Responses of soil Collembola to long-term atmospheric CO_2 enrichment in a mature temperate forest

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ABSTRACT

Responses of Collembola to 7 years of CO_2 enrichment (550 ppm) in a Swiss free-air CO_2 enrichment (FACE) experiment in a forest with 80- to 120-year-old trees were investigated in this study. Contrary to our expectations, increased CO_2 caused a significant decrease in Collembola numbers, including a significant decrease in euedaphic Collembola. Increased CO_2, however, did not affect community group richness. Collembola biomass was not significantly changed by CO_2 enrichment, regardless of whether it was considered in terms of the total community, life-strategy groups, or individual species (with an exception of *Mesaphorura krausbaueri*). The reason for this is that CO_2 enrichment caused a general increase in individual body size, which compensated for reduced abundances. The results are consistent with the idea that the rhizosphere is important for soil fauna, and the combination of reduced fine root growth and increased soil moisture might trigger a reduction in Collembola abundance.

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1. Introduction

Atmospheric CO_2 concentrations are expected to double relative to pre-industrial concentrations by the end of the 21st century (Canadell et al., 2007). This atmospheric CO_2 enrichment is likely to have considerable impacts on ecosystems (Körner, 2000; Li et al., 2006), as it stimulates photosynthetic rates for many plant species, leading to increased plant growth and biomass production, increased fine root production, and possibly an increased rate of root turnover and exudation (Rogers et al., 1994; Körner, 2000). However, less is known about how CO_2-induced alterations may affect the soil food web (Sticht et al., 2008).

Previous studies dealing with increases in atmospheric CO_2 have concentrated on aboveground responses of plants and few have considered belowground responses (Makkonen et al., 2011). Soil, however, is the single largest organic carbon pool on land and practically the only long-term carbon sink (Jagadamma, 2009). Whether terrestrial ecosystems act as a carbon source or sink will depend largely upon belowground processes (Körner, 2000).

Soil fauna organisms are very diverse and occur in large numbers. They have low mobility and relatively short lifecycles, and are easily affected by environmental changes. Collembola, for example, live for only a few weeks or months, and have been found to be very sensitive to soil acidification (Rusek, 1998) and/or nitrogen (N) deposition (Xu et al., 2009). Hence, Collembola have been proposed as good indicators of environmental changes and soil quality (Rusek, 1998; Chauvat et al., 2007; Xu et al., 2009).

CO_2 enrichment often leads to more carbon being allocated to roots (Norby et al., 2004). Root turnover is a key process supplying energy and nutrients to soil biota (Pollierer et al., 2007). Moreover, it has been shown that recent photosynthate-C can be rapidly assimilated by the mesofauna of the rhizosphere, mainly by Collembola (Ostle et al., 2007). Increased atmospheric CO_2 levels are assumed to have negligible direct effects on soil fauna because it is adapted to much higher CO_2 concentrations in the soil atmosphere (van Veen et al., 1991). However, indirect impacts can be expected through trophic relationships, such as increases in the quality and quantity of litter (Coûteaux et al., 1999).

The soil food web is complex, but ultimately it relies almost entirely on plant-derived nutrients (Pollierer et al., 2007). These affect the composition and biomass of soil communities (Dhillion et al., 1996). N and lignin concentrations in plant tissues are greatly affected by atmospheric CO_2 (Coûteaux et al., 1999). It is widely known that CO_2 enrichment can cause a significant reduction in N concentrations in plant tissues, resulting in reduction of litter quality. Changes in lignin concentration have been found in a very broad range, from −46 to +62% (Coûteaux et al., 1999), generally with significant increases for woody plants and non-significant reductions for herbaceous species. Increased CO_2 concentrations could further induce the production of more defensive carbon

compounds such as phenols, with a negative effect on litter decomposition, at least during its early stages (Coûteaux and Bolger, 2000). However, on the other hand, soil biota represent a link between plant detritus and plant-available nutrients. They are thus of primary importance for all biogeochemical cycles. Changes in biodiversity, community structure and the activity of soil biota due to environmental change will ultimately feed back on plants and thus, via their photosynthesis, on atmospheric CO_2.

