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Plant diversity generates enhanced soil microbial access to recently photosynthesized carbon in the rhizosphere

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ABSTRACT

Plant diversity positively impacts ecosystem services such as biomass production and soil organic matter (SOM) storage. Both processes counteract increasing atmospheric CO_2 concentration and global warming and consequently need better understanding. In general it is assumed that complementary resource use is driving the positive biomass effect and that the rhizospheric microbial community provides the necessary nutrients mineralizing SOM. So far however, it remains unclear how this link between the above and the belowground system is functioning; in detail it remains unclear if a more efficient CO_2 uptake at higher diversity levels leads to higher root exudation that stimulate the microbial mineralization. Contrastingly we show here for the first time that more diverse grassland communities provide a better access to root exudates for the rhizospheric community. We applied a continuous $^{13}CO_2$ label in a controlled environment (The Montpellier European Ecotron) to ecosystem monoliths from the long-term The Jena Experiment and showed analyzing the $\delta^{13}C$ content of phospholipid fatty acids and neutral lipid fatty acid that plant diversity increased the plant-derived C uptake of Gram negative bacteria and arbuscular mycorrhizal fungi (AMF). Root biomass but not the amount and $\delta^{13}C$ content of root sugars positively influenced the plant diversity effect observed on Gram negative bacteria whereas the specific interaction between plant and AMF was independent from any plant trait. Our results demonstrate that plant diversity facilitated the accessibility of plant derived C but not the above-belowground transfer rates. This facilitating effect enabled more diverse plant communities to use complementary C and most likely nutrient resources both from soil organic matter mineralization for better growth. We anticipate from our results that plant diversity effects are less driven by the performance of individuals in mixtures (trait plasticity) but by the combination of individuals that interact independently (trait complementarity).

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1. Introduction

Biodiversity is an important regulator of ecosystem functioning (Hooper et al., 2005; Cardinale et al., 2012; Bardgett and van der Putten, 2014). During the last two decades numerous studies have demonstrated negative effects of biodiversity loss on key ecosystem processes (reviewed in Hooper et al., 2012) such as primary productivity and soil organic carbon (SOC) storage (Tilman et al., 2001; Fornara and Tilman, 2008; Steinbeiss et al., 2008a; Marquard et al., 2009). Yet, primary productivity and SOC storage are not independent from each other, as enhanced belowground inputs of plant-derived carbon (C) associated with increased biomass production at higher diversity levels might lead to increased SOC accumulation (Steinbeiss et al., 2008a; Lange et al., 2015). This plant–soil relationship is likely to be mediated by soil microorganisms, since they are the main agents transferring C from plants to SOC (Gleixner, 2013). Soil microorganisms can be classified in several ways, for instance the soil microbial community has

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been divided into ecological categories related to their preferentially decomposed C sources: copiotrophs are able to decompose labile C sources (e.g. root exudates (Wardle, 2002)) and oligotrophs have higher nutrient affinity and are capable of decomposing SOC and plant-derived litter (Fierer et al., 2007). Another commonly way of classifying soil microorganisms is by their abundance in different compartments of the soil (Denef et al., 2007; Elfstrand et al., 2008; Denef et al., 2009; Esperschutz et al., 2009; Bird et al., 2011; De Deyn et al., 2011; Bahn et al., 2013; Fanin et al., 2015). In general, Gram negative (G−) bacteria are recognized as rhizospheric microorganisms (Denef et al., 2009), which preferentially decompose simple substrates; such as recently fixed plant-derived C (i.e. root exudates). Gram positive (G+) bacteria are slow growing and stress tolerant microorganisms (Waldrop et al., 2000) that dominate the bacterial community in the bulk soil. They are known to decompose complex substrates and are able to use older and more stabilized SOC for growth (Kramer and Gleixner, 2008; Bahn et al., 2013). Saprotrophic fungi can actively access their C substrates through hyphal growth (Strickland and Rousk, 2010). They have extensive enzymatic capabilities (Denef et al., 2007) and are able to decompose a wider variety of C substrates like root exudates, plant litter (Treonis et al., 2004) and SOC (Garcia-Pausas and Paterson, 2011). Arbuscular mycorrhizal fungi (AMF) are obligate symbionts that actively form associations with most of the known terrestrial plants (Engels et al., 2000). AMF colonize the intracellular space of plant roots and actively trade C for nutrients with the host plant (Bonfante and Genre, 2008; Drigo et al., 2010).

