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Community structure of ectomycorrhizal fungi across an alpine/subalpine ecotone

G. Kernaghan and K. A. Harper

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In order to assess changes in the community structure of ectomycorrhizal fungi across the tree line, data on distributions of fungi and their host plants, as well as on edaphic factors and stand age, were collected at two montane sites in the Front Range of the Canadian Rockies. Canonical correspondence analysis (CCA) was used to explore relationships between fungal species composition and environmental factors. Richness and diversity of ectomycorrhizal fungi decreased with elevation, in spite of the fact that host plant diversity was highest at the ecotone between the subalpine forest and the alpine zone. Both host plant distribution and edaphic factors were important in explaining the observed changes in fungal species diversity and composition. The majority of ectomycorrhizal fungi found in the subalpine forest and at the ecotone were conifer associates, while a large proportion of those in the alpine zone were non-host specific and able to form mycorrhizae with both angiosperms and gymnosperms. The abundance of non-host specific fungi in the alpine zone is expected to provide a favorable environment for the establishment of conifer seedlings above the present tree line.

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Ecotones, or zones of transition between habitats, are often areas of enriched species diversity due to the co-occurrence of species from adjacent habitats (Hansen et al. 1992, Risser 1995). Leopold (1933) coined the term "edge effect" for this phenomenon at abrupt ecotones, and it has since been demonstrated in a wide range of organisms at various scales, including vascular plants (Jones and Peterson 1970, Scheiner and Istock 1994), small mammals (Sekgororoane and Dilworth 1995), soil fauna (Rusek 1992) and other insects (Downie et al. 1996).

At the alpine/subalpine ecotone of the Canadian Rockies, the *Picea-Abies* forest merges with the low growing shrubs dominating the alpine zone, resulting in a mosaic of alpine and subalpine vegetation. Because many of the plant genera in this habitat are obligately ectomycorrhizal, and because many of the fungi involved are host specific (Molina et al. 1992), the distribution of ectomycorrhizal fungi might be expected to mirror patterns seen in ectotrophic vegetation, such as high diversity at the ecotone.

Moser (1967, 1980) studied the distribution of fungal sporocarps across montane tree line (or "Kampfzone") in the Alps. He found the community of ectomycorrhizal fungi at the ecotone to be an amalgamation of species from the subalpine forest and the alpine zone and hypothesized on the importance of mycorrhizal fungi in determining the upper elevation limit of conifer establishment.

Studies on the distributions of sporocarps of ectomycorrhizal fungi in other forest ecosystems have implicated either host plant composition (Nantel and Neumann 1992, Såstad 1995) or edaphic factors (Hansen 1988, Tyler 1989, Rühling and Tyler 1990) as the major

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determinants of fungal community structure. The number and distribution of sporocarps, however, may not be reliable indicators of the distribution of fungal thalli in the soil environment (Gardes and Bruns 1996). Ectomycorrhizae, on the other hand, are less ephemeral than sporocarps, and analysis of ectomycorrhizal roots is a more direct measure of the level of plant-fungus association. Relatively few studies, however, have attempted to relate the abundance of ectomycorrhizal roots to environmental variables (Agerer 1985, Rao et al. 1997, Väre et al. 1997).

The objective of this study was to assess the diversity and species composition of ectomycorrhizal fungi across an elevational tree line on the basis of sporocarp and ectomycorrhizal root collections, and to determine the relative influences of host plants and abiotic factors on fungal distribution. A dominant influence of ectotrophic host plants on the distribution of ectomycorrhizal fungi should be evidenced by relatively high fungal diversity at the ecotone.

Materials and methods

Collection and identification of fungi

Field work was conducted at two tree line sites in the Front Range of the Canadian Rockies: 1) between 2000 and 2200 m a.s.l. on the southeast slope of Mt. Tripoli, in the Nikanassin Range, Alberta (52°52′N, 117°17′W), and 2) between 2300 and 2500 m a.s.l. on the southwest slope of Mt. Rae, Peter Lougheed Provincial Park, Alberta (50°36′N, 114°59′W). At both sites, the subalpine forest was co-dominated by mature *Picea engelmannii* Parry and *Abies lasiocarpa* (Hook.) Nutt. and also supported scattered *Larix lyallii* Parl. The ecotone supported stunted (krummholz) *Picea* and *Abies*, separated by *Salix barrattiana* Hook., *S. glauca* L., *S. arctica* Pall., *Betula glandulosa* Michx., and ericaceous shrubs. Plant cover in the alpine zone was similar to that of the ecotone but also included *Dryas octopetala* L. and *D. integrifolia* M. Vahl. Soils were Dystric and Eutric Brunisols, and Orthic and Orthic Humic Regosols (Trottier 1972, Mortimer 1978). Snowpack is generally heavy from October to May. In July and August the mean daily temperature range is from 6 to 10°C, and mean monthly precipitation is from 66 to 105 mm (Environment Canada, Archive of Climatological Data). See Kernaghan and Currah (1998) for more detailed site descriptions.

