sample of *P. bracteosa,* from Glacier View Ridge, had high levels of DS (Table 1.10); DS had been reported for this species by Currah & Van Dyk (1986). Of the eight samples of *P. groenlandica*, four were NM, four had low to high levels of DS and one had a low level of VAM (Tables 1.3, 1.4, 1.6, 1.7); Thomas (1943) had earlier reported VAM on this species. *Pedicularis* sp. from Glacier View Ridge had a low level of DS (Table 1.10). Other *Pedicularis* spp. have variously been reported as NM or having VAM, DS or EC (Currah & Van Dyk, 1986; Katenin, 1964; Stutz, 1972; Sycheva, 1955).

Of the three plants of *Penstemon davidsonii* sampled, one was NM, one had a low level of DS and one had a low level of VAM with spores on the root surface (Tables 1.3, 1.9). Ours is the first report of VAM for this species and of DS for the genus. Other *Penstemon* spp. have been variously recorded as NM or having VAM (Currah & Van Dyk, 1986; Thomas, 1943).

All of the four plants of *Veronica cusickii* sampled had low to high levels of VAM and two additionally had low levels of DS (Tables 1.8, 1.10). All of the 16 plants of *V. wormskjoldii* sampled had low to high levels of VAM and six had low to high levels of DS. These are the first reports of mycotrophy for both

species. Other *Veronica* spp. have been variously reported as NM or having DS or VAM (Currah & Van Dyk, 1986; Dominik, *et al.*,1954; Katenin,1964; Saif *et al.*, 1977; Sycheva, 1955).

DISCUSSION

Plant communities. -In general, the vegetation is widely spaced throughout the Lyman glacier forefront. The chronosequence sites (CO, C1, C2, C3, C4, E2, E3, W2 and W3) showed differences in their plant communities.

The central chronosequence line clearly showed the development of plant communities over time. In site C0, after ca 15 years exposure, vegetation has yet to established. Site C1,exposed ca 25 years, showed the first plant community closest to the base of the glacier. This plant community of *Juncus mertensianus*, *J. drummondii*, and *Saxifraga ferruginea* is widely spaced and low cover. The plant community in site C2, exposed ca 35 years, differs considerably from that of C1, with *Salix planifolia* and *Juncus drummondii* as co-dominant species. Ericaceae and Pinaceae members colonized this site in low numbers. A more diverse plant community is established in sites C3 and C4 (exposed ca 45 and 60 years respectively), with *Salix planifolia* and *Phyllodoce empetriformis* as the main co-dominant species.

The plant communities established in the central chronosequence showed a "patch" or "island" pattern of its mycorrhiza-dependent components. *Salix commutata*, *S. planifolia*, *Phyllodoce empetriformis*, *Cassiope mertensiana, Abies lasiocarpa* and *Tsuga mertensiana* commonly form patches of vegetation throughout these sites. This phenomenon is not well understood, but it does not occur with mycorrhiza-independent plants such as *Carex*, *Juncus* and *Saxifraga* spp. Hence, we speculate that, although patch formers probably

provide a microclimate favorable for establishment of seedlings, *Salix* shrubs seem particularly important in this regard and may develop a soil microflora that improves the substrate for other plant colonizers. Their development of mycorrhizal mycelium in surrounding soil also enables mycorrhiza-dependent seedlings to establish by plugging into the mycorrhizal system. The dark septate endophytes appear to be common to all species in this respect and thus may be important in the process.

The plant communities of the east chronosequence differed little between the two sites. E2 is co-dominated by *Phyllodoce empetriformis* and *Cassiope mertensiana* and site E3 is co-dominated by *Luetkea pectinata*, *Juncus mertensianus* and *Phyllodoce empetriformis*. *Salix* shrubs were not common in this chronosequence, and the patch pattern common in the central chronosequences was not observed in these sites. Animal traffic on the trail to Spider Pass, which runs, near the chronosequence, may have dispersed mycorrhizal propagules to the more recently exposed sites.

Plant communities in the west chronosequence are influenced by the wet environment resulting from melting of snow that persists far into summer and by frequent soil disturbances such as soil and rock avalanches. Site W2 is co-dominated by *Juncus drummondii* and *Mimulus tilingii* both typical of wet soils, but also had many mycorrhizal plants, especially VAM hosts. Avalanche debris from vegetated benches on the cliffs above, including soil and plants, was scattered near site W2 and probably was the source of VAM inoculum. The plant community of site W3 was wetter, had fewer species and less mycorrhizal plants than W2. Also, the patching pattern was not observed in these sites.

Glacier View Ridge is characterized by heathlands, wet and dry meadows, and conifer parklands which are the main seed sources for many of the mycorrhiza-dependent plant colonizers of the glacier forefront. These

communities are predominantly of mycotrophic species, Cloudy Peak supports an alpine community. However, a few species established in this area are also found in the glacier forefront. It represents the type of high ridges that are potential seed and inoculum sources above the glacier forefront.

Soil characteristics. - Although our soil analyses were not replicated within sites, some differences were observed. The pH was almost neutral for site C0 but acid for the older of the sites. C and N were considerable lower in the forefront sites than in GVR (C-6.6% and N-2580mg/l). The carbon content in site C0 (0.069%) may be of microbial origin, a safe assumption due to the fact that no vegetation is present in this site. Even though nitrogen content in site C0 is low (55mg/l), it may not be a limit for plant establishment; however the rates of depletion are not known. Phosphorus content differed little between sites and may not be a limiting factor in the forefront (Table 1.12).

Total contents of most cations analyzed were higher in the forefront sites than those in the GVR site except for Na, was about the same for all sites (Table 1.13). Most extractable cations analyzed (Ca, Mg, K and Cu) were higher in the forefront than in GVR. Extractable Al was considerable lower in the forefront sites than in GVR (Table 1.14).

Plant growth is slower on the forefront sites than on the GVR site, judging from annual tree height of the Pinaceae. Because cations were generally more abundant on the forefront than on GVR, the low N and low organic matter are the most likely nutitional factors limiting growth rates on the forefront. No strong trends were evident between rhizosphere and nonrhizosphere soils. Soil pH differed little between NR and RZ. In all cases pH was above 4; which is suitable for plant growth. Carbon (NR-0.060-0.077, RZ-0.077-0.115%) was slightly higher in RZ than in NR, but no pattern of change along the

chronosequence was detected. Apparently, carbon accretion in the forefront soil is both slow and erratic. Slow carbon buildup by slow plant growth may be nearly balanced by decomposition rates. Total nitrogen content decreased along the chronosequence in both NR and RZ. Total nitrogen is low in the forefront sites compared to GVR. Nitrogen-fixing plants are almost absent on the forefront and their contribution to the N budget is limited. Evidently, substantial N accretion requires far more than 65 years in this habitat. Total phosphorus content differed little between NR and RZ of all sites. Mycorrhizae and P uptake are undoubtedly important for plant growth. The phosphorus supply and uptake by plants interact with mycorrhizal colonization to affect plant colonization and growth. Additional research is needed to explore these interactions at Lyman Glacier.

Total cation content showed few differences between NR and RZ.(Table 1.16). Ca was lower in C1 than in older sites for both NR and RZ. Total K tended to decrease with exposure time (from C1 to C4) in RZ but not in NR. No strong trends were discernable in extractable cations over the chronosequence except for K of NR soil which decreased along the chronosequence. Potassium losses by leaching may be higher and faster in plant communities on the older moraines (Table 1.17).

Our soil sampling was limited and intended primarily to characterized the sites. Detecting patterns of change over time would require much more sampling than we were able to do.

Soil propagules. - Mycorrhizal fungi propagules were distributely erratically on the forefront soil. The mycorrhizal status of the plant communities represents a kind of natural bioassay of the distribution patterns of the mycorrhizal fungi on the forefront, assuming random dispersal of host seed over the forefront (Table

1.19). For instance, VAM colonizations of plants sampled were generally low (less than 30%), except in W2 (49%) which is under frequent soil disturbances caused by rock avalanches from the upper rock benches and cliffs. Site C1 had a very low VAM incidence and W3 lacked VAM altogether. The Ericaceae tipically formed ERM on the forefront and the Salicaceae and Pinaceae consistently formed EM.

Bioassay seedlings grown in forefront soils under greenhouse conditions showed no VAM colonization. All species grown in GVR soil except *V. deliciosum* consistently formed VAM. *V. deliciosum* formed ERM in samples from C2, E2, W2 and GVR in at least one seedling of each soil site except CO.

Mycotrophy of the plant communities. - Changes in the proportion of plant species of different mycotrophic habit could be detected along the central chronosequence. A high proportion of species established on site C1 are nonmycorrhizal (NM) or facultatively mycorrhizal (F). Mycorrhizal hosts with mycobionts dispersed by air occur in small proportion in this site. VAM dependent hosts are completely absent. The proportion of NM and F plant species to mycorrhizal species declined over time along the central chronosequence (Table 1.18). An exception to this pattern occurred at C2 (14% - VAM dependent) which is located along a drainage from the West chronosequence, where soil from avalanches from the cliffs may deposit VAM propagules. During spring runoff, VAM propagules may be water borne to C2. Soil movement by animal traffic may be another mechanism of VAM spore dispersal to this site. Nonmycorrhizal and facultatively mycorrhizal hosts are earliest colonizers in the youngest sites, where mycorrhizal propagules have not been established yet.

Occurrence of mycorrhizal colonization types throughout the Lyman Glacier forefront is summarized in Table 1.19. Again, nonmycorrhizal species decreased over time along the central chronosequence. VAM occurrence showed an erratic pattern, even when on facultative plants. EM and ERM colonizers generally increased along the central chronosequence. East and west chronosequences show quite different patterns of VAM, probably due to the spore transport factors along both sides of the forefront. The east chronosequence is affected by rock, soil and plant avalanches, hikers and animal traffic that move soil which may contain VAM spores. Both W2 and W3 sites are the foot of cliffs with unstable soil on benches that avalanche affecting both sites. Both E3 and W3 sites are located in semiaquatic areas in which NM species are the main colonizers.

Dark septate endophytes. - DS colonizations were observed in most plant families present throughout the forefront except the Polypodiaceae. However, we had too few samples of Polypodiaceae to be able to say that DS never occur on them. DS colonizations were occasional in the Caryophyllaceae and Saxifragaceae, occurred in 18% (4/22) of the Cyperaceae sampled, and were most common in the Salicaceae (84%, 26/31), Rosaceae (54%, 7/13) and Ericaceae (51%, 40/78). DS appeared in the central chronosequence (C2- 35%, C3- 46%, C4- 42%), East chronosequence (E2- 35%, E3- 32%), and West chronosequence (W2- 41%, W3- 24%).

Because the DS endophytes have been become widely established in the forefront, we infer that their propagules are aerially dispersed. However, their sporulating stages are not known for the Lyman Glacier area. Other dispersal methods may include hyphal fragments carried by air currents,

surface water flow or soil movement caused by disturbance avalanches or strong winds.

Mycotrophy of plant families. - The highest percentages of nonmycorrhizal samples were observed in commonly nonmycorrhizal families (Table 1.20): Caryophyllaceae (81%, 17/21), Cyperaceae (82%, 14/22), and Saxifragaceae (85%, 46/54). Only one sample from site W2, a *Carex nigricans* was colonized by VAM. Low levels of VAM and DS were occasional in the Saxifragaceae. VAM were most abundant in Polypodiaceae (100%, 7/7), Rosaceae (92%, 12/13), Asteraceae (76%, 13/17), Scrophulariaceae (54%, 36/67) and Poaceae (45%, 9/20). ERM were observed only in the Ericaceae (97%, 76/78). EM occurred in the Pinaceae (96%, 26/27), Salicaceae (94%, 29/31) and Polygonaceae (6%, 1/16).

General conclusions. - These studies were conducted in an area that has experienced little disturbance from man. The patterns of plant community initiation and development have evolved naturally from Pleistocene or pre-Pleistocene times. The results support the hypothesis that patterns of colonization are determined by the availability of propagules of mycorrhizal fungi.

Nonmycorrhizal or facultatively mycorrhizal host plants prevail initially but are gradually replaced by mycorrhizal species. Those with propagules dispersed by air then gain dominance with time. Entry of plants with mycorrhizal fungi dispersed by movement of soil is slow and erratic.

These studies also confirm the observations of Peyronel (1924), Read & Haselwandter (1981) and Currah & Van Dyk (1986) that DS fungi are pervasive in subalpine and alpine systems. The biology and role of these endophytes

clearly deserves high priority in research programs designed to clarify the important organisms, their processes and interactions, in belowground ecosystems.

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Fig. 1.1. Fungal colonization within root cortical cells of ***Vaccinium deliciosum***. (a) Dark-walled septate endophyte microsclerotia. Bar=5 μm. (b) Ericoid mycorrhizal endophyte. Bar=5μm.

