Distribution of Mycorrhizal Types among Alpine Vascular Plant Families on the Beartooth Plateau, Rocky Mountains, U.S.A., in Reference to Large-Scale Patterns in Arctic–Alpine Habitats

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Abstract

Mycorrhizal symbiosis is critical to plant establishment and survival, influences plant community structure and function, and could be particularly important in harsh environments such as the alpine tundra. An examination of 53 vascular plant species in 21 families from alpine areas of the Beartooth Plateau (Rocky Mountains) revealed most were mycorrhizal (68%) and four distinct types of symbioses were present. They differ in fungal groups involved, plant taxa, physiology, ecology, morphology, and resource acquisition. *Betula*, *Dryas*, *Salix*, and *Polygonum viviparum* consistently form ectomycorrhizae (ECT) with basidiomycete fungi. *Phyllodoce*, *Kalmia*, and *Vaccinium* (Ericaceae) form ericoid mycorrhizae with ascomycete fungi, and *Arctostaphylos* an arbutoid type with basidiomycetes. Eight families (18 species) had only arbuscular mycorrhizae (AM) of glomalean fungi: Apiaceae, Asteraceae, Campanulaceae, Fabaceae, Hydrophyllaceae, Onagraceae, Poaceae, Ranunculaceae. Nonmycorrhizal (NM) families were Brassicaceae, Caryophyllaceae, Crassulaceae, Cyperaceae, Gentianaceae, and Juncaceae. Split families included Polygonaceae (NM/AM/ECT), Portulacaceae (NM/AM), Rosaceae (AM/ECT), and Scrophulariaceae (NM/AM). This is the first report of mycorrhizae for 25 alpine plant species, and most others are new reports for the Rocky Mountains. The distribution of mycorrhizal types among plant families is reasonably consistent across the arctic-alpine biome (reviewed here) with exceptions. The patchy distribution of mycorrhizal types associated with large-scale perennial vegetation mosaics suggests microbial functioning is not uniform across tundra landscapes.

Introduction

Mycorrhizae occur in a broad range of habitats and ecosystems, are geographically widespread, and occur in a majority of plant species and families. Fungi confer benefits to host plants by increasing nutrient and water uptake as well as by providing protection from biotic and abiotic pressures (Smith and Read, 1997). This mutualistic symbiosis contributes to the fitness of the plant, and the structure and function of the plant community, and, in a sense, can be said to regulate that functioning (Allen, 1991). Mycorrhizae may play a particularly crucial role in the survival and diversity of vegetation in harsh environments such as the alpine (Gardes and Dahlberg, 1996; Haselwandter and Read, 1987). Several distinct types of mycorrhizal association are possible, each with its own unique physiology, differential use of resources (Michelsen et al., 1996), and particular taxa of fungi (Smith and Read, 1997), all of which has implications for overall ecosystem functioning.

The arctic-alpine biome covers 8% of the earth's land and is defined by its cold climate (Chapin and Körner, 1995; Körner, 1999). The alpine life zone (3%) is defined as the vegetation zone above treeline and is known for its low compact vegetation and severe abiotic conditions. Alpine plants endure low temperatures and air pressure, intense solar radiation, nutrient poor soils, a short growing season, and intense winds (Billings, 1979; Körner, 1999). In addition, areas of the Rocky Mountains have continental climates with relatively low humidity. Yet a select group of plants adapted to these extreme conditions manages to grow and reproduce in alpine areas (Körner, 1999; Billings, 1973). Varied topography and wide-ranging snow

accumulation creates diverse alpine microhabitats, often spatially compressed into intricate mosaic patterns. Snowbed communities in cold, wet soil exist within a short distance of soils made desert-like by extreme sunlight and critical aspect (Johnson and Billings, 1962). Plants are often dormant up to 10 months of the year and can be either snow covered or exposed and frozen on ridge tops. These short, steep environmental gradients result in development of plant ecotypes that differ in many respects, possibly including mycorrhizal status.

In the larger picture, on a biome scale, it has been suggested that nonmycorrhizal plants are more widespread in high arctic areas than in alpine areas, that infective levels of arbuscular mycorrhizal (AM) fungi varies greatly in cold regions, and that ectomycorrhizae occur primarily with a few widespread woody shrubs in arctic-alpine habitats (Gardes and Dalberg, 1996). Surveys of these microbial fungal communities provide basic information, and are the necessary precursors to understanding how mutualisms aid in plant survival and influence plant community structure in cold-dominated regions on both large and small scales.

Information on the distribution and host specificity of mycorrhizal types with vascular plant species is limited in arctic-alpine situations (Table 1). In the Eurasian Arctic, mycorrhizae have been surveyed in Spitsbergen (Hesselman, 1900; Väre et al., 1992), northwest Finland (Väre et al., 1997), and Siberia (Katenin, 1964). In North America, the mycorrhizal status of arctic plants has been examined in Barrow, Alaska (Miller and Laursen, 1978) and on Eagle Summit (Miller, 1982), Ellesmere Island in Canada (Kohn and Stasovski, 1990), and the Truelove Lowland in Canada (Bledsoe et al., 1990; Stutz, 1972).

Alpine Regions		
Austrian Alps	39 species examined: 4 ECT, 20 AM, 8 ER, 7 other	Haselwandter and Read (1980)
Austrian Alps	113 spp: 14 ECT, 93 AM, 6 NM	Read and Haselwandter (1981)
Tatra Mts, Poland	83 spp: 2 ECT, 64 AM, 1 ECTENDO, 14 NM	Nespiak (1953)
Alaska: Denali Park	38 spp: 6 ECT, 2 AM, 7 ER, 1 AR, 22 NM/MS	Treu et al. (1996)
Colorado alpine	81 spp: unknown	Trappe and Luoma (1992)
N. Rocky Mountains	32 spp: 2 ECT, 27 AM, 3 NM	Lesica and Antibus (1986)
N. Rocky Mountains	53 spp: 7 ECT, 25 AM, 3 ER, 1 AR, 17 NM	Cripps and Eddington (this paper)
Arctic Regions		
Spitsbergen	76 spp: 3 ECT, 0 AM, 2 ER, 71 NM	Väre et al. (1992)
NW Finland	42 spp: 4 ECT, 22 AM, 9 ER, 7 NM	Väre et al. (1997)
Ellesmere Island	24 spp: 6 ECT, 1 AM, 1 AR, 4 ER, 12 NM	Kohn and Stasovski (1990)
Truelove: Canada	55 spp: 3 ECT, 2 ER, 34 internal hypha, 16 NM	Bledsoe et al. (1990)
Truelove: Canada	43 spp: 6 ECT/AR/ER, 7 AM, 30 NM	Stutz (1972)
Alaska: Barrow	16 spp: 6 ECT, 6 AM, 1 ECTENDO, 3 NM	Miller (1982)
N Sweden (subarctic)	23 spp: 6 ECT, 3 AM, 5 ER, 9 NM	Michelsen et al. (1996)
Antarctic/Subantarctic		
S. Orkney and Antarctica	2 spp: 137 samples: 137 NM	Christie and Nicolson (1983)
Marion Island	24 spp: 23 AM, 1 NM	Smith and Newton (1986)
Macquarie Island	36 spp: 15 am, 1 OR, 20 NM	Laursen et al. (1997)

* AM = arbuscular mycorrhizae, AR = arbutoid mycorrhizae, ECTENDO = ectendomycorrhizae, ECT = ectomycorrhizae, ER = ericoid mycorrhizae, OR = orchid, MS = microsclerotia, NM = not mycorrhizal.

Studies have been done in the Antarctic (Christie and Nicolson, 1983; Smith and Newton, 1986), and the subantarctic Macquarie Island (Laursen et al., 1997). Alpine studies include those in the Tatra Mountains of Poland (Nespiak, 1953), the Austrian Alps (Haselwandter and Read, 1980; Read and Haselwandter, 1981), and Denali Park, Alaska (Treu et al., 1996).