The aim of this study was to explore the effects of long-term CO_2 enrichment on soil Collembola community in a natural, mature temperate forest. We hypothesized that the density and diversity of Collembola would increase with CO_2 enrichment. Since Collembola show well-differentiated ecomorphological life forms each with their own feeding habits (Klironomos and Kendrick, 1995), we further hypothesized that different life strategy groups would react differently to the CO_2 enrichment, depending on whether they are more dependent on aboveground plant litter or on root-derived nutrition.

2. Materials and methods

2.1. Study site

The study was conducted at the Swiss Canopy Crane-CO_2 enrichment facility in Hofstetten (47°28′ N, 7°30′ E, elevation 550 m a.s.l.), near Basel, Switzerland, where a free-air CO_2 enrichment (FACE) experiment was performed from 2001 to 2008 in a mature mixed forest, with trees 80–120 years old. The dominant species in the experimental area are *Fagus sylvatica* (L.), *Quercus petraea* (Matt.) Liebl., *Quercus robur* (L.) and *Carpinus betulus* (L.), with *Tilia platyphyllos* (Scop.), *Acer campestre* (L.) and *Prunus avium* (L.) present as companion species. The area has a typical humid temperate climate, characterized by mild winter and moderately warm summer, with mean January and July air temperatures of 2.1 and 19.1 °C, respectively. The total annual precipitation for the region averages 990 mm. The soil is a shallow Rendzina on calcareous bedrock, and in the upper 10 cm, the soil is a silty loam with a pH (KCl) of 5.8 (Pepin and Körner, 2002; Schleppi et al., 2012).

The web-FACE system consisted of three parts: a CO_2 release system, a CO_2 concentration measurement system and a computer-based control system. Food-grade liquid CO_2 was delivered from a 22-m³ insulated reservoir to two heat-exchangers, where it was vaporized. CO_2 gas was released from thin plastic tubes woven into the crown of trees. These tubes had laser-drilled holes (0.5 mm diameter, spaced at 30-cm intervals). The CO_2 concentration was 550 ppm during the growing seasons, May to September or October. See Pepin and Körner (2002) for a detailed description of this web-FACE system.

2.2. Soil sampling and classification of the Collembola specimens

Ten sampling plots were well-distributed in the inner part of the CO_2-enriched area (i.e. to avoid the edge effects) and in a control area (30–50 m apart from the CO_2-enriched area) within the same forest, respectively. Soil cores (5 cm depth) were taken with a steel cylinder (3 cm diameter) in November 2007, after 7-years of CO_2 enrichment. At each sampling plot, four cores were taken and pooled to provide one mixed sample, giving 10 soil samples for each area ($n = 10$). Collembola were collected from the soil samples using Tullgren funnels. Collembola specimens were sorted and counted under a microscope and identified to species level with a dissecting microscope Olympus Bx41 (Olympus, Tokyo, Japan). For identification, we used the keys in "Checklist of the Collembola of the world" (Janssens, 2007), as well as those in Potapov (2001), Bretfeld (1999), Pomorski (1998), and Gisin (1960). All Collembola specimens found were further categorized into three life-strategy groups, euedaphic, hemiedaphic and atmobiont, which live in different soil layers and have different feeding habits. This classification was done according to Gisin (1943), Ponge (2000), Chauvat (2004), Stierhof (2003), and Sticht et al. (2008). The body length of individuals was measured to 0.01 mm precision using a microscope at 10–80× magnification with a microscope ocular meter.

2.3. Data analysis

The dry biomass of individual Collembola was derived from its body length because body length is related to the biomass of invertebrates and is easier to measure than biomass (Rogers et al., 1976; Hódar José, 1996). The biomass was then calculated using the equation:

$$W = 0.0024L^{3.676} \tag{1}$$

where W is the biomass (mg) and L is the length (mm) of individuals (Hódar José, 1996).

Comparisons of Collembola abundance, group richness, and biomass between the control and the CO_2 treatment were based on t-tests for independent samples. For these analyses, the data were grouped in three ways: according to individual species, life-strategy group or the whole community. To test the abundance of the whole community and *Isotomiella minor*, the data were square-root transformed to ensure the homogeneity of variances. SPSS 13.0 was used for all analyses.