At each site, six 16 m transects were constructed; 2 in the subalpine forest, 2 at the ecotone and 2 in the alpine zone. Transects paralleled elevational contours and were ca 200 m apart. Ectomycorrhizae were sampled by taking 3.5 cm diameter soil cores from the organic horizon at 1 m intervals along each transect. Ectomycorrhizae were removed from the organic material by wet sieving and characterized by light and scanning electron microscopy (Kernaghan et al. 1997, Kernaghan 2001). Anatomical characters were then compared to literature descriptions, including Agerer (1987), Ingelby et al. (1990) and Goodman et al. (1996).

Sporocarps of all ectomycorrhizal fungi fruiting in 10×26 m quadrats centered around each transect were collected during each snow-free month (June–Sept.) from 1994 to 1997, dried, identified and deposited in the Univ. of Alberta Cryptogamic Herbarium (ALTA). Taxonomic details are in Kernaghan and Currah (1998). Sporocarp ribosomal DNA, extracted from 42 representative taxa, was amplified by the polymerase chain reaction (PCR) and used to construct a restriction fragment length polymorphism (RFLP) data base for comparison to DNA extracted from examples of each anatomically distinct ectomycorrhizal type. Detailed protocols for PCR amplification and RFLP analyses are described in Kernaghan et al. (1997) and Kernaghan (2001).

Environmental factors

Relative abundances of ectotrophic host plants (based on Molina et al. 1992) in each 10×26 m quadrat were estimated by basal diameter measurements (expressed as basal area) for *Abies*, *Picea* and *Larix*, and by visual cover estimates for *Salix* and *Dryas*. Stand age was determined from increment cores of the two largest trees in each quadrat. Monthly temperature amplitude of the organic soil horizon was measured during the sampling period using buried max./min. thermometers. Depth of organic material (L, F and H horizons combined) was measured at four points along each transect and averaged. For pH and soil moisture determinations, one 10×10 cm section of organic horizon was removed adjacent to each transect each month during the sampling period. Moisture content was determined by weight loss after oven drying 10 g subsamples at 60°C for 24 h. For pH determination, a second subsample was air dried, homogenized, mixed with distilled water at 1:10 wt./vol. for 12 h and measured with a digital pH meter. Geometric averages of the four pH values were used in subsequent analyses. All environmental factors were measured in the summer of 1997.

Richness and diversity indices

Ectomycorrhizal richness was based on the number of different fungi colonizing roots along each transect. For ectomycorrhizal diversity, the abundance of each fungal genus forming ectomycorrhizae in each soil core was estimated as heavy (50–100%), moderate (25–50%), scant (5–25%) or nominal ($< 5\%$). Diversity was then calculated for each transect using the Shannon index (Shannon and Weaver 1949). The relative proportion of

each genus in each core was calculated by dividing the median value for the category of abundance (0.75, 0.375, 0.15 or 0.025) by the sum of median values within each core. The relative proportion for each genus along each transect was the sum of the relative proportions in all the cores along the transect. Richness of host plants was based on the number of ectotrophic genera present within each quadrat. Diversity of host plants was also quantified by the Shannon index, using basal area measurements and cover estimates for relative abundance of ectotrophic plants. For sporocarps, richness was based on the number of different fungi fruiting within the quadrats. Diversity indices were not calculated for sporocarps due to difficulty in quantifying relative abundance.

Analyses of variance were used to assess the effect of site and elevation on host plant richness, ectomycorrhizal richness, sporocarp richness, ectomycorrhizal diversity and host plant diversity. A complete block design was used in which sites acted as blocks (site effects were random and elevation effects were fixed). Because there were no significant site effects or site × elevation interactions, data were re-analyzed without the site term as one-way ANOVAs with subsequent Tukey tests. All analyses were performed using SPSS 7.5. (SPSS, Chicago, IL).

