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Effects of soil substrate quality, microbial diversity and community composition on the plant community during primary succession

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ABSTRACT

The study addresses the role of microbial community and soil properties development on species replacement during succession. During succession, plants directly and indirectly affect microbial communities and soil properties. Such belowground changes then feedback on plants. Although of both substrate-plant and microflora–plant interactions have been studied, the joint interactions of all three remain underexplored. We studied the effects of the microbial community and substrate on plants in a full-factorial experiment. Substrates from 10- and 50-year-old post-mining sites were sterilized. Suspensions from the early and late substrate, each applied in two dilutions (high and low diversity), were used to inoculate each substrate. Substrates were sown with three early and three late successional plant species both with one grass and two herbs.

Aboveground plant biomass was higher in the late than early successional substrate. Grasses were not stimulated by higher diversity of microbial community while herbs grew better with the more diverse microbial community. Late successional herbs grew better with the late successional microbial community but early successional herbs grew well with both early and late microbial community. Grasses were thus very responsive to substrate quality and were not stimulated by microbial diversity while herbs responded positively to microbial diversity. This may affect species replacement during succession, from early succession herbs not showing strong responses to microbial community composition to late succession herbs showing specific responses to microbial communities, with grasses responding to nutrient conditions. Also nutrient supply and reduction of microbial community is likely to support grasses over herbs.

1. Introduction

Ecological succession has been a central topic in ecology for more than 100 years (Odum, 1969; Glenn-Lewin et al., 1992; Prach and Walker, 2011). Although the interactions among plants greatly affect succession, complex interactions between various trophic levels, including plant microbial symbionts, decomposers that contribute to nutrient release and ecosystem engineers that contribute to soil formation and modification of soil properties, might be even more important and might greatly affect plant community development (Thompson et al., 1993; De Deyn et al., 2003; Frouz et al., 2008).

In addition to altering the community of other organisms as a consequence of their interactions, plants and other organisms also alter the abiotic environment. One of the most important changes to the abiotic environment is the formation of soil. For example, during succession in post-mining soils, initial plant development enables colonization by earthworms (Frouz et al., 2008). Earthworms then cause massive changes in the soil substrate, which in turn causes changes in plant community composition (Frouz et al., 2008; Mudrák et al., 2012). Plants affect soil directly and also indirectly by modifying the community of soil organisms, which in turn may affect soil formation (Frouz et al., 2008). These effects of plants occur via two major pathways: one pathway is associated with litter, and the other is associated with roots (Wardle et al.,

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Litter provides a substantial proportion of the carbon, energy, and nutrients that support soil organisms (Ponge, 2003). During litter decomposition nutrients become available to plants. Moreover soil organisms that decompose litter also redistribute organic matter, increase soil porosity and enhance soil aggregate formation, which greatly alters soil sorption capacity, water holding capacity, and other soil properties (Ponge, 2003; Six et al., 2004) and consequently modifies the soil as a substrate for plants (Thompson et al., 1993; Roubíčková et al., 2009). During succession in post-mining soils, for example, initial plant development enables colonization by earthworms which then alter plant community (Frouz et al., 2008; Mudrák et al., 2012). In general, soil substrate development during succession affects the competition among individual plant species and plant functional groups (such as grasses and herbs) due to their different preferences for soil conditions and nutrient supply (Frouz et al., 2008; Xia and Wan, 2008).

Roots transfer large amounts of assimilates to symbionts and especially to mycorrhizal fungi that help plants acquire phosphorus (P), nitrogen (N), and water (Smith and Read, 2008). Roots also support a large number of microorganisms in their rhizospheres (Bonkowski et al., 2000; Berg and Smalla, 2009). Root-associated organisms substantially affect plant growth and consequently plant community composition during succession (De Deyn et al., 2003; Nara, 2006; Püschel et al., 2007). Plant effects on soil microorganisms may result in the accumulation of plant pathogens or symbionts, which may positively or negatively affect the next plant generation in a phenomenon referred to as plant–soil feedback, with negative feedback being more common in early successional species and positive feedback in late successional species (Kardol et al., 2006). Pioneer plants may lack root symbionts (Cazarés et al., 2005) and may not effectively protect themselves against pathogens. Accumulation of pathogens in a soil supporting pioneer plants may cause a negative plant-soil feedback. Late successional species with root symbionts effectively compete for nutrients (Titus and del Moral, 1998; Püschel et al., 2007), and the accumulation of symbionts in soil may explain why intermediate or late stages of succession exhibit positive plant-soil feedback. Dependence on rhizosphere microorganisms differs between species and plant guilds; for example, herbs are more dependent than grasses on mycorrhizae (van der Heijden et al., 2006). Other studies show that forbs seem to have a stronger effect on microbial communities than grasses (Farrer et al., 2013; Xia et al., 2016). This suggests that in general symbiotic plant microbial interactions may be more important for herbs than grasses. Manipulation studies also show that microbial diversity affects plant fitness, suggesting that some important interactions may be maintained by rare microbial species (Hol et al., 2010). Roots and associated soil organisms also greatly affect the development of soil aggregates (Six et al., 2004), which in turn affects subsequent generations of plants and other soil organisms.