3. Results

3.1. Collembola abundance and species richness

A total of 26 Collembola species were collected from the soil of the Hofstetten web-FACE experiment (Table 1). The total abundance of all species was lower in the CO_2-enriched plots than in the control plots ($t = 2.24$, $P = 0.04$, $n = 10$) (Table 2). Of the 13 species common to both plots, the abundances of seven were lower in the CO_2-enriched area than in the control. The four dominant species (>10% of the total abundance) were *Mesaphorura krausbaueri*, *Marcuzziella tripartite*, *Isotomiella minor* and *Isotomiella* sp. (Table 1). The abundance of all of them was lower in the CO_2-enriched area than in the control. The individuals of the most abundant species, *Mesaphorura krausbaueri*, and genus, *Isotomiella*, represented 27.6% and 37.7%, respectively, of the total community in the control, but in the CO_2-enriched area they were significantly less abundant, by 54.6% ($t = 2.23$, $P = 0.03$, $n = 10$) and by 57.3% ($t = 2.35$, $P = 0.03$, $n = 10$), respectively. When abundances were analyzed according to life-strategy group, the effect of the CO_2 was significant only for the euedaphic group ($t = 2.45$, $P = 0.02$, $n = 10$)

Table 1

Abundance of Collembola species in the Free Air CO_2 Enrichment (FACE) experiment at Hofstetten.

Collembola species	Life strategy[a]	Control Abundance (ind. m^{-2})[b]	Elevated CO_2 Abundance (ind. m^{-2})
Cyphoderus albinus Nicolet, 1842	eu	0	35 (35)
Cyphoderus bidenticulatus Womersley, 1934	eu	71 (47)	0
Entomobrya nivalis Linnaeus, 1758	at	0	35 (35)
Folsomia sp.	he	106 (76)	0
Folsomides parvulus Stach, 1922	eu	177 (79)	389 (244)
Isotomiella minor Schäffer, 1896	eu	1380 (327)*	531 (177)
Isotomiella sp.	eu	1274 (355)	602 (140)
Isotomodes productus Axelson, 1906	eu	0	35 (35)
Lepidocyrtus cyaneus Tullberg, 1871	at	212 (78)	71 (47)
Lepidocyrtus paradoxus Uzel, 1890	at	0	35 (35)
Marcuzziella tripartita Rusek, 1975	eu	743 (305)	425 (196)
Mesaphorura krausbaueri Börner, 1901	eu	1946 (378)*	885 (254)
Neelides minutus Folsom, 1901	eu	212 (108)	35 (35)
Onychiuroides pseudogranulosus Delamare Deboutteville & Gisin, 1951	eu	0	106 (76)
Parisotoma notabilis Schäffer, 1896	he	212 (151)	318 (144)
Pogonognathellus flavescens Tullberg, 1871	at	35 (35)	0
Proisotoma minuta Tullberg, 1871	he	71 (47)	71 (47)
Proisotoma spp.	he	318 (162)	35 (35)
Protaphorura sp.	eu	0	35 (35)
Sminthurus viridis Linnaeus, 1758	at	35 (35)	359 (35)
Thalassaphorura alborufescens Vogler, 1895	eu	71 (71)	106 (54)
Thalassaphorura sp.	eu	106 (76)	0
Tomocerina minuta Tullberg, 1877	at	0	142 (58)
Tomocerus vulgaris Tullberg, 1871	he	35 (35)	35 (35)
Triacanthella perfecta Denis, 1926	he	35 (35)	0
Willowsia platani Gisin, 1960	at	0	71 (71)
Sum		7042	4034

*Significant differences between elevated CO_2 and control plots ($P < 0.05$).
[a] Life strategy of species: eu, euedaphic; he, hemiedaphic; at, atmobiont.
[b] Values are the means (standard error) of 10 samples.

Table 2
Effects of CO_2 treatments on soil Collembola (density, group richness, and biomass) for the whole community and the two most abundant species, analyzed using t-test ($n = 10$). Values of t and p are given.

