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Independent role of belowground organisms and plant cultivar diversity in legume-grass communities

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ABSTRACT

Plant diversity and different groups of belowground organisms have been shown to influence the characteristics of plant communities and their associated aboveground organisms; however, little is known about the interactions and combined effects of these biotic factors. Furthermore, while plant species richness has received a lot of attention, intraspecific diversity has only recently come into the focus of community ecology. The objective of this study was to determine whether the addition of beneficial soil organisms (arbuscular mycorrhizal fungi (AMF) and anecic earthworms (*Lumbricus terrestris* L.) and different levels of plant cultivar diversity interactively influence productivity, weed establishment, leaf damage by herbivores and pathogens, and the diversity of aboveground herbivores in legume-grass communities. Our results indicated that the addition of AMF increased aboveground plant productivity and tended to decrease the diversity of aboveground herbivores. Earthworms attenuated the effect of AMF addition on AMF root colonization, but had no effect on plant productivity or herbivore diversity. Weed biomass was significantly lower in plant communities with high cultivar diversity compared to low cultivar diversity. We did not find interactive effects of the two soil organism groups and plant cultivar diversity. Our results demonstrate the independent roles and additive positive effects of AMF and plant cultivar diversity on functions such as productivity and resistance against weeds in the field. We suggest that AMF and plant cultivar diversity manipulations may be applied more frequently in agriculture management programs that aim for sustainable yield enhancement and biocontrol of herbivores and weeds.

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1. Introduction

An increasing body of work demonstrates that plant diversity and aboveground communities are influenced by belowground organisms (Wardle et al., 2004; van der Heijden et al., 2008). Plant diversity itself has been found to lead to increased plant productivity and to alter herbivore performance (Hughes et al., 2008; Scherber et al., 2010). However, most studies have focused on species diversity (van der Heijden et al., 1998; Scherber et al., 2010; Eisenhauer et al., 2012), while the role of intraspecific diversity for ecosystem functions has only recently drawn interest (Kotowska et al., 2010; Ostfeld and Keesing, 2012). Moreover, little is known about the interactive effects that intraspecific plant diversity and soil biota may have on plant and aboveground herbivore communities, and ecosystem functions.

Arbuscular mycorrhizal fungi (AMF) and earthworms are vital components of the rhizosphere and soil biota community. Previous studies have shown that AMF and earthworms can positively influence plant nutrition and productivity (Milleret et al., 2008; Kohler-Milleret et al., 2013; Willis et al., 2013). AMF are generally known to improve plant growth by enhancing nutrient uptake such as available phosphorus (P) and inorganic nitrogen (N), by inducing root system modifications, and by influencing soil structure (Rillig and Mummey, 2006; Smith and Read, 2008). Moreover, the plants' symbiosis with AMF is thought to improve plant resistance against aboveground herbivores (Pineda et al., 2010). Earthworms, as ecosystem engineers which dominate the biomass of soil invertebrates, are also known to alter the soil environment and nutrient availability through their feeding, burrowing, casting, and dispersing activities (Lavelle, 1988). Furthermore, a review article by Wurst (2010) illustrated that aboveground herbivores can be affected by earthworms either

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negatively or positively depending on abiotic and biotic soil conditions and species identity.

Previous studies reported conflicting results about AMF and earthworm interactions and their consequences for plant performance (Eisenhauer et al., 2009; Mammitzsch et al., 2012). Earthworms have been documented to stimulate mycorrhizal infection (Ma et al., 2006), increase the AMF root colonization rate and dispersal of AMF spores (Zarea et al., 2009). However, earthworms may also have no effects on the symbiosis between AMF and plants (Wurst et al., 2004; Eisenhauer et al., 2009), or may reduce the arbuscular mycorrhizal symbiosis by damaging or grazing on fungal mycelia (Pattinson et al., 1997; Bonkowski et al., 2000; Lawrence et al., 2003). Earthworms and AMF were found to have mainly independent effects on plant community productivity (Wurst et al., 2011; Wurst and Rillig, 2011), but this may change with the successional stage of the plant community (Mammitzsch et al., 2012). These results and a previous study on the effect of diverse soil organisms on a plant community (Ladygina et al., 2010) suggest that direct interactions between functionally dissimilar soil organisms exist, but are usually not strong enough to change their individual impacts on ecosystem functions such as primary productivity.

