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Belowground Tritrophic Food Chain Modulates Soil Respiration in Grasslands

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ABSTRACT

Edaphic biota significantly affects several essential ecological functions such as C-storage, nutrient turnover, and productivity. However, it is not completely understood how belowground animal contribution to these functions changes in grasslands subject to different land use types. A microcosm experiment was carried out to test the effect of a tritrophic food chain on CO_2 release from grassland soils. Soil was collected from three differently managed grassland systems (meadow, pasture, and mown pasture) located in three distinct German regions that cover a north-south gradient of approximately 500 km. The tritrophic food chain comprised natural edaphic microflora, nematodes, and predatory gamasid mites. The experimental design involved a full factorial combination of the presence and absence of nematodes and gamasid mites. Nematodes significantly increased the CO_2 emissions in most treatments, but the extent of this effect varied with land use type. The fact that grazing by nematodes stimulated the metabolic activity of the edaphic microflora over a wide range of grassland soils highlighted the critical impact of the microfauna on ecosystem services associated with soil organic matter dynamics. Gamasids slightly amplified the effect of nematodes on microbial metabolic activity, but only in the pastures. This effect was most probably due to the control of nematode abundance. The fact that gamasid addition also augmented the impact of environmental conditions on nematode-induced modulation of soil respiration highlighted the need for including land use differences while evaluating soil fauna contribution to soil processes. To conclude, the differential response of the investigated tritrophic food chain to different grassland management systems suggests that adverse effects of land use intensification on important soil processes such as atmospheric C-release could potentially be reduced by using management methods that preserve essential features of the belowground food web.

Key Words: CO_2 emission, land use, microcosm, nematodes, predatory mites, soil fauna, soil food webs

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INTRODUCTION

Grasslands comprise about 26% of the total land area and 80% of the agriculturally productive land area worldwide (Boval and Dixon, 2012). They play an important role in greenhouse gas emission, preserving water, and maintaining biodiversity (De Fries and Rosenzweig, 2010), with the edaphic biota significantly affecting several essential ecological functions such as C-storage, nutrient turnover, and productivity (van Eekeren *et al.*, 2010). In general, the framework for soil biological activities is set by environmental factors such as climate (Wall *et al.*, 2008; Briones *et al.*, 2009; Carrera *et al.*, 2009; Wang *et al.*, 2009; Briones *et al.*, 2014), edaphic conditions (*e.g.*, Ekschmitt *et al.*, 2008; Sun *et al.*, 2013), plant community composition (Birkhofer *et al.*, 2011), and land use intensity (Manning *et al.*, 2008; De Vries *et al.*, 2013; Ma *et al.*, 2013; Norris *et al.*, 2013). However, the soil systems of grasslands differ from those of other ecosystems such as forests due to the high turnover of shoot and root biomass, and consequently the absence of long-term C storage in timber (Bardgett and Cook, 1998). In a broader sense, identifying the biotic mechanisms suitable for C emission mitigation from grassland soils remains one of the major challenges in modern soil ecology.

Agricultural management modifies gas fluxes from soils mainly by changing both the composition of microbial and invertebrate communities and the interactions between them (Bjørnlund *et al.*, 2006; Brussaard *et al.*, 2007; Menyailo *et al.*, 2008; De Vries *et al.*, 2013). Thus, the impact of human intervention on the release of CO_2 and other trace gases can be understood only by accounting for the complex relationships among edaphic organisms. While the microflora generally me-

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diates up to 90% of the C turnover in soils (Anderson, 1995), edaphic invertebrates contribute to soil respiration with only 1% to 13% (but normally 4%–5%) (Persson, 1989; Juang *et al.*, 2016). However, soil animals are of enormous quantitative importance as they alter the microbial activity (Wolters, 2000). For example, invertebrate grazers preying on soil microbes (*e.g.*, Conrad, 1996) are themselves an important food source for higher-level predators (Berg and Bengtsson, 2007). Thus, many feedback loops between different trophic levels of the soil food webs may affect soil respiration (Griffiths and Bardgett, 1997). Moreover, different soil faunal groups may exert opposing effects on decomposition (Vetter *et al.*, 2004). For example, the stimulation of bacterial activity caused by moderate nematode grazing outweighs the overall loss of bacterial cells due to microbivore trophic activity (De Mesel *et al.*, 2004; Vetter *et al.*, 2004). This may further be complicated by non-trophic effects of the fauna, such as bacterivorous nematodes increasing the bacterial activity through active stirring of oxygen in the soil water, leading to its enrichment (Standing *et al.*, 2006). Possible implications of these processes and mechanisms on the CO_2 release from soil are shown schematically in Fig. 1. Finally, as the role of different trophic groups in food chains can dramatically change with environmental conditions and land use type (De Ruiter *et al.*, 2005), the impact of soil biota on CO_2 release is dependent on the environmental context (Hooper *et al.*, 2000; De Vries *et al.*, 2013).