Ordination analyses

Canonical correspondence analysis (CCA, Ter Braak 1986) was performed on a sporocarp species-quadrat data matrix which contained presence/absence data on 70 fungal species collected in the 12 quadrats. This ordination was detrended by 26 segments with nonlinear rescaling of the axes (Hill and Gauch 1980), to improve clarity of the diagram. The abundances of the ectotrophic host plant genera were used as environmental variables to constrain the ordination axes. Abiotic factors (pH, depth of organic material, soil moisture, and monthly temperature amplitude) and stand age were highly correlated surrogates of host plant composition and were therefore added to the ordination diagram as passive variables.

Canonical correspondence analysis (CCA) was also performed on the ectomycorrhiza data in a similar manner. In this case, however, the species-transect matrix represented frequency of occurrence (0–16) of the different ectomycorrhizae in soil cores along the transects. Unlike the ordination based on sporocarp data, no detrending was necessary for the ectomycorrhiza data set. All ordination analysis were performed using CANOCO software (Ter Braak 1988).

In order to assess the importance of ectotrophic host plant abundance relative to other measured environmental variables we also performed 2 additional canonical correspondence analyses for each data set (sporocarp and mycorrhizae). Each used a different set of environmental variables; either host plant abundance only or edaphic factors and stand age only. Variation was then partitioned into components explained by the different sets of environmental factors (Borcard et al. 1992).

Results

Sporocarps and ectomycorrhizae collected

A total of 70 ectomycorrhizal species were collected as sporocarps within the 12 quadrats: 54 of these were found in the subalpine forest, 29 at the ecotone and ten in the alpine zone. Fourteen fungal genera were represented in the subalpine forest, while a subset of eight of these, plus the genus *Suillus*, was collected in the ecotone, and a further subset of five genera in the alpine zone (Fig. 1). *Cortinarius* was the most species-rich genus in all habitats, although the number of species decreased with elevation, as was the case with most other genera. The number of *Russula* and *Lactarius* species was greatest at the ecotone, however, and *Amphinema* and *Tomentella* were similar in the alpine zone and the subalpine forest.

Ectomycorrhizae collected along the 12 transects were sorted into 15 genera and one unknown ascomycete taxon. *Cenococcum geophilum* Fr.: Fr. was the most common fungal symbiont, and along with *Inocybe*, *Tomentella* and an unidentified ascomycete, showed greatest abundance in the alpine zone (Fig. 2). Mycorrhizae formed by *Cortinarius* were also common and were similar in abundance in the subalpine forest and the alpine zone. *Amphinema*, as well as several less abundant genera, decreased in abundance with elevation. As with sporocarps, the mycorrhizae of *Russula* and *Lactarius* were most abundant at the ecotone. For detailed discus-

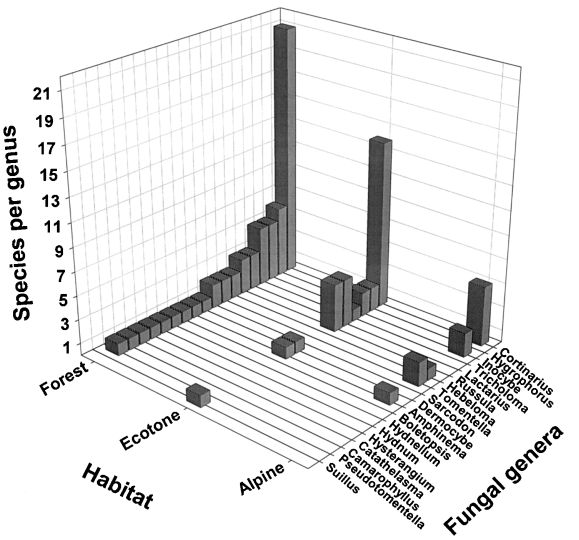

Fig. 1. Number of fungal species belonging to each genus at each elevation based on sporocarp collections.

