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Belowground interactive effects of elevated CO_2, plant diversity and earthworms in grassland microcosms

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Abstract

The potential interactive effects of future atmospheric CO_2 concentrations and plant diversity loss on the functioning of belowground systems are still poorly understood. Using a microcosm greenhouse approach with assembled grassland plant communities of different diversity (1, 4 and 8 species), we explored the interactive effects between plant species richness and elevated CO_2 (ambient and +200 p.p.m.v. CO_2) on earthworms (*Lumbricus terrestris*) and microbial biomass. We hypothesised that the beneficial effect of increasing plant species richness on earthworm performance and microbial biomass would be modified by elevated CO_2 through impacts on belowground organic matter inputs, soil water availability and nitrogen availability. We found higher earthworm biomass in the 8-species mixtures under elevated CO_2, and higher microbial biomass under elevated CO_2 in the 4 and 8-species mixtures where earthworms were present. The results suggest that plant driven changes in belowground organic matter inputs, soil water availability and nitrogen availability explain the interactive effects of CO_2 and plant diversity on the belowground compartment. The interacting mechanisms by which elevated CO_2 modified the impact of plant diversity on earthworms and microorganisms are discussed.

Zusammenfassung

Die potentiellen wechselwirkenden Effekte von zukünftigen atmosphärischen CO_2-Konzentrationen und der Pflanzendiversität auf Bodensysteme sind nur unvollkommen bekannt. Im Gewächshaus nutzten wir Mikrokosmen mit zusammengestellten Grasland-Pflanzengesellschaften unterschiedlicher Diversität (1, 4 und 8 Arten) und untersuchten die wechselwirkenden Effekte von Artenzahl und CO_2-Konzentration (Umgebungswert und + 200 p.p.m.v. CO_2) auf Regenwürmer (*Lumbricus terrestris*) und die mikrobielle Biomasse. Wir vermuteten, dass der positive Effekt zunehmender Pflanzenartenzahlen auf die Leistung der Regenwürmer und die mikrobielle Biomasse durch erhöhtes CO_2 modifiziert werden würde, indem es den organischen Stoffeintrag im Boden und die Verfügbarkeit von Wasser und Stickstoff im Boden beeinflusst. Wir fanden erhöhte Regenwurmbiomasse in den 8-Arten-Mikrokosmen bei erhöhtem CO_2 und eine höhere mikrobielle Biomasse bei erhöhtem CO_2 in den 4- und 8-Arten-Ansätzen mit Regenwürmern. Die Ergebnisse legen nahe, dass pflanzengesteuerte Änderungen des organischen Stoffeintrags im Boden und die Verfügbarkeit von Wasser und Stickstoff im Boden die interagierenden Effekte von CO_2 und Pflanzendiversität auf das Bodenkompartiment erklären. Die wechselwirkenden Mechanismen, durch die erhöhtes CO_2 den Einfluss der Pflanzendiversität auf Regenwürmer und Mikroorganismen modifiziert, werden diskutiert.

Keywords: Climate change; Species richness; Above-belowground interactions; Water availability; Soil N; *Lumbricus terrestris*

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Introduction

Understanding the relationship between biodiversity, climate change and the ecosystem services upon which we are heavily reliant emerged as a critical issue in the face of increasing human-induced environmental change (Millennium Ecosystem Assessment 2005). Whilst much attention has been devoted to separately studying the impacts of climate change and biodiversity loss, considerably less is known about their interactive effects on ecosystems and the services they provide (Balvanera et al. 2006). Studies which include the effects of climate change factors on the functioning of the belowground compartment are even fewer and generally highlight the considerable lack of knowledge in this area (Chung, Zak, Reich, & Ellsworth 2007; Kardol, Cregger, Campany, & Classen 2010). Since the biological functioning and the species composition of the belowground compartment is dependent on organic matter inputs from plants, understanding the links between producer and decomposer subsystems is essential for predicting ecosystem-level responses to global change (Wardle 2002).