The final mechanisms how plant diversity interacts through the soil microbial community on soil C storage remain unclear so far. Several possible mechanisms have been put forward to explain how more diverse plant communities could increase the C transfer into the soil microbial community. For instance, more diverse plant communities could be more effective in photosynthetic assimilation (Milcu et al., 2014) resulting in higher root exudation rates (Amos and Walters, 2006; Lange et al., 2015; Shahzad et al., 2015), which might promote growth of the soil microbial community (Chung et al., 2009). Alternatively, more diverse plant communities do not only produce higher aboveground biomass, but also higher root biomass (Ravenek et al., 2014). The increased root biomass might, in turn, foster soil microorganisms, in particularly root-associated microbes in several ways, for instance via a higher input of root litter (Phillipson et al., 1975; Latz et al., in press) which would act on the longer term; through increased rhizodeposition (Van Der Krift et al., 2001) and by facilitating a better access to recently fixed plant derived C (Guo et al., 2005).

Labelling experiments have been extensively used to determine the C transfer from plants to soil microorganisms. Different experimental approaches have been developed, for example, labelling experiments can be based on the application of either enriched ^{13}C substrates that mimic root exudates (Lemanski and Scheu, 2014) or enriched $^{13}CO_2$ that label all photosynthetic products (Denef et al., 2007; Staddon et al., 2014). However, different outcomes might be obtained by the use of distinct labelling techniques, e.g. pulse labelling or continuous labelling. Metabolic fluxes that are dependent on turnover of different pools are best investigated using pulse labelling (Wolfe and Chinkes, 2005). However, the results depend on the duration of the labelling as slow pools are not completely labelled and this is known to bias for example the release of plant C to the soil system (Paterson et al., 1997; Malik et al., 2015). In contrast, continuous labelling experiments allow even slow pools to reach steady-state and are therefore more suitable to determine C resource availability and C sources for different compartments of the ecosystem (e.g. soil, soil microorganisms, plants) (Schimel, 1993).

In order to identify the influence of plant diversity and the mechanisms behind the C transfer from plants to soil microbial communities, we took advantage of a long-term biodiversity experiment (The Jena Experiment (Roscher et al., 2004)) and an advanced controlled environment facility for ecosystem research (The Montpellier European Ecotron (Milcu et al., 2014)). Atmospheric $^{13}CO_2$ labelling of large monoliths originating from The Jena Experiment with four and 16 species allowed us to investigate how the flow of C between the different ecosystem compartments was affected by plant diversity. We extracted phospholipid fatty acids (PLFA) and neutral lipid fatty acid (NLFA) from all soil samples to account for differences in $\delta^{13}C$ values of distinct soil microbial groups and to identify changes in both the microbial biomass and the isotopic ratios of the microbial groups related to increased plant diversity. Following the argumentation by Lange et al. (2015) that emphasized the importance of increased microbial activity in the rhizosphere under high plant diversity for triggering the C cycling and ultimately promoting SOC accumulation, we explored more deeply the mechanisms of C transfer from aboveground to belowground through the soil microbial community and hypothesize that 1) higher photosynthetic activity at higher plant diversity results in increased microbial C uptake, as a result of a better access to recently photosynthesized plant derived C (i.e. root exudates) and 2) this plant diversity effect is more pronounced in root-associated soil microorganisms.

2. Materials and methods

2.1. Plant communities originating from the Jena experiment

The Jena Experiment, is a long-term grassland biodiversity experiment located in Jena Germany (50°55′ N, 11°35′ E, 130 m a.s.l.) established in 2002 on a former agricultural land. The field site comprises 82 plots (20 × 20 m) with a diversity gradient that ranged from one to 60 plant species and from one to four functional groups (grasses, small herbs, tall herbs and legumes). The mean sand content in the field varied from 5.3 to 45%; clay content from 14.4 to 26.3% and silt content between 40.6 and 73.1%, pH values were in the range of 7.1–8.4 (Roscher et al., 2004). The initial values of SOC and soil N were between 1.5% and 2.8% and from 0.2% to 0.3%, respectively. For this experiment, 12 plots were selected according to the following criteria: (1) grasses, legumes and herbs were present and (2) realized species numbers were close to sown species. The selected plots (see Table S1 in Supporting information) included two sown diversity levels (four and 16 species) with six replicates per diversity level. In December 2011, soil monoliths (2 m depth; 1.6 m dia.) were excavated from the selected plots using steel lysimeters (UMS GMBH, Munich, Germany). The soil monoliths were representative in terms of percentage vegetation cover and standing biomass of the plots from which they originated. All monoliths were stored over winter in the soil at the field site. In spring 2012, they were transported to the Montpellier European Ecotron in France.

2.2. Setting up the Jena-Ecotron experiment

The soil monoliths were randomly allocated to the 12 controlled environment units of the macrocosm platform in the Ecotron facility in Montpellier, France (Milcu et al., 2014). In each unit the aboveground compartment of the ecosystems was confined in a transparent dome with a volume of ca. 30 m^3, while the belowground compartment was maintained in a lysimeter. The imposed environmental conditions in the Ecotron simulated the average climatic conditions in the Jena Experiment since 2002. A continuous atmospheric $^{13}CO_2$ labelling was applied inside all domes for a

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