A few studies have addressed the mycorrhizal status of plants above timberline in the northern Rocky Mountains. Lesica and Antibus (1986a) examined 32 species of vascular plants from six alpine sites in Montana, including the Beartooth Plateau. Of these, 27 (85%) were AM infected, two were ectomycorrhizal, and three nonmycorrhizal. At least eight of these were from the Beartooth Plateau and seven hosted AM fungi (*Smelowskia calycina*, *Trisetum spicatum*, *Carex rupestris*, *Eritrichium nanum*, *Arenaria obtusiloba*, *Silene acaulis*, and *Castilleja pulchella*). They also found four of six species of alpine hemiparasitic plants (Scrophulariaceae) to have very low levels of AM infection in the Montana alpine (Lesica and Antibus, 1986b).

To examine patterns of symbiosis among plant families at both local (ecotype) and global (arctic-alpine biome) levels, roots of 53 plant species in 21 families from the Beartooth Plateau alpine (Rocky Mountains) were examined, and results compared to that from other arctic-alpine regions, and plant families worldwide. This information can contribute to an understanding of mycorrhizal patterns and functioning of particular plant species and within plant families in an evolutionary context, and can help reveal ecological anomalies and variation in plant-fungal symbiosis in the harsh cold regions of the world.

Methods

STUDY AREA

The study area is located in the alpine vegetation zone of the Beartooth Plateau (45°N, 109°30′W) situated along the Montana-Wyoming border, U.S.A. (Fig. 1). The study sites are a few miles west of Cooke City, in Park County, Wyoming and Carbon County, Montana. The Beartooth Plateau constitutes one of many plateaus in

a fault-block complex, separated by streams and glacial valleys. It contains a broad area of alpine habitats that include boulder fields, talus slopes, moist and dry meadows, snowbeds, patterned ground, and bedrock outcrops (Eversman, 1995). The vegetation as described by Johnson and Billings (1962) is a continuum of four types: alpine turf, alpine meadow, alpine bog, and willow thicket. Within these types are cushion plant communities, *Geum rossii* turf communities, and grass/sedge turf communities. Vegetation types can stretch over large slopes, and run from xeric windy ridge tops to mesic areas and wet bogs. Sharp boundaries can occur due to steep environmental gradients (Johnson and Billings, 1962; Cooper et al., 1997). The average daily temperature during the growing season is 8°C and the average length of the growing season is 81 d. In comparison to arctic regions there are places of high snow accumulation with low air and soil temperatures, resulting in a growing season that varies from 0 to 90 d, depending on snowmelt, topographic site, and year. Thus summers can be longer and warmer, or shorter and colder than in arctic regions (Billings, 1973). Five study sites were selected along U.S. Highway 212 which traverses the Beartooth Plateau, ranging from elevations of 2950 to 3250 m, all above treeline in various alpine habitats within specific plant communities.

COLLECTION AND PROCESSING

Vascular plants were collected from selected habitats at each site during July and August, 2001 and 2002. Plants were either flowering or just past this state. Plants were pressed, dried, and identified according to the nomenclature of Dorn (1984) and Scott (1995). Dried specimens were mounted on herbarium paper, labeled with location data and mycorrhizal status, and deposited in the MONT Herbarium at Montana State University.

Two to three specimens with roots and soil were collected for each plant species. Roots with soil were put in plastic bags, kept cool, and quickly transported. Roots were carefully washed to remove soil and intertwined roots. Because roots were so intertwined and matted, only those that could be traced back to the main root were considered. Once cleaned, roots were clipped, put into plastic cages and kept cool

FIGURE 1. Panorama of the Beartooth Plateau alpine zone in the Northern Rocky Mountains, U.S.A.

and moist until processing. To observe fungi, roots were cleared by simmering in a 10% KOH solution for 3 min, rinsed in tap water for 20 min, simmered in a 5% ink and vinegar solution for 3 min., and rinsed in tap water for 5 to 10 min., following a technique from Vierheilig et al. (1998). Roots were examined under a dissecting scope for ectomycorrhizae and possible colonization of endomycorrhizae. Selected root lengths were mounted on microscope slides and examined under a compound microscope for infection. Levels were not quantified in detail, but particular roots were visually accessed for the extent of mycorrhizal colonization relative to the total root length. If diagnostic hyphae or other mycorrhizal structures were present in a few areas, it was considered lightly infected (+), twice that was considered medium (++), and if a majority of the root was colonized, it was considered a heavy infection (+++). Semipermanent slides were made of infected roots using glycerol as a mounting medium and nail polish to seal edges. These are housed in the MONT Herbarium at Montana State University with dried plant vouchers.

Mycorrhizal types were identified according to Brundrett et al. (1996). Ectomycorrhizae were identified by the presence of a Hartig net, intercellular hyphae, and mantle surrounding the exterior of the root (Fig. 2A). Arbuscular mycorrhizal (AM) fungi were identified by the presence of nonseptate hyphae with arbuscules and/or vesicles (Fig. 2B) within the root and/or the presence of attached spores. Arbutoid

mycorrhizae were identified from root cross sections showing a fungal sheath with hyphal penetration into individual root cells. Ericoid mycorrhizae were recognized by coils or knots of hyphae within cells, and the lack of a sheath. The presence of dark septate hyphae characteristic of endophytic fungi was observed in some plants but was not included as a consistent part of the assessment.

Results

Of the 53 species of alpine vascular plants examined, 36 (68%) were mycorrhizal, and 17 (32%) were not mycorrhizal (Table 2). Four basic types of symbiosis were present in the plant roots examined: ecto-, ericoid, arbutoid, and arbuscular mycorrhizae. Of the mycorrhizal plants, seven species supported ectomycorrhizae (*Betula glandulosa*, *Dryas octopetala*, *Polygonum viviparum*, *Salix arctica*, *S. glauca*, *S. planifolia*, and *S. reticulata*). Twenty-five species were infected with arbuscular mycorrhizal (AM) fungi, primarily in the Asteraceae (10) and Rosaceae (3), plus two in Scrophulariaceae, one in Fabaceae, one in Apiaceae, one in Hydrophyllaceae, two in Ranunculaceae, one in Poaceae, one in Campanulaceae, one in Polygonaceae, one in Onagraceae and one in Portulacaceae (*Lewisia pygmaea*). Three ericaceous plants, *Phyllodoce glanduliflora*, *Kalmia microphylla* and *Vaccinium scoparium* were lightly infected with ericoid fungi
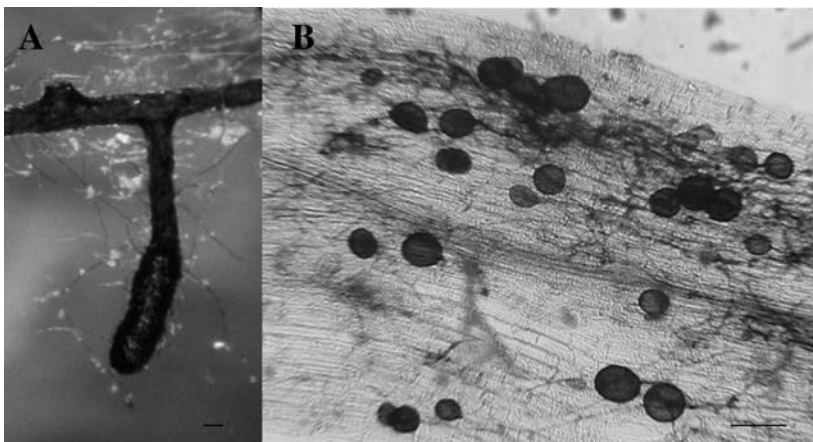

FIGURE 2. Micro-level symbiosis. (A) Ectomycorrhizal root tip of Dryas octopetala *and ascomycete fungus* Cenococcum geophilum. Bar = 1 cm. (B) Vesicles, spores, and hyphae of an arbuscular mycorrhizal fungus within Senecio roots. Bar = 50 μm.

