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Root-associated fungal communities along a primary succession on a mine spoil: Distinct ecological guilds assemble differently



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ABSTRACT

The aim of the study was to explore fungal community assembly during spontaneous primary succession. Pyrosequencing was used to investigate the root-associated fungal communities of two dominant trees *Salix caprea* and *Betula pendula* along a primary successional chronosequence (12-, 20-, 30- and 50-year-old sites) on a mine spoil bank in the Czech Republic. Ecological guilds were parsed to fungal OTUs and subsequent multivariate analyses revealed that communities of ectomycorrhizal fungi (EcMF), fungal plant pathogens (PaF) and fungal root endophytes (EndF) changed statistically significantly along the successional chronosequence. Arbuscular mycorrhizal fungi (AMF) were very rare across all samples. EcMF and PaF communities were strongly related to the development of the entire plant community along the succession, while this relationship was much less pronounced for EndF communities. Early stage EcMF communities dominated by Pezizales were subsequently replaced by Thelephorales and Russulales in later successional sites. Positive correlation with site age was also found for EndF from order Helotiales. No significant differences were observed between the fungal communities of *S. caprea* and *B. pendula* in our study. We conclude that fungal taxa with tight ecological relationship to plants assemble with close feedback to plant communities, which change along the chronosequence, whereas communities of fungal endophytes develop more stochastically during the primary succession.

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1. Introduction

Primary succession is generally characterized by soil development and change in vegetation structure (Odum, 1969). It naturally occurs in environments, where new substrate is deposited or revealed, such as lava flows or areas after glacier retreat. Primary succession can also occur on spoil banks, which are created from a large amount of spoil material after mining activities (Prach et al., 2013). Spoil material excavated from great depth has typically no or only very low biological activity (Frouz et al., 2001). The subsequent succession process involves accumulation of soil organic matter, nitrogen and available phosphorus contents along with increasing plant cover, plant community richness and diversity and microbial biomass (Baldrian et al., 2008; Frouz et al., 2001, 2008). Mine spoils represent an excellent system for primary succession investigations encompassing locations of different age in a restricted area; moreover, understanding the factors that influence primary succession in these areas is important for their reintegration into the landscape.

Plant succession is inseparably linked to succession of heterotrophic microorganisms, which utilize all forms of plant-derived carbon and are important drivers of plant community productivity and diversity (van der Heijden et al., 2008). Among them, rootassociated fungi have evolved close links to living plants, but at the same time, constitute a highly heterogeneous group. Roots are colonized by obligately or facultatively biotrophic mycorrhizal fungi and pathogens, but also by many other fungi commonly termed root endophytes, which have variable and only partially explored trophic and functional relationship to the plant (Brundrett, 2006; Porras-Alfaro and Bayman, 2011).

In contrast to successional dynamics of plants, primary succession of root-associated fungi has so far received less attention. Vast



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majority of studies on fungal community dynamics in primary successional environments have focused solely on a single fungal ecological guild with predominance of those focused on ectomycorrhizal (Muhlmann and Peintner, 2008; Trowbridge and Jumpponen, 2004) and arbuscular mycorrhizal (de León et al., 2016; Krüger et al., 2017) fungi. Despite variable successional systems and methodical approaches, the pattern emerging from these studies suggests that succession of root-associated fungi follows different and less predictable trajectories than plant succession (Dickie et al., 2013; Jumpponen et al., 2012). For example, increasing species richness, a main feature of early plant succession (Walker and Del Moral, 2003), is usually less evident or not encountered at all in the succession of root-associated fungi (Jumpponen et al., 2012; Martínez-García et al., 2015).

Species richness and composition of fungal communities in general co-varies with vegetation and responds to abiotic soil characteristics (Kohout et al., 2015; Tedersoo et al., 2014). Among soil parameters, extractable soil P concentration and C:N ratio were important predictors of fungal community composition at the landscape scale (Lauber et al., 2008). However, different fungal ecological guilds respond to vegetation and abiotic factors to a different degree, with communities of biotrophic symbionts and pathogens being more tightly linked to vegetation characteristics than those of saprotrophs (Bahram et al., 2016; Nguyen et al., 2016a). Different degree of dependence upon plant resources and soil resources has been also suggested as one possible explanation for different successional patterns of EcM and AM fungi (Dickie et al., 2013). However, a direct comparison of successional patterns among fungal ecological guilds, such as available for fungi and plants (Davey et al., 2015) or fungi and bacteria (Brown and Jumpponen, 2014) has been presented rarely so far (Welc et al., 2014).

