

Atmospheric CO₂ enrichment induces life strategy- and species-specific responses of collembolans in the rhizosphere of sugar beet and winter wheat

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Abstract

We studied atmospheric CO₂ enrichment effects on life form types, species composition, dominance structure and individual density of collembolans under cultivation of sugar beet and winter wheat. The study was part of a long-term CO₂ enrichment field experiment (FACE: Free Air CO₂ Enrichment) at the Federal Agricultural Research Centre (FAL) in Braunschweig (Germany), using isotopically labelled CO₂. The stable C-isotopic signature ($\delta^{13}\text{C}$) of collembolan species, plant material, and soil indicated CO₂ impacts on C translocation. The $\delta^{13}\text{C}$ values of both crops significantly increased from above-ground to below-ground plant parts and significantly decreased under FACE conditions. The $\delta^{13}\text{C}$ values of collembolan species differed significantly depending on CO₂ treatment and crop and showed a distinct tendency depending on plant growth stage. The extent, to which $\delta^{13}\text{C}$ values of collembolans decreased under FACE conditions, was species- and life strategy-dependent. The stable C-isotopic signatures of euedaphic and hemiedaphic species were similar in the control, but, depending on crop, differently affected by atmospheric CO₂ enrichment. Under winter wheat cultivation, hemiedaphic species showed more negative $\delta^{13}\text{C}$ values than euedaphic ones under FACE conditions. CO₂ enrichment effects on occurrence, density and dominance distribution of the collembolan species differed strongly between crops and their developmental stages, which reveal crop-specific below-ground effects due to different food qualities in the rhizosphere. CO₂ impacts were stronger under sugar beet compared to winter wheat cultivation. Independent of crop, CO₂ enrichment enhanced the diversity of collembolans before harvest and increased the proportion of hemiedaphic in relation to euedaphic species in a community. Our results on collembolan communities imply CO₂-induced changes in the root-derived carbon resources used by the soil food web. The present study reveals atmospheric CO₂ enrichment impacts to specifically affect collembolan species according to their food preferences.

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1. Introduction

Atmospheric CO₂ elevation, one of the most important climate change drivers (IPCC, 2007), is known to enhance plant photosynthetic rates (Körner, 2000) and water use efficiency (e.g., Conley et al., 2001). Elevated CO₂ can also affect the chemical composition of plant tissues, e.g., by changing the carbon (C) to nitrogen (N) ratio. Due to an increased biomass (e.g., Bender et al., 1999; Demmers-Derks et al., 1998) and wider plant C/N ratios, the quality

and quantity of litter, and therefore C input into the soil, is also affected by CO₂ elevation (Weigel et al., 2005). Thus, future atmospheric CO₂ conditions will have considerable impacts on ecosystem processes and services.

Studies which deal with impacts of CO₂ elevation on agro-ecosystems are dominated by measurements of plant-mediated processes (Canadell et al., 1996). Less is known about CO₂-induced alterations concerning the soil food web, which is indirectly affected through changes in litter quantity and quality, as well as shifts in root turnover rates and nutrient exudation into the rhizosphere (Coûteaux and Bolger, 2000; Wardle et al., 2004). Recent results of Pollierer et al. (2007) give evidence that root-derived

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carbon resources seem to be much more important for soil animal food webs than previously estimated. Knowledge of this influence is of great importance to fully understand agro-ecosystem responses to atmospheric CO₂ enrichment, since soil biota communities are drivers of the soil C-turnover through the decomposition of organic matter and nutrient mobilisation (for Collembola see Chamberlain et al., 2006; Rusek, 1998). Changes in the diversity structure of the decomposer food web would, therefore, have the potential to alter soil ecological processes and services in agriculture.