TABLE 2

*Mycorrhizal status of vascular plants from the alpine zone of the Beartooth Plateau, Rocky Mountains, U.S.A New reports for the alpine are starred.**

Family	Species	NM	ECT	AM	ER	AR	Site
APIACEAE	*Bupleurum americanum* Coult. & Rose		−	+++	−	−	mesic
ASTERACEAE	*Achillea millefolium* L.		−	+++	−	−	mesic
	Antennaria lanata (Hook.) Greene		−	+++	−	−	mesic
	Artemisia scopulorum Gray		−	++	−	−	wet
	Aster alpigenus (T. & G.) Gray		−	+++	−	−	mesic
	Erigeron simplex Greene		−	+++	−	−	mesic
	Senecio cymbalarioides Buek		−	+++	−	−	mesic
	Senecio fremontii T. & G.		−	+	−	−	mesic
	Senecio fuscatus Hayek		−	+++	−	−	mesic
	Senecio triangularis Hook.		−	+++	−	−	mesic
	Solidago multiradiata Ait.		−	+++	−	−	mesic
BETULACEAE	*Betula glandulosa* Michx.=*nana* L.		+++	−	−	−	mesic
BRASSICACEAE	*Arabis lemmonii* S. Wats.	*	−	−	−	−	xeric
CAMPANULACEAE	*Campanula rotundifolia* L.		−	+	−	−	mesic
CARYOPHYLLACEAE	*Minuartia obtusiloba* (Rydb.) House	*	−	−	−	−	xeric
	Silene acaulis (L.) Jacq.	*	−	−	−	−	xeric
CRASSULACEAE	*Sedum lanceolatum* Torr.	*	−	−	−	−	mesic
	Sedum rhodanthum Gray	*	−	−	−	−	wet
CYPERACEAE	*Carex scirpoidea* Michx.	*	−	−	−	−	mesic
	Carex sp. 1	*	−	−	−	−	mesic
	Carex sp. 2	*	−	−	−	−	mesic
	Eriophorum callitrix Cham. ex C.A. Mey.	*	−	−	−	−	wet
ERICACEAE	*Arctostaphylos uva-ursi* (L.) Spreng.		?	−	−	+?	mesic
	Kalmia microphylla (Hook.) A. Heller		−	−	+	−	mesic
	Phyllodoce glanduliflora (Hook.) Cov.		−	−	+	−	mesic
	Vaccinium scoparium Leiberg ex Cov.		−	−	+	−	mesic
FABACEAE	*Trifolium parryi* Gray		−	+	−	−	mesic
GENTIANACEAE	*Gentiana algida* Pall.	*	−	−	−	−	mesic
HYDROPHYLLACEAE	*Phacelia hastata* Dougl. ex Lehm.		−	+++	−	−	xeric
JUNCACEAE	*Juncus parryi* Engelm.	*	−	−	−	−	wet
ONAGRACEAE	*Epilobium atpinum* L.		−	++	−	−	wet
POACEAE	*Poa alpina* L.		−	++	−	−	mesic
POLYGONACEAE	*Oxyria digyna* (L.) Hill	*	−	−	−	−	mesic
	Polygonum bistortoides Pursh.	*	−	−	−	−	mesic
	Polygonum vivparum L.		+	−	−	−	mesic
	Rumex paucifolius Nutt.		−	+	−	−	wet
PORTULACACEAE	*Lewisia pygmaea* (Gray) Robins. in Gray		−	+++	−	−	xeric
	Spraguea umbellata Torr.	*	−	−	−	−	xeric
RANUNCULACEAE	*Caltha leptosepala* DC.		−	+	−	−	mesic
	Ranunculus eschscholtzii Schlecht.		−	+	−	−	wet
ROSACEAE	*Dryas octopetala* L.		+++	−	−	−	xeric
	Geum rossii (R.Br.) Ser in DC.		−	+++	−	−	mesic
	Potentilla diversifolia Lehm.		−	+++	−	−	mesic
	Sibbaldia procumbens L.		−	+++	−	−	mesic
SALICACEAE	*Salix arctica* Pall.		+++	−	−	−	mesic
	Salix glauca L.		+++	−	−	−	mesic
	Salix planifolia Pursh		+++	−	−	−	mesic
	Salix reticulata L.		+++	−	−	−	mesic
SCROPHULARIACEAE	*Castilleja pulchella* Rydb.	*	−	−	−	−	mesic
	Pedicularis groenlandica Retz.	*	−	−	−	−	wet
	Pedicularis oederi Vahl ex Homem.	*	−	−	−	−	mesic
	Penstemon procerus Dougl. Ex Grah.		−	+++	−	−	mesic
	Veronica nutans Bong.		−	+++	−	−	wet

* NM = not mycorrhizal, ECT = ectomycorrhizae, AM = arbuscular mycorrhizae, ER = ericoid mycorrhizae, AR = arbutoid mycorrhizae, OR = orchid mycorrhizae, MS = microsclerotia.

and *Arctostaphylos uva-ursi* had arbutoid-type mycorrhizae. One third of the plants were not mycorrhizal, primarily those in Caryophyllaceae, Cyperaceae, Crassulaceae, Brassicaceae, Juncaceae, Portulacaceae, plus two in Scrophulariaceae, and one in Polygonaceae. *Penstemon procerus* and *Veronica nutans*, plants in Scrophulariaceae, a family generally not considered mycorrhizal, were AM infected.

Mycorrhizal Associations by Plant Family in Arctic-Alpine Regions

APIACEAE

The species *Bupleurum americanum*, collected in a dense turf grass community on the Beartooth Plateau, was heavily colonized with

AM fungi. Lesica and Antibus (1986a) found it to be AM colonized as well. In the Subantarctic, Laursen et al. (1997) examined other genera in this family and found internal vesicles and dark septate (DS) hyphae in *Azorella macquariensis* and vesicles and arbuscles in roots of *Hydrocotyle novae-zeelandiae*.

ASTERACEAE

All 10 alpine species examined in this family were well colonized with AM fungi. *Achillea millefolium*, *Antennaria lanata*, *Aster alpigenus*, *Erigeron simplex*, *Senecio cymbalarioides*, *S. fuscatus*, *S. fremontii*, *S. triangularis*, and *Solidago multiradiata* were heavily colonized whereas *Artemisia scopulorum* was less infected. Other arctic-alpine researchers examined different species of *Senecio*, *Erigeron*, and *Solidago* and found them to be AM colonized, including *Senecio canus* (Lesica and Antibus, 1986a; Read and Haselwandter, 1981), *S. subalpinus*, *S. uniflorus* (Nespiak, 1953), and *Solidago virgaurea* (Nespiak, 1953; Väre et al., 1997). Read and Haselwandter (1981) found *Achillea clavennae* to be AM colonized. Väre et al. (1992) reported *Erigeron humilis* to be nonmycorrhizal in the High Arctic, and (Väre et al., 1997) reported *Antennaria dioica* to be AM colonized. In other studies, *Artemisia umbelliformis* supported AM fungi, *A. alpinus* was not mycorrhizal (Read and Haselwandter, 1981), and *Artemisia* sp. had microsclerotia (Treu et al., 1996). AM infection was observed in *Aster bellidiastrum* in the Alps (Haselwandter and Read, 1980; Read and Haselwandter, 1981).

BETULACEAE

Betula glandulosa was not examined in detail as for the other families, but roots were ectomycorrhizal, and mushrooms of particular basidiomycete fungi such as *Leccinum rotundifoliae*, and *Lactarius glyciosmus*, specific for birch on the Beartooth Plateau, indicated an ectomycorrhizal status (Cripps, 2002). Other arctic studies have shown *Betula nana* to be associated with a diversity of ectomycorrhizal fungi in arctic-alpine regions, primarily basidiomycetes, but with a few ascomycetes as well (Gardes and Dahlberg, 1996).