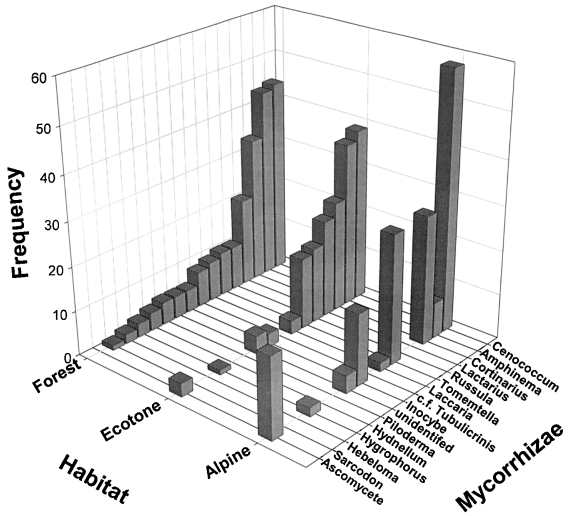

Fig. 2. Frequency (out of 72 soil cores) of different ectomycorrhizae collected at each elevation.

sion of ectomycorrhizae see Kernaghan et al. (1997) and Kernaghan (2001).

Species richness and diversity indices

Richness of ectomycorrhizal fungi based on sporocarp collections was significantly higher in the subalpine forest than in the other two habitats ($F = 13.863$, $p = 0.002$) and was most variable among ecotone transects (Fig. 3a). Richness values for ectomycorrhizae also decreased with increasing elevation (Fig. 3b), although the differences among habitats were not significant ($F = 1.631$, $p = 0.249$). As with sporocarp richness, the greatest within-habitat variability was at the ecotone. Richness of ectotrophic host plant genera was highest at the ecotone ($F = 5.727$, $p = 0.025$), although multiple comparison tests indicated that only the difference between the subalpine forest and the ecotone was significant. Within-habitat variability in host plant richness was similar in each of the three habitats (Fig. 3c).

Ectomycorrhizal diversity decreased with increasing elevation ($F = 9.389$, $p = 0.006$), although the decrease from the ecotone to the alpine zone was not significant (Fig. 3d). Host plant diversity was highest at the ecotone ($F = 18.945$, $p = 0.001$), but only the difference between the ecotone and the alpine zone was significant (Fig. 3e). Within-habitat variability was highest at the ecotone for mycorrhizal diversity, and in the alpine zone for host plant diversity. One of the ecotone transects on Mount Rae (Rae 2) supported a greater cover of non-ectotrophic plants (grasses) than the other transects through the same habitat. Measures of fungal richness and diversity on this transect were substantially lower than for other ecotone transects (Figs 3a, b and d).

Environmental factors

Trends in measured environmental variables with increasing elevation include decreases in organic material, stand age and abundance of *Abies* and *Picea*, and increases in the abundance of *Salix* and *Dryas*. Differences between the two sites include higher soil pH and more *Salix* in the alpine zone at Mt. Tripoli, greater temperature amplitude and more *Dryas* and *Abies* in the alpine zone at Mt. Rae, and the presence of *Larix* at Mt. Rae (Table 1).

Correspondence analyses

In the detrended canonical correspondence analysis (DCCA) of fungal species based on the presence of sporocarps (Fig. 4), the first ordination axis ($\lambda_1 = 0.752$, species-environment correlation = 0.987) reflects the elevational gradient. Fungi on the left side of the diagram (e.g. species of *Boletopsis*, *Catathelasma*, *Hydnellum*, *Sarcodon* and *Hysterangium*) were associated with the mature subalpine conifer forests with deep, moist organic horizon. Fungi on the right side of the diagram (e.g. *Inocybe lacera* (Fr.:Fr.) Kumm., *I. lanuginella* (Schroet.) J. E. Lange, *Tomentella elissii* (Sacc.) Jülich & Stalpers,