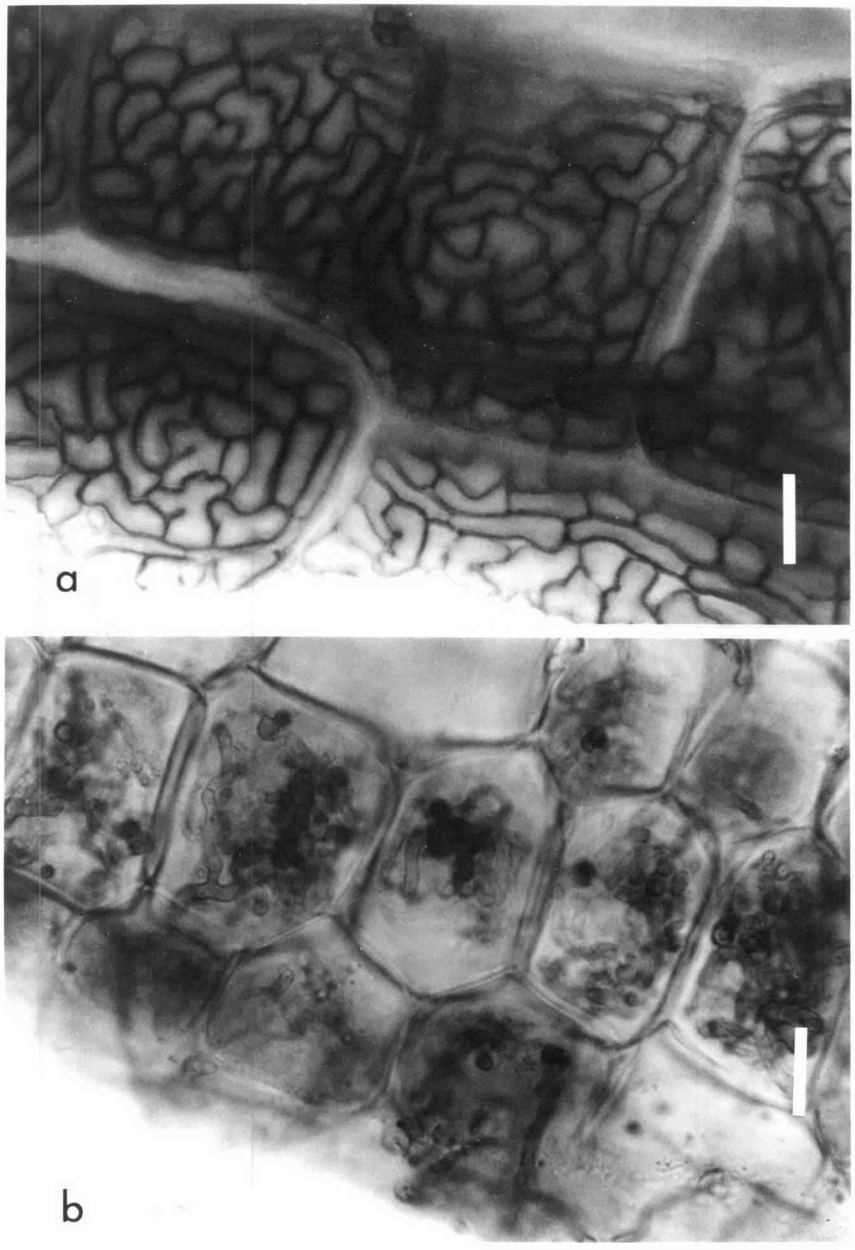

Fig.1.1

Table 1.1 Plant species from Lyman Glacier forefront and nearby areas collected for root examination.

Taxa	No. sampled	Collection Site[a]
ASTERACEAE	**20**	
Anaphalis margaritacea (L.) Benth. & Hook.	1	GV
Aster alpigenus (T. & G.) Gray	4	C2
Crepis nana Rich.	5	E3,W2
Erigeron aureus Greene	1	CP
Senecio cymbalarioides Buek	1	E3
Senecio fremontiii T. & G.	7	C2,W2
BRASSICACEAE	**1**	
Draba oligosperma Hook.	1	CP
CARYOPHYLLACEAE	**21**	
Arenaria rubella (Wahl.) Smith	21	C1, C2,C3,C4, W2, W3
CYPERACEAE	**23**	
Carex scopulorum Holm	10	C2,C3,E2,W2
C. spectabilis Dewey	2	E3
C. nigricans Retz.	6	C1,E3,W2
Carex sp. 1	4	C4
Carex sp. 2	1	GV
EQUISETACEAE	**1**	
Equisetum arvense L.	1	E2
ERICACEAE	**83**	
Cassiope mertensiana (Bong.) G. Don	17	C2,C3,C4,E2,E3,W2,GV
Ledum glandulosum Nutt.	5	C4,E3
Phyllodoce empetriformis (Sw.) D. Don	25	C2,C3,C4,E2,E3,W2,CP,GV,
P. glanduliflora (Hook.)Cov.	12	E2,E3,W2
Vaccinium deliciosum Piper	23	C2,C3,C4,E2,E3,W2,GV
V. caespitosum Michx.	1	CP
FABACEAE	**1**	
Lupinus lepidus Dougl.	1	GV
JUNCACEAE	**69**	
Juncus drummondii var. *subtriflorus* (Mey.)Hitchc.	27	C1,C2,C3,E3,W2,W3
J. mertensianus Bong.	18	C1,C2,C3,E3,W2,W3
Luzula hitchcockii Hamet-Ahti	22	C1,C2,C3,C4,E2,W2,GV
Luzula parviflora (Ehrh.) Desv.	2	E3

[a] C = Central Chronosequence, E = East Chronosequence, W = West Chronosequence, CP = Cloudy Peak, GV = Glacier View Ridge.

Table 1.1 Plant species from Lyman Glacier forefront and nearby areas collected for root examination (continued).

Taxa	No. sampled	Collection Site[a]
LILIACEAE	**3**	
Erythronium grandiflorum Pursh	1	GV
Tofieldia glutinosa (Michx.) Pers.	1	E3
Veratrum viride Ait.	1	GV
ONAGRACEAE	**35**	
Epilobium alpinum L.	17	C1,C2,E2,W2,W3
E. angustifolium L.	1	GV
E. latifolium L.	15	C2,C4,E2,W2,W3
E. watsonii Barb.	2	E2,E3
PINACEAE	**27**	
Abies lasiocarpa (Hook.) Nutt.	10	C3,C4,E2
Larix lyallii Parl.	2	E2
Picea engelmanii Parry	2	E2
Tsuga mertensiana (Bong.) Carr.	13	C2,C4,E2,E3
POACEAE	**23**	
Agrostis variabilis Rydb.	2	E2
Deschampsia caespitosa (L.) Beauv.	3	E2
Festuca sp.	1	GV
Poa cusickii Vasey	4	E2
P. nevadensis Vasey	7	C2
Poa sp.	4	W2
Grass#1	1	GV
Grass#2	1	GV
POLEMONIACEAE	**1**	
Phlox diffusa Benth.	1	CP
POLYGONACEAE	**17**	
Oxyria digyna (L.) Hill.	15	C1,C2,C4,W2,W3
Polygonum bistortoides Pursh	2	C2, GV
POLYPODIACEAE	**7**	
Cryptogramma crispa (L.) R. Br.	4	W2
Cystopteris fragilis (L.) Bernh.	3	C2
ROSACEAE	**17**	
Luetkea pectinata (Pursh) Kuntze	15	C2,C3,C4,E2,CP, GV
Potentilla flabellifolia Hook.	1	GV
Sorbus sitchensis Roem.	1	GV

[a] C = Central Chronosequence, E = East Chronosequence, W = West Chronosequence, CP = Cloudy Peak, GV = Glacier View Ridge.

Table 1.1. Plant species from Lyman glacier forefront and nearby areas collected for root examination (continued).

Taxa	No. sampled	Collection Site[a]
SALICACEAE	**31**	
Salix commutata Bebb.	11	C2,C4,E3
S. nivalis Hook.	2	W2
S. planifolia Pursh	18	C1,C2,C3,C4,E3,W2
SAXIFRAGACEAE	**54**	
Saxifraga ferruginea Grah.	27	C1,C2,C3,C4,E2,E3
S. punctata L.	1	E2
S. tolmiei T. & G.	26	C1,C2,C3,C4,E2,W3
SCROPHULARIACEAE	**70**	
Castilleja parviflora Bong.	3	C2
Mimulus lewisii Pursh	12	C1,C2,E2,W2
M. tilingii Regel	15	C2,C3,C4,E2,W2,W3
Pedicularis attollens Gray	6	E2,E3
P. bracteosa Benth.	1	GV
P. groenlandica Retz.	8	C2,C3,E2,E3
Pedicularis sp.	1	GV
Penstemon davidsonii Greene	3	C2,W3
Veronica cusickii Gray	5	W2, GV
V. wormskjoldii Roem. & Schult.	16	C2,4,C4,E2,W2

[a] C = Central Chronosequence, E = East Chronosequence, W = West Chronosequence, CP = Cloudy Peak, GV = Glacier View Ridge.

Table 1.2. Plants species from Lyman Glacier forefront and their mycorrhizal status (1 Central Chronosequence).

