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ORIGINAL PAPER

Ectomycorrhiza of *Kobresia myosuroides* at a primary successional glacier forefront

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Abstract The bog sedge *Kobresia myosuroides* is among the first ectomycorrhizal (EM) plants forming dense pads on receding glacier forefronts of the Austrian Alps. This is the only Cyperaceae species known to form EM. To date, little is known about fungal species involved in these EM associations. Therefore, the main aim of this study was to detect EM fungal communities of *K. myosuroides* (1) by describing mycorrhizal morphotypes (MT) and (2) by identifying the mycobionts by rDNA internal transcribed spacer (ITS) sequencing. Furthermore, seasonal dynamics of *Kobresia* mycobionts were investigated. Sampling was performed in all four seasons (also under snow cover) during the years 2005 and 2006 at the Rotmoos glacier forefront, a well-characterized alpine primary successional habitat in the Austrian alps (2,300 m above sea level). The degree of EM infection of *K. myosuroides* roots was high (95%). Ten MTs were described and sequences of 18 fungal taxa were obtained. This was the highest mycobiont diversity ever reported for this plant. *Cenococcum geophilum* was the most abundant mycobiont (37–46%) and shared dominancy with *Sebacina incrustans* (16–44%) and *Tomentella* spp. (7–37%). *Tomentella* (including *Thelephora*) was the most species-rich mycobiont genus with five taxa, followed by *Cortinarius*, *Inocybe*, and *Sebacina* with two taxa each and one *Hebeloma* species. Other ascomycete mycobionts beside *C. geophilum* were *Helvella* sp., *Lecythophora* sp., and one Pezizales species. Due to high interannual differences in the EM fungal community, no significant seasonal changes could be detected. The importance of fungal mycobionts in alpine habitats is discussed.

Keywords *Kobresia myosuroides* · Bellardi bog sedge · Ectomycorrhiza · Spatial variation · Glacier forefront · Primary succession · Interannual differences

Introduction

Kobresia myosuroides (= *Kobresia bellardii*, Bellardi bog sedge) belongs to the Cyperaceae with circumboreal distribution in arctic and alpine habitats. It is the only sedge known to have ectomycorrhizal (EM) associations (Schadt 2002; Wang and Qiu 2006). However, EM-like structures have been described for *Carex flacca* and *Carex pilulifera* with *Cortinarius cinnamomeus* (Harrington and Mitchell 2002).

Research on the mycorrhizal status of *K. myosuroides* has started early in alpine and arctic habitats with classical morphological methods (Fontana 1963; Haselwandter and Read 1980; Kohn and Stasovski 1990; Massicotte et al. 1998). Schadt (2002) was the first to use molecular tools for his investigation of the fungal EM partners of this sedge; he detected *Inocybe*, *Russula*, *Cenococcum*, and *Hymenoscyphus* as mycobionts of *K. myosuroides* in Colorado (USA) and a *Tuber* species was also recently described as mycobiont of this sedge (Ammarellou and Saremi 2007). Concomitant

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studies (Lipson et al. 1999; review by Näsholm and Persson 2001) suggested a potential role of EM associations of *K. myosuroides* for nitrogen uptake and transfer. Schadt et al. (2003) also studied the seasonal dynamics of bulk soil fungal communities associated with this plant and found previously unknown fungal lineages in winter and spring. These and additional data (Lipson et al. 2002) indicated that the time of snowmelt is a period with high fungal activity.

However, fungi involved in EM associations with *K. myosuroides* in alpine habitats were so far more or less unknown. Therefore, the main aim of this study was to characterize EM fungal communities of *K. myosuroides* by (1) quantifying the degree of EM colonization, (2) describing mycorrhizal morphotypes, and (3) by identifying the mycobionts based on rDNA internal transcribed spacer (ITS) sequencing. Furthermore, seasonal dynamics in species composition of the *Kobresia* mycobionts was monitored by sampling over four seasons (also under snow cover) in 2005 and 2006 at the Rotmoos glacier forefront, a well-characterized alpine primary successional habitat in the Austrian Alps at approximately 2,300 m above sea level.