	Density (10^3 m^{-2})		Group richness		Biomass (mg m^{-2})	
	t	p	t	p	t	p
Whole community	2.24	0.04*	0.51	0.62	0.35	0.73
Mesaphorura krausbaueri	2.23	0.03*	NA	NA	2.15	0.05*
Isotomiella minor	2.08	0.05*	NA	NA	1.67	0.11

*Significant differences between control and CO_2-treated plots ($P < 0.05$).
NA: not applicable.

(Fig. 1A). Group richness did not significantly differ between the control and CO_2-enriched area (Table 2).

3.2. Collembola biomass

None of the biomasses of the total community, of the three life-strategy groups, and of the individual species were affected by the CO_2 treatment except for that of *Mesaphorura krausbaueri* (Fig. 1B, Table 2). Although the number of euedaphic individuals decreased significantly in the CO_2 treatment (Fig. 1A), the difference in biomass was not significant ($t = 1.78$, $P = 0.09$, $n = 10$) (Fig. 1B). The average size of individual Collembola generally increased with increased CO_2 concentrations, where the mean body length was 0.51 mm compared with 0.46 mm under control conditions. With the CO_2 treatment, the frequency distribution of body lengths tended to shift toward larger values (Fig. 2). Among the eight most abundant species (i.e., with an abundance >1% the total) that occurred in both treatments, body length was greater in the FACE area than in the control for six species: *Thalassaphorura albor-ufescens*, *Mesaphorura krausbaueri*, *Isotomiella minor*, *Folsomides parvulus*, *Parisotoma notabilis*, and *Lepidocyrtus cyaneus* (Table 3). In contrast, the length of the two species *Marcuzziella tripartite* and *Isotomiella* sp. was lower in the CO_2-enriched area than in the control (Table 3).

4. Discussion

Our initial hypothesis was that Collembola populations would increase because of the abilities to assimilate efficiently the input C (Ostle et al., 2007). Contrary to this hypothesis, long-term CO_2 enrichment was found not to affect Collembola group richness and biomass, but it did appear to reduce Collembola abundance significantly. Responses of Collembola to elevated atmospheric CO_2 concentrations have been reported in a few previous studies, but with inconsistent results. In a boreal pine forest in eastern Finland, Haimi et al. (2005) found that both the total number of Collembola and the number of the most abundant genera and species, *Mesaphorura* and *Isotomiella minor*, were smaller under CO_2 enrichment in an experiment using single-tree closed chambers. A similar outcome was found in a plantation of deciduous trees in Wisconsin, USA, where Loranger et al. (2004) reported a significant decrease in Collembola abundance under free-air CO_2 enrichment. Another study in a pine plantation (Hansen et al., 2001) did not focus on Collembola but on microarthropods in general, which were 33% less abundant with CO_2 enrichment. This effect was already detected at an early stage of the experiment, which means that it is unlikely that it was due to the availability of litter for the soil biota.

In contrast, CO_2 enrichment was found to increase the abundance and biodiversity of Collembola in an agro-ecosystem in Germany (Sticht et al., 2006). This FACE experiment in a crop rotation with wheat and sugar beets had more effect on the community composition of Collembola than on the abundance of individual species, with a marked increase in hemiedaphic compared to euedaphic species. The authors attributed the observed effects to changes in root-derived carbon resources. These results are very different from ours as we observed a significant decrease in Collembola abundance but not in group richness. Our findings are thus more similar to those from other forests and may differ from those of Sticht et al. (2006) because of the other type of ecosystem they studied. The main factors affecting the responses of Collembola to CO_2 enrichment may thus be linked to soil tilling and to the higher nutrient availability in a fertilized agricultural soil, but not enough research has been done to draw general conclusions.

The different responses of ecosystems to rising CO_2 levels largely result, according to Körner (2000) from different experimental conditions, i.e. from interactions between CO_2 and other factors. Similarly, local conditions seem to significantly affect the responses of soil fauna to elevated CO_2. For example, nematode responses to long-term CO_2 enrichment vary locally with soil patterns (Yeates et al., 1999).