Taxa	No. Sampled	Mycorrhizal Status [a,b]
Arenaria rubella	3	NM; NM; NM.
Carex nigricans	3	NM; NM; NM.
Epilobium alpina	3	NM; NM; NM.
Juncus drummondii var. *subtriflorus*	4	NM; NM; NM; DS +.
J. mertensianus	3	NM; NM; NM.
Luzula hitchcokii	3	NM; NM; DS +.
Mimulus lewisii	2	NM; VAM +.
Oxyria dygina	2	NM; NM.
Salix planifolia	1	DS +, EM +++.
Saxifraga ferruginea	3	NM; NM; DS +.
S. tolmiei	4	NM; NM; NM; NM.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.3. Plants species from Lyman Glacier forefront and their mycorrhizal status (2 Central Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Arenaria rubella	3	NM; NM; DS +.
Aster alpigenum	4	DS ++, VAM ++; DS ++, VAM ++; DS +++, VAM +; DS ++++, VAM +.
Carex scopulorum	3	NM; NM; DS ++.
Cassiope mertensiana	3	ER ++; ER ++++; ER ++.
Castilleja parviflora	3	VAM +; VAM +; VAM +, *G. tenue.*
Cystopteris fragilis	3	VAM +++; VAM ++; VAM +.
Epilobium alpinum	6	NM; DS +++, VAM ++++; VAM +; DS +, VAM +; DS +, VAM +; DS +, VAM +.
E. latifolium	5	NM; NM; NM; NM; DS +.
Juncus drummondii var. *subtriflorus*	6	NM; NM; NM; NM; DS ++; DS +++.
J. mertensianus	3	NM; NM; NM, Hyphae with arthrospores.
Luetkea pectinata	4	NM; DS +, VAM +; DS ++, VAM +; VAM +.
Luzula hitchcockii	3	NM; NM; DS +, many dark brown conidia on the surface.
Mimulus lewisii	5	NM; NM; NM; VAM +; VAM +.
M. tilingii	1	NM.
Oxyria dygina	3	NM; NM; NM.
Pedicularis groenlandica	3	NM; NM; DS +++.
Penstemon davidsonii	2	NM; VAM ++, hyphae and VAM spores on the surface.
Phyllodoce empetriformis	3	DS ++++, ER ++; ER +++; ER +.
Poa nevadensis	7	NM; DS +, VAM ++; VAM +++; VAM ++; DS +; DS +; DS ++, VAM +.
Polygonum bistortoides	1	EM +.
Salix commutata	5	DS +, EM ++++; DS ++, EM ++; EM ++; DS ++++, EM ++; DS +++, EM ++.
S. planifolia	3	DS ++++, VAM ++, EM +; DS ++, EM +++; DS ++, EM ++.
Saxifraga ferruginea	3	NM; NM; DS +.
S. tolmiei	9	DS +; NM all the rest.
Senecio fremontii	3	NM; NM; NM.
Tsuga mertensiana	4	NM; DS ++, EM +++; DS +, EM +++; DS ++, EM +++.
Vaccinium deliciosum	4	NM; ER ++++; ER +; ER +++.
Veronica wormskjoldii	3	DS +++, VAM +; DS ++, VAM +; DS +, VAM +.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.4. Plants species from Lyman Glacier forefront and their mycorrhizal status (3 Central Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Abies lasiocarpa	2	DS +, EM +; DS +, EM ++++.
Arenaria rubella	2	NM; NM.
Carex scopulorum	3	NM; NM; DS +.
Cassiope mertensiana	4	DS ++, ER ++; ER +; ER +; ER ++++.
Juncus drummondii var. *subtriflorus*	3	NM; NM; DS +.
J. mertensianus	3	NM; NM; DS ++.
Luetkea pectinata	2	DS +, VAM +; DS +, VAM +.
Luzula hitchcockii	3	NM; DS +; DS +.
Mimulus tilinguii	3	NM; NM; NM.
Pedicularis groenlandica	3	NM; DS +; DS +.
Phyllodoce empetriformis	3	DS +, ER ++; DS +, VAM ?, ER ++++; DS +++, ER +++.
Salix planifolia	5	DS +; DS +, EM ++++; DS +++, EM ++; DS ++++, EM +++; DS ++++, EM ++++.
Saxifraga ferruginea	5	NM; NM; NM; NM; NM.
S. tolmiei	2	NM; NM.
Vaccinium deliciosum	3	DS ++, ER +++; ER ++; ER ++.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.5. Plants species from Lyman Glacier forefront and their mycorrhizal status (4 Central Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Abies lasiocarpa	5	DS +, EM +++; EM ++; EM ++; EM +++; EM ++.
Arenaria rubella	7	NM; NM; NM; NM; DS +; DS ++, hyaline hyphae inside cells; VAM ++, fine endophyte, *G tenue*.
Carex sp.	4	NM; NM; NM; NM.
Cassiope mertensiana	3	DS ++++, ER +; DS ++, ER +++; DS ++, ER ++++.
Epilobium latifolium	3	NM, but many septate hyphae outside; VAM ++; VAM +.
Ledum glandulosum	2	DS +, ER +++; DS ++, ER +.
Luetkea pectinata	3	DS +++, VAM +++; DS ++, VAM +; VAM +.
Luzula hitchcokii	3	DS ++; DS ++; DS +.
Mimulus tilingii	2	NM; NM.
Oxyria dygina	1	NM.
Phyllodoce empetriformis	4	NM; DS +++, ER +; DS +, ER ++; DS +, VAM ?, ER ++++.
Salix commutata	4	DS ++++, VAM ++, EM ++++; DS +++, EM ++; DS +++, EM +; EM ++++.
S. planifolia	4	DS ++, EM +; DS ++, EM ++; DS +++, EM +++; EM ++.
Saxifraga ferruginea	7	All NM, but one sample had hyaline hyphae inside.
S. tolmiei	6	All NM. but one sample had hyaline hyphae inside.
Tsuga mertensiana	2	DS +, EM ++; DS ++, EM +++.
Vaccinium deliciosum	5	DS ++, ER ++++; DS ++, ER ++++; DS ++, ER ++++; ER +; ER +.
Veronica wormskjoldii	4	DS +++, VAM +; DS +, VAM +; VAM +; VAM +.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.6. Plants species from Lyman Glacier forefront and their mycorrhizal status (2 East Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Abies lasiocarpa	3	DS +, EM ++; VAM +, EM ++; EM +++.
Carex scopulorum	3	NM; NM; DS +.
Cassiope mertensiana	2	ER +; ER +.
Deschampsia caespitosa	3	NM; DS +, VAM ++, *G. tenue*; VAM +, *G. tenue*.
Epilobium alpinum	1	DS +, VAM +++.
E. latifolium	1	DS +, VAM +.
E. watsonii	1	NM.
Equisetum arvense	1	VAM +.
Juncus drummondii var. *subtriflorus*	7	NM; NM; NM; NM; NM; NM, clamp connections inside cells; DS ++.
Larix lyallii	2	EM +; EM ++++.
Luetkea pectinata	4	DS +++, VAM +; VAM +; VAM ++++; VAM ++.
Luzula hitchcockii	4	NM; NM; DS +; DS +, VAM +.
Mimulus lewisii	1	VAM +++.
M. tilingii	4	NM; NM; VAM +; DS +.
Pedicularis attollens	3	NM; NM; NM.
P. groenlandica	1	DS +, VAM ++.
Phyllodoce empetriformis	7	DS +, ER ++++; ER ++; ER ++; ER ++; DS +, ER ++; DS +, ER ++; DS +, VAM ?, ER ++++.
P. glanduliflora	7	DS +++, ER ++; ER ++; DS +++, ER ++; DS +, ER ++; DS +, ER +++; DS +, ER ++; ER ++.
Picea engelmanii	2	EM ++; EM ++.
Poa cusickii	4	NM; NM; DS +; VAM +++.
Saxifraga ferruginea	5	NM; NM; NM; DS +; VAM +.
S. punctata	1	DS +, VAM +.
S. tolmiei	3	NM; NM; NM.
Tsuga mertensiana	5	DS ++, EM ++; EM ++++; EM +++; DS +++, EM ++; DS +, EM ++.
Vaccinium deliciosum	4	DS +, ER +++; DS +, ER +++; DS +, ER; DS ++++, ER ++.
Veronica wormskjoldii	6	VAM ++; VAM +++; VAM ++++; VAM +; VAM ++; VAM ++.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.7. Plants species from Lyman Glacier forefront and their mycorrhizal status (3 East Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Agrostis variabilis	2	NM; NM.
Carex nigricans	1	NM.
C. spectabilis	2	NM; NM.
Cassiope mertensiana	3	DS +, ER ++; ER +; ER ++.
Crepis nana	2	DS +, VAM +++, *G. tenue;* VAM +++.
Epilobium watsonii	1	NM.
Juncus drummondii var. *subtriflorus*	3	NM; NM; NM.
J. mertensianus	3	NM; NM; DS +.
Ledum glandulosum	3	DS ++, ER +++; ER +; VAM ?, ER ++.
Luzula parviflora	2	NM; NM.
Pedicularis attollens	3	NM; NM; NM.
P. groenlandica	1	NM.
Phyllodoce empetriformis	2	ER +++; VAM ?, ER +++.
P. glanduliflora	3	VAM ?, ER ++++; DS ++, ER ++++; ER +++.
Salix commutata	2	DS ++++, VAM ++, EM +++; DS +, VAM +, EM +++.
S. planifolia	3	NM,young root tips; DS +, EM ++++; EM +++.
Saxifraga ferruginea	4	NM; NM; NM; DS +, VAM ?.
Senecio cymbalarioides	1	DS ++, VAM +++.
Tofieldia glutinosa	1	DS +.
Tsuga mertensiana	2	DS +, VAM ?, EM +++; DS ++, EM ++.
Vaccinium deliciosum	3	DS +, ER ++; DS +, VAM +, ER +++; VAM ?, ER +++.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.8. Plants species from Lyman Glacier forefront and their mycorrhizal status (2 West Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Arenaria rubella	3	NM; NM; NM, but many VAM spores and hyphae in the outside.
Carex nigricans	2	NM; DS +, VAM +, Hyphae, arbuscules and spores, but no vesicles.
C. scopulorum	1	NM.
Cassiope mertensiana	1	ER +.
Crepis nana	3	VAM ++; VAM ++; VAM +.
Cryptogramma crispa	4	VAM ++; VAM +; VAM +; VAM +, spore outside.
Epilobium alpinum	4	NM; NM; DS +, VAM +; DS +, many superficial hyphae.
E. latifolium	3	DS ++, VAM +++; VAM +, spores; DS ++, VAM +.
Juncus drummondii var. *subtriflorus*	4	NM; NM; DS +, VAM +++; DS +.
J. mertensianus	3	NM; NM, but VAM spores outside the roots; DS +, VAM +.
Luzula hitchcockii	4	NM; DS +; DS +; VAM +.
Mimulus lewisii	4	DS +; VAM ++; VAM +++, *G. intraradices*; VAM ++.
M. tilingii	4	NM; VAM ++; VAM +; VAM +.
Oxyria digyna	8	NM; NM; DS +; DS ++; DS ++; VAM +; DS ++, VAM ++; DS +++, VAM +.
Phyllodoce empetriformis	4	DS +, ER +++, many brown conidia; DS +, ER +; DS +, ER +++; ER +.
P. glanduliflora	2	DS ++, ER +++; DS +, ER +.
Poa sp.	4	NM; DS +; DS ++, VAM +++; DS ++, VAM +.
Salix nivalis	2	DS +, VAM ++, EM ++; DS +, EM +++.
S. planifolia	2	DS +, EM ++; DS +, EM +++.
Senecio fremontii	4	NM; VAM +++; VAM ++; VAM +++.
Vaccinium deliciosum	3	ER +; ER ++; ER ++.
Veronica cusickii	4	DS +, VAM ++; VAM ++; DS ++, VAM ++; VAM +++.
V. wormskjoldii	3	DS +, VAM +; VAM +; VAM +++.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.9. Plants species from Lyman Glacier forefront and their mycorrhizal status (3 West Chronosequence).

Taxa	No. sampled	Mycorrhizal Status [a,b]
Arenaria rubella	3	NM; NM; NM.
Epilobium alpinum	3	NM; NM; NM.
E. latifolium	3	NM; NM; NM.
Juncus mertensianus	3	NM; NM; DS +.
Mimulus tilingii	1	DS +.
Oxyria digyna	1	NM
Penstemon davidsonii	1	DS +, many hyphae outside.
Saxifraga tolmiei	2	DS +, hyaline hyphae inside; NM, hyaline hyphae inside.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.10. Plants species from Glacier view ridge top (adjacent meadow) and their mycorrhizal status.

Taxa	Mycorrhizal Status [a, b]
Anaphalis margaritacea	DS ++, VAM +.
Anemone occidentalis	DS ++, VAM +++.
Carex sp.	DS +++, VAM +.
Cassiope mertensiana	ER +.
Epilobium angustifolium	DS ++, VAM +.
Erythronium grandiflorum	DS ++, VAM ++.
Grass (984)	DS +, VAM +.
Grass (987)	DS ++, VAM +.
Festuca sp.	DS ++.
Luetkea pectinata	DS ++.
Lupinus lepideus	DS ++.
Luzula hitchcockii	DS +++, VAM +.
Pedicularis bracteosa	DS ++++.
Pedicularis sp.	DS +.
Phyllodoce empetriformis	DS ++, ER ++++.
Polygonum bistortoides	DS +++, EM +.
Potentilla flabellifolia	DS ++++, VAM ++++, EM +.
Sorbus sitchensis	DS +, VAM +++, EM +.
Vaccinium deliciosum	DS ++, ER +++.
Veratrum viride	DS ++, VAM ++.
Veronica cusickii	DS +++.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.11. Plants species from Cloudy peak ridge top (adjacent meadow) and their mycorrhizal status.

Taxa	Mycorrhizal Status [a, b]
Anemone occidentalis	DS +, VAM +.
Draba oligosperma	DS +.
Erigeron aureus	DS ++, VAM ++.
Luetkea pectinata	DS +.
Phlox diffusa	DS +, VAM ++.
Phyllodoce empetriformis	DS +++, VAM +++, ER +.
Vaccinium caespitosum	DS +.

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage of mycorrhizal roots from the random sample as well dark-walled septate endophytes; (+), 1-25%; (++), 26-50%; (+++), 51-75%; (++++), 76-100%.

Table 1.12. Soil pH and carbon, nitrogen and phosphorus contents for the Lyman Glacier forefront and an adjacent meadow.

Site	pH	C	N	P
		%	mg/l	
Central 0	7.02	0.069	55	398
Central 2	4.49	0.055	118	411
East 2	4.51	0.110	223	394
West 2	6.08	0.055	120	379
Glacier View Ridge	4.80	6.590	2580	438

Table 1.13. Total cations of soils of the Lyman Glacier forefront and an adjacent meadow.

Site	Al	Ca	Mg	Na	K	Cu	Fe
	Perchloric acid digest method (mg/Kg)						
Central 0	21700	7400	8600	2100	7100	110	29100
Central 2	20800	5300	8900	1700	7400	96	29300
East 2	30700	7200	8500	2600	5400	58	31600
West 2	21700	9300	7000	2500	3800	50	26600
Glacier View Ridge	10300	1700	450	2000	530	7	8500

Table 1.14. Extractable cations of soils of the Lyman Glacier forefront and an adjacent meadow.

Site	Al	Ca	Mg	Na	K	Cu	Fe
	Ammonium Acetate method (mg/Kg)						
Central 0	8	580	101	26	246	3.5	9.3
Central 2	10	143	24	14	128	11.1	8.2
East 2	17	51	4	12	38	2.7	6.4
West 2	11	362	39	12	81	1.8	9.9
Glacier View Ridge	83	66	13	12	60	0.7	11.4

Table 1.15. Comparison of pH, and totals of carbon, nitrogen and phosphorus for the central chronosequence of the Lyman glacier forefront.

	pH		C %		N mg/l		P mg/l	
Site	N R [a]	R Z [b]	N R	R Z	N R	R Z	N R	R Z
1	4.81	5.80	0.061	0.089	53.6	66.4	244	293
2	5.26	6.19	0.069	0.115	49.7	73.7	276	297
3	6.21	6.23	0.077	0.077	40.9	31.7	282	211
4	6.58	6.34	0.060	0.079	22.1	32.4	225	225

a N R= Soil sample collected where no plants were growing.

b R Z= Soil sample collected from the plant root zone.

Table 1.16. Comparison of total cations for the central chronosequence of the Lyman glacier forefront.

	Al		Ca		Mg		Na		K		Cu		Fe	
	Perchloric acid digest method (Total mg/Kg)													
Site	NR [a]	RZ [b]	NR	RZ	NR	RZ	NR	RZ	NR	RZ	NR	RZ	NR	RZ
1	21600	21200	2900	3300	8300	8700	2900	2900	7200	8000	83	65	26500	26900
2	21000	22100	4600	4400	8400	8600	2200	2500	7300	7200	75	83	24800	26200
3	27400	27800	4300	4600	10700	9900	2200	2200	9100	4600	115	107	29300	27800
4	26900	27400	4600	4300	9800	10200	2200	2200	7800	4300	93	109	26800	28400

a NR= Soil sample collected where no plants were growing.

b RZ= Soil sample collected from the plant root zone.

Table 1.17. Comparison of extractable cations for the central chronosequence of the Lyman glacier forefront.