Material and methods

Study site

Sampling was performed on the Rotmoos glacier forefront, a primary successional site in the Tyrolean Alps (Ötz valley, Austria). This glacier forefront in the Rotmoos valley lies 2,280–2,450 m above sea level. The sampling area of about 100×200 m was chosen at the moraine of 1858 (46° 50' N, 11° 01' E), thus being approximately 150 years without ice cover. Plant cover varied between 50% and 90%. The vegetation at this site was described in detail by Erschbamer et al. (1999). Briefly, the plant community is considered a grassland community (Raffl and Erschbamer 2004; Raffl et al. 2006) with the following abundant and potentially ectomycorrhizal plants in a patchy distribution: *K. myosuroides*, *Polygonum viviparum*, *Salix herbacea*, and *Salix retusa*. Soil composition is very heterogeneous due to dependence on microhabitats; the content of organic matter is about 7% (Erschbamer et al. 1999).

Sampling

Each sampling year, five sampling plots (K1 to K5, 1×1 m each) were selected at the study site where *K. myosuroides* occurred as the dominant plant. From each sampling plot, five samples of roots and surrounding soil were taken with a small scoop in the middle and at the margin of the dense *Kobresia* turfs. The resulting holes measured approximately 5×5×5 cm. Samples were stored in the original soil at 4°C until further treatment for no longer than 2 weeks. Sampling was conducted four times a year in 2005 and 2006. Spring samples were taken 2 weeks after snow melt, on June 15, 2005 and June 27, 2006. Summer samples were taken on August 4, 2005 and August 22, 2006. Fall samples were taken on September 15, 2005 and October 3, 2006. Winter samples were taken under an approximately 40-cm-high snow cover on December 14, 2005 and December 12, 2006. Environmental data (mean temperature and moisture) were measured in a 2-week period before the respective sampling date and shown in supplementary Table S1.

In order to obtain reference sequences for species-level identification of mycorrhizal fungi, we harvested all occurring fruitbodies in the study site during 2005 and 2006. Voucher material was deposited in the Herbarium IB (University of Innsbruck). IB voucher material, harvested earlier at the study site, was also used.

Sample processing

After careful washing, fine roots were separated from *Kobresia* main roots. For each of the five sampling plots, 100 mycorrhizal root tips were randomly selected yielding a total of 500 root tips studied from each sampling date. Root tips were examined at ten to 100-fold magnification and sorted into morphotypes (MTs) based on color, emanating elements, mantle layer, and hyphal anatomy (Agerer 1991; supplementary Table S2).

At least three representatives of each MT were transferred into cetyltrimethylammonium bromide buffer and stored at −20°C until later molecular investigations. At least three samples of each MT, deriving from different samples, were analyzed. If only one sequence pattern (operational taxonomical unit = OTU) was obtained, the MT was considered as this OTU. Otherwise, additional root tips of this MT were sequenced. The most abundant OTU was then regarded as the mycorrhizal partner.

Molecular methods

DNA was extracted from single root tips according to Southworth (2000). Polymerase chain reaction (PCR) was performed as described by Mühlmann et al. (2008) using the primer combinations ITS1F × LR15 or ITS1F × NL4 (O'Donnell 1993; Gardes and Bruns 1993; Vilgalys 2005). DNA isolation and sequencing protocols for fruitbody processing followed those of a previous study (Peintner et al. 2001). Primers used for PCR amplification and sequencing were ITS1 combined with LR15 or NL4 (White et al. 1990; O'Donnell 1993; Vilgalys 2005). Purified PCR products were sequenced by MWG AG Biotech (Germany) or Genecust (Custom Services for

Research; France) with the primer ITS1. Sequences were analyzed using Sequencer software (version 4.6; Gene Codes Inc. Ann Arbor, MI, USA).

Sequence analyses

Basic Local Alignment Search Tool searches were carried out against the public sequence databases National Center for Biotechnology Information and UNITE (Kõljalg et al. 2005). OTUs were defined as sequences with at least 97% similarity and regarded as belonging to one species. Furthermore, sequences of the EM were compared to those generated from EM of other host plants (*S. herbacea* and *P. viviparum*) or from reference fruitbodies collected at this study site. Molecular analyses of MT 2 resulted in unclear results (heterogeneous sequences or sequences belonging to fungal groups not known to form EM associations: *Alatospora* sp., Helotiales sp.). This MT appeared unhealthy and was characterized by a gaunt surface. Therefore, MT 2 was defined as degenerating or senescent EM root tips but remained included in all statistical calculations.

Statistical analyses

Statistical analyses were carried out with relative abundances of MTs. We calculated the abundance of MTs (including senescent and nonmycorrhizal root tips) as percent of investigated root tips per plot (supplementary Table S3). Frequency of MTs was calculated as percentage of plots where the individual MT was detected. We divided the MTs into main MTs and rare MTs: main MTs were defined as found on ≥5% of all investigated root tips in both years together, whereas rare MTs showed abundances of <5%.

To analyze seasonal and spatial variation of the EM fungal communities associated with *K. myosuroides*, we calculated richness (*S*) for total number of species, evenness (*E*) for their distribution, and Shannon and Simpson's diversity indices according to McCune and Grace (2002) with PC-ORD version 5.0 (McCune and Mefford 1999).

Analysis of variance (ANOVA) was performed with SigmaStat Software (SigmaStat for Windows 3.5, 2006, Systat Software) using several datasets: the whole dataset including data of both sampling years and reduced datasets using data for each year, separately: as the dependant variable, we used either Shannon and Simpson's diversity indices or relative abundances of the main MTs (MT 14, MT 6, MT 3) and the pooled abundances of the remaining MTs. After passing the normality test, one-way ANOVA was calculated with either "season" or "plot" as independent variable. If normality test failed, Kruskal–Wallis one-way ANOVA on ranks was used for detection of significant differences between the groups. The pairwise multiple comparison procedures (Tukey test) were applied to detect groups differing significantly from the others ($p>0.050$).

To minimize underestimation of species richness (because of the sampling methodology itself), the true richness was estimated with four methods for the data from both years and all combined: (1) abundance-based coverage estimator of species richness (ACE), which relies on the abundances of rare species for estimation of the true species richness; (2) incidence-based coverage estimator of species richness (ICE) is based on presence or absence data; (3) Chao estimators (Chao1 and Chao2) use common species as well as singletons and doubletons to estimate the number of missing species; and (4) the second-order Jackknife richness estimator (Jack2) is very sensitive to the number of rare species and can perform poorly with a small sample size. Samples were randomized without replacement. All estimations were calculated in EstimateS 8.0 (Colwell 2006).

Results

Ninety-five percent of all 4,000 examined *K. myosuroides* root tips were colonized by EM fungi. In total, ten EM MTs with well-developed mantle layers were detected (supplementary Table S2). The main MTs were identified as *Cenococcum geophilum* (MT 14), *Sebacina incrustans* (MT 6), and *Tomentella* spp. (MT 3), which together colonized 83% of the root tips (Table 1). Three rare MTs were assigned to the fungal genera *Cortinarius* (MT 8) and *Inocybe* (MT 27) and to Thelephoraceae (MT 15) with two species each. Four rare MTs remained unidentified.

In total, 18 fungal taxa were found on the roots of *K. myosuroides* (Table 2). Ribosomal DNA ITS sequences for six ascomycete and 12 basidiomycete species were obtained. *Tomentella* (including *Thelephora*) was the most species-rich mycobiont genus with five taxa, followed by *Cortinarius*, *Inocybe*, and *Sebacina* with two taxa each. One *Hebeloma* species was found. Ascomycete mycobionts were *C. geophilum*, *Helvella* sp., *Lecythophora* sp., and one Pezizales species. Two sequences showed high similarity to reference sequences of *Alatospora* or Helotiales.

Estimates of actual species richness (based on MTs, including senescent root tips) reached 100% (ICE, Chao1, and Chao2) or 96% (ACE) and 91% (Jack2) of the observed species (compare Fig. 1).