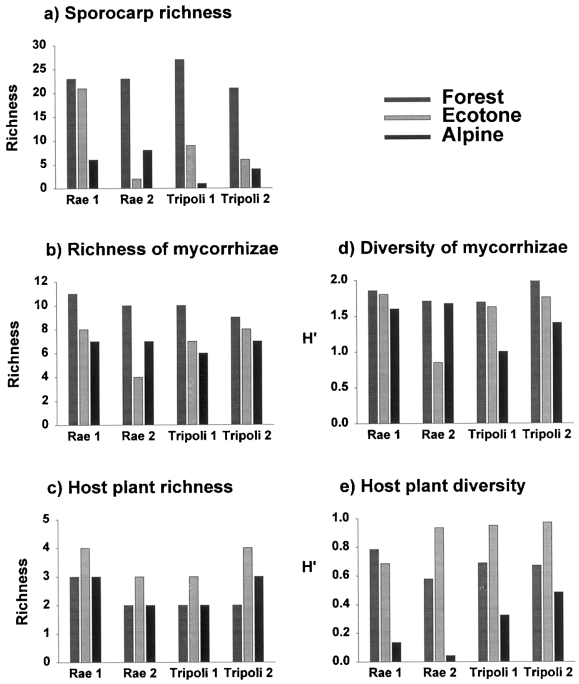

Fig. 3. a–e. Richness and Shannon-Weaver diversity indices (H') on four transects through the subalpine forest, through the ecotone and through the alpine zone. a) Richness of ectomycorrhizal fungi based on sporocarp collections. b) Richness of ectomycorrhizal fungi based on ectomycorrhizae in soil cores. c) Richness of ectotrophic host plant genera. d) Diversity of ectomycorrhizal fungi based on ectomycorrhizae in soil cores. e) Diversity of ectotrophic host plants. Bars represent individual transects.

Table 1. Measured environmental variables at each habitat at each site. Values are averages from two quadrats.

Variable	Forest		Ecotone		Alpine	
	Mt. Rae	Mt. Tripoli	Mt. Rae	Mt. Tripoli	Mt. Rae	Mt. Tripoli
Soil pH	5.8	5.8	5.5	5.7	5.6	6.6
Soil moisture (%)	53.7	51.3	42.2	52.3	45.2	51.9
Organic horizon (cm)	5.8	6.2	2.8	3.5	1.2	1.7
Conifer age (yr)	112	110	65	75	10	5
Soil temp. amplitude (°C)	16	19	15.7	23	15.5	27
Basal area of *Abies* (cm)	13 227	10 792	6702	3915	117	4
Basal area of *Picea* (cm)	16 025	22 114	4560	1909	49	42
Basal area of *Larix* (cm)	490	0	11.4	0	9.8	0
Cover of *Salix* (%)	2.5	0	20	37.5	0.8	80
Cover of *Dryas* (%)	0	0	0	0	43.5	7.5