Microarthropods, as important members of the decomposer community, are very abundant and their role in soil formation is well recognised (Parisi et al., 2005). They have also been shown to respond sensitively to land use changes (for Collembola see Dittmer and Schrader, 2000; Schrader et al., 2006; Chauvat et al., 2007) and to improve soil functions. Collembolans, as a highly diverse microarthropod group, represent a valuable biological indicator of soil quality, as they include several species representing different soil adaptation levels (Parisi et al., 2005). Furthermore, collembolans show well-differentiated ecomorphological life forms (Gisin, 1943; Rusek, 1998) and feeding guilds (Berg et al., 2004), are selective feeders comprising a wide range of food sources (Bracht Jørgensen et al., 2005; Filser, 2002; Klironomos and Kendrick, 1995), modify soil organic matter at the molecular level, and influence microbial community size through their grazing activity (Chamberlain et al., 2006). These characteristics indicate that collembolans are well suited for analysing impacts of atmospheric CO₂ elevation on the decomposer food web. Previous results range from increasing (Jones et al., 1998) to decreasing densities of collembolans (Klironomos et al., 1997) under atmospheric CO₂ elevation. Within the first crop rotation cycle of the Braunschweig Free Air CO₂ Enrichment (FACE) experiment, collembolan abundances significantly increased under atmospheric CO₂ enrichment when winter wheat was cultivated (Sticht et al., 2006b). These contradictory findings reveal the need for more detailed field studies concerning CO₂ impacts on species level of collembolans and their ecological classification. Furthermore, studies on atmospheric CO₂ impacts on collembolan communities in arable soil, including developmental stages of different crops, have been missing up to now.

To improve knowledge on crop-dependent effects regarding CO₂ impacts, the Braunschweig FACE experiment provided a unique opportunity, since it represented the only European FACE experiment in an agro-ecosystem under crop rotation (Weigel et al., 2006). Future atmospheric CO₂ concentrations were simulated under field conditions by fumigating the standing crop with isotopically labelled CO₂.

The aim of the present study was to investigate CO₂ enrichment effects on individual density and dominance structure of collembolans in arable soil, and to detect whether impacts differ between life strategies and species.

Two developmental stages of sugar beet and winter wheat were studied within the second crop rotation cycle to consider crop-dependent nutritional conditions for collembolans below-ground.

The stable C-isotopic composition ($\delta^{13}\text{C}$) of animal tissues is correlated with the respective diet (DeNiro and Epstein, 1978). Moreover, recent photosynthate-C is known to be rapidly assimilated by the mesofauna of the rhizosphere, mainly by collembolans (Ostle et al., 2007). Therefore, in the present study, stable C-isotopic analysis was used to trace the C translocation from the CO₂-enriched atmosphere to the plant soil system and to test plant-mediated impacts on life form types and species of collembolans.

2. Materials and methods

2.1. Site description and management

A FACE field experiment (Lewin et al., 1992) was conducted in an agro-ecosystem at the Federal Agricultural Research Centre (FAL) in Braunschweig, Lower Saxony, Germany (10°26'E 52°18'N, 79 m a.s.l.) (details in Hendrey, 1992; Sticht et al., 2006b; Weigel et al., 2006). The local climate is characterized by a mean annual air temperature of 8.8 °C and a total precipitation rate of 618 mm year⁻¹. The soil at the site is a luvisol of a loamy sand texture, with a pH of 6.3–6.5 and a mean organic carbon content of 1.4% in the Ap horizon (Weigel et al., 2006). The field (total 22 ha) has been used for agriculture, cultivating only C3 plants, for at least 30 years. During the FACE experiment, the field was managed in a locally typical crop rotation, including winter barley (*Hordeum vulgare*), ryegrass (*Lolium multiflorum*) as a cover crop, sugar beet (*Beta vulgaris*) and winter wheat (*Triticum aestivum*) as sequential crops. The rotation cycle was repeated once, resulting in a total duration of the CO₂ enrichment experiment of 6 years (1999–2005). All soil, fertilizer, irrigation, and pesticide management measures were carried out according to local farming practices (Weigel et al., 2006). Crop management measures and CO₂ treatment details during sugar beet (*B. vulgaris*, spp. Altissima Döll, cv. “Impuls”) cultivation in 2004 and winter wheat (*T. aestivum*, cv. “Batis”) cultivation in 2005 are briefly summarised in Table 1.

2.2. Experimental design

The FACE system consisted of four circular plots (rings) of 20 m diameter. Each ring was surrounded by vertical vent pipes engineered by the Brookhaven National Laboratory, NY, USA. The pipes extended to the top of the crop canopy and were equipped with blowers. More detailed information about the experimental design, the ventilation system, and the performance of FACE techniques were outlined by Lewin et al. (1992) and Hendrey (1992).

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