The reason why the abundance of Collembola in forest soils decreases with higher atmospheric CO_2 is possibly that N becomes
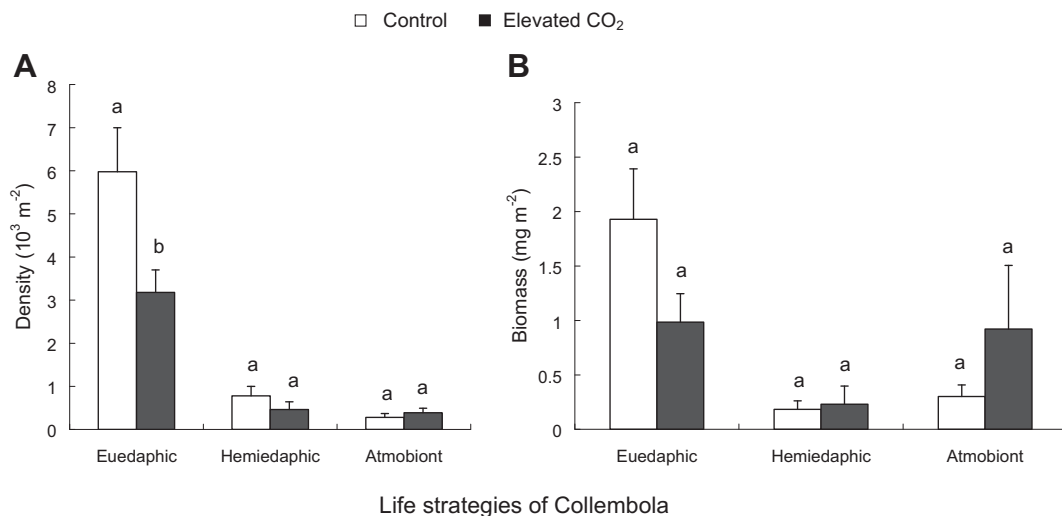
□ Control ■ Elevated CO_2

Fig. 1. Effects of the CO_2 treatment on the abundance of Collembola species in three life-strategy groups (euedaphic, hemiedaphic, and atmobiont) in the Free Air CO_2 Enrichment (FACE) experiment at Hofstetten. Values are the means (standard error) of 10 samples. For each life-strategy group, values with different letters are significantly different ($P < 0.05$).
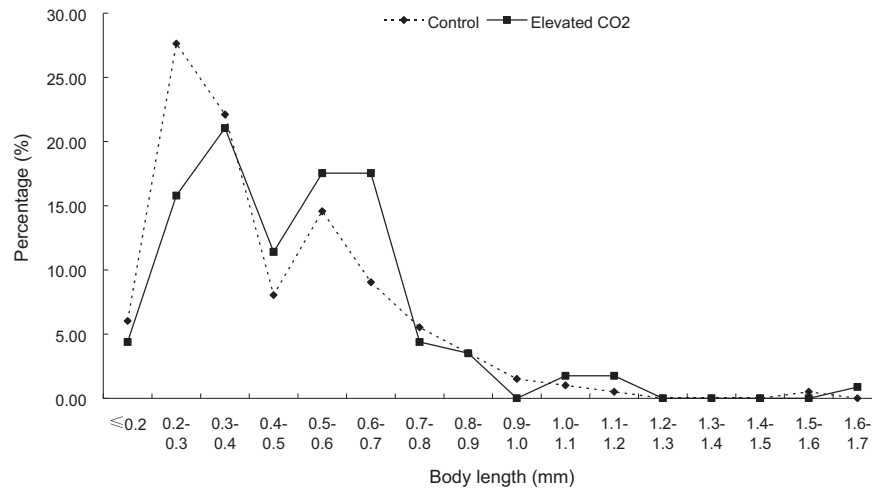
Fig. 2. Effect of the atmospheric CO_2 enrichment on the distribution of the body lengths of Collembola in the Free Air CO_2 Enrichment (FACE) experiment at Hofstetten.

insufficiently availabile. Collembola are indeed affected by both the atmospheric CO_2 concentration and soil N. In studies with poplar trees in open-top chambers, Klironomos et al. (1996, 1997) found that Collembola were negatively affected by CO_2 enrichment under N-poor conditions, but not in N-rich soils. The calