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Rhizosphere fungal assemblages and soil enzymatic activities in a 110-years alpine chronosequence

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ABSTRACT

The abundance, distribution and functions of soil fungi in alpine ecosystems remain poorly understood. We aimed at linking the fungal community structure with soil enzymatic activities in the rhizospheres of several plants associating with mycorrhizal fungi (arbuscular, ecto- and ericoid) and growing along a soil developmental gradient on the forefield of an alpine glacier. Fungal communities in roots and in rhizosphere soils were assessed using a site-tailored set of quantitative PCR assays with fluorescent hydrolysis probes. Enzymatic activities of mycorrhizal roots and rhizosphere soils were assessed using fluorogenic substrates. In this study we addressed: i) whether and how the structure of fungal communities and enzymatic activities in rhizosphere soils change along the soil developmental gradient, ii) whether the type of mycorrhiza shows a clear relationship to the pattern of enzymatic activities in the rhizosphere, and iii) how the structure of fungal communities and enzymatic activities in rhizosphere soils is related to plant species abundances along the soil chronosequence. The results suggest that plant identity affected the structure of both ecto- and arbuscular mycorrhizal fungal communities in rhizosphere soil and roots, whereas the community of non-mycorrhizal fungi was rather dictated by the soil developmental stage. Both plant identity and associated mycorrhizal fungi affected the enzymatic activity in the rhizosphere soil. Species-specific elevations of rhizosphere enzyme activities were detected for *Salix helvetica* (chitinase and α-glucosidase), *Rhododendron ferrugineum* (α-glucosidase and sulfatase), and *Agrostis gigantea* (phosphatase and xylosidase). These results indicate different functional roles played by different types of mycorrhizal symbiosis in a young alpine ecosystem.

1. Introduction

Land gradually emerging from underneath retreating glaciers provides a natural laboratory for studying ecosystem development (Huggett, 1998; Walker et al., 2010). Living organisms – especially plants – contribute substantially to ecosystem development in general and to soil formation in particular (Chapin et al., 1994). Acting as islands of available nutrients and carbon, their rhizospheres harbor a great diversity of highly active microorganisms (Hawkes et al., 2007), including mycorrhizal fungi.

Read (1993) proposed that occurrence and distribution of mycorrhizal fungal communities in primary succession ecosystems presented a predictable pattern: early successional stages were mainly colonized by non-mycorrhizal plants which were subsequently replaced by plants hosting arbuscular mycorrhizal fungi (AMF), followed by ectomycorrhizal (ECM) and eventually by the ericoid mycorrhizal (ER) plants. However, reviewing the most recent research on fungal communities during long-term soil development, Dickie et al. (2013) postulated that the distribution pattern of mycorrhizal fungi in newly developing ecosystems cannot be infallibly predicted. Firstly, the distribution pattern of mycorrhizal fungi in a given environment is affected by local edaphic conditions and plant community composition. Secondly, driven by ecosystem disturbances, the distribution pattern of mycorrhizal fungi comprises both progressive and retrogressive stages. This means that a given mycorrhizal type can occur at any developmental stage which provides persistent local conditions for its establishment and further development. For example, AMF commonly associated with early succession plants can still occur at later stages of ecosystem development. This can be either due to colonization of spaces opened by disturbance or due to persistence of AMF in the ecosystem as it develops (Lambers et al., 2008; Oehl

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et al., 2011). Reversely, the presence of ECM and ER fungi not only at the mature but also at the pioneering stages of ecosystem development has been repeatedly reported in the literature (Jumpponen, 2003; Cázares et al., 2005).

Different plant species are colonized by specific mycorrhizal type/s and preferentially associate with selected mycorrhizal fungal taxa (Smith and Read, 2008). Thus, the composition of mycorrhizal fungal communities is not random. The specificity of mycorrhizal fungi towards the host as well as the uneven distribution of a plant species in the landscape are likely to underlie observed fluctuations in the density and composition of mycorrhizal fungal communities in a given environment. Following this concept, Becklin et al. (2012) reported that richness and diversity of the AMF communities vary for different herbaceous plants (i.e., *Taraxacum ceratophorum*, *Taraxacum officinale*, and *Polemonium viscosum*) colonizing alpine meadows or shrublands. Similarly, Sykorová et al. (2007) noted qualitative differences in AMF communities associated with three plant taxa (i.e., *Gentiana verna*, *Gentiana acaulis*, and *Trifolium* spp.) in a Swiss alpine meadow. Like for AMF, plants often tend to share ECM symbionts rather than to harbor distinctive ECM communities (Ryberg et al., 2011), although cases of strict association between some fungal and plant partners are known (e.g. *Lactarius* sp. and *Larix* sp.). However, more investigations are needed to test how widespread is the sharing of symbionts between plant species or which factors decide about distinctiveness of the fungal communities associated with them.

The distribution, density and structure of mycorrhizal fungal communities in the environment are directly related to their functioning. Mycorrhizal fungi support the host plant in nutrient/water acquisition and alleviate various environmental stresses, and thus their functioning can directly influence development, establishment and fitness of the plant communities (Smith and Read, 2008). Among the mycorrhizal functions, enzymatic activity as a strategy for nutrient acquisition has received substantial attention. A variety of hydrolytic exoenzymes are produced by ECM and ER fungi (Read and Perez-Moreno, 2003). Upon hydrolysis of complex biomolecules immobilized in soil organic matter (SOM), essential nutrients are released to the soil. These are then taken up by mycorrhizal hyphae and further transferred to the mycorrhizal host plant (Smith and Read, 2008). Unlike for ECM and ER, production of large amounts of hydrolytic exoenzymes by AMF has not been consistently shown (Hodge and Fitter, 2010). Although bacteria, fungi and plants all contribute to the pool of enzymes in the soil, and a given enzyme cannot be traced back to a specific organism (Tabatabai and Dick, 2002), there is evidence that large amounts of numerous exoenzymes are actively produced and released to the hyphosphere of specific ECM and ER fungi (Courty et al., 2005; Mitchell and Gibson, 2006). This suggests that enzymatic activities in the rhizosphere soil of different plant species are to a great extent determined by their associated mycorrhizal partners.

Using a soil development sequence in a glacier forefield as a model, the aims of this work were to determine i) the contribution of plant identity and soil properties on the structure (composition and abundance) of mycorrhizal fungal communities and ii) the enzymatic activities in the rhizosphere soils of four different plant species (*Salix helvetica*, *Agrostis gigantea*, *Leucanthemopsis alpina* and *Rhododendron ferrugineum*) hosting different mycorrhizal types. We hypothesized that i) the structure of fungal communities associated with different plant species would change along a soil developmental gradient; ii) enzymatic activities in the rhizosphere soil of different plant species would change along the same gradient; iii) exoenzyme activities would be greater in the rhizospheres of plants associated with ecto- and ericoid mycorrhizal fungi (*S. helvetica* and *R. ferrugineum*, respectively) than of plants harboring arbuscular mycorrhizal fungi (*A. gigantea* and *L. alpina*).

2. Materials and methods

2.1. Sampling sites

Sampling was performed at the forefield of the Damma glacier situated in the Central Swiss Alps (Canton of Uri, N46°38.117′, E8°27.677′). The same study site was used intensively for the multidisciplinary project “BigLink” and has been described in detail elsewhere (Bernasconi et al., 2011; Welc et al., 2012). In July 2009, eight experimental sites were selected for further investigations (see Fig. S1 in electronic supplement). The approximate ages of soils on these sites ranged from 7 to 110 years (see Electronic supplement for details). Soil ages were calculated according to the historical glaciological records available at The Swiss Glacier Monitoring Network (http://glaciology.ethz.ch/messnetz/glaciers/damma, accessed 13th December 2013). The experimental sites lay at elevations between 1966 and 2025 m. Precipitation in the area is about 2600 mm per year (Bernasconi et al., 2011), without expected significant differences in precipitation between the sites. To minimize differences in soil moisture and runoff patterns between the sites, we selected the sites most distant from streams, terrain depressions or elevations. Soils at the experimental sites were shallow (max. 10 cm) Hyperskeletic Leptosols (Bernasconi et al., 2011). An organic layer (thickness of approximately 0.5 cm) was discernible only at the oldest sites (more than 100 years after deglaciation). Soils were slightly acidic, generally poor in total C and N, and rather high in available P levels, although the values varied quite strongly across the chronosequence (Table 1).

Plant cover at the studied sites ranged between 5 and 100%. Herbs and grasses (e.g., *L. alpina*, *A. gigantea*, *Poa alpina*) predominated at the younger sites, while the woody plants (*S. helvetica*, *R. ferrugineum*, *Vaccinum* sp.) increased their coverage toward the older sites. *S. helvetica* (a shrub approximately 60–80 cm high, see Fig. S2A in electronic supplement) was present at all experimental sites, with maximum abundance (~30% surface coverage; Göransson, personal communication) on the middle sites, deglaciated 60–65 years ago. Single seedlings of willow colonized already young sites. Willows decreased their abundance towards the older sites and were completely outcompeted by *R. ferrugineum* on the area deglaciated >110 years ago (i.e., outside of the chronosequence investigated here). *A. gigantea* (a perennial grass approximately 20–30 cm high, see Fig. S2B in electronic supplement) was present at all experimental sites. At the middle sites it reached coverages between 20 and 40%, occupying areas between the canopy of woody plants (Göransson, personal communication). On the young (i.e., deglaciated 7 and 8 years ago) and older sites (i.e., deglaciated >78 years ago), *A. gigantea* occurred as single plants rather than in dense stands. *L. alpina* (herb approximately 10–20 cm high, see Fig. S2C in electronic supplement) was found on all experimental sites but was more common in the young and middle sites. Its surface coverage never exceeded 5%. This plant species tended to colonize open spaces in the canopy away from the woody plants. *R. ferrugineum* (a woody shrub approximately 50–80 cm high, see Fig. S2D in electronic supplement) was absent at the sites deglaciated 7 and 8 years ago either because of insufficient time to establish, insufficient local conditions (low temperature close to the ice) or due to poor seed dispersion. It was more abundant in the middle sites and gradually increased its abundance towards the older sites (i.e., deglaciated 78–110 years ago), where its surface coverage reached over 50% (Göransson, personal communication).

2.2. Soil and root sampling

At each experimental site, the following plants representing different mycorrhizal types were sampled: *S. helvetica* (dual mycorrhizal plant, with scarce AMF and predominant ECM colonization), *L.*