Interannual comparison of fungal community

Species diversity was significantly higher in 2005 than in 2006 (Simpson, $p=0.013$; Shannon, $p=0.003$; Table 3). A more detailed analysis indicated that the diversity of only the winter samples was significantly higher in 2005 than in 2006 (Simpson, $p=0.034$; Shannon, $p=0.009$), whereas

Table 1 Relative abundances and frequencies (both in percent) of *K. myosuroides* ectomycorrhizal morphotypes (MT) including taxon names, senescent root tips, and nonmycorrhizal root tips are presented for each season (spring, summer, fall, winter), for each plot (K1 to K5), and in total for both sampling years (2005 and 2006) separately; *n* of samples are given in brackets

		Spring (5)	Summer (5)	Fall (5)	Winter (5)	K1 (4)	K2 (4)	K3 (4)	K4 (4)	K5 (4)	Total (20)
Abundances											
MT 14, *Cenococcum geophilum*	2005	28.0	38.2	29.4	36.2	17.5	26.8	48.8	56.8	15.0	33.0
	2006	25.8	29.6	17.2	46.0	24.3	36.3	48.0	17.0	22.8	29.7
MT 6, *Sebacina incrustans*	2005	16.4	22.2	24.8	26.4	23.0	13.0	8.3	31.3	36.8	22.5
	2006	30.2	42.4	38.0	43.8	39.3	48.5	29.0	33.5	42.8	38.6
MT 3, *Tomentella* spp.	2005	31.8	18.6	24.0	13.0	28.5	15.8	35.3	0.0	29.8	21.9
	2006	26.4	7.6	37.0	10.2	29.0	0.0	20.3	39.0	13.3	20.3
Senescent root tips	2005	4.6	9.6	10.6	6.8	5.5	23.8	1.8	0.0	8.5	7.9
	2006	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MT 8, *Cortinarius* spp.	2005	1.8	7.4	7.2	3.2	18.5	0.0	0.0	0.0	6.0	4.9
	2006	0.0	0.6	2.2	0.0	0.0	1.8	0.0	1.8	0.0	0.7
MT 11, n.d.	2005	0.0	2.8	0.0	0.0	1.0	0.0	0.0	2.5	0.0	0.7
	2006	0.0	11.6	0.0	0.0	0.0	0.0	0.0	0.0	14.5	2.9
MT 24, n.d.	2005	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	2006	9.4	3.6	0.0	0.0	0.0	10.0	0.0	0.0	6.3	3.3
MT 15, *Thelephoraceae* spp.	2005	7.4	0.0	1.2	0.0	1.8	7.5	1.5	0.0	0.0	2.2
	2006	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MT 5, n.d.	2005	4.4	0.0	0.0	0.0	0.0	2.3	0.0	3.3	0.0	1.1
	2006	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MT 27, *Inocybe* spp.	2005	0.0	0.0	0.0	0.4	0.0	0.5	0.0	0.0	0.0	0.1
	2006	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nonmycorrhizal root tips	2005	5.6	1.2	2.8	14.0	4.3	10.5	4.5	6.3	4.0	5.9
	2006	8.2	4.6	5.6	0.0	7.5	3.5	2.8	8.8	0.5	4.6
Frequencies											
MT 14, *Cenococcum geophilum*	2005	100	100	100	100	100	100	100	100	100	100
	2006	80	100	80	100	100	100	100	100	50	90
MT 6, *Sebacina incrustans*	2005	60	100	100	80	100	50	75	100	100	85
	2006	100	100	80	100	100	100	100	75	100	95
MT 3, *Tomentella* spp.	2005	80	80	80	80	100	100	100	0	100	80
	2006	80	40	80	60	75	0	100	100	50	65
Senescent root tips	2005	40	40	40	80	75	100	25	0	50	50
	2006	0	0	0	0	0	0	0	0	0	0
MT 8, *Cortinarius* spp.	2005	20	40	40	20	100	0	0	0	50	30
	2006	0	20	40	0	0	25	0	50	0	15
MT 11, n.d.	2005	0	40	0	0	25	0	0	25	0	10
	2006	0	20	0	0	0	0	0	0	25	5
MT 24, n.d.	2005	0	0	0	0	0	0	0	0	0	0
	2006	40	20	0	0	0	50	0	0	25	15
MT 15, *Thelephoraceae* spp.	2005	40	0	20	0	25	25	25	0	0	15
	2006	0	0	0	0	0	0	0	0	0	0
MT 5, n.d.	2005	40	0	0	0	0	25	0	25	0	10
	2006	0	0	0	0	0	0	0	0	0	0
MT 27, *Inocybe* spp.	2005	0	0	0	20	0	25	0	0	0	5
	2006	0	0	0	0	0	0	0	0	0	0
Nonmycorrhizal root tips	2005	100	40	60	100	75	75	75	75	75	75
	2006	100	40	40	0	75	25	25	75	25	45

MTs are sorted based on their abundances in all samples.
n.d. Not determined

diversities of the other seasons, compared year to year, did not differ significantly.