BRASSICACEAE

Arabis lemmonii collected from a disturbed area was nonmycorrhizal. In the Tatra mountains, Nespiak (1953) found *A. alpina* and *A. neglecta* to be nonmycorrhizal.

CAMPANULACEAE

Campanula rotundifolia had slight AM colonization. In another alpine study, it was also AM colonized (Nespiak, 1953). *Campanula alpina* and *C. scheuchzeri* supported AM fungi in the Tatras and Alps (Nespiak, 1953; Read and Haselwandter, 1981), but *C. uniflora* was nonmycorrhizal in the Arctic (Väre et al., 1992).

CARYOPHYLLACEAE

Both *Minuartia obtusiloba* and *Silene acaulis* were nonmycorrhizal in our Beartooth samples. Other studies showed mixed reports on these species. In other alpine areas, *S. acaulis* was either AM colonized (Nespiak, 1953; Haselwandter and Read, 1980), or nonmycorrhizal (Read and Haselwandter, 1981; Treu et al., 1996). In arctic regions, all *Silene acaulis* specimens examined were nonmycorrhizal (Väre et al., 1992, 1997) except one in the Canadian Arctic that was AM infected (Bledsoe et al., 1990). Kohn and Stasovski (1990) suggest evidence of ericoid-like fungi in this species. Other species of *Minuartia* (*M. verna*, *M. rubella*, *M. biflora*) have been assessed as

primarily nonmycorrhizal (Read and Haselwandter, 1981; Väre et al., 1992), but Bledsoe et al. (1990) have two reports of AM fungi on *M. rubella* and *M. rossii*.

CYPERACEAE

The two unidentified *Carex* species examined were nonmycorrhizal as was *Carex scirpoidea*, and *Eriophorum callitrix*. In other studies, some *Carex* species (*C. curvula*, *C. leporinella*, *C. misandra*, *C. nardina*, *C. stans*) were AM colonized (Bledsoe et al., 1990; Haselwandter and Read, 1980; Read and Haselwandter, 1981; Lesica and Antibus, 1986a) while other species (*C. bigelowi*, *C. firma*, *C. lachenalii*, *C. membranacea*, *C. mirochaeta*, *C. nardina*, *C. podocarpa*, *C. rupestris*, *C. scirpoidea*, *C. sempervirens*, *C. subspathecea*, *C. trifida*, *C. ursina*, *C. vaginata*) were nonmycorrhizal (Nespiak, 1953; Haselwandter and Read, 1980; Read and Haselwandter, 1981; Miller, 1982; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Väre et al., 1992, 1997; Michelsen et al., 1996; Treu et al., 1996; Laursen et al., 1997). *Kobresia mysurioides* (not examined in the present study) is consistently ectomycorrhizal in arctic and alpine regions, and this symbiosis type is exceptional for a sedge (Read and Haselwandter, 1981; Kohn and Stasovski, 1990; Massicotte et al., 1998; Schadt et al., 2001). Kohn and Stasovski (1990) found one species of *Carex* to possibly have ericoid-like mycorrhizae. In arctic regions, *Eriophorum scheuchceri*, *E. triste*, and *E. vaginatum* were all nonmycorrhizal (Miller, 1982; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Väre et al., 1992) however, Bledsoe et al. (1990) found *E. scheuchzeri* to have AM fungi in the Canadian Arctic.

CRASSULACEAE

Sedum lanceolatum and *S. rhodanthum* were nonmycorrhizal in our study. Nespiak (1953) found *Sedum alprestre* to be nonmycorrhizal and Väre et al. (1997) reported a species in a different genus of this family, *Rhodiola rosea*, to be AM colonized.

ERICACEAE

Three of the ericacous plants in our study, *Phyllodoce glanduliflora*, *Kalmia microphylla*, and *Vaccinium scoparium* were well colonized with ericoid mycorrhizae, however, colonization was light in *Arctostaphylos uva-ursi* which had an arbutoid type infection and was also possibly ectomycorrhizal. In other surveys, species of *Arctostaphylos* (*A. alpina*, *A. rubra*) had arbutoid (Miller, 1982; Treu et al., 1996) as well as ectomycorrhizae. *Vaccinium* species (*V. myrtillus*, *V. uliginosum*, *V. vitis idaea*) from most other studies displayed ericoid mycorrhizae (Miller and Laursen, 1978; Haselwandter and Read, 1980; Miller, 1982; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Treu et al., 1996; Väre et al., 1997), but *V. uliginosum* was reported ectomycorrhizal by Stutz (1972). *Loiseleuria procumbens* and *Calluna vulgaris* also host ericoid fungi in the alpine (Haselwandter, 1979). Some discrepancies might be explained by recent changes in terminology.

FABACEAE

Trifolium parryi was lightly colonized with AM fungi on the Beartooth. Lesica and Antibus (1986a) found *T. haydnii* to be AM colonized as well. Other species in this family that have been examined include *Oxytropis nigrescens* which was nonmycorrhizal (Miller, 1982) and *Astragalus alpinus* (Väre et al., 1997), also nonmycorrhizal.

FIGURE 3. *Organism level symbiosis. (A)* Caltha leptosepala *hosts arbuscular mycorrhizal fungi in its roots. (B)* Dryas *is ectomycorrhizal with mushroom-producing fungus* Entoloma alpicola.

GENTIANACEAE

Gentiana algida (Arctic gentian) was not mycorrhizal, however a very uniform type colonization of dark septate hyphae was observed within cells with clusters of small round cells (microsclerotia). Other studies reported *G. algida* to be nonmycorrhizal but with micro-sclerotia (Read and Haselwandter, 1981; Treu et al., 1996), and *G. punctata* and *G. frigida* to be endomycorrhizal (Nespiak, 1953).

HYDROPHYLLACEAE

Phacelia hastata collected from a recently disturbed (3 yr) site was heavily colonized with AM fungi. No other reports on this species and family could be found.

JUNCACEAE

Juncus parryi was nonmycorrhizal in alpine areas of the Bear-tooth Plateau. Species examined in the other studies such as *J. biglumis* and *J. trifidus* were also nonmycorrhizal (Kohn and Stasovski, 1990; Väre et al., 1992, 1997), however, there are reports of AM fungi on *J. trifidus* and *J. biglumis*i (Nespiak, 1953; Bledsoe et al., 1990).

ONAGRACEAE

Epilobium alpinum was moderately colonized with AM fungi. In the Arctic, Väre et al. (1997) found *E. anagallidifolium* to have AM fungi, and in the Subantarctic, Laursen et al. (1997) found *E. brun-nescens* to be nonmycorrhizal and *E. pendunculara* to have AM fungi and dark septate hyphae.

POACEAE

Poa alpina was AM colonized in this study. Other alpine studies found it to have AM fungi as well (Nespiak, 1953; Haselwandter and Read, 1980; Read and Haselwandter, 1981). For other species, *Poa laxa* was AM colonized (Nespiak, 1953; Haselwandter and Read, 1980) and *P. arctica* was nonmycorrhizal (Treu et al., 1996). *Poa alpina* was nonmycorrhizal in Väre et al.'s (1992) arctic study. In arctic regions, many *Poa* species are reported nonmycorrhizal including *P. phryganodes*, *P. algida*, *P. alpigena*, *P. arctica*, and *P. abbreviata*. (Bledsoe et al., 1990; Väre et al., 1992), however, *P. alpigena* and *P. arctica* have been found with AM fungi (Bledsoe et al., 1990; Väre et al., 1997). For antarctic and subantarctic areas, *P. flabellata* and *P. annaua* were nonmycorrhizal (Christie and Nicolson, 1983; Laursen et al., 1997). *Poa cookii* was reported AM colonized by Smith and Newton (1986) and with vesicles by Laursen et al. (1997). *Poa foliosa* and *P. literosa* were infected with dark septate hyphae in the Subantarctic (Laursen et al., 1997). The grass *Deschampsia* (not examined in this study) can be completely nonmycorrhizal in the Arctic (DeMars and Boerneer, 1995).