	Al		Ca		Mg		Na		K		Cu		Fe	
	Ammonium acetate method (mg/Kg)													
Site	NR [a]	RZ [b]	NR	RZ	NR	RZ	NR	RZ	NR	RZ	NR	RZ	NR	RZ
1	4.45	0.05	884	637	124	135	120	121	205	141	3.02	0.32	0.11	0.43
2	7.21	10.82	893	1025	123	152	117	116	111	195	4.80	3.95	0.16	0.05
3	3.55	4.69	562	910	95	169	119	126	122	167	7.10	2.21	0.05	0.21
4	3.15	7.07	827	409	93	77	118	118	70	131	2.29	2.40	0.05	0.11

a N R= Soil sample collected where no plants were growing.

b R Z= Soil sample collected from the plant root zone.

Table 1.18. Proportion of plant species of different mycotrophic habit along the central chronosequence sampling line on the Lyman Glacier forefront.

		Mycotrophic Habit [b]			
				Mycorrhiza Dependent	
Site	Years of exposure [a]	NM	F	A	S
0	15	0	0	0	0
1	25	55	36	9	0
2	35	25	36	25	14
3	45	40	27	33	0
4	60	22	28	44	6

[a] Number of years since the ground was exposed from under the receding glacier.

[b] NM= nonmycorrhizal, F= facultatively mycorrhizal, A= mycobiont dispersed by air, S= mycobiont dispersed by soil movement.

Table 1.19. Occurrence of mycorrhizal colonization in the Lyman Glacier forefront.

Site	No. sampled	Mycorrhizal status [a]				
		NM	DS	VAM	ER	EM
		%				
0 central [b]		0	0	0	0	0
1 central	31	84[c]	13	3	0	3
2 central	105	43	35	28	9	11
3 central	46	43	46	4	22	13
4 central	69	38	42	16	19	22
2 east	85	29	35	27	23	14
3 east	47	45	32	13	30	13
2 west	76	22	41	49	13	5
3 west	17	76	24	0	0	0
Total	476	40	36	23	16	12

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b This site lacked of vegetation.

c Percentage is number of samples colonized, except NM in which is number of samples noncolonized.

Table 1.20. Plant families from Lyman Glacier and their mycorrhizal status.

Family	No sampled	Mycorrhizal Status [a]				
		NM	DS	VAM	ERM	EM
				%		
Asteraceae	17	23 [b]	35	**76**	0	0
Caryophyllaceae	**21**	**81**	14	5	0	0
Cyperaceae	**22**	**82**	18	4	0	0
Equisetaceae	1	0	0	**100**	0	0
Ericaceae	78	2	51	1	**97**	0
Juncaceae	**67**	**64**	34	6	0	0
Liliaceae	1	0	**100**	0	0	0
Onagraceae	**34**	**56**	38	38	0	0
Pinaceae	27	4	52	4	0	**96**
Poaceae	20	35	**45**	**45**	0	0
Polygonaceae	**16**	**56**	31	19	0	7
Polypodiaceae	7	0	0	**100**	0	0
Rosaceae	13	8	54	**92**	0	0
Salicaceae	31	3	84	16	0	**94**
Saxifragaceae	**54**	**85**	13	4	0	0
Scrophulariaceae	67	36	24	**54**	0	0

a Fungal root colonizers and mycorrhizae types: NM= Nonmycorrhizal; DS= Dark-walled septate endophyte; VAM= Vesicular-arbuscular; ER= Ericoid and EM= Ectomycorrhizal.

b Percentage is number of samples colonized, except in NM in which is number of samples noncolonized.

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Chapter 2

Vesicular-Arbuscular Mycorrhizae in the Pinaceae

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SUMMARY

Vesicular-arbuscular mycorrhizae are reported for seedlings of *Abies lasiocarpa*, *Pseudotsuga menziesii*, *Tsuga heterophylla* and *T. mertensiana* growing in their natural habitats. Collected seedlings grew in openings and under a closed forest canopy. Different rates of VAM colonization were observed among conifer species and between forest canopies.

INTRODUCTION

Vesicular-arbuscular mycorrhizae (VAM) are characteristic of most herbaceous plant species (Harley and Harley, 1987; Trappe, 1987). In the Coniferophyta VAM characteristically form on all families except the Pinaceae, which usually have been assumed to be ectomycorrhizal (EM)(Harley and Smith, 1983).

"Endotrophic mycorrhizae" were reported for *Pinus monophylla* Torr. & Frém. and *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco (as *Pseudotsuga mucronata* Sudw.) by McDougall & Jacobs (1927). Their drawing of the *Pseudotsuga* mycorrhiza, though not detailed, shows hyphal coils similar to those common in VAM of the Cupressaceae. Henry (1933, 1934), Asai (1934), Dominik (1951) and Shvartsman (1955) recorded "endotrophic mycorrhizae" on various species of Pinaceae, but they did not differentiate between VAM and other intracellular forms such as ericoid or ectendomycorrhizae, so their reports cannot be evaluated.

The first unequivocal record of VAM in the Pinaceae was by Golubinskaya (1967), who presented a convincing drawing of VAM hyphae and vesicles in roolets of *Picea obovata* Led. She also found typical VAM vesicles in *Larix sibirica* (DuRoi) Koch, *Pinus sibirica* DuTour and *Pinus sylvestris* L. Similar hyphae were observed in *Abies sibirica* Led., but no vesicles were observed. Dowgiallo and Rambelli (1972) subsequently described VAM on *Pinus halepensis* Mill., and Malloch and Malloch (1981) reported VAM vesicles in rootlets of *Abies balsamea* (L.) Mill. and *Larix laricina* (DuRoi)Koch.

Mycorrhiza researchers, ourselves included, either ignored these findings or dismissed them as atavistic curiosities with little relevance to the biology of the Pinaceae. Recently, however, Douglas-fir [*Pseudotsuga*

menziesii (Mirb.) Franco var. *menziesii*] and western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] were discovered to form VAM in a soil bioassay study (Cázares and Smith, 1991). This led us to examine field-grown members of these species for VAM to determine whether or not the phenomenon was common in natural habitats. Subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] and mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.] were also examined because of our studies on mycorrhizal ecology of those species.

MATERIALS AND METHODS

Study area

Douglas-fir seedlings were collected along the side of Higley Peak Rd. (47° 31' N. lat., 123° 54 W. long., elev ca 1000 m), Jefferson Co. Washington. Western hemlock seedlings were collected near Lake Quinault (47° 30' N. lat., 123° 58 W. long, elev ca 500 m), Grays Harbor Co. Washington. Subalpine fir and mountain hemlock seedlings were collected near Lyman lake (48° 12' N. lat., 120° 551 W. long. elev1708 m) Glacier Peak Wilderness Area, Wenatchee National Forest, Chelan Co., Washington. The vegetation is typical for the mountain hemlock subalpine forest (Franklin and Dyrness, 1973). Annual precipitation averages 2750 mm, mostly as snow which accumulates from November through April (Mann and Dull, 1979).

Sampling

All seedlings sampled were 2 to 4 years old. Eight seedlings of Douglas-fir were from a gravelly roadbank among grasses and forbs. Fifteen seedlings of western hemlock were from under a closed forest canopy among understory shrubs and forbs. Twenty-five seedlings of subalpine fir and two of mountain

hemlock were from openings among grasses and forbs along the edge of a trail. Thirteen seedlings of subalpine fir and ten seedlings of mountain hemlock were collected from under a closed forest canopy with little ground vegetation.

Clearing and staining

Entire root systems were washed in running tap water, cut in pieces to fit in Tissue-Tek plastic capsules (Fisher Scientific Co., Pittsburgh, PA), cleared in a 15% H_2O_2 solution for 10 min, rinsed with tapwater, and autoclaved for 3 min at 121 ^oC in a 10% KOH solution. The KOH solution was decanted and root samples were rinsed with tapwater, steamed for 30 min in a 10% KOH solution, rinsed again with tap water, placed in 1% HCL for 30 min and again rinsed with tapwater. Cleared samples were steamed for 30 min in a staining solution of 0.5% trypan-blue in lactoglycerol, rinsed with tapwater and stored in lactoglycerol or water at 4 ^oC until microscopic examination.

Assessing VAM colonization

VAM colonization was evaluated by stereo- and compound microscopy by the following categories: (+), presence of more than ten vesicles per root system; (+ -), presence of less than ten vesicles per root system; (-), complete absence of vesicles. In many cases apparent VAM-type hyphae were present but vesicles were absent. To avoid overestimating the presence of true VAM, however, we chose vesicles as the criterion for demonstrating VAM. No arbuscules were seen, although Cázares and Smith (1991) reported them from Pinaceae.

RESULTS AND DISCUSSION

For seedlings grown in openings, ten or more VAM vesicles were observed in 15 of the 25 subalpine firs, three of the eight Douglas-firs, and both of the mountain hemlocks. Western hemlock were not collected from openings. For seedlings grown under the closed forest canopy, ten or more vesicles were observed in one of the 13 subalpine firs, one of the 15 western hemlocks, and none of the ten mountain hemlocks. No Douglas-fir seedlings were collected from under a closed canopy forest (Table 2.1).

VAM were more common in seedlings from openings than from under the closed forest canopy. In the openings, at least some vesicles were present in 76% of the subalpine firs, 87% of the Douglas-firs and both of the mountain hemlocks. In the closed forest canopy, VAM were present in 16% of the subalpine firs, 12% of the western hemlocks seedlings and 20% of the mountain hemlocks.

Ectomycorrhizae were always present on the seedlings examined, and dark-walled septate endophytes were commonly present in roots of subalpine fir and mountain hemlock. Seedlings from under a closed forest canopy were more heavily colonized by *Cenococcum geophilum* Fr. than those from openings.

Differences in vegetation and soil characteristics were observed between openings and closed forest canopy. The openings were located along a trail of a loose, exposed soil or along a roadbank, mainly colonized by forbs and grasses. The understory vegetation under the closed forest canopy was sparse and growing among considerable woody debris. VAM inoculum potential was not determined, but we hypothesize that VAM colonization of Pinaceae relates to the presence of higher levels of VAM fungi propagules in the openings then

under the canopy and possibly to the presence of typically VAM companion plants.

Succession from VAM to EM in the same root system has been described for *Helianthemum* (Read *et al.*, 1977), *Eucalyptus* (Lapeyrie and Chilvers, 1985; Chilvers *et al.*, 1987) and *Alnus* (Lin *et al.*, 1987). Malajczuk *et al.* (1981) demonstrated that eucalypts, which are normally strongly ectomycorrhizal, would readily form VAM when inoculated with suitable fungi and hypothesized that this ability could be important in early succession on disturbed soil.

We have no evidence on the effects of VAM colonization in the Pinaceae. Our intent was to determine if it occurs in nature. More studies on the occurrence of this phenomenon among the members of the Pinaceae in their natural habitats are needed. VAM are important in revegetation of disturbed habitats (Allen *et al.*, 1987). And, once VAM hosts become established, they are a main source of inoculum for new host plants (Read *et al.*, 1976). The ecological importance of VAM in survival and growth of Pinaceae in open habitats with high VAM inoculum potential (such as clearcuts), as well as in forests where the overstory species are EM hosts, remains to be determined. It is clear to us at this stage, however, that studies of the role of mycorrhizae in establishment of Pinaceae in clearcuts, burns, and other disturbed habitats is incomplete if only ectomycorrhizae are considered. Staining root systems for VAM determination should be routine for such work.

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Table 2.1. Occurrence of VAM in seedlings of the Pinaceae

	Forest canopy					
	Open			Closed		
	VAM status (%) [d]					
Taxa	(+) [a]	(+ -) [b]	(-) [c]	(+)	(+ -)	(-)
Abies lasiocarpa	60 (15/25)	16 (4/25)	24 (6/25)	8 (1/13)	8 (1/13)	84 (11/13)
Pseudotsuga menziesii	37 (3/8)	50 (4/8)	12 (1/8)	---	---	---
Tsuga heterophylla	---	---	---	6 (1/15)	6 (1/15)	87 (13/15)
Tsuga mertensiana	100 (2/2)	---	---	0 (0/10)	20 (2/10)	80 (8/10)

[a] Presence of more than ten vesicles per root sample.

[b] Presence of less than ten vesicles per root sample.

[c] Complete absence of vesicles in the root sample.

[d] Percentage is number of samples colonized, fraction is number of colonized over total number of samples examined of each species.

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Chapter 3

Spore Dispersal of Hypogeous, Ectomycorrhizal Fungi on a Glacier Forefront by Mammal Mycophagy

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SUMMARY

To assess the role of mammal mycophagy in ectomycorrhizal inoculation of outwash and moraines exposed by recession of a subalpine glacier, fecal pellets of animals inhabiting the glacier forefront and nearby, well established plant communities were examined for fungal spore content. Tracks, sightings and feces of deer and mountain goats indicated that they commonly visited the forefront. Pikas, marmots and chipmunks resided in the older, partly vegetated areas of the forefront, especially among morainal rocks. Spores of

ectomycorrhizal fungi, especially hypogeous species, were found in feces of all these animals on the forefront, indicating that mycophagy disperses fungi from nearby sources onto the forefront.