The objectives of our study were therefore (i) to describe the communities of four ecological guilds of root-associated fungi - arbuscular mycorrhizal fungi (AMF), ectomycorrhizal fungi (EcMF), pathogen fungi (PaF) and root endophytic fungi (EndF) in roots of two dominant tree species, *Salix caprea* and *Betula pendula*, growing in a primary successional chronosequence on a coal mine spoil bank; (ii) to assess the relationships of host tree species, soil chemistry, plant communities and site age with richness and community composition of each of these guilds. Specifically, we tested the following hypotheses:

i). Communities of AMF, PaF and EcMF will differ more between the two host plants than those of EndF due to the tighter association with the host plants of the former.

ii). Development of AMF, PaF and EcMF communities will show a strong relationship with composition of plant communities during the primary succession, while EndF communities will be more influenced by soil factors.

2. Material and methods

2.1. Site description

The studied spoil bank in the Sokolov brown-coal mining district (NW Bohemia, Czech Republic; $50^{\circ}14'40.6''$ N, $12^{\circ}40'27.1''$ E) covers an area of approx. 2.5×10 km and is situated at 500-600 m a.s.l. The mean annual precipitation is 650 mm and median annual temperature reaches 6.8 °C. The spoil bank is composed of deposits of tertiary clays (mainly kaolinite, illite and montmorillonite) that formed the overburden layers of coal seam (Kříbek et al., 1998) and encompasses patches of land left to spontaneous plant succession. The clay substrates were not rearranged after heaping and become

first colonized by herbs and grasses (Frouz et al., 2008). The first trees (mainly willows - *Salix caprea* and birches - *Betula pendula*) appear already at the youngest sites and visually dominate the 20-year-old sites ('site age' means number of years after mine spoil deposition across the whole manuscript). After 30 years, *S. caprea* clearly dominates, creating a closed canopy that shades nearly the entire soil surface and a thick layer of litter. Grasses and herbs occur only sporadically at the 30-year-old sites. Subsequently, willows almost completely vanish, and the 50-year-old forest is composed mainly of birches with a dense understory of herbs and grasses. For additional descriptive information about the studied sites (soil characteristics, vegetation cover) see Rydlová et al. (2016), illustrative pictures of the sampled sites are shown in Krüger et al. (2017).

2.2. Root sampling

Four successional stages (approx. 12, 20, 30 and 50 years old) were studied. Each successional stage was replicated at three sites distant at least 100 m apart. Altogether, 12 sites were sampled in June 2013. The GPS coordinates and elevation of each site were recorded using a Trimble GeoExplorer GeoXH 2008 differential GNSS (Trimble Inc., California, USA) with post-processing in Trimble Pathfinder Office using CZEPOS correction data. Six individuals of both target tree species (*S. caprea* and *B. pendula*) located several meters apart and of approximately the same age (approaching the site age) were selected and labeled at each site in order to cover an area of 50×50 m. Two samples containing soil and roots of size approx. $15 \times 15 \times 20$ cm were collected near each tree and mixed, which yielded 144 samples in total. The samples were then individually placed into plastic bags and immediately transferred to the laboratory.

The tree roots were washed, cut into pieces and from each sample, one random subsample of 0.1 g root fresh weight was frozen in liquid nitrogen and stored at -80 °C for later DNA isolation. Remaining roots were stained with Trypan blue (Koske and Gemma, 1989). Post-clearing bleaching with alkaline hydrogen peroxide was applied when needed to remove brownish root discoloration of some samples (Brundrett et al., 1996). Thirty root segments per sample, each approx. 1.5 cm long, were mounted on microscopic slides. Frequency of colonization by EcMF, AMF and dark septate endophytes (DSE) was scored in 150 visual fields uncompound microscope der а (Olympus BX60) at $200 \times$ magnification. Ambiguous root segments/structures were sorted out as such and not evaluated. They accounted for less than 5% of the analyzed visual fields. Only fine roots (<2 mm in diameter) were inspected and therefore, no old suberized roots occurred in our samples.

In each plot, soil pH, conductivity, total carbon (C_{tot}), total nitrogen (N_{tot}), total phosphorus (P_{tot}), available P (P_{avail}), available calcium (Ca_{avail}), magnesium (Mg_{avail}) and potassium (K_{avail}) were assessed as described in Krüger et al. (2017), the values are listed in Supplementary Table S1. All plant species present within a radius of 0.75 m around each sampled tree were recorded in September 2013 (in order to determine the plants securely in their flowering/fruiting stage). The plant community of a site was then described as presence/absence of each plant species in the six circles evaluated per site for each tree species (Supplementary Table S2).

2.3. Molecular analyses

All frozen root samples were disrupted in the tissue lyser. Subsequently, DNA was extracted using the NucleoSpin PlantII Kit (Macherey-Nagel, Germany) according to the manufacturer's instructions and eluted in 100 μ l double distilled water (ddH₂O). The Download English Version:

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