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Does plant diversity influence phosphorus cycling in experimental grasslands?

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ABSTRACT

Plant diversity was shown to influence the N cycle, but plant diversity effects on other nutrients remain unclear. We tested whether plant species richness or the presence/absence of particular functional plant groups influences P partitioning among differently extractable pools in soil, P concentrations in soil solution, and exploitation of P resources (i.e. the proportion of total bioavailable P in plants and soil that was stored in aboveground biomass) by the plant community in a 5-year biodiversity experiment in grassland.

The experimental grassland site established in 2002 had 82 plots with different combinations of numbers of species (1, 2, 4, 8, 16, 60) and functional groups (grasses, small non-leguminous herbs, tall non-leguminous herbs, legumes). In 2007, we determined P partitioning (Hedley) in soil of all experimental plots. We sampled plant community biomass and continuously extracted soil solution with suction plates from March 2003 to February 2007 and determined PO_4-P concentrations in all samples.

The presence of legumes increased aboveground P storage in plants and decreased labile P_i concentrations in soil because of their higher demands for P associated with N_2 fixation. During cold periods, readily plant-available PO_4-P concentrations in soil solution increased in legume-containing mixtures likely caused by leaching from P-rich residues. We found a consistently positive effect of plant species richness on P exploitation by the plant community which was independent of the presence of particular plant functional groups. With proceeding time after establishment, plant species richness increasingly contributed to the explanation of the variance in P exploitation. Therefore, plant strategies to efficiently acquire P seem to become increasingly important in these grasslands. We conclude that diverse plant communities are better prepared than less diverse mixtures to respond to P limitation induced by continuously high atmospheric N deposition.

1. Introduction

Plant species richness is partly driven by nutrient supply (Janssens et al., 1998; McCrea et al., 2001; Wassen et al., 2005). However, at similar nutrient supply, plant species richness in turn has been shown to influence ecosystem functioning including the nutrient cycle (Scherer-Lorenzen et al., 2003; Spehn et al., 2005; Tilman et al., 1996). A number of manipulative field experiments have been conducted to investigate the effect of plant species richness on ecosystem processes to assess the potential consequences of the currently observed biodiversity loss (Hooper et al., 2005; Schmid et al., 2002). Most experimental studies have focused on biomass production and the N cycle so far, since N limits plant productivity at many locations of the temperate zone (Vitousek and Howarth, 1991). As a result of anthropogenic N deposition and the associated shift in N:P ratios in biomass, however, P is becoming increasingly important for plant growth and biodiversity (Galloway et al., 2004; Vitousek et al., 2010; Wassen et al., 2005).

The underlying mechanistic hypothesis to explain the plant species richness-nutrient cycling relationship is that plants can use available nutrients in a complementary way (Trenbath, 1974). Thus, niche differentiation in space and/or time in more diverse systems may result in a more complete resource use at the community level compared to less diverse systems (Hooper et al., 2005). Positive complementarity effects have explained increased biomass production in a number of plant diversity experiments (Marquard et al., 2009; Spehn et al., 2005; van Ruijven and Berendse, 2003). If plants take up more N because of increased biomass production in diverse systems, the uptake of all other essential elements, e.g. P, must also increase. Karanika et al. (2007) presented support for this hypothesis based on a pot

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experiment. It remains, however, unclear whether any positive relationship between plant diversity and P exploitation holds true for established grassland systems.

Driven by complementary N uptake, increasing plant species diversity decreased plant-available soil N concentrations (Niklaus et al., 2001; Scherer-Lorenzen et al., 2003; Tilman et al., 1996). This effect was also observed at our study site, the Jena Experiment (Oelmann et al., 2007b) where, however, the effect of plant species diversity on the P cycle has not yet been tested. Hooper and Vitousek (1998) found an effect of functional groups on resin-extractable P in soil mainly caused by the difference between vegetated and non-vegetated plots. The study of the plant diversity-P cycle relationship is in contrast to N complicated by the strong physicochemical control of P solubility (Hinsinger, 2001). Furthermore, it is difficult to identify the plant-available P fraction in soil, because i) extractions with salt solutions often yield no correlations between P concentrations in the extraction solution and measures of plant P uptake (Gilbert et al., 2009), and ii) the soil solution as the most sensitive measure of P availability is characterized by low P concentrations due to the low solubility product of the associated P-containing minerals posing problems to analytical accuracy. Therefore, several P fractions ranging from the instantaneous measure of P concentrations in soil solution to total P storage in soil must be included to gain insight into the relationship between plant diversity and P availability in soil. Although P concentrations in either soil (labile fraction) or plant material is commonly used for evaluating bioavailability of P (Alt et al., 2011; Critchley et al., 2002; Gilbert et al., 2009; Janssens et al., 1998), to our knowledge, no study has linked aboveground P exploitation and P fractions in soil of differently diverse grasslands yet. The potential effect of plant diversity could vary among different soil depths and among seasons because of complementary P uptake in space and time as was observed for N (Bardgett et al., 2003; McKane et al., 2002; von Felten et al., 2009).