INTRODUCTION

Fungi are an important food for many animals, and the animals in turn disperse spores of the fungi; most fungi consumed are mycorrhizal symbionts with plant roots (Maser *et al.*, 1978; Fogel and Trappe, 1978; Hayes *et al.*, 1986). Hypogeous fungi (truffles and false truffles) particularly depend on animal mycophagists for spore dispersal (Trappe and Maser, 1977). The spores remain viable after passage through the mammalian digestive tract (Trappe and Maser, 1976; McIlveen and Cole, 1976; Rothwell and Holt, 1978; Kotter and Farentinos, 1984; Trappe and Castellano, unpublished data). Most hypogeous fungi can be identified to family or genus by spore morphology (Castellano *et al.,* 1989).

Free-living nitrogen-fixing bacteria resident in sporocarps of mycorrhizal fungi are also dispersed along with the fungal spores by mammal mycophagy (Li and Castellano, 1985; Li *et al.*, 1986). These bacteria could be significant to the nitrogen budgets of plants colonizing new substrates such as glacial deposits.

Our discovery of a hypogeous fungus associated with *Salix* mycorrhizae on the forefront of the receding Lyman Glacier (Cázares and Trappe, 1990) suggested that animals have transported spores of such fungi from adjacent plant communities onto the forefront itself. Lyman Glacier terminates in the mountain hemlock vegetation zone in the the Glacier Peak Wilderness Area of

the North Cascade Mountains, Chelan County, Washington (Franklin and Dyrness, 1973). Its forefront supports an evolving, subalpine plant community.

Adjacent to the forefront is a long established subalpine parkland of meadows, heather, and clumps of *Abies lasiocarpa* (Hook.) Nutt., *Larix lyallii* Parl., *Tsuga mertensiana* (Bong.) Carr., and *Salix* spp. These trees and shrubs support hypogeous, ectomycorrhizal fungi such as *Elaphomyces granulatus* Fr., *E. muricatus* Fr., *Gastroboletus ruber* (Zell.) Cázares. & Trappe, *Hymenogaster glacialis* Cázares & Trappe, *Macowanites lymanensis* Cázares & Trappe, *Rhizopogon subsalmonius* Smith, *R. vulgaris* (Vitt.) Lange, and *Thaxterogaster pingue* (Zeller) Singer & Smith.

Tracks, sightings and fecal deposits of mule deer (*Odocoileus hemionus*) and mountain goats (*Oreamnos americanus*) attested to travel on the forefront by these animals. No sign of black bear (*Ursus americanus*) was detected on the forefront, but feces were collected at nearby Lyman Lake. Yellow-pine chipmunks (*Eutamias amoenus*), hoary marmots (*Marmota caligata*), and pikas (*Ochotona princeps*) were resident in the more vegetated, older parts of the forefront, especially near rocky moraines. Heather voles (*Phenacomys intermedius*) lived in adjacent parkland and possibly in older, vegetated parts of the forefront. Mycophagy was investigated by examination of fecal pellets of these mammals collected from the Lyman glacier forefront and nearby habitats. Several other small mammals, as listed by Reichel (1986), were likely active on or near the forefront, but we neither observed them nor found identifiable feces.

MATERIALS AND METHODS

Fecal pellets were collected opportunistically, air dried and stored in paper bags. The mammal sources of the fecal pellets were determined by size, shape and correlation with the mammals inhabiting the collection area. The methods for identification of fungal spores in the fecal pellets were those of Castellano *et al.* (1989). Fragments of several pellets from each collection were soaked in Melzer's reagent, then examined by use of a compound microscope.

RESULTS AND DISCUSSION

Of the 41 fecal samples collected (Table 3.1), 29 were from the glacier forefront and 12 were from nearby areas. Pika pellets were largely aggregated near nests among piles of rocks in terminal moraines. Marmot and chipmunk pellets were mostly scattered near burrows among rocks, although marmot feces were also present at distances of more than a hundred meters from the nearest burrow. Heather voles defecate in latrines, which consequently may contain thousands of pellets; we found heather vole latrines only in meadow and heather communities near the forefront. Deer pellets were widely distributed, although not generally abundant, on the forefront and adjacent parkland. Mountain goat pellets were found only within 200 m of the present glacier terminus; on some occasions a mountain goat watched us sampling soils and plants in study plots. The one black bear collection was from a forested area below the forefront.

None of the samples contained large concentrations of spores. When present, spores were scattered or in small clusters in the samples. In all 41

samples, 19 contained spores identifiable to genus or family, six had unidentifiable spores, and 16 lacked spores.

Of 11 collections of pika pellets, nine were from the forefront and two from nearby areas. Seven of the 11 contained spores of ectomycorrhizal fungi, including two species of *Rhizopogon* plus *Elaphomyces*, *Genea*, *Melanogaster*, and *Tuber*, species, one species each in the Octavianinaceae, Boletaceae, and Cortinariaceae, and at least 12 spore types that could not be identified to family or genus. Pikas have been earlier reported as mycophagists (Maser *et al.*, 1978)

All 12 samples of hoary marmot feces were from the forefront. Nine contained fungi, including the ectomycorrhizal genera *Cortinarius*, *Elaphomyces*, *Rhizopogon*, *Tuber*, the hyperparasitic genus *Microthecium*, and four types in the Ascomycotina that could not be identified to family.

Two of the three chipmunk fecal collections were from the forefront, one from a nearby area. Two of the three had ectomycorrhizal fungal spores, including species in the ectomycorrhizal genera *Elaphomyces* and *Genea*, plus at least two that could not be identified to family. Yellow-pine chipmunks are well established as mycophagists (Maser *et al.*, 1978).

Two of the four samples of heather vole fecal pellets contained spores not identifiable to family: two in the Ascomycotina and one in the Basidiomycotina. Heather voles are little studied in relation to mycophagy, but the one record in the literature indicates that they eat hypogeous fungi (Maser *et al.*, 1978).

Five of the six samples of deer fecal pellets were from the forefront. Two of the six contained ectomycorrhizal fungal spores, all in the Cortinariaceae, including one probably being *Thaxterogaster pingue*. Deer often eat

hypogeous fungi, especially in late fall when browse species have dried out (Trappe, unpublished data).

The one black bear collection contained spores of a member of the Ascomycotina not identifiable to family. Black bears are omniverous and often eat hypogeous fungi (Trappe, unpublished data).

One of four samples of mountain goat pellets contained fungi, at least one ectomycorrhizal species in the Cortinariaceae and one not identifiable to family in the Ascomycotina. To our knowledge, this is the first report of mycophagy by mountain goats.

Most spores identifiable to family or genus in these samples were of ectomycorrhizal fungi commonly associated with trees near the glacier forefront or shrub willows on or near the forefront. One exception was the *Microthecium* sp., which was likely a hyperparasite on the fruiting body of one of the ectomycorrhizal, hypogeous fungi.

Animal mycophagists clearly disperse ectomycorrhizal inoculum onto the forefront for receptive colonizing hosts. Pikas, marmots and chipmunks eat and excrete spores of *Elaphomyces* and *Rhizopogon* spp., common hypogeous mycobionts of the Pinaceae in the area. *Hymenogaster glacialis* Cázares & Trappe was associated with mycorrhizae of *Salix* spp. established on 60-80 year-old moraines on the Lyman Glacier forefront (Cázares and Trappe, 1990). Quite likely that fungus was dispersed by an animal mycophagist from nearby willow communities.

Because these small mammals do not travel long distances, their transport of spores from established tree or shrub hosts to uncolonized soil probably proceeds at a slow, erratic, stepwise pace. Deer, on the other hand, can be effective agents of long-distance dispersal. We found spores of only one hypogeous fungus, *Thaxterogaster pingue,* a mycobiont of *Abies lasiocarpa,* in

the deer feces examined. However, deer can be avid eaters of hypogeous fungi (Trappe, unpublished data); *Elaphomyces granulatus,* the hypogeous fungus we most often found in the Lyman glacier area, is known in Europe as the "stag truffle" because it is so commonly dug up and eaten by deer. The very name of the genus, from Greek, indicates this: *Elapho-* (deer) and *-myces* (fungus). Mule deer are also documented as eaters of *Rhizopogon* spp. (Trappe, unpublished data).

Except for *Hymenogaster glacialis,* the ectomycorrhizal fungi that we observed to fruit in association with willows or Pinaceae on the forefront were of mushroom-forming species, particularly in the genera *Cortinarius, Dermocybe, Inocybe* and *Russula.* Their spores are primarily dispersed by air, so they would predictably be the most effective in inoculating the forefront soil for early establishment of ectomycorrhizal hosts (Trappe, 1988). In that sense they are more important for initial colonization than the hypogeous fungi dispersed by animal mycophagy. Establishment of the hypogeous species in seral plant communities, however, inserts diversity that may be useful to maintenance of plant health and survival in stressful habitats such as the Lyman Glacier forefront.

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Table 3.1. Occurrence of spores of fungal taxa in mammal feces collected from Lyman Glacier forefront and nearby habitats.

Animal species	No. of samples	Fungal genera
Pika	11	*Rhizopogon* , *Melanogaster*, *Cortinarius*, *Elaphomyces*, *Genea*, *Tuber*, four unidentified Basidiomycotina and five unidentified Ascomycotina
Hoary marmot	12	*Rhizopogon* (two spp.) *Cortinarius*, *Elaphomyces*, *Tuber*, *Microthecium* and two unidentified Ascomycotina
Yellow-pine chimpmunk	3	*Genea*, *Elaphomyces* and one unidentified Ascomycotina
Heather vole	4	Two unidentified ascomycetes and one Basidiomycotina
Mule deer	6	*Cortinarius*
Mountain goat	4	*Cortinarius* and one unidentified Ascomycotina
Black bear	1	One unidentified Ascomycotina

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Chapter 4

Alpine and Subalpine Fungi of the Cascade Mountains. I. *Hymenogaster glacialis* sp. nov.

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SUMMARY

A new *Hymenogaster* species is described from a fungal community in the recently exposed forefront of Lyman glacier in the North Cascades, Washington.

INTRODUCTION

The Cascade mountains run north-south from southern British Columbia to northern California, forming a barrier to storms blowing east from the Pacific Ocean. The range creates a sharp west to east moisture gradient, with heavy precipitation on the west slopes grading in a pronounced rain shadow to steppe and tundra on the farthest eastern slopes. Heavy snowfall near the crest has produced heavy glaciation in the past. Glaciers are presently active on higher peaks in the south and even relatively low summits to the north, especially in northern Washington state. Glaciation has produced deeply dissected topography, resulting in strikingly different habitats over distances of less than a hundred meters. Ancient and recent volcanism has further imprinted the Cascade landscape with diversity, ranging from high volcanic peaks to tephra deposits of varying texture and depth.

This is the first report of our studies of fungi of the Cascades. One area that we have studied intensively is the forefront of the receding Lyman glacier (Fig. 4.1a). This subalpine area (elev. ca. 1900 m.) is characterized by well-developed moraines, fluting, and outwash. The newest plant colonization is on moraines exposed from the receding ice for 40-60 years; these infant communities include nonmycorrhizal *Carex*, *Juncus*, and *Saxifraga* spp. and ectomycorrhizal *Salix spp.* and *Abies lasiocarpa* (Hook.) Nutt. Older moraines support increasingly diverse communities, with *Salix* spp. as low, scattered shrub dominants.

METHODS

Methods of collection and study of macroscopical features are essentially those of Smith (Smith and Zeller, 1966). Glacier forefronts are very stony, however, we have discovered many sporocarps, even of agarics, by looking under stones. That was how the undescribed *Hymenogaster* was discovered. Microscopical features are essentialy those used by Fogel (1985). Color names are given as the ISCC-NBS color number (Kelly and Judd, 1955).

DESCRIPTION

Hymenogaster glacialis Cazares & Trappe, *sp. nov.*

Fig. 4.2a-c.

BASIDIOMATA *3-6 mm in diam, subglobosa, coacta, sordide alba.* ***GLEBA*** *brunnea, loculis irregularibus, usque ad 1 mm in diam.* ***COLUMELLA*** *absens.* ***PERIDIUM*** *evanescens, 30-150 µm crassum; epicute 20-100 µm crassa, hyphis hyalinis, cellulis elongatis vel subglobosis usque ad 20 µm in diam; subcute 30-60 µm crassa, hyphis hyalinis, intertextis, usque ad 5 µm in diam.* ***TRAMA*** *20-80 µm crassa, hyphis confertim subparallelis vel intertextis, usque ad 5 µm in diam.* ***SUBHYMENIUM*** *cellulis hyalinis, subglobosis, usque ad 5-20 µm in diam.* ***BASIDIA*** *20-25 x 5-9 µm, cylindrica, hyalina, 4-spora.* ***SPORAE*** *15-18 (-19) x (-11) 12-15 (-16) µm, ornamentum includens, L/W= 1.18-1.25 late ellipsoideae vel ellipsoideae, ornamento verrucoso-rugoso usque ad 2 µm alto; apex papillatus; basis truncata, 1-2 µm crassa; in KOH singulatim brunneae, aggregatae obscure brunneae.* ***HOLOTYPUS:*** *Trappe # 10418 (OSC).*

BASIDIOMATA 3-6 mm in diam, subglobose, surface felty, sordid white, unchanging upon drying. **GLEBA** deep brown (ISCC-NBS 56), locules irregularly shaped and up to 1 mm in diam, randomly arranged. **COLUMELLA** absent, but some young sporocarps have cottony sterile tissue at the base. **RHIZOMORPHS** absent. **ODOR** not distinctive, taste not determined.