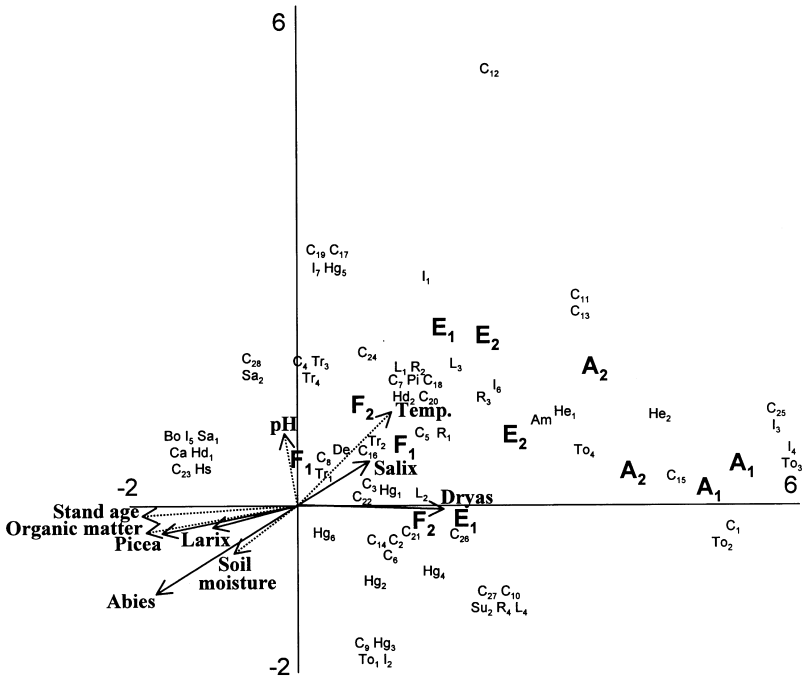

Fig. 4. Detrended canonical correspondence analysis of sites, environmental factors and fungal species based on sporocarps. Site scores are labeled with bold capital letters: F = subalpine forest, E = ecotone and A = alpine zone; subscripts on site labels indicate Mt. Rae (1) or Mt. Tripoli (2). Environmental factors used to constrain ordination axes are represented by arrows; those added as passive variables are represented by dashed arrows. Abbreviations of taxa are as follows (for clarity, species of *Hydnum* are grouped with *Hydnellum*, *Camarophyllus* with *Hygrophorus* and *Pseudotomentella* with *Tomentella*): *Amphinema byssoides* Am, *Boletopsis subsquamosa* Bo, *Catathelasma imperiale* Ca, *Cortinarius albonigrellus* C_1, *C.* cf. *biformis* C_2, *C. brunneus* C_3, *C. metarius* C_4, *C. chrysomallus* C_5, *C. colus* C_6, *C. crassus* C_7, *C delibutus* C_8, *C. dilutus* C_9, *C. evernius* C_{10}, *C. favrei* C_{11}, *C. fulminoides* C_{12}, *C. galerinoides* C_{13}, *C. hinnuleus* C_{14}, *C. inops* C_{15}, *C. multiformis* C_{16}, *C. paragaudis* C_{17}, *C. percomis* C_{18}, *C. scandens* C_{19}, *C. traganus* C_{20}, *C. triformis* C_{21}, *C. uraceus* C_{22}, *C. venetus* C_{23}, *C. zinziberatus* C_{24}, *C.* sp. subgen. *Phlegmacium* C_{25}, *C.* sp. subgen *Sereciocybe* C_{26}, *C.* sp. subgen *Telamonia* C_{27}, *C.* sp. subgen *Telamonia* C_{28}, *Dermocybe crocea* De, *Hebeloma crustuliniforme* He_1, *H.* cf. *subfastigiatum* He_2, *Hydnellum caeruleum* Hd_1, *Hydnum repandum* Hd_2, *Camarophyllus pratensis* Hg_1, *Hygrophorus chrysodon* Hg_2, *H. erubescens* Hg_3, *H. korhonenii* Hg_4, *H. pudorinus* Hg_5, *H. pustulatus* Hg_6, *Hysterangium separabile* Hs, *Inocybe dulcamara* I_1, *I. flocculosa* I_2, *I. lacera* I_3, *I. lanuginella* I_4, *I. rimosa* I_5, *I. whitei* I_6, *I.* sp. I_7, *Lactarius alnicola* L_1, *L. caespitosus* L_2, *L. deliciosus* L_3, *L. luculentus* L_4, *Russula brevipes* R_1, *R. integra* R_2, *R. silvicola* R_3, *R. torulosa* R_4, *Sarcodon scabrosus* Sa_1, *Sarcodon* sp. Sa_2, *Suillus aeruginascens* Su_2, *Piloderma fallax* Pi, *Pseudotomentella tristis* To_1, *Tomentella ellisii* To_2, *T. sublilacina* To_3, *T.* sp. To_4, *Tricholoma myomyces* Tr_1, *T. saponaceum* Tr_2, *T. vaccinum* Tr_3, *T. virgatum* Tr_4.

T. sublilacina (Ellis & Holw.) Wakef. and *Cortinarius albonigrellus* Favre) were characteristic of the *Salix* and *Dryas* dominated alpine zone which has less organic material and greater temperature amplitude. The majority of fungi were associated with both the subalpine forest and the ecotone and are located near the center of the diagram.

The second axis of the DCCA based on sporocarps ($\lambda_2 = 0.220$, species-environment correlation = 0.939) differentiates species composition between the two sites (Fig. 4). Species toward the top of the diagram were more abundant on Mt. Tripoli, with higher alpine soil pH, greater soil temperature amplitude and a higher proportion of *Salix*. Conversely, species toward the bottom of