POLYGONACEAE

Polygonum bistortoides was nonmycorrhizal in our study. It was nonmycorrhizal in the Alaskan alpine as well (Treu et al., 1996), but noted with AM fungi in Montana (Lesica and Antibus, 1986a) and the Tatra mountains of Poland (Nespiak, 1953). In contrast, *Polygonum viviparum* was ectomycorrhizal in our study with a black morphotype on root tips similar to the ascomycete *Cenococcum*. *Polygonum viviparum* is also reported to be ectomycorrhizal in the Alps, the Alaskan alpine, Norway, and alpine areas of Montana (Lesica and Antibus, 1986a; Read and Haselwandter, 1981; Sønstebo, 2002; Treu et al., 1996), the only exception being Nespiak (1953) who found endomycorrhizae. In arctic regions, it was entirely nonmycorrhizal (Bledsoe et al., 1990; Väre et al., 1992, 1997).

In our study, *Rumex paucifolius* from wet areas, was lightly colonized with AM fungi, and this is the first report for this species to our knowledge. *Oxyria digynia*, a plant found by itself near a melting snow bank on the Beartooth Mountains was nonmycorrhizal. In other studies, Nespiak (1953) and Väre et al. (1992) also found it to be nonmycorrhizal, but AM fungi are reported by Bledsoe et al. (1990).

PORTULACACEAE

Lewisia pygmaea, found in very open dry rocky areas near lichen-encrusted soil within dense grassy meadows, was heavily colonized with AM fungi. *Spraguea umbellata* from an erosional area was nonmycorrhizal. There are no previous reports of mycorrhizal status for these species.

RANUNCULACEAE

Caltha leptosepala (Fig. 3A) was lightly colonized with AM fungi. Different genera and species in this family are typically noted to be associated with AM fungi (Nespiak, 1953; Haselwandter and Read, 1980; Read and Haselwandter, 1981; Bledsoe et al., 1990; Treu et al., 1996; Väre et al., 1997). However, Väre et al. (1992) found all species examined in the family to lack mycorrhizae in the High Arctic. *Ranunculus eschscholtzii*, a snowbed buttercup, was possibly AM colonized in our study. Other studies in the alpine found *R. alpestris*, *R. glacialis*, and *R. montanus* to have AM fungi or at least endo-mycorrhizae (Nespiak, 1953; Haselwandter and Read, 1980; Read and Haselwandter, 1981). Väre et al. (1992) in Spitsbergen found all the *Ranunculus* examined to be nonmycorrhizal (*R. hyperboreus*, *R. lapponicus*, *R. nivalis*, *R. pygmaeus*, *R. spitsbergensis*, and

R. sulphureus). Other arctic studies reported *R. acris*, *R. nivalis*, *R. pygmaeus*, and *R. sulphureus* to be AM colonized (Bledsoe et al., 1990; Väre et al., 1997). Antarctic and subantarctic studies found *R. biternatus* and *R. crassipes* to have AM fungi (Christie and Nicolson, 1983; Smith and Newton, 1986; Laursen et al., 1997).

ROSACEAE

Three of the species examined in this family, *Potentilla diversifolia*, *Geum rossii*, and *Sibbaldia procumbens* were heavily colonized with AM fungi. *Dryas octopetala* (Fig. 3B) was ectomycorrhizal in all specimens, and *Oxyria digyna* was not mycorrhizal. Many species of *Potentilla* have been reported with AM infections, including *P. aurea*, *P. brauniana*, *P. cranzii*, and *P. ovina* in other arctic-alpine surveys (Nespiak, 1953; Haselwandter and Read, 1980; Read and Haselwandter, 1981; Lesica and Antibus, 1986a; Väre et al., 1997). Nonmycorrhizal reports include *Potentilla hyparctica* and *P. pulchella* in the Arctic (Väre et al., 1992). Bledsoe et al. (1990) reported *Potentilla hyparctica* ectomycorrhizal in Canada. *Geum rossii* has been found with AM fungi (Lesica and Antibus, 1986a) as has *G. montanum* and *G. reptans* (Nespiak, 1953; Read and Haselwandter, 1981). *Sibbaldia procumbens* likewise can be colonized by AM fungi (Treu et al., 1996; Väre et al., 1997).

Dryas octopetala is consistently ectomycorrhizal (Haselwandter and Read, 1980; Read and Haselwandter, 1981; Miller, 1982; Lesica and Antibus, 1986a; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Treu et al., 1996; Väre et al., 1992). A survey of macrofungi on the Beartooth Plateau shows *Dryas octopetala* (Fig. 3A) to be mycorrhizal with several basidiomycetes, including species of *Cortinarius*, *Inocybe*, *Entoloma*, and *Hebeloma*, however, the ascomycete *Cenococcum geophilum* (Fig. 3B) is the most common fungus on *Dryas* roots in this area (Cripps, 2002). *Dryas* is ectomycorrhizal in other arctic-alpine areas where it hosts a more diverse ectomycorrhizal flora, compared to the depauperate one on the Beartooth Plateau. *Dryas* supports a large array of macrofungi in the Scottish Highlands, including *Boletus edulis* and *Cantharellus cibarius* which appears to be a result of historical factors (Harrington and Mitchell, 2002). Mycorrhizae have been synthesized with *Dryas* in the laboratory (Debaud et al., 1981).

SALICACEAE

Dwarf willows *Salix arctica* and *S. reticulata*, and shrub willows *S. planifolia* and *S. glauca* are all ectomycorrizal. To date, over 60 species of ectomycorrhizal fungi have been catalogued with *Salix* species on the Beartooth Plateau, with some specificity involved. Primary ectomycorrhizal genera are *Amanita*, *Cortinarius*, *Entoloma* (Fig. 3B), *Hebeloma*, *Inocybe*, *Lactarius*, and *Russula* (Cripps, 2002). A black morphotype is common on *Salix* root tips. In one case, the mantle was dissected, pressed on a slide and the characteristic "star pattern" of *Cenococcum* observed. Pieces of the mantle and adjacent sclerotia were surface sterilized and cultured on agar. However, when the ITS region of the cultured fungus was sequenced, it matched *Phialocephala fortinii* at 99%, a species also known to occur on alpine plants. At this point we do not understand the result, but report it here. Possible conclusions are that (1) both fungi were present in the characteristic mantle, and *Philalocephala* grew while *Cenococcum* did not, (2) that the molecular data is in error, or (3) that *Philalocephala* produced a *Cenococcum*-like mantle which appears unlikely. It is possible that surface sterilization kills ectomycorrhizal fungi and releases endophytic fungi.

In other studies, *Salix* species were ectomycorrhizal (Haselwandter and Read, 1980; Read and Haselwandter, 1981; Miller, 1982; Bledsoe et al., 1990; Kohn and Stasovski, 1990; Treu et al., 1996; Väre

et al., 1992, 1997). However, AM fungi can occur along with ectomycorrhizal fungi in *Salix reticulata*, *S. herbacea*, *S. myrsinites*, *S. glauca*, *S. lanata*, *S. hastata*, and *S. nigricans* (Dhillion, 1994). Nespiak (1953) reported *Salix herbacea* to be ect-endomycorrhizal which might be explained by Dhillion's report of both endo- and ectomycorrhizal fungi in roots. Alpine willows are known to have a diverse mycoflora (Gardes and Dahlberg, 1996) and mycorrhizae have been synthesized on dwarf willows (Antibus et al., 1981; Graf and Brunner, 1997).

SCROPHULARIACEAE

Penstemon procerus and *Veronica nutans* were heavily colonized with AM fungi. Other alpine researchers reported *Veronica alpina* (Nespiak, 1953; Väre et al., 1997) and *V. fruticans* (Haselwandter and Read, 1980; Read and Haselwandter, 1981) to have AM mycorrhizae.