The main mycobionts (*C. geophilum*, *S. incrustans*, and *Tomentella* spp.) were very abundant during the whole investigation period (Table 1, supplementary Table S3, supplementary Fig. S1). *C. geophilum* colonized between 17.2% and 46.0% of the root tips and occurred in 80% to 100% of the samples. *S. incrustans* colonized between

Table 2 Ectomycorrhizal mycobionts of *K. myosuroides* detected at a primary successional site

ID	Length	Gb Acc Nr	Reference	Score	Identities (%)	Name
178	503	EU498729	AY204590	823	96	*Alatospora* sp.[a]
1202	896	EU498730	EF434154	1,598	97	*Cenococcum geophilum*
1478	550	EU498731	EU326172		100[b]	EM root tip *Salix* (*Cortinarius*)
181	576	EU498732	EU292268	1,108	99	*Cortinarius* sp.
198	464	EU498733	AY948495	817	97	*Hebeloma bruchetii*
759	1,417	EU498734	EU292653	1,014	95	Helotiales sp.[a]
855	800	EU498735	UDB000177	579	Locked	*Helvella* sp.
1034	670	EU498736	EU326177		100[b]	*Inocybe johannae* IB20050451
784	414	EU498737	AY940653	387	97	*Inocybe* sp.
221	515	EU498738	EF433985	930	98	*Lecythophora* sp.
168	598	EU498739	AJ968676	1,053	99	Pezizales sp.
761	634	EU498740	EU326168		100[b]	EM root tip *Salix* (*Sebacina*)
1031	693	EU498741	EF655701		100[b]	*Sebacina incrustans* IB20060213
194	643	EU498742	AF184747	1,086	97	*Thelephoraceae* sp. 1
872	695	EU498743	EF411132	1,106	96	*Thelephoraceae* sp. 2
851	268	EU498744	EF655700		100[b]	EM root tip *Polygonum* (*Tomentella*)
199	757	EU498745	EU326163		100[b]	EM root tip *Salix* (*Tomentella*)
838	273	EU498746	EF655702		100[b]	*Tomentella* sp. IB20060231

Root tip ID, sequence length, Genbank accession number (Gb Acc Nr) of rDNA ITS sequences, best BLAST match (Reference) and score, identities (%), and identification on genus, family, or order level are shown.

[a] Taxa identified from senescent root tips

[b] Samples identified based on reference fruitbody material (IB number included) or reference EM root tips (*Salix herbacea* and *Polygonum viviparum*)

16.4% and 43.8% of the root tips and occurred in 60% to 100% of the samples. *Tomentella* spp. colonized between 7.6% and 37.0% of the root tips and occurred in 40% to 80% of the samples. Five rare MTs were found in 2005 together colonizing 16.8% of the root tips and three in 2006 colonizing 6.8% of the root tips. Senescent root tips were recorded in 2005 only.

Spatial and seasonal variation of main mycobionts

The main MTs were found in every season and all plots of both sampling years with the exception of *Tomentella* spp. (MT 3; lacking in plot K4 in 2005 and in plot K2 in 2006). These main MTs were observed with frequencies between 40% and 100% (Table 1). Statistically significant spatial