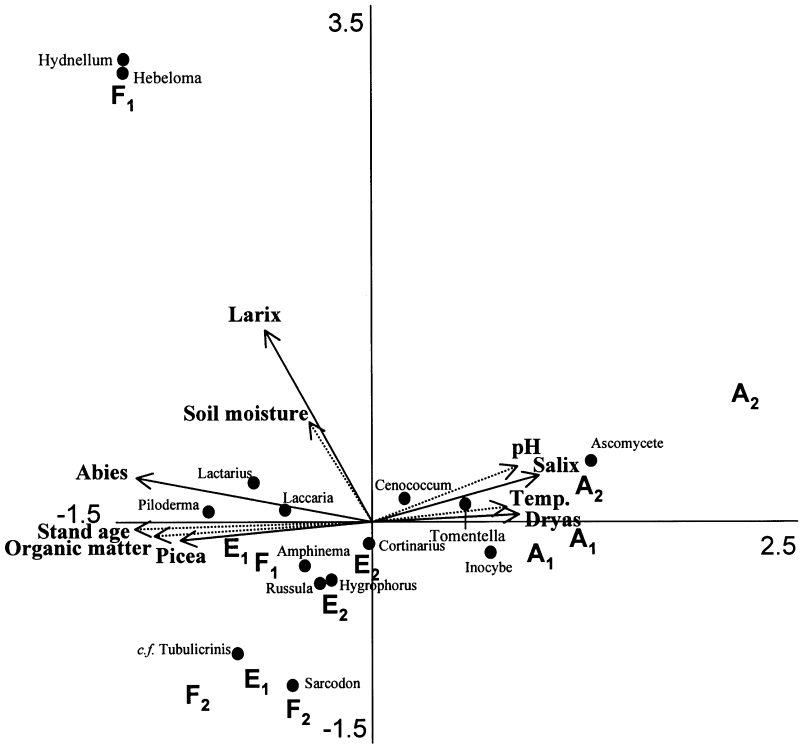

Fig. 5. Canonical correspondence analysis diagram of sites, environmental factors and fungal genera based on ectomycorrhizae. Genera are represented by closed circles. Sites are labeled with bold capital letters: F = subalpine forest, E = ecotone and A = alpine zone; subscripts on site labels indicate Mt. Rae (1) or Mt. Tripoli (2). Environmental factors used to constrain ordination axes are represented by arrows and those added as passive variables are represented by dashed arrows.

the diagram were more abundant on Mt. Rae, with lower soil temperature amplitude, more acidic alpine soils and a higher proportion of *Abies* and *Larix*.

The canonical correspondence analysis (CCA) of fungal genera based on ectomycorrhizae (Fig. 5) is similar to the DCCA based on sporocarps (Fig. 4), in that the first ordination axis ($\lambda_1 = 0.250$, species-environment correlation = 0.970) reflects the elevational gradient. In this case, however, separation of the two sites along the second axis ($\lambda_2 = 0.172$, species-environment correlation = 0.972) is less clear. A relatively distinct community, characterized by mycorrhizae formed by *Tomentella*, *Inocybe* and an unidentified ascomycete, is apparent in the alpine zone, whereas the ecotone and forest communities are not well separated. One of the forest transects at Mt. Rae (F_1) supported a relatively distinct fungal species composition which included *Hydnellum* and *Hebeloma* mycorrhizae, which were not found on other transects.

In partitioning the variation in fungal species composition by using CCAs with different sets of environmental variables (biotic, abiotic and both), we found that host plant abundance and abiotic factors explained similar proportions of the variation in both the sporocarp and ectomycorrhizae data sets (Table 2). Also, the interaction of host plant abundance and abiotic factors explained more variation in the ectomycorrhizae data set than in the sporocarp data set.

Discussion

Elevated diversity at the ecotone was evident in the community of ectotrophic host plants, but absent in community of ectomycorrhizal fungi. This result was somewhat surprising, given the obligate nature of mycorrhizal symbioses and the high levels of host specificity of many ectomycorrhizal fungi (Molina et al. 1992). An explanation for this difference in diversity between plants and their symbiotic fungi may lie in the decreasing richness of ectomycorrhizal fungi with elevation. The communities of subalpine and alpine ectotrophic plants are similar in richness (Fig. 3c), and their amalgamation at the ecotone leads to higher diversity. Because the richness of the alpine fungal community was much lower

Table 2. Variation partitioning for the sporocarp and ectomycorrhizae data sets for different sets of environmental variables using canonical correspondence analysis. Numbers are expressed as percentages of total variation.

Source of variation	Sporocarp data set (%)	Mycorrhiza data set (%)
Only host plant abundance	39	39
Other environmental variables	38	35
Host plant abundance × other variables	13	21
Neither host plants nor other variables	10	6

than that of the subalpine forest, however, their amalgamation at the ecotone resulted in intermediate diversity.

The observed decrease in fungal richness with elevation is likely governed by a number of factors, including changes in edaphic properties such as soil structure, pH, temperature, moisture, and nutrient content. Mason et al. (1986) observed variation in the potential of ectomycorrhizal fungi to colonize plant roots in different soil types, and Hansen (1988) and Rühling and Tyler (1990) identified soil base saturation and organic matter content as the most important factors governing fungal distribution in Swedish deciduous forests. Depth of organic material also appeared to be the most important edaphic factor in the present study (Figs 4, 5).