PERIDIUM evanescent, 30-150 µm thick, two-layered: epicutis 20-100 µm thick, of hyaline, thin-walled hyphae up to 5 µm at septa,with elongated to inflated cells up to 20 µm in diam; subcutis 30-60 µm thick, of hyaline, thin-walled, interwoven hyphae up to 5 µm in diam; clamp connections absent.

TRAMA 20-80 µm wide, of compact, thin-walled, subparallel to interwoven, hyaline, nongelatinous hyphae up to 5 µm in diam; clamp connections absent. **SUBHYMENIUM** of 2-3 rows of hyaline, thin-walled, compactly arranged, subglobose cells, 5-20 µm in diam. **BASIDIA** 20-25 x 5-9 µm, cylindrical, hyaline, thin-walled, 4-spored, clamp connections absent at base.

SPORES 15-18 (-19) x (-11) 12-15 (-16) µm including ornamentation, but not beak or pedicel, L/W=1.18-1.25; broadly ellipsoid to ellipsoid; the ornamentation warty-wrinkled and up to 2 µm tall; apex papillate, 1-3 x 1-3 µm, paler than spore proper, not ornamented; base truncate, 1-2 µm wide. In KOH, brown singly, dark brown in mass; in Melzer's reagent, golden brown singly, orange brown to reddish brown in mass.

ETYMOLOGY: Latin, "of glacial".

HOLOTYPE: Washington, Chelan County, Lyman Glacier forefront, 2 September 1988, elevation 1900 m, hypogeous under stones in wet area among dwarf *Salix* roots in raw moraine, leg. Efrén Cázares and Jim Trappe # 10418 (OSC).

NOTES: Spore dimensions of this species clearly relates it to *H. gilkeyae* Zeller & Dodge (Zeller & Dodge, 1934), which has spores 15-22 x 10-11 μm. The small size of the basidiomata, the evanescent, thin peridium and the relatively large locules of the gleba distinguish *H. glacialis* from the other *Hymenogaster* spp.

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Fig. 4.1. (a) Lyman glacier forefront. Arrow marks dwarf willow clumps.

Fig. 4.1

Fig. 4.2. ***Hymenogaster glacialis.*** (a) Dried sporocarps in surface view and in cross-section, photo courtesy of Dr. D. Luoma. Bar= 1 mm. (b) Basidiospores. Bar= 10 µm. (c) Basidiospores attached to basidia.

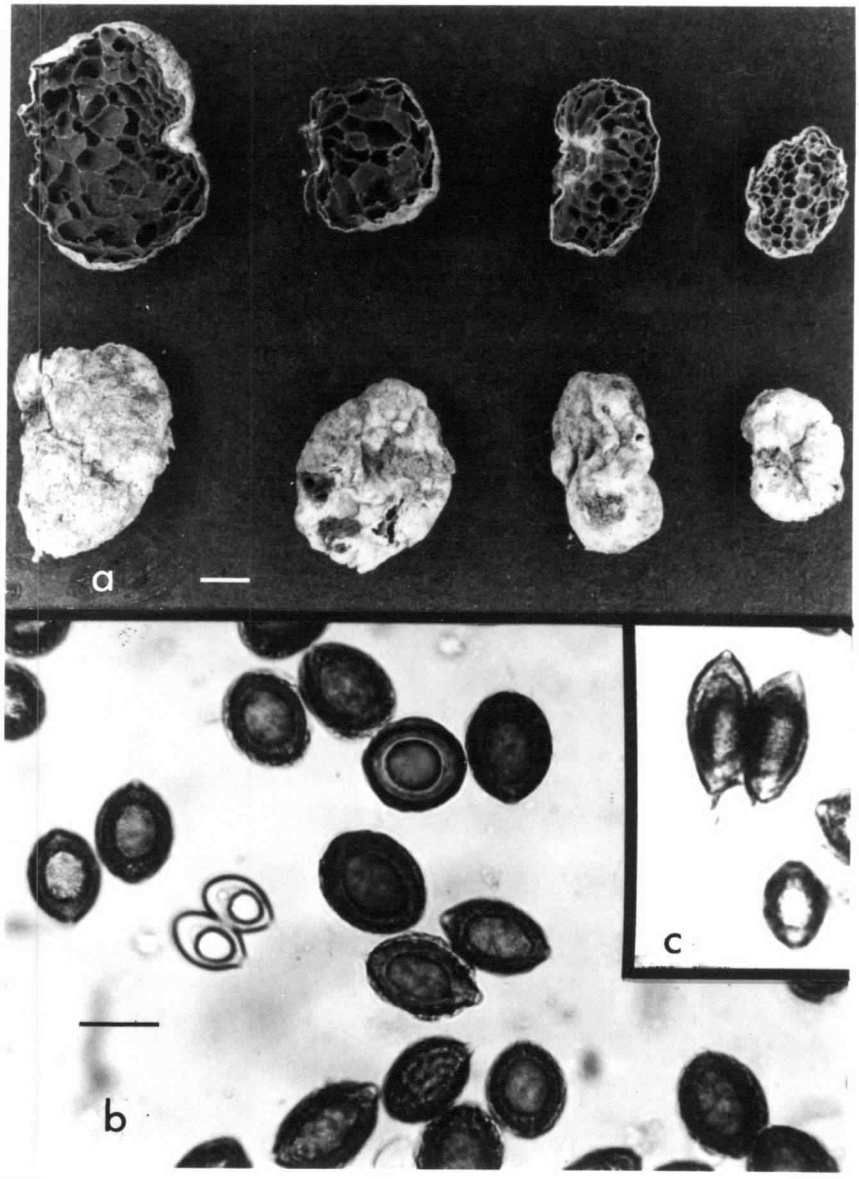

Fig. 4.2

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Chapter 5

Alpine and Subalpine Fungi of the Cascade and Olympic Mountains.

2. *Macowanites lymanensis* sp. nov.

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SUMMARY

A new *Macowanites* species is described from near Lyman Lake, Glacier Peak Wilderness Area, in the North Cascade Range, Washington.

INTRODUCTION

Lyman Lake is in the Glacier Peak Wilderness Area of the Wenatchee National Forest, North Cascade Mountains, Chelan County, Washington. Fig. 5.1a The vegetation is typical of mountain hemlock [*Tsuga mertensiana* (Bong.) Carr.] subalpine forests (Franklin and Dyrness, 1973). In the old forest on the north and west shores of Lyman Lake, where this new species was found, the dominant tree species, in addition to mountain hemlock, are noble fir (*Abies procera* Rehd.), Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.]. The mountain hemlock zone is wet and cool: the annual precipitation at Lyman Lake averages 2750 mm, mostly as snow, which accumulates from November through April (Mann and Dull, 1979). The fleshy fungi fruit primarily July through September.

METHODS

The single collection was noticed because several sporocarps were emergent in the bare, compacted soil of a heavily used campsite about 10 m from a small stream. All sporocarps were found in a roughly circular area about 1 m in diam, some single, others in clusters, and a few joined at the base. After fresh characters were recorded, specimens were dried and saved for microscopic study. Microscopic features were described according to Smith (1963). Color names and numbers were determined with the ISCC-NBS manual (Kelly and Judd, 1955).

DESCRIPTION

Macowanites lymanensis Cázares & Trappe, *sp. nov.*

Figs. 5.1b-c, 5.2a-b.

BASIDIOMATA *7-23 x 12-36 mm, subglobosa, turbinata, lobata vel depressa.* ***PERIDIUM*** *glabrum, pallide luteolum labibus brunneis, 20-70 µm crassum, hyphis 2-5 µm ad septa, cellulis inflatis usque ad 10-20 µm.* ***GLEBA*** *pallide armeniaca, loculata.* ***STIPES-COLUMELLA*** *alba, vix vel manifeste projecta, percurrens vel truncata.* ***BASIDIA*** *28-45 x 11-17 µm, clavata, sterigmatibus 2-4.* ***SPORAE*** *7-13 (-17) x 7-12 (-14) µm, globosae vel subglobosae, symmetricae, amyloideae, virgis vel verrucis singularibus, lineis vel subreticulo ornatae.* ***HOLOTYPUS:*** *Trappe # 10611 (OSC).*

BASIDIOMATA single to gregarious or caespitose, 7-23 x 12-36 mm in diam, subglobose to turbinate, lobed or depressed at the center. **PERIDIUM** pale dull yellow with brown stains on disc, grading to white towards the margin, glabrous, recurved and often attached to stipe but sometimes separated to reveal the basal locules. **GLEBA** pale orangish yellow (ISCC-NBS 73) or slightly yellower, loculate, locules 0.3-1 mm broad. **STIPE-COLUMELLA** barely projecting or prominent, white, percurrent or truncated, context white. **RHIZOMORPHS** absent. **ODOR** strongly yeasty with a slight wine essence, taste mild.

SPORES 7-13 (-17) x 7-12 (-14) µm, excluding ornamentation, globose to subglobose, symmetrical, the wall and ornamentation amyloid, ornamentation 1-2 µm tall, consisting of rods or warts, separate or often

connected by lines, occasionally forming a partial reticulum, sterigmal appendage with an amyloid collar or amyloid deposit on one side.

BASIDIA 28-45 x 11-17 µm, thin-walled, clavate, with 2 or 4 sterigmata, hyaline in KOH, pale yellow in Melzer's reagent. **CYSTIDIA** absent.

TRAMA 35-140 µm wide, of thin-walled, hyaline sphaerocysts but ocasionally also with a central strand of interwoven, thin-walled hyphae 3-6 µm in diam at septa. **SUBHYMENIUM** cellular, 1-3 (-5) cells deep, the cells 10-15 (-20) µm in diam, hyaline in KOH, pale yellow in Melzer's reagent. **STIPE-COLUMELLA** of hyaline, thin-walled, tightly interwoven hyphae, 2-8 µm in diam at septa, many cells inflated up to 10-20 µm in diam. Epicutis of **PERIDIUM** 20-70 µm thick, composed of appressed, thin-walled hyphae 2-5 µm in diam at septa, with most cells inflated up to 10-20 µm in diam, light yellow in KOH and Melzer's reagent, and a subcutis composed of thin-walled, hyaline, inflated cells and sphaerocysts 10-40 µm in diam. **CLAMP CONNECTIONS** absent.

ETYMOLOGY: in reference to Lyman Lake, near which the holotype was collected.

HOLOTYPE: Washington, Chelan County, Wenatchee National Forest, Glacier Peak Wilderness Area, Lyman Lake, campsite on E shore near the inlet of Cloudy Pass Creek, 48° 12' N. Lat., 120° 551 W. Long., elevation 1708 m, hypogeous to emergent in bare, compacted soil among *Abies amabilis-A. lasiocarpa* roots, Jim Trappe # 10611, 25 September 1990 (OSC).

DISCUSSION

The distinctive features of this species are the thin peridial epicutis of appressed hyphae, the relatively large spores with ornamentation 1-2 µm tall, consisting of individual rods or warts often connected in lines or forming a partial reticulum, and a total absence of cystidia. Of the species with similar spores, all have different peridial coloration except *M. citrinus* Singer & Smith. *M. citrinus*, however, has a peridial epicutis comprised of a turf of filaments (Singer & Smith, 1960) as opposed to the epicutis of appressed hyphae of *M. lymanensis. Macowanites mexicanus* Guzmán and *M. duranguensis* Guzmán recently described from México (Guzmán, 1988) both have spores with ornamentation < 1 µm tall and cystidia in the hymenium.

Singer and Smith (1960) used the presence of sphaerocysts in the glebal mediostratum in *Macowanites* as the major character that distinguishes it from *Elasmomyces*, which lacks these cells in the mediostratum. We have followed this concept in assigning the new species to *Macowanites.* In the scheme of Pegler and Young (1979), the species would be placed in *Elasmomyces.* They place genera with statismospores (symmetrical spores that lack the forcible discharge mechanism) in the Elasmomycetaceae, a segregate from the Russulaceae (with asymmetrical ballistospores). As defined by Pegler and Young, the Elasmomycetaceae cuts across the distinct phylogenetic lines leading from *Russula* and *Lactarius* and thus is polyphyletic. We prefer to leave all hypogeous russuloid and lactarioid taxa in the family Russulaceae. The various genera form a continuum from *Russula* and *Lactarius* with pileus, stipe, lamellae and ballistospores to *Gymnomyces* and *Zelleromyces,* respectively, with no pileus or stipe, a peridium-enclosed, loculate gleba, and statismospores. *Macowanites* fits in this continuum between *Russula* and

Gymnomyces. Elasmomyces and *Martellia* may form a side branch continuum from *Macowanites.*

ACKNOWLEDGMENTS

This study was supported by National Science Foundation Grant BSR-8717427 and the U. S. Forest Service, PNW Research Station. Drs. Harry Thiers and Michael Castellano reviewed the manuscript and offered many helpful suggestions. Personnel of the U. S. Forest Service, Wenatchee National Forest, Chelan Ranger District, encouraged and facilitated our field work. SEM photomicrographs were prepared by Dr. Al Soeldner. The senior author thanks "Consejo Nacional de Ciencia y Tecnología" in México for their support.