While the interactions between plant roots and microorganisms may result in relatively rapid changes in the microbial community and relatively rapid feedback to plants, changes to the substrate resulting from interactions with litter tend to occur relatively slowly (Bever et al., 1997; Ponge, 2003; Ehrenfeld et al., 2005).

Changes in soil microorganisms and changes in substrate during plant succession have been extensively studied (Kardol et al., 2006; Nara, 2006; Frouz et al., 2008; Mudrák et al., 2012), but their relative importance to succession and their interactions have seldom been considered. The aim of this contribution was to assess the separate and interactive effects of microbial diversity, microbial community composition, and soil substrate quality on plant performance during primary succession.

We hypothesize that both substrate quality (i.e., soil quality) and microbial diversity will affect plant growth but that the nature of the effects will differ between grasses and herbs and early and late successional species. We expect that late successional species will respond equally to substrate quality and microbial diversity, that grasses will be generally more responsive to substrate quality than to microbial properties, and that herbs will be more responsive to microbial diversity and community composition than to substrate quality.

2. Materials and methods

2.1. Sampling of substrates

The substrates used in this experiment were obtained from a chronosequence of post-mining soil developing on the overburden, material that lies above coal seam that was excavated and deposited on heaps Fduring open-cast mining of brown coal near Sokolov, Czech Republic. The substrate was deposited mainly in the form of alkaline mudstones, which subsequently decomposed into smaller particles and amorphous clay. During soil formation in this chronosequence, pH gradually decreases, carbon (C) and N accumulate, and P becomes more available (Frouz et al., 2008).

We used substrates from two sites in the same chronosequence. At the 10-year-old site (i.e., the overburden had been deposited 10 years earlier), the mudstones had broken into pieces <2 mm, and vegetation was scarce. At the second site, which was 50 years old, the substrate had been influenced by roots, litter, and soil fauna for several decades, which resulted in the formation of an A soil horizon that was about 8–10 cm thick. We had two substrates of a contrasting quality, the early successional substrate supported much lower plant biomass in field than the late successional substrate (Frouz et al., 2008). The chemical properties of the two substrates are summarized in Table 1. Substrate was sampled from a depth of 3–8 cm at both sites. At each site, five spots about 50 m apart were sampled, and the material was combined to obtain one composite sample of about 10 kg.

2.2. Substrate preparation

The substrates were used for an experiment that followed the approach described by Hol et al. (2010) with some modifications. About 1 kg of substrate was stored at 4 °C, and the remainder was placed in four sealable plastic bags, each containing about 1.5 kg of substrate. These fresh substrates were then sterilized with a 40-kGy dose of γ radiation. Sterilized substrates were inoculated with a suspension of non-sterile substrates to obtain dilutions of 10^{-2} and 10^{-7}; dilution in this case refers to the proportion of inoculated soil to sterilized soil. Suspensions were sonicated and filtered through a 40 μm mesh before use. The volume of suspension added to each replicate was always the same but the quantity of non-sterile substrate in the suspension differed according to the treatment. As has been already shown on several soils by Wertz et al. (2006) almost all microbial species would be present in the less-diluted suspension (high microbial diversity treatment) but that only the most common species would be present in the more-diluted suspension (low microbial diversity treatment). Both sterilized substrates were inoculated with suspensions from both substrates using these two dilutions. This yielded eight combinations (with one bag of substrate for each combination): early successional substrate inoculated with a suspension of early successional substrate at low and high microbial diversity (EEL, EEH); early successional substrate inoculated with a suspension of late successional substrate at low and high microbial diversity (ELL, ELH); late successional substrate inoculated with a suspension of late successional substrate at low and high microbial diversity (LLL,