Microclimate may also be an important factor in the decrease in fungal richness with elevation. Not only does it directly impact soil temperature and moisture, but transpiration rates of sporocarps have been shown to play a significant role in the elevational distribution of macrofungi (Moser 1980). In exposed alpine areas, elaborate sporocarps with large surface areas are few, and dwarfism, presumably a strategy to protect against desiccation, is a common trait (Favre 1955). In the present study, the community of ectomycorrhizal fungi above the tree line was characterized by fungi with small sporocarps which do not protrude above the ground cover (e.g. *Inocybe*) and corticioid fungi (e.g. *Tomentella* and *Amphinema*), which fruited beneath stones or prostrate *Salix* branches.

The change in vegetation type from the subalpine coniferous forest to the angiosperm dominated alpine zone is also likely to impact fungal richness. Sporocarp surveys have shown fewer species of ectomycorrhizal fungi occur in angiosperm forests than in adjacent conifer forests (Richardson 1970, Bieri et al. 1992) and because less photosynthesis occurs in small alpine plants than in forest conifers, less carbon is available to support ectomycorrhizal fungi (Newman 1988).

Along with the decrease in fungal richness with elevation came significant changes in species composition. Specificity for particular host plant genera (Molina et al. 1992, Newton and Haigh 1998) is expected to have a major influence on the distribution of ectomycorrhizal fungi; Nantel and Neumann (1992) found a high correlation between ectomycorrhizal fungi and host trees in a mixed forest, regardless of soil characteristics. Hansen (1988), however, suggests that the distributions of mycorrhizal fungi, even those specific to a particular host plant species, are further attenuated by edaphic factors.

Results of our constrained ordinations using different combinations of environmental variables indicated that the variation in fungal composition explained by host plant distributions was similar to the amount explained by the other environmental variables (Table 2). However, this is a generalization based on the entire community of ectomycorhizal fungi, and there is considerable variation in levels of host specificity among species. In the present study, this variation was clearly evident in soil cores taken at the ecotone. In this case, angiosperm and gymnosperm roots were present under identical climatic and edaphic conditions, and any differences in fungal species colonizing the two were due to host specificity. Some fungi, e.g. *Amphinema byssoides*, *Cenococcum geophilum* and *Tomentella* spp., were found on both angiosperm and gymnosperm roots, while others, such as *Russula* and *Lactarius* were found on only gymnosperm roots. The relative influence of host plants should therefore be greatest on the host specific fungi, and the influence of abiotic factors should be greater on non-host specific fungi. Biotic and abiotic determinants of fungal distribution are not independent of course, and host plant distributions are themselves determined by local geology (parent material) and climatic conditions. Geology and climate can also affect ectomycorrhizal fungi directly, or have indirect effects via soil development.

Another observed trend was a decrease in host specificity with elevation, resulting in a high proportion of non-host specific fungi (species which could form symbioses with angiosperms or gymnosperms) in the alpine zone (Figs 1, 2). Strong specificity for either angiosperms or gymnosperms was seen in 60% of the species (collected as sporocarps) in the subalpine forest, 65% of those in the ecotone and 45% of those in the alpine zone (see Kernaghan and Currah 1998). This trend is even clearer in the ectomycorhizal roots, with non-host specific fungi such as *Cenococcum*, *Inocybe*, *Amphinema* and *Tomentella* dominating the alpine community (Fig. 2).

An explanation for the higher levels of host specificity for gymnosperms relative to angiosperms may lie in the role of these plants in community succession. A generalized model of ectomycorrhizal host specificity during succession is given by Last et al. (1987), in which seedlings first form mycorrhizae with a few generalistic fungi and diversity and specificity then increase with tree age until canopy closure. In the alpine zone of the Front Range, *Dryas* acts as an early pioneer, facilitating colonization by *Salix* and then *Picea* (Blundon et al. 1993), and we expect it to be advantageous for *Dryas* and *Salix* to form relatively non-specific symbioses with the limited number of fungal species available during primary succession after deglaciation.

This relative lack of host specificity in the alpine zone, together with the negative influences of alpine climate and soils on ectomycorrhizal richness, would seem to explain many of the observed changes in ectomycorrhizal community structure across tree line.

Recently, conifer recruitment into many low alpine areas has been increasing due to warmer global temperatures (Kupfer and Cairns 1996, Rochefort and Peterson 1996). If the alpine zone were dominated by angiosperm specific ectomycorrhizal fungi, conifers might be at a disadvantage with respect to seedling establishment in the alpine zone. However, because the community of ectomycorrhizal fungi associated with alpine plants in the

Front Range of the Canadian Rockies is relatively non-host specific, it should therefore facilitate conifer recruitment above the present tree line.

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