Fig. 5.1. (a) Lyman Lake area (Type locality). (b) Fresh basidiome of ***M. lymanensis*** in cross section. Bar=1 cm. (c) Exterior of the basidiome and some exposed locules. Bar=1 cm. (Photos a and b courtesy of Dr. M. A. Castellano).

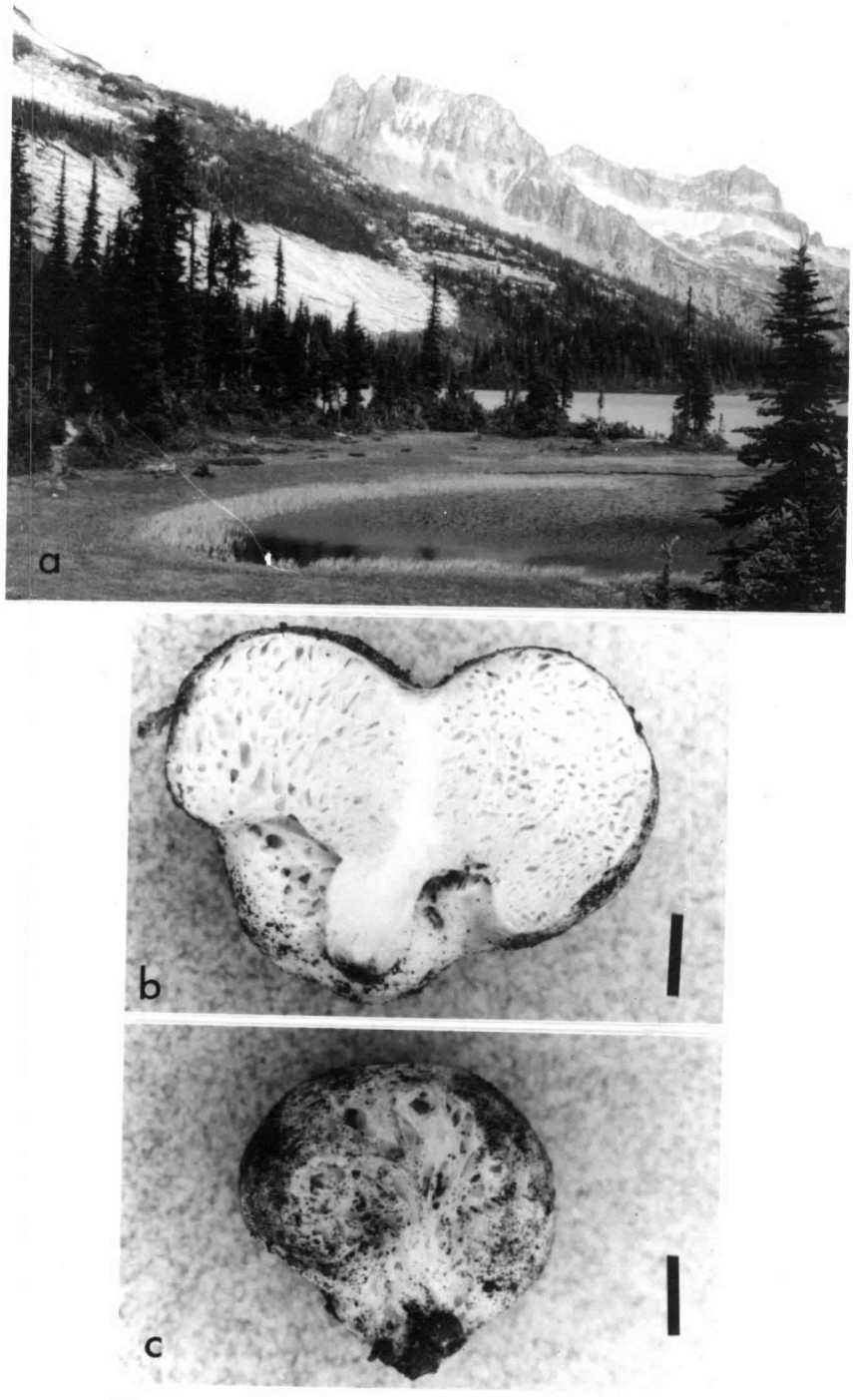

Fig. 5.1

Fig. 5.2. ***Macowanites lymanensis***. (a) Basidiospores (Nomarsky differential interference contrast photomicrograph). Bar=10 µm. (b) Basidiospores (Scaning Electron photomicrograph). Bar= 5 µm.

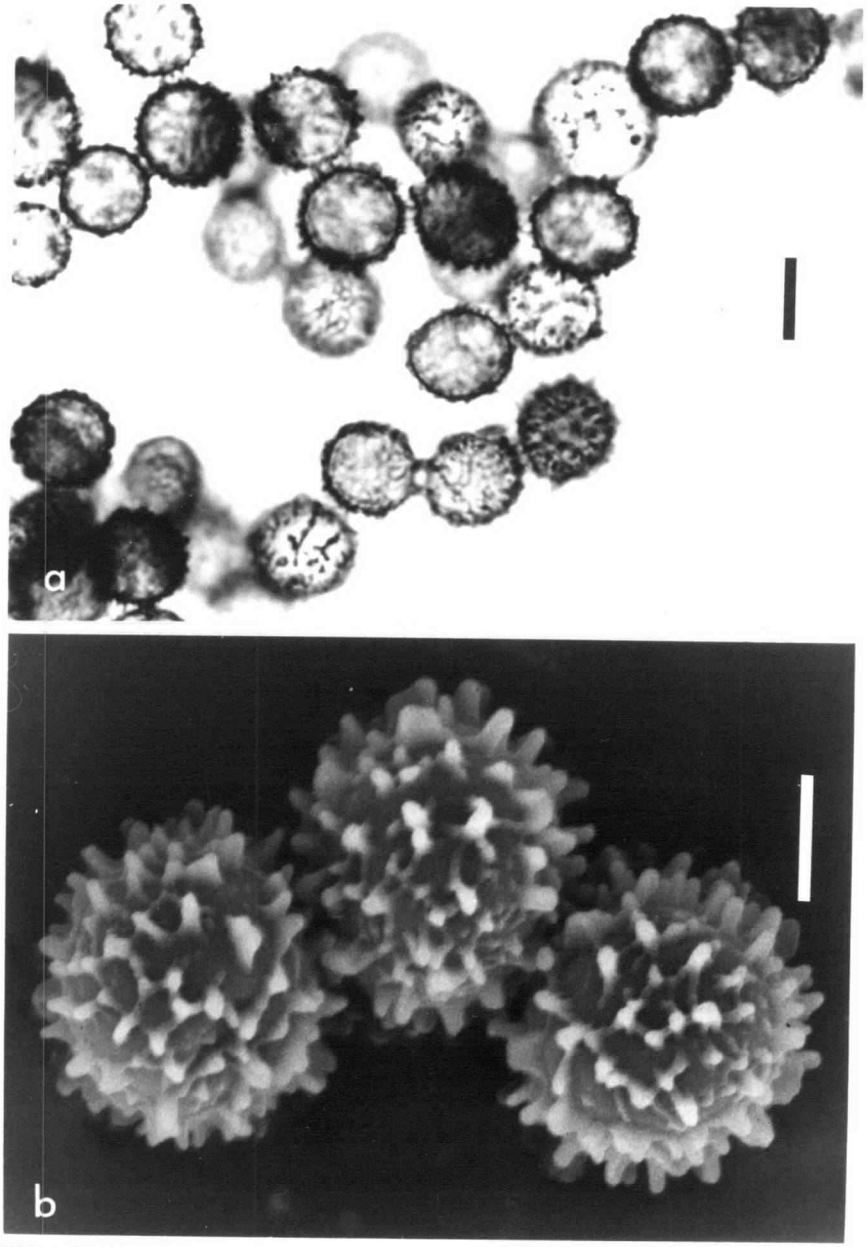

Fig. 5.2

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Chapter 6

Alpine and Subalpine Fungi of the Cascade and Olympic Mountains.
3. *Gastroboletus ruber* comb. nov.

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SUMMARY

A new combination of *Gastroboletus ruber* is made from *Truncocolumella rubra* Zeller. The range of the species in the Cascade mountains is extended from northern Washington to mid Oregon.

INTRODUCTION

Zeller (1939) described *Truncocolumella rubra* from a single collection, and Smith & Singer (1959) recorded a second collection. Since then, no further material has been reported in the literature. We have seen 13 additional collections, most of them our own and most containing many basidiomata. In 1989 and 1990 we found it fruiting abundantly near Lyman Lake in the Glacier Peak Wilderness Area of the North Cascades, not far from the type locality of *Macowanites lymanensis* Cázares & Trappe (see this issue of *Mycotaxon*). Observing *T. rubra* in its substantial variation, we became aware that it is intermediate between *Gastroboletus* and *Truncocolumella.* This is not surprising, in that evolutionary progression from a gymnocarpic to a angiocarpic habit predictably produces occasional intermediates.

Truncocolumella rubra retains strongly boletoid characters, including asymmetric ballistospores, whereas the type of the genus, *T. citrina,* has lost most boletoid features, has symmetric statismospores, and resembles the genus *Rhizopogon.* Moreover, *T. citrina* seems to have been derived from *Suillus* through *Gastrosuillus,* whereas *T. rubra* is clearly related to *Boletus* through *Gastroboletus.* Accordingly, we regard the placement of *T. rubra* as phylogenetically inappropriate and move the species to *Gastroboletus.* We prefer this solution to the erection of a new monotypic genus, because the *Gastroboletus* affinity of the species is clear and it retains ballistospores.

METHODS

Macro- and microscopic features were described according to the standard methods used by Smith & Singer (1959). Colors of *G. ruber* sporocarps vary greatly and thus are given in general color terms.

DESCRIPTION

Gastroboletus ruber (Zeller) Cázares & Trappe, comb. nov.
≡*Truncocolumella rubra* Zeller, Mycologia 31:7-8, Figs. 5, 6, 21, 22. 1939.

Figs. 6.1a-b, 6.2a-b and 6.3a.

BASIDIOMATA 20-40 x 20-55 mm, subglobose to turbinate or lobed, solitary to gregarious or caespitose, hypogeous to emergent. **PERIDIUM** rose to brownish red or reddish brown and persistent on apex of percurrent stipe-columellae, dingy pale yellow to dark reddish brown and usually evanescent where covering mouths of exposed tubular glebal locules, but sometimes partially persisting and then becoming yellowish brown to cinnamon and depressed in the tube mouths to give a reticulate appearance. **GLEBA** light yellow in youth, dark olive at maturity, initially of separable tubes 0.5-1 mm in diam divided into labyrinthine locules ±0.2 mm in diam, upon expansion the tubular organization becomes disrupted but the labyrinthine locules still radiate and are up to 0.5 (-0.8) mm in diam, the exposed locule mouths tinged reddish orange to red at maturity, turning blue where bruised or cut, separable from the columella. **STIPE-COLUMELLA** pale yellow with a concolorous context, turning blue instantly where cut, columnar to dendroid, percurrent or not, with many branches reaching or nearly reaching the peridium, projecting as much as 1 cm

below the glebal base, up to 1.5 cm broad at the apex when percurrent. Basal hyphae white to pale yellow. **ODOR** not distinctive.

SPORES (8-) 9-15 (-20) x 4-6 µm, smooth, asymmetric, subfusiform, walls up to 0.5 µm thick, pale green to olive in KOH, pale orangish yellow in Melzer's reagent.

BASIDIA 26-40 x 7-11 µm, thin-walled, cylindical to clavate, hyaline, 2- to 4- spored, sterigmata 4-5 µm long. **CYSTIDIA** 25-50 x 4-14 µm, scattered, thin-walled, fusoid-ventricose, hyaline to pale olive in KOH, lacking incrustations. **SUBHYMENIUM** cellular, 2-3 cells deep, cells 3-10 µm in diam. **TRAMA** 25-170 µm thick, of hyaline, thin-walled, subparallel to interwoven hyphae 2-12 µm in diam, laticiferous hyphae occasional. **STIPE-COLUMELLA** composed of thin-walled, hyaline, branched hyphae, 3-12 (-15) µm in diam, laticiferous hyphae scattered near the peridium. **CLAMP CONNECTIONS** absent. **PERIDIAL EPICUTIS** initially differentiated as a palisade of cylindric to clavate dermatocystidia 15-30(-70) x 3-10 µm, hyaline to pale yellow in KOH, becoming a disrupted turf over the gleba as the basidiome expands but remaining a palisade over the percurrent columellar apices, in age the contents turning yellow to brown.

ETYMOLOGY: Latin, *ruber* (red), in reference to the red mouths of exposed glebal tubes.

DISTRIBUTION, HABITAT, AND SEASON: Cascade Mountains of Oregon and Washington, probably ectomycorrhizal with *Tsuga mertensiana* but *Abies amabilis*, *A. lasiocarpa*, *A. procera*, *Picea engelmannii*, *Pinus contorta* or *P. monticola* often present as well; at elevations of 4000-5800 ft.; August through September.