Diversity in functional plant properties relevant for nutrient acquisition and use among co-existing plant species might favor complementary P uptake. Therefore, the consideration of plant functional groups for P cycling in differently diverse grassland systems is essential. For example, the high P demand of legumes because of the energy costs associated with N_2 fixation which is supplied by the synthesis of adenosinetriphosphate (ATP) is well known (Aerts and Chapin, 2000; Pate, 1986). Because of their extensive rooting system, grasses might more efficiently explore P resources in soil and thus, reduce PO_4-P concentrations in soil solution (Hooda et al., 1999). However, the exploitation of nutrient resources in soil by grasses might not be as efficient for P as was reported for N, because of reduced infestation of grasses with arbuscular mycorrhizal fungi (Brundrett, 2002).

All reported plant diversity or functional group effects on above- and belowground nutrient pools in grasslands were based on short-term experiments. In short-term studies weather conditions might strongly affect biomass production (Ciais et al., 2005) and thus, short-term ecosystem P cycling. Therefore, plant diversity or functional group effects might be restricted to a particular study year. Furthermore, in particular belowground processes are known to respond to plant diversity only after a time lag (Eisenhauer et al., 2010). Recently, Oelmann et al. (2011) have shown that the relationship between plant diversity and N availability in soil changed systematically during the first five years after establishment of the experimental grassland mainly induced by organic matter accumulation because of conversion from arable land to grassland. Availability of P in soil might change with time because of periodic removal of nutrients with the mowing and harvesting of grassland plants and continuous depletion of P-fertilizer remains (applied during agricultural use frequently preceding conversion to grassland in central Europe). Therefore, it is likely that competitive interactions among plant species – mainly driven by resource availability – are changing and reduced P availability with time also modulates plant diversity effects. Taken together, these arguments illustrate that longer-term studies are required to derive general conclusions about plant diversity or functional group effects on P cycling.

The objective of our study was to test if plant species richness *per se* or the presence of plant functional groups influences P cycling i.e., P exploitation by the plant community, P concentrations and partitioning in solid soil, and P concentrations in soil solution in artificial grassland systems established by conversion from arable land during the first five years after sowing.

We hypothesized that (i) plant species richness is positively correlated with P exploitation of plant communities and correspondingly negatively with P availability in soil similar to N, (ii) plant functional identity influences aboveground P exploitation of plant communities and P availability in soil, and (iii) plant species richness gains importance for P exploitation of plant communities and P availability in soil with time after establishment of the grassland.

2. Materials and methods

This study was conducted in the framework of the "Jena Experiment" (www.the-jena-experiment.de) which addresses the role of biodiversity on element cycling and trophic interactions in experimental grassland systems (Roscher et al., 2004).

2.1. Study site

The field site is located near the German city of Jena (50°55′ N, 11°35′ E; 130 m above sea level). Mean annual air temperature is 9.3 °C, and mean annual precipitation amounts to 587 mm (Kluge and Müller-Westermeier, 2000). A comparison of this long-term mean (LTM, 1960–1990) with the study years is given in Table 1. The soil is an Eutric Fluvisol developed from up to 2 m-thick fluvial sediments that are almost free of stones. The systematic variation in soil texture as a consequence of fluvial dynamics is considered in the experimental design by arranging the plots in four blocks parallel to the river. The study site was converted from grassland to arable land in the early 1960s. Organic C concentrations ranged from 13 to 33 g kg^{-1}, organic C:N ratios from 8 to 15, and pH (H_2O) from 7.1 to 8.4 at the start of the experiment in 2002.

The experimental design is described in Roscher et al. (2004). Briefly, the main experiment comprises 82 plots (20 × 20 m) of different levels of species richness (1, 2, 4, 8, 16, 60) and different numbers (1, 2, 3, 4) of plant functional groups (grasses, [non-leguminous] small herbs, [non-leguminous] tall herbs, legumes) chosen from a species pool of 60 species representing species typically occurring in Molinio-Arrhenatheretea meadows (Ellenberg, 1996). Each plant-diversity level had 16 replicates except for 14 mixtures with 16 species and four replicates of the 60-species mixture. The management of all plots was adapted to extensive meadows used for hay production, and all plots were mown twice a year in June and September. Plots were not fertilized during the experimental period. To maintain the sown species diversity level, plots were weeded regularly by cutting the weeds at the soil surface.

Table 1
Weather conditions during the study period. Significant differences between the Long-Term Mean (LTM) and the respective years are indicated by different letters. For statistical details see methods. no. = number, n.a. = not available

	Mean T (°C)	Rainfall sum (mm)	No.[a] of days T<0 °C (March)	No.[a] of days T<0 °C (Winter)
LTM	9.3 a	587 a	n.a	n.a
2003	9.9 a	436 b	0	30
2004	9.4 a	573 a	1	37
2005	9.2 a	422 b	8	47
2006	10.0 a	493 a	14	6
2007	10.2 a	710 a	0	n.a

[a] no. = number.