The aim of this study was to investigate the effect of management on the faunal modulation of microbial CO_2 release from temperate grassland soils. The food chain in our experiment comprised the natural edaphic microflora, nematodes, and predatory mesofauna represented by gamasid mites. We hypothesized that the introduction of nematode-feeding predators would hinder overgrazing of soil bacteria by microbivores and additionally stimulate the bacterial activity. As a result of this, the presence of gamasid mites would augment the microbial CO_2 emission in microcosms inoculated with nematodes. The findings of Coleman *et al.* (2004) and Zhang *et al.* (2012) indicate that the strength of such trophic and non-trophic effects would vary with the intensity of grassland management, as microbial biomass and activity are generally higher under more vigorous management. Hence, our second hypothesis was that cascading effects in the food chain would amplify CO_2 emission most strongly in intensively used grasslands.

MATERIALS AND METHODS

Study sites

Grassland soils were sampled in each of three German regions, jointly covering a north-south gradient of about 500 km: Schorfheide-Chorin Biosphere Reserve (NE Germany, mean annual temperature (MAT) of 8–

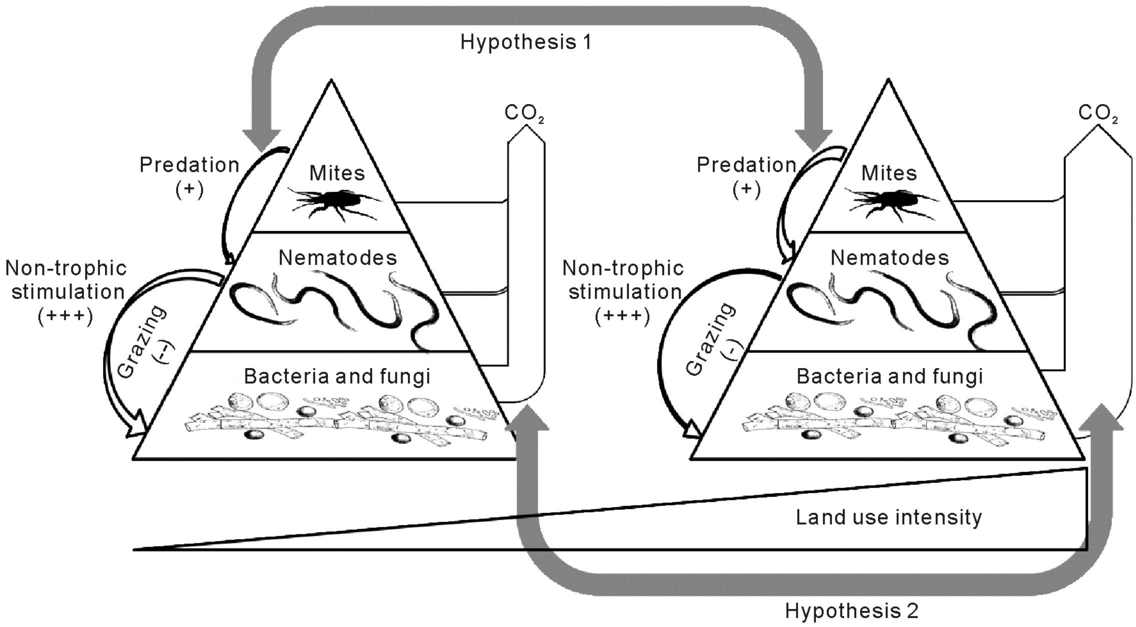

Fig. 1 Schematic diagram of the potential effects of trophic and non-trophic interactions between soil microflora, nematodes, and predatory mites in a tritrophic soil food chain on the CO_2 emission levels from grassland soils tested in the microcosm experiment in this study. Numbers of "+" and "−" under each process name indicate the presumable relative strength of their positive and negative impact on soil respiration, respectively.

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