COLLECTIONS EXAMINED: **OREGON**: **Clackamas Co.**-Mt. Hood, McNeil Point trail, J. Lindgren (Trappe 8206 in OSC); **Hood River Co.**-Mt. Hood, Tilly

Jane Forest Camp, T. Hongo (Trappe 5056 in OSC). **Jefferson Co**.-Mt. Jefferson Wilderness Area, Shirley Lake, J. Trappe 5900 (OSC), Cabot Lake trail, J. Trappe 5896 (OSC) & Carl Lake, J. Trappe 5902 (OSC). **Lane Co**.-McKenzie Drainage, English Mtn., S. Berch (Trappe 7505 in OSC); Three Sisters Wilderness Area, Obsidian trail, D. Luoma 818 (OSC) and S. M. Miller 977 (OSC). **WASHINGTON**: **Chelan Co**.-Lyman Lake, E. Cázares and J. Trappe (Trappe 10412 & 10439 in OSC), E. Cázares (Trappe 10614 in OSC). **King Co**.-Snoqualmie Pass, D. E. Stuntz [Zeller 8272 (NY, holotype of *Truncocolumella rubra*)]. **Skamania Co**.-Indian Heaven, Tombstone Lake, J. Lindgren (Trappe 9018 in OSC). **Whatcom Co**.-4 mi. N. of Copper Lake, J. Trappe 674 (OSC); Hannegan Pass, A. H. Smith #16218 (MICH, OSC); Upper Chilliwack River, J. Trappe 675 (OSC).

DISCUSSION

Originally described as a *Truncocolumella,* this species is actually intermediate between *Gastroboletus* and *Truncocolumella.* The stipe-columella is reduced more than usual for *Gastroboletus* spp. (Thiers & Trappe, 1969, Thiers, 1989) but still shows stipe-like characteristics and, when percurrent, is covered with a boletoid epicutis [the two collections available to Smith & Singer (1959) evidently had no specimens with a percurrent columella]. The gleba is decidedly tubular in youth, the "mouths" of the outermost locules being stuffed in the manner of many *Boletus* spp. The overall color and bluing reactions are boletoid.

The only other described *Truncolumella, T. citrina* Zeller, the type species for the genus, appears essentially as a *Rhizopogon* with a dendroid columella and bears no macroscopic resemblance to boletes. We suspect it is derived

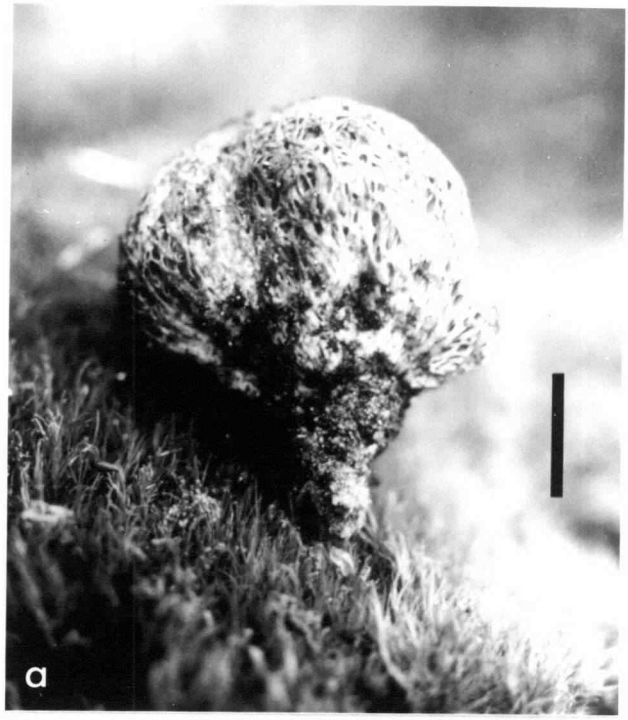
from the genus *Suillus,* whereas *G. ruber* is clearly derived from *Boletus.* Indeed, it so strongly resembles the pileate *Gastroboletus turbinatus* (Snell) Smith & Singer in microscopic features that we are tempted to regard it as a direct descendent from that species. Both relate directly to *Boletus* sect. *subtomentosi sensu* Thiers.

Until now, *G. ruber* was reported only from two collections in northern Washington (Smith & Singer, 1959). Apparently confined to the Cascade Mountains, its range is now extended some 400 km south to Lane County, Oregon. We are pleased to note that the first Oregon specimens were found by Prof. Tsuguo Hongo of Shiga University, Japan, when he and Trappe were collecting at Mt. Hood in 1977. Prof. Hongo discovered this exciting find while Trappe was finishing his lunch!

ACKNOWLEDGMENTS

This study was supported by National Science Foundation Grant BSR-8717427 and the U. S. Forest Service, PNW Research Station. Drs. Harry Thiers and Michael Castellano reviewed the manuscript and offered many helpful suggestions. Personnel of the U. S. Forest Service, Wenatchee National Forest, Chelan Ranger District, encouraged and facilitated our field work. SEM photomicrographs were prepared by Dr. Al Soeldner. The senior author thanks "Consejo Nacional de Ciencia y Tecnología" in México for their support.

Fig. 6.1. ***Gastroboletus ruber***. (a) Fresh basidiome, photo courtesy of Dr. D. Luoma. Bar=1 cm. (b) Basidiospores (Nomarsky differential interference contrast photomicrograph). Bar=10 μm.



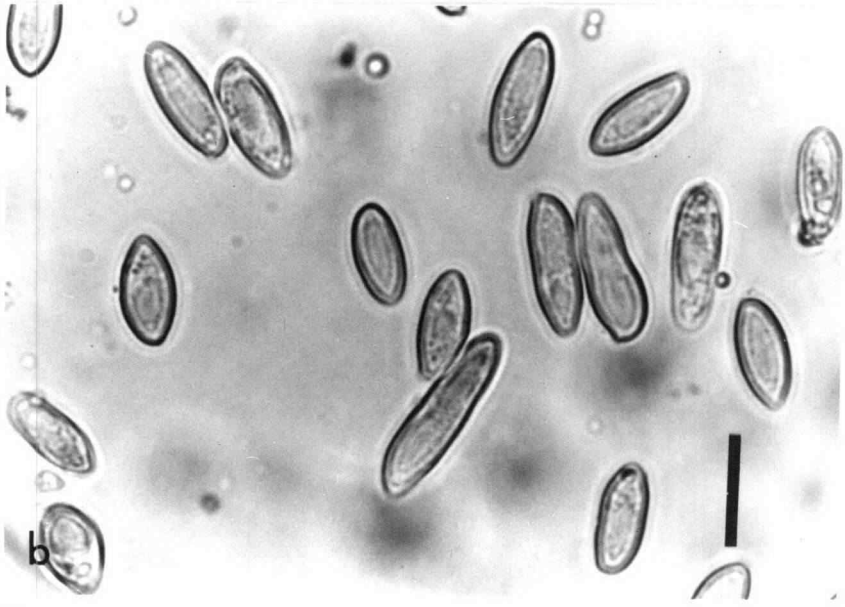


Fig.6.1

Fig. 6.2. (a) and (b) Scaninig electron photomicrographs of basidiospores of ***G. ruber***. Bar=5 μm.

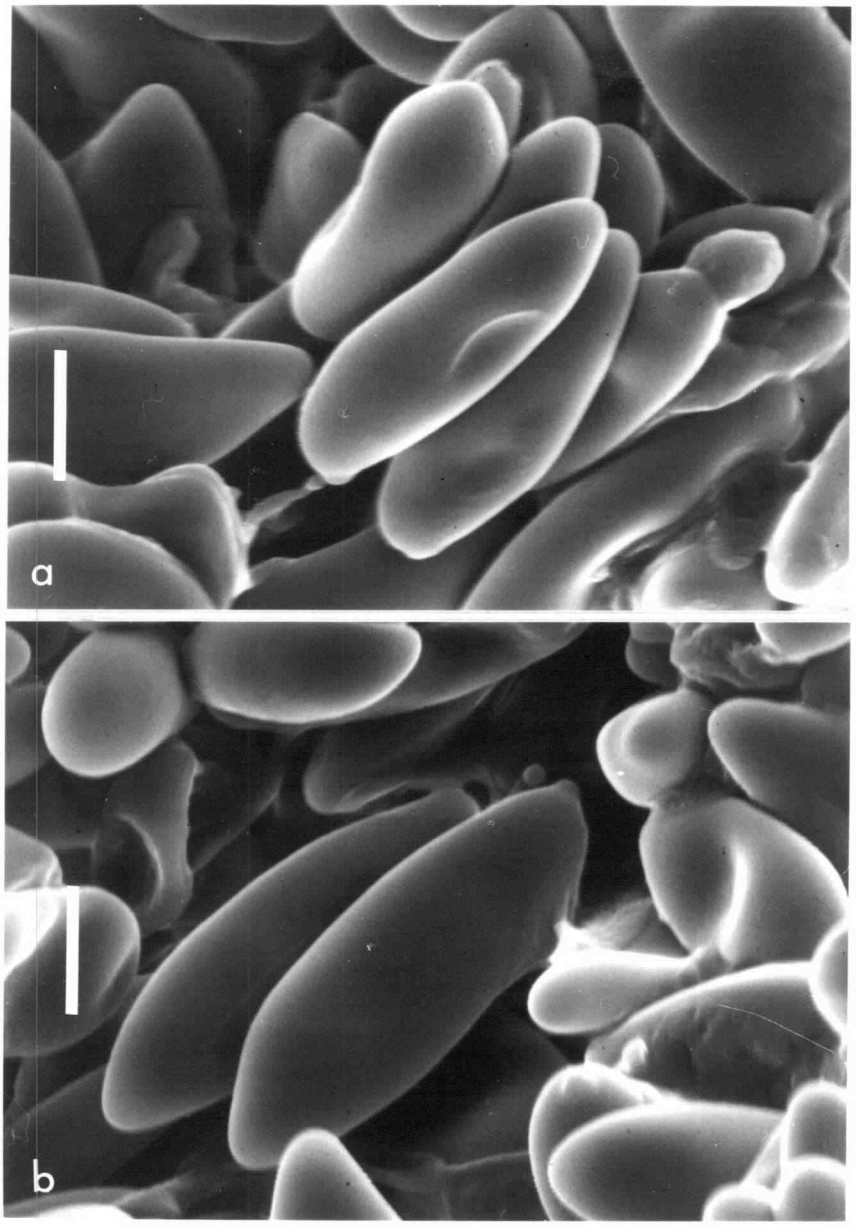


Fig.6.2

Fig. 6.3. (a) Diagrammatic cross sections of basidiomata of ***G. ruber***, showing columellae and surrounding glebae. Bar=1 cm.

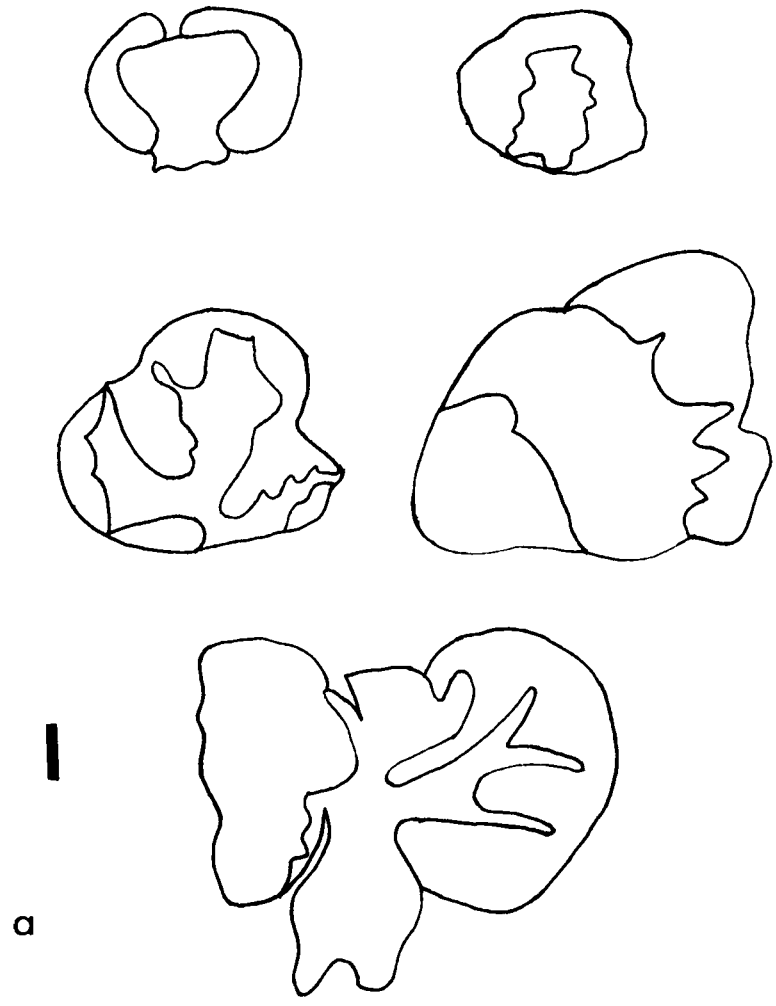


Fig.6.3

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