Plant species diversity was reported to interact with soil biota and to influence multiple trophic levels and alter ecosystem functions, such as community productivity and plant resistance toward herbivores and plant invaders (van der Heijden et al., 1998; Ladygina et al., 2010; Scherber et al., 2010; Eisenhauer et al., 2012). Yet intraspecific plant diversity has only recently received increasing attention. For example, the diversity of different cultivars of single plant species, such as *Oryzae sativa* L. (Zhu et al., 2000), *Gossypium hirsutum* L. (Yang et al., 2012) and *Arabidopsis thaliana* L. (Kotowska et al., 2010), was reported to have direct and indirect impacts on the enhancement of plant productivity, the resistance to herbivory and plant pathogens, as well as on predators of herbivores. Compared to single cultivars, high cultivar diversity of host plants was found to lead to increased resistance against plant pathogens and insect pests (Ostfeld and Keesing, 2012; Tooker and Frank, 2012). Furthermore, plant cultivar diversity has been reported to influence the genetic diversity (Paffetti et al., 1996; Dalmastri et al., 1999) and community composition of soil microorganisms (Schweitzer et al., 2008). However, to date it remains untested whether plant cultivar diversity interacts with belowground organisms to affect aboveground organisms and ecosystem functions. If these factors have combined positive additive or even synergistic effects, their interactive effects could be exploited to promote ecosystem functions in sustainable agriculture.

Many studies on plant-mediated above–belowground interactions have been conducted in highly controlled environments such as greenhouses and climate chambers (Poveda et al., 2005; Olson et al., 2008; Johnson et al., 2012; Kostenko et al., 2012; Singh et al., 2014). However, to evaluate the importance of results obtained under controlled environmental conditions for natural environments, field studies are necessary (Soler et al., 2012). The challenge of field studies manipulating soil biota is to establish a meaningful control treatment.

In contrast to former field studies on above–belowground interactions, in the present study soil organisms were added to field soil rather than reducing them by the application of pesticides, because of their potentially severe and uncontrollable side effects (Smith et al., 2000). For instance, to demonstrate the impact of fungi in communities, fungicides are often applied as a control treatment to suppress mutualistic or pathogenic soil fungi. However, fungicides have also been shown to affect earthworms (Xu et al., 2011), soil protozoan (Ekelund, 1999), bacterial diversity (Johnsen et al., 2001) and community structure of soil oribatid mites (Al-Assiuty et al., 2014). The resulting feedback from the modified belowground community can then affect plant growth and productivity in natural and agricultural systems. By adding certain groups of soil organisms to background levels of the soil biotic community, we took an approach that has the advantage to avoid artificial side effects by treating the control treatments with pesticides, but the disadvantage of potentially underestimating the impact of the soil biota, since they are also present in low numbers in the control treatments.

We set up a field experiment with grass–legume mixtures of high and low cultivar diversity and investigated the impacts of AMF and earthworm additions on the plant community, associated antagonistic organisms (e.g., pathogens and herbivores), and ecosystem functions (plant community productivity, resistance against weeds and aboveground antagonists). We worked in an agricultural setting with typical agriculturally–relevant mixtures of the legume *Trifolium pratense* L. and the grass *Lolium perenne* L. and used a number of different cultivars (one or four per species) to test effects of plant cultivar diversity. Intraspecific diversity can refer to a number of hierarchical levels of diversity such as the richness of genotypes or subspecies; in our study higher cultivar diversity was used as a proxy for higher intraspecific diversity. Furthermore, several investigations about perennial grass and legume cultivars have been reporting consistent differences in traits including canopy structure, nutritional quality or resistance to fungal diseases among different cultivars (Gilliland et al., 2002; Smit et al., 2005; Jacob et al., 2010; Swieter et al., 2014).

Overall, we hypothesized that (1) the addition of AMF, the addition of earthworms, and higher plant cultivar diversity increase plant productivity, and enhance plant community resistance against weeds, aboveground herbivores and plant pathogens. Further, we hypothesized that (2) AMF, earthworms and plant cultivar diversity may interact directly, but their interactions will not be strong enough to alter their individual impacts on ecosystem functions leading to additive combined effects.

2. Materials and methods

2.1. Experiment design

2.1.1. Plot set-up

On the campus of Freie Universität Berlin, Germany, we chose an 11 m × 23 m area of a former cornfield with sandy loamy soil. Soil samples were randomly taken and mixed for nutrient analyses. The experimental site contained 1.5 g total N kg^{-1}, 19.3 g organic C kg^{-1}, 325 mg available P kg^{-1}, 200 mg available K kg^{-1}, and pH 7.4 (LUFA, Rostock, Germany; see the methods in Table S1). The area was ploughed before it was divided into 64 1 m × 1 m plots. We established the plots with a distance of 1 m from each other. Between the plots we left a path for management purposes and to reduce the interference between them. A fully-factorial field experiment with three different categorical treatments was designed. The treatments were: arbuscular mycorrhizal fungi addition (no/yes), earthworm addition (no/yes) and cultivar diversity of the plant community (low/high) each with 8 replicates. The treatments were randomly assigned to the plots.

2.1.2. Plant material

Differing in characteristics (Table S2), *T. pratense* cultivars 'Milvus' 'Larus' 'Diplomat' and 'Taifun' as well as *L. perenne* cultivars 'Lipresso' 'Lacerta' 'Licampo' and 'Sures' were used for the experiment. The two species were chosen because they are widely grown as commercial grassland species and because they are colonized by AMF in the field (Oehl et al., 2004); furthermore, information relating to impacts of earthworms and AMF is

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