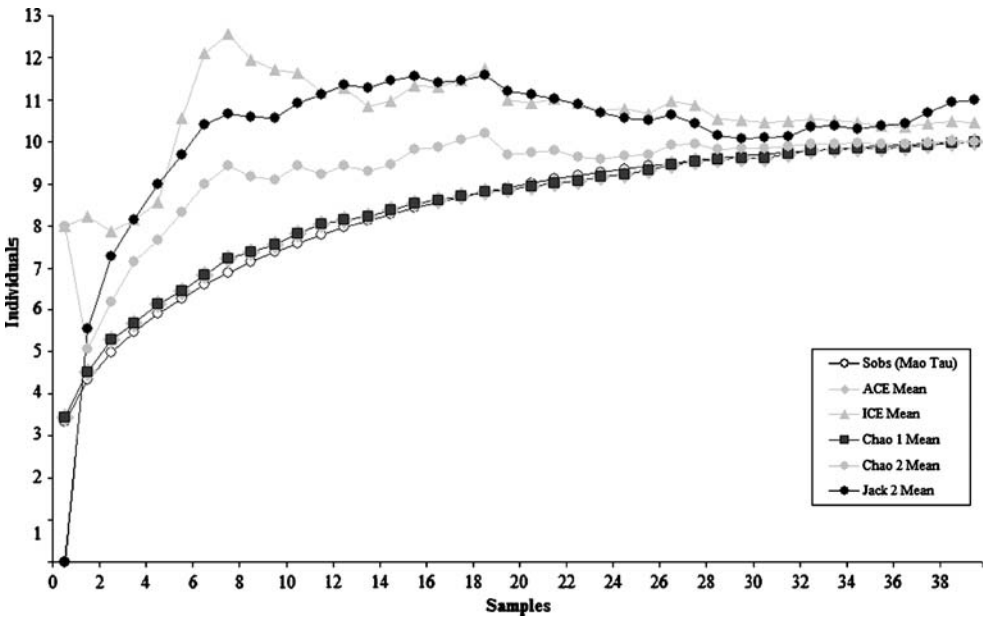

Fig. 1 Species richness estimation curves of *K. myosuroides* ectomycorrhizae in all samples of the years 2005 and 2006 (Species observed (*Sobs*), abundance-based coverage estimator of species richness (*ACE*), incidence-based coverage estimator of species richness (*ICE*), Chao estimator 1 and 2 (*Chao1*, *Chao2*), and second-order Jackknife richness estimator (*Jack2*))

Table 3 Diversity indices for *K. myosuroides* ectomycorrhizal morphotypes for all samples in each year separately (2005, 2006), for all samples in both years together and for seasons or plots (K1–K5) in each year, separately

		Richness	Evenness	Shannon	Simpson's
2005	All samples	4.6	0.832	1.256	0.6620
2006		3.3	0.850	0.981	0.5702
Both years		4.0	0.841	1.118	0.6161
2005	Spring	4.8	0.831	1.283	0.6701
	Summer	4.4	0.800	1.189	0.6305
	Fall	4.4	0.885	1.306	0.6950
	Winter	4.8	0.812	1.246	0.6523
	K1	6.0	0.898	1.601	0.7731
	K2	5.0	0.856	1.371	0.7083
	K3	4.0	0.780	1.070	0.6063
	K4	3.3	0.771	0.907	0.5275
	K5	4.8	0.855	1.333	0.6948
2006	Spring	4.0	0.848	1.176	0.6483
	Summer	3.4	0.865	1.034	0.6028
	Fall	3.2	0.825	0.915	0.5336
	Winter	2.6	0.862	0.798	0.4962
	K1	3.5	0.893	1.108	0.6344
	K2	3.0	0.880	0.935	0.5570
	K3	3.3	0.912	1.069	0.6274
	K4	4.0	0.714	0.990	0.5320
	K5	2.8	0.851	0.802	0.5006

differences were observed for the abundances of the main MTs in 2005 for the following plots: *C. geophilum* (plot K4 vs. K5, K1, K2 and plot K3 vs. K5, K2; $p \leq 0.027$), *S. incrustans* (plot K3 vs. K5; $p = 0.048$), and *Tomentella spp.* (plot K4 vs. K1, K3, K5; $p \leq 0.010$). No significant seasonal variations were found.

Discussion

Ectomycorrhizal degree of *K. myosuroides*

The degree of EM infection of *K. myosuroides* detected in this study was comparable to the EM infection degree of *P. viviparum* (100%, Mühlmann et al. 2008) and *S. herbacea* (93%; Mühlmann and Peintner 2008) at the same study site. However, such high EM degrees were rarely detected in similar habitats. Trowbridge and Jumpponen (2004) reported an average of 25% of *Salix* root tips to be EM on the Lyman glacier forefront (WA, USA). On the same study site, Cázares et al. (2005) reported an EM degree up to 25% for *Polygonum bistortoides* and up to 100% for dwarf *Salix* spp. Blaschke (1991) found that EM infection of young adventitious rootlets of *Dryas octopetala* was low whereas the major root system of this plant was strongly ectomycorrhizal (up to 90%) when growing in humus layer. In the same study, *P. viviparum* root rips were EM up to 73%. To our knowledge, no available study described the EM degree of *K. myosuroides*.