Grasslands constitute a widespread ecosystem type covering ∼27% of the terrestrial surface (Henwood 1998). This highlights their importance as model systems used for investigating the consequences of biodiversity loss (Roscher et al. 2005; Tilman, Reich, & Knops 2006) or elevated CO_2 (Niklaus et al. 2007; Reich 2009). Reich et al. (2001) showed that plant diversity interacts with elevated CO_2 and nitrogen availability to modify ecosystem functioning. Furthermore, elevated atmospheric CO_2 concentrations usually reduce stomatal density and conductance (Woodward & Bazzaz 1988; Tricker et al. 2005), which may result in increased soil water availability by reducing evapotranspiratory loss of water (Morgan, Lecain, Mosier, & Milchunas 2001; Nelson et al. 2004). Although both CO_2 and plant diversity loss have been shown to impact the decomposer functioning through changes in the quality and quantity of organic matter inputs and impacts on soil moisture and nutrient availability, we have a limited understanding of their combined effects on the decomposer functioning (Niklaus et al. 2007) despite their important role in biogeochemical cycling, plant performance and soil C storage (Bardgett 2005).

Both earthworms and microorganisms are key decomposer groups which are sensitive to changes in aboveground inputs as well as soil water and nutrient regimes, but we only have a limited mechanistic understanding of the interactive effects of elevated CO_2 and plant diversity loss on their performance. The few studies that report effects of elevated CO_2 on earthworms, predominantly measuring their response in terms of activity, indicate increased activity with increasing levels of CO_2 (Arnone & Zaller 1997; Yeates, Tate, & Newton 1997; Zaller & Arnone 1999b). However, an observation of community biomass and composition by Zaller and Arnone (1999b) found no effects of elevated CO_2. Available data also show that increasing plant species diversity (Zaller & Arnone 1999a; Spehn, Joshi, Schmid, Alphei, & Körner 2000; Niklaus et al. 2007) can lead to increased earthworm biomass and activity. Often specific relationships between plant species or functional groups and earthworms (Zaller & Arnone 1999b; Milcu, Partsch, Langel, & Scheu 2006) have been reported, whilst Milcu, Partsch, Scherber, Weisser, and Scheu (2008) suggested that it is the change in the quality rather than quantity of plant inputs associated with changes in species diversity that affect earthworm performance. The consequences of elevated CO_2 on microorganisms are still unclear since there is insufficient data to predict how microbial biomass and functioning will change as atmospheric CO_2 concentration continues to rise (Zak, Pregitzer, King, & Holmes 2000; Bardgett, Freeman, & Ostle 2008). The consequences of diversity loss for soil microorganisms are, however, somewhat clearer with recent publications pointing out the positive relationship between plant diversity and the functioning and biomass of microbial communities (Eisenhauer et al. 2009).

The scope for interacting effects of diversity loss and elevated CO_2 on soil organisms is clearly large. Climatic change is likely to affect soil biota both directly and indirectly (via plant responses), with associated consequences for ecosystem functioning. In this study we explored the interaction between plant species richness, elevated CO_2 and the presence of earthworms and its effects on the belowground compartment of model grasslands, using a microcosm greenhouse experiment. Our overarching hypothesis is that the frequently observed beneficial effects of increasing the richness of plant species on earthworm performance and microbial biomass will be altered by elevated CO_2, through changes in belowground organic matter inputs and altered soil water and nitrogen availability.

Materials and methods

Experimental setup

Experimental grassland communities of varied plant species richness (1, 4 and 8 species) were established in cylindrical microcosms made of PVC tubes, 10.3 cm in diameter and 25 cm in height. The microcosms were sealed at the base with 0.5 mm^2-mesh, and a layer of sand (0.25 kg) was added to the bottom of the microcosms to ensure efficient drainage. The sand was topped by 1.6 kg of sieved soil (1 cm diameter sieve) taken from the "A" horizon of a mesotrophic grassland (MG5, *Cynosurus cristatus* – *Centaurea nigra*; Rodwell et al. 1992) in Silwood Park, Ascot, UK (N51°24.3 W00°38.5). Prior to use, the soil (Bagshot sands, pH 5.35) was homogenised and defaunated by freezing at −22 °C for two weeks (Huhta, Wright, & Coleman 1989). Subsequently, the soil was watered intermittently over a 12 day period with deionised water to remove excess nutrients released by the perturbation.