Pedicularis groenlandica, *P. oederi*, and *Castilleja pulchella* were nonmycorrhizal for our specimens. However, in a study of hemiparasitic plants in Montana, *P. groenlandica*, *P. parryi* and some species of *Castilleja* including *C. pulchella* had traces of AM infection (Lesica and Antibus, 1986b). The genus *Pedicularis* apparently varies in its mycorrhizal status, and has been reported as ectomycorrhizal (*P. capitata*, *P. hirsuta*, *P. dasyantha*) by Stutz (1972), Kohn and Stasovski (1990), and Väre et al. (1992) in the Arctic. In contrast, *P. capitata*, *P. hirsuta*, *P. lanata*, and *P. sudetica* are reported to host AM fungi in the Arctic in another study (Bledsloe et al., 1990). In the alpine, Treu et al. (1996) found four species of *Pedicularis* (*P. capitata*, *P. kanei*, *P. langsdorffii*, *P. verticillata*) to be devoid of mycorrhizal fungi, but most had microslerotia in the roots. Kohn and Stasovski (1990) found one species, *P. hirsuta*, to be nonmycorrhizal.

Discussion

Worldwide, the alpine flora consists of 8000 to 10,000 species of vascular plants, in approximately 2000 genera and 100 families. About one fourth of all higher plant families include alpine representatives (Körner, 1999). Prominent alpine families are Asteraceae, Brassicaceae, Caryophyllaceae, Cyperaceae, Ericaceae, Gentianaceae, Poaceae, Ranunculaceae, and Rosaceae, all of which were sampled on the Beartooth Plateau. Over 400 species in about 43 alpine plant families occur on the Beartooth Plateau (Lackschewitz, 1994), and several are considered rare taxa (Lesica, 1991). A majority of the plant species examined from the Beartooth Plateau had mycorrhizae (68%), and while the remainder did not, many hosted fungi of unknown ecology. This suggests few plants are free of fungi in their roots in the alpine. The mycorrhizal status of twenty-five alpine plant species are new reports for the alpine (Table 2), and most are new reports for the Beartooth Plateau and the Rocky Mountains where information is substantially lacking. To gain a larger perspective, results were compared to those from other arctic-alpine regions, and to general mycorrhizal patterns of vascular plant families worldwide in all terrestrial habitats (Newman and Reddell, 1987; Smith and Read, 1997). Patterns for the Beartooth Plateau were similar to that for other arctic-alpine regions, however, different plant species were often examined making direct comparisons difficult, and differences between arctic and alpine regions need to be taken into account.

ECTOMYCORRHIZAL PLANT FAMILIES OF THE BEARTOOTH PLATEAU

Betulaceae (*Betula glandulosa*) and Salicaceae (*Salix arctica*, *S. glauca*, *S. planifolia*, *S. reticulata*) are woody, deciduous, dicot taxa, and both families were entirely ectomycorrhizal with basidiomycete

fungi in our study. These families are consistently ectomycorrhizal in other arctic-alpine studies, although AM fungi were noted as well in one study of willow (Dhillon, 1994). Worldwide for all habitats and 74 species, these two families are 100% mycorrhizal with no records of nonmycorrhizal plants in nature (Newman and Reddell, 1987). Globally, Betulaceae is ectomycorrhizal in 70% of species, or hosts both ecto- and AM fungi (22%), with rare reports of other types (Newman and Reddell, 1987). Similarly, Salicaceae hosts ectomycorrhizal fungi in 83% of species, AM in 4%, and both 11% of the time (Newman and Reddell, 1987). There are thousands of species of possible fungal symbionts worldwide (Smith and Read, 1997), hundreds possible in arctic-alpine regions (Gardes and Dahlberg, 1996), and over 60 are recorded with willow from the Beartooth Plateau alpine zone (Cripps, 2002). Ectomycorrhizal outliers (in typically AM or nonmycorrhizal families) such as *Kobresia mysurioides*, *Polygonum viviparum*, and *Dryas* are discussed within their respective families.

ERICOID AND ARBUTOID PLANT FAMILIES OF THE BEARTOOTH PLATEAU

Plants examined in the Ericaceae formed either ericoid mycorrhizae (*Phyllodoce glanduliflora*, *Kalmia microphylla*, *Vaccinium scoparium*) with ascomycete fungi, or arbutoid mycorrhizae (*Arctostaphylos uva-ursi*) with basidiomycete fungi. Beartooth plants followed a pattern similar to that of ericaceous plants in other arctic-alpine habitats where nonwoody species associate with particular ascomycete (ericoid) fungi, and woody species associate with basidiomycete fungi forming arbutoid mycorrhizae (Haselwandter, 1979; Read, 1983). It is generally thought that the basidiomycete fungi involved in the arbutoid symbiosis are the same as those that form ectomycorrhizae on plants in other families. Worldwide, the Ericaceae (for 81 spp.) are mycorrhizal 95% of the time (Newman and Reddell, 1987), and the family is important in arctic-alpine regions.

ARBUSCULAR MYCORRHIZAL (AM) PLANT FAMILIES OF THE BEARTOOTH PLATEAU

Eight families from the Beartooth Plateau formed only arbuscular mycorrhizae (AM, VA) with glomalean fungi in this study, and are: Apiaceae, Asteraceae, Campanulaceae, Fabaceae, Hydrophyllaceae, Onagraceae, Poaceae, and Ranunculaceae. These families are reported to host AM fungi in other arctic-alpine studies, but often different species were examined, and there are occasional reports of nonmycorrhizal plants. This is the most widespread type of mycorrhiza occurring on a majority of plant species worldwide (Smith and Read, 1997).

Asteraceae is well established as an AM family in arctic-alpine regions, and this was confirmed by our 10 heavily infected species. There are, however, reports of nonmycorrhizal plants and only microsclerotia in roots (Read and Haselwandter, 1981; Treu et al., 1996). Worldwide the family contains 80% mycorrhizal species, and 98% of these are with AM fungi (Newman and Reddell, 1987). In Ranunculaceae, all of our species were AM infected, similar to different species in other alpine habitats, but plants in high arctic communities are commonly nonmycorrhizal, and this difference is particularly true for the genus *Ranunculus* (Väre et al., 1992). Globally, Ranunculaceae species are mycorrhizal 80% of the time, and 94% of these are with AM fungi (Newman and Reddell, 1987). Similarly, most grasses in Poaceae host AM fungi in the alpine (as in our study), but many plants are nonmycorrhizal in the High Arctic and Antarctic (Bledsloe et al., 1990; Laursen et al., 1997; Väre et al., 1992). For example, 75 samples of *Deschampsia antarctica* from the Arctic were totally devoid of mycorrhizae, but the same species was capable of

mycorrhization by AM fungi in greenhouse studies (DeMars and Boerner, 1995). Calcicole grasses in the Bavarian alpine heath, on the other hand, have a high degree of AM infection (Blaschke, 1991). Two species of grasses in subarctic Sweden were AM infected in harsh fellfields and lacked infection in heaths, suggesting environmental factors can play a role in mycorrhizal status, but taxonomic considerations were also important in the study (Michelsen et al., 1996). Worldwide, Poaceae (202 species) is reported mycorrhizal 84% of the time, almost always with AM fungi (99%) (Newman and Reddell, 1987). More research is necessary to determine if the nonmycorrhizal status of some grass plants are a result of taxonomic or environmental factors. In the Fabaceae, the one species (*Trifolium parryi*) examined from the Beartooth hosted AM fungi in the roots, but both mycorrhizal and nonmycorrhizal plants are known from arctic and alpine regions. Worldwide, also for 202 species, over 90% are mycorrhizal, 82% with AM fungi, 16% with ectomycorrhizal fungi, and 2% with both. While generally considered a nitrogen-fixing family, leguminous plants also depend on mycorrhizal fungi.

In general for AM families, plants can apparently lack mycorrhizae under particular environmental conditions, and this is more likely in the Arctic than in the alpine. Wet anaerobic soils, lack of appropriate inocula, seasonality, and absence of an advantage for symbiosis could preclude some plant-AM unions.