EM fungal community of *K. myosuroides*

Eighteen fungal taxa were found on the roots of *K. myosuroides* at this alpine site. This is the highest mycobiont diversity ever reported for this bog sedge. All 12 basidiomycete and four ascomycete mycobionts (*C. geophilum*, *Helvella* sp., *Lecythophora* sp., and Pezizales sp.) of *K. myosuroides* are known as EM partners of various host plant genera (e.g., Tedersoo et al. 2006).

The detected species richness of *K. myosuroides* mycobionts is similar to the mycobiont diversity of two other EM plants occurring at the same study site: 19 fungal taxa were found on *S. herbacea* roots (Mühlmann and Peintner 2008) and 18 taxa were found on *P. viviparum* roots (Mühlmann et al. 2008). However, the number of EM morphotypes was much lower in *Kobresia* (ten MT) than in *S. herbacea* (21 MT) or *P. viviparum* (19 MT). This reflects the low morphological differentiation of EM in sedges, compared to other EM plants. The problem that several fungi were forming one MT on *K. myosuroides* roots was already reported by Schadt (2002). He found at least two fungal taxa (*Inocybe* sp., *Russula* sp.) forming the same EM MT on *Kobresia* roots in the Rocky Mountains. This makes it difficult to identify and quantify mycobiont communities of *K. myosuroides* based on morphotyping (Schadt 2002) and, consequently, highlights the importance of sequence-based methodologies for the identification of EM.

Dynamics of EM fungi

Although this study included winter samplings of *K. myosuroides* root tips, no significant seasonal changes in the EM community were detected. The three main MTs were always abundant, whereas rare MTs decreased in abundance or disappeared in winter. EM fungi are generally very dynamic (Parrent and Vilgalys 2007). We speculate that the dominating mycobiont taxa are stress tolerant and competitive and therefore readily replace rare mycobionts especially during periods of stagnating plant growth; in spring, new root tips can be colonized by all EM fungi present in the soil.

Important alpine mycobiont genera

Early mycobiont studies were performed based on fruitbody surveys. Such data were also used for estimating the importance of fungal taxa as mycobiont partners for arctic–alpine EM host plants: *Cortinarius*, *Inocybe*, *Lactarius*, and *Russula* were therefore long regarded as important myco-

bionts in arctic–alpine areas (e.g., Gardes and Dahlberg 1996). However, *C. geophilum* clearly dominated mycobiont communities of *K. myosuroides* in the Rocky Mountains (Massicotte et al. 1998; Schadt 2002), followed by a MT related to the *Hymenoscyphus* aggregate. *C. geophilum* also dominated *Kobresia* mycobiont communities of the Rotmoosferner glacier forefront (mean abundance 31%) but shared this dominancy with *S. incrustans* (30%) and *Tomentella* spp. (21%). Schadt (2002) noted that fruitbodies related to the dominant EM taxa were not found in his study site. In contrast, *Sebacina* and *Tomentella* basidiomes were found in our sampling area but only after targeted and extensive search. Recent sequence-based studies of the EM communities of *D. octopetala* (Harrington and Mitchell 2005), *Arctostaphylos uva-ursi* (Krpata et al. 2007), *P. viviparum* (Mühlmann et al. 2008), and *S. herbacea* (Mühlmann and Peintner 2008) suggest that the importance of some genera mentioned by Gardes and Dahlberg (1996) might have been overestimated: although *Cortinarius* and *Inocybe* spp. were found in association with most of these alpine plants, these genera were not abundant mycobionts. Moreover, only one *Russula* sp. was found on *P. viviparum* and *A. uva-ursi* roots, respectively, and no *Lactarius* species was ever detected in alpine habitats using molecular methods. Therefore, we conclude that fruitbody occurrence of these taxa is not related to EM abundances.

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