PRIMARILY AM FAMILIES, WITH VARIABLE STATUS IN OUR STUDY

Four families were not consistent in their mycorrhizal status on the Beartooth Plateau. Polygonaceae contained two nonmycorrhizal, one AM, and one ectomycorrhizal species. In arctic-alpine habitats, two closely related species are of interest: *Polygonum bistortoides* which is generally nonmycorrhizal (or with AM fungi), and *P. viviparum* which is typically ectomycorrhizal in the alpine (Sønstebo, 2002). This was true for our study as well; however, *P. viviparum* can be nonmycorrhizal in the Arctic (Bledsoe et al., 1990; Väre et al., 1992, 1997). Other genera in this family host AM fungi, but there are numerous reports of nonmycorrhizal plants in both arctic and alpine habitats. Worldwide for 30 species, 40% are mycorrhizal, 23% are variable, and 37% lack mycorrhizae (Newman and Reddell, 1987).

Rosaceae is primarily an AM family, and this was true for *Potentilla* and *Geum* species in our study, but *Dryas octopetala* hosted ectomycorrhizal fungi, and this pattern is consistent for other arctic-alpine habitats as well. Occasionally, other species in this family, primarily woody types, are reported to be ectomycorrhizal under some circumstances (Bledsloe et al., 1990), and nonmycorrhizal plants occur as well. Worldwide the Rosaceae (84 species tested) is mycorrhizal 82% of the time, mostly with AM fungi (74%), occasionally with ectomycorrhizal fungi (12%), or both (14%) (Newman and Reddell, 1987). There is scant information for the Portulacaeae, and we report for the first time that *Lewisia pygmaea* (pygmy bitterroot) was AM infected, and that *Spraguea umbellata* lacked mycorrhizae. The Scrophulariaceae was once considered a nonmycorrhizal family, and while three species lacked mycorrhizae on the Beartooth Plateau, two were infected with AM fungi. The genus *Pedicularis* is particularly interesting because it has been reported with AM fungi, as nonmycorrhizal, or as ectomycorrhizal in the Arctic. This variability appears environmentally induced and not stable within a species (Stutz, 1972; Kohn and Stasovski, 1990; Treu et al., 1996; Vare et al., 1992). *Castilleja* is also of interest in this regard, and while our species were nonmycorrhizal, some plants on the Beartooth Plateau apparently can host AM fungi (Lesica and Antibus, 1986b). Worldwide in Scrophulariaceae, 66% of the species are mycorrhizal, 13% variable, and 22% nonmycorrhizal as reported by Newman and Reddell (1987). Of the mycorrhizal species, 96% are reported with AM fungi.

Six families (Brassicaceae, Caryophyllaceae, Cyperaceae, Crassulaceae, Gentianaceae, Juncaceae) were entirely nonmycorrhizal on the Beartooth Plateau above treeline for all the plants examined. Four of the families were previously considered essentially nonmycorrhizal (the other two unknown), but there is growing evidence that mycorrhizae are not rare in these groups, and that frequency varies with the family. This also appears to be true in arctic-alpine regions. While we found all plants in the Brassicaceae, Caryophyllaceae, Cyperaceae, and Juncaceae to be nonmycorrhizal on the Beartooth Plateau, there are a growing number of reports of AM fungi in these families. A detailed study of *Carex* (Cyperaceae) found 16 of 23 species capable of hosting AM mycorrhizae, and reported that mycorrhizae are more widespread than once thought in the genus (Miller et al., 1999). Discrepancies appear to arise because sedges in wet, anaerobic soils often lack mycorrhizae, and because of seasonal variation (Miller et al., 1999; Ruotsalainen et al., 2002). Both taxonomic position and environmental conditions can apparently play a role in determining mycorrhizal status. On the other hand, the sedge *Kobresia mysurioides* (Cyperaceae) appears to be consistently ectomycorrhizal in the alpine (Massicotte et al., 1998; Lipson et al., 1999), and this is a taxonomically stable union. It is rare for any kind of grass or sedge to be ectomycorrhizal, particularly with consistency. Worldwide, the sedge family is 74% nonmycorrhizal for 123 species studied, and of the 26% reported as mycorrhizal, most (97%) were with AM fungi. Worldwide, families once considered nonmycorrhizal range from 8% mycorrhizal in Brassicaceae (63 species studied), 11% in Cyperaceae (123 spp.), 15% in Juncaceae (39 spp.), 36% in Caryophyllaceae (28 spp.), to 66% in Scrophulariaceae (32 spp.) according to Newman and Reddell (1987). When plants are mycorrhizal in these families, it is primarily with AM fungi, with rare exceptions.

ENDOPHYTIC FUNGI WITHIN ARCTIC-ALPINE PLANTS

Many root systems (both mycorrhizal and nonmycorrhizal) in our study, hosted a diversity of root-associated fungi that could be categorized as fine endophytes, dark septate endophytes, root parasites, and/or saprophytes. These were not recorded consistently in our study, but were prevalent on some plant species such as the Arctic gentian (*Gentiana algida*). Endophytic fungi are common in alpine plants (Stoyke and Currah, 1991; Jumpponen et al., 1998; Jumponnen, 2001; Grünig et al., 2002), although their ecological roles are not clear. They also occur in plants in other terrestrial habitats as reviewed in Jumponnen and Trappe (1998). Dark septate root fungi re-inoculated onto alpine *Carex* increased biomass, suggesting a putatively mutualistic role (Haselwandter and Read, 1982), and some species have enzymes for decomposition of detritus (Caldwell et al., 2000). The alpine plant *Ranunculus adoneus* is associated with endophytic fungi in Colorado (Schadt et al., 2001), including *Phialophora gregata*, and we add to this our putative discovery of *Philalocephala fortinii* on *Salix arctica* in Wyoming.

NUTRIENT PARTITIONING AND RECYCLING
BY MYOCORRHIZAL FUNGI IN ARCTIC-ALPINE HABITATS

Arctic and alpine soils are generally nutrient deficient, and often low in inorganic N and P (Kielland, 1994). While all mycorrhizal types are thought to confer nutritional and protective benefits to plants, these vary depending on the symbionts involved, and biotic and abiotic factors (Smith and Read, 1997). There is evidence that plants with different types of mycorrhizae access different nutritional resources. For example, some ectomycorrhizal fungi have phosphatase activity

that promotes the use of inorganic P by plants (Antibus et al., 1981). Nitrogen is particularly limiting in arctic-alpine habitats, where the largest portion of N is in organic form, and tied up in recalcitrant organic matter (Kielland, 1994). Further, N and P in plant tissue from the Colorado alpine region are not directly proportional to that in the soil, which suggests other factors are at work (Bowman et al., 2003), perhaps at the soil-plant interface. A study of ^{15}N, showed that various types of mycorrhizae access different nitrogen sources (Michelsen et al., 1996). Interestingly, the ectomycorrhizal symbiosis accessed mostly organic N, probably from fresh leaf litter, and had a limited ability to use NO^{3-} if available. These results were for ectomycorrhizal *Salix*, *Betula*, and *Dryas* mats in subarctic Sweden. Several strains of *Hebeloma*, an important ectomycorrhizal fungal genus in the arctic and alpine, were tested for the ability to assimilate amino acids. Arctic *Hebeloma* strains actually preferred an organic source of N over inorganic NH^{4+} forms (Tibbett et al., 1998). Similarly, the ectomycorrhizal sedge *Kobresia* is able to access amino acids as an N source (Lipson et al., 1999). Plants with ericoid mycorrhizae also access organic N in litter, and appear to be even more dependent on this N source (Michelsen et al., 1996). Neither mycorrhizal type used complexed N in the recalcitrant part of the organic matter.

In the same study, plants with AM fungi had access to mostly inorganic N in the form of NH^{4+}, as did nonmycorrhizal plants. This might help explain why the same grass species were AM infected in fellfields but lacked infection in heaths where high organic matter was present (Michelsen et al., 1996). Plants with nitrogen-fixing organisms on their roots (Fabaceae) used atmospheric N^2, but also supported mycorrhizal fungi that accessed other N sources (Michelsen et al., 1996). Endophytic ascomycetes such as *Philophora finlandia* and *Phialocephala fortinii* are capable of utilizing detrital substates as carbon and nitrogen sources as well as functioning as biotrophs in mycorrhizal associations (Caldwell et al., 2000). In addition, the ecological roles of these fungi can change seasonally, or with plant condition. Microbes (including mycorrhizal fungi) are in competition for scarce resources in arctic-alpine habitats, and nutrient partitioning and recycling are two strategies that optimize the use of available resources. The various mycorrhizal types function differently in vascular plant communities, and, in addition, not much is known about how they interact.

DISTURBANCE IN TUNDRA ECOSYSTEMS

Knowledge of specific plant-fungal associations could also lead to useful reclamation practices in cold regions. Disturbance can deplete microbial communities in the alpine. For example, the 10 alpine plant species examined during high-elevation reclamation work on the Beartooth Plateau all hosted AM fungi in revegetation plots, but the diversity of fungi was low (one species) compared to that of undisturbed areas (11 species) (Allen et al., 1987). It is not known if microbial communities recover in alpine habitats, or if plant access to appropriate microbes speeds the revegetation process. In a subalpine study, fungal inoculum reduced ruderal species (nonmycorrhizal weeds and exotics), and increased succession rates in some plots. However, in other plots, the lack of ruderals to hold the soil was detrimental (Allen and Allen, 1988). The use of nonobligate mycorrhizal species such as *Deschampsia* could offer a more flexible system in the alpine. An additional benefit of mycorrhizal fungi is that mycelium aggregates and stabilizes soils at high elevations (Graf and Brunner, 1995). Reconstruction of the Beartooth Highway, which began in 2004, will disturb alpine habitat along the corridor. Revegetation efforts will be extensive and challenging, and success will depend on many factors, possibly including recovery of microbes in the soil. The prevalence and diversity of mycorrhizal symbioses can be indicators of the health and sustainability of plant communities. In the larger picture, information
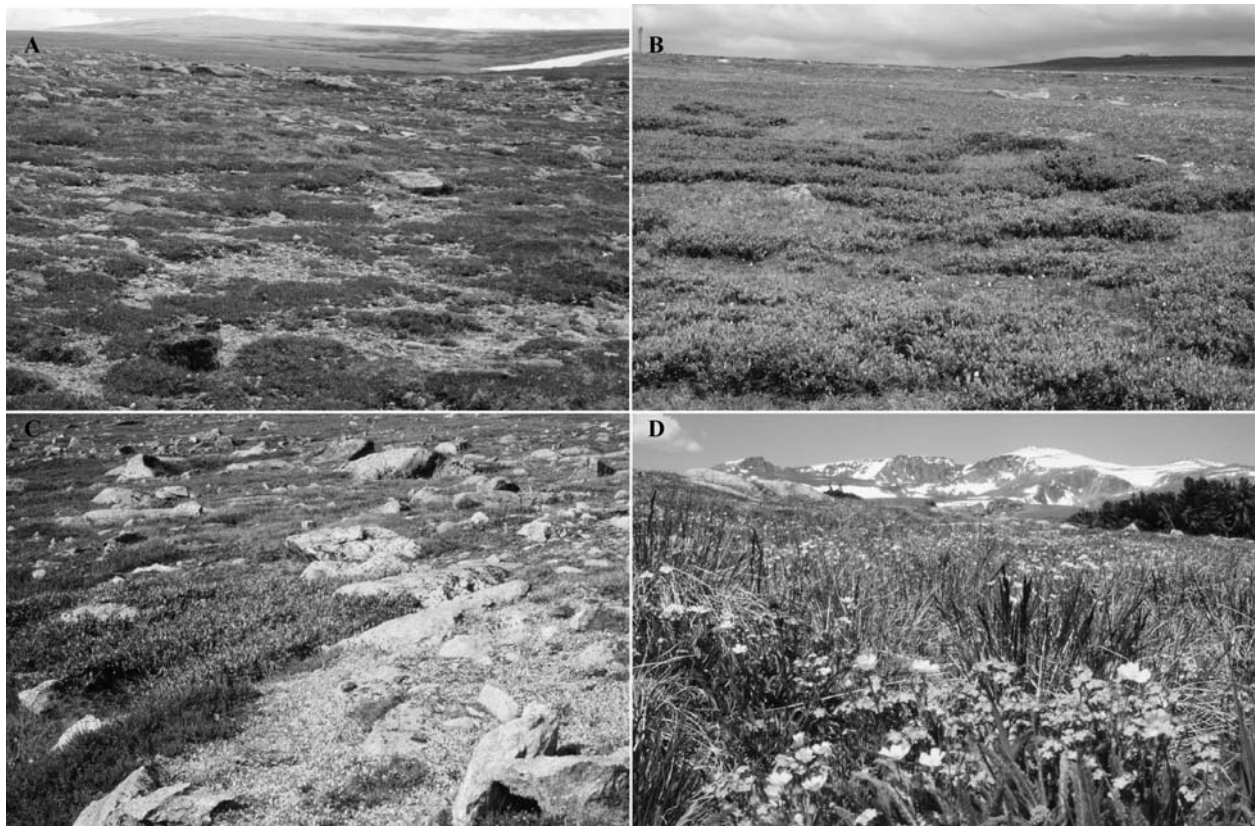
FIGURE 4. *Alpine plant-fungal level mosaics on the Beartooth Plateau. (A) Ectomycorrhizal system of discontinuous* Dryas octopetala *patches. (B) Ectomycorrhizal system of shrubby willow surrounded by predominantly arbuscular mycorrhizal meadows. (C) Exclusively ectomycorrhizal mats of dwarf willow. (D) Open meadows of alpine flowering plants supported by arbuscular mycorrhizal fungi.*

on mycorrhizal associations is critical if one is to foresee any future loss of diversity or changes in plant communities caused by global climate alteration or other major disturbance in the sensitive arctic-alpine biome (Gardes and Dahlberg, 1996).

OVERVIEW OF MYCORRHIZAL DISTRIBUTIONS IN ARCTIC-ALPINE REGIONS

Most ectomycorrhizal systems in arctic-alpine habitats are of woody, perennial, deciduous plants that form extensive mats such as *Salix*, *Betula*, and *Dryas* (Fig. 4A–C). These low plant forms serve not only as protection from wind and cold, but also to capture fallen leaf litter in place. This *in situ* N source can then be recycled by both saprophytic and ectotrophic fungi, with both promoting access of organic N to plants (Michelsen et al., 1996). *Kobresia* (another ectomycorrhizal species) also forms large tussock mats. Ericoid systems follow a similar pattern and woody species of *Phyllodoce*, *Vaccinium*, and *Arctostaphylos* can likewise form large mats. Arbuscular mycorrhizal systems, which access inorganic forms of N, are important in alpine turfs, alpine meadows, and fellfields (Fig. 4D). These vegetation types can stretch over large areas and be entirely supported by glomalean (AM) fungi. Nonmycorrhizal systems can be extensive as well, for example sedges can cover large areas of wet terrain. The diversity of micro- and macrohabitats in the alpine, determined by abiotic factors including soil type, is reflected in these plant patterns. The patchy distribution of the different mycorrhizal systems associated with large-scale, perennial vegetation mosaics suggests microbial functioning is not uniform across tundra landscapes.

Additionally, microbial activity in the alpine tundra was recently found to reach its peak under snow, and models of carbon dioxide dynamics (which impact global climate change) may need to be reassessed (Schadt et al., 2003). The study also revealed there was a seasonal shift of the microbial community type, and numerous unknown taxa were discovered as well, indicating how little we know of cold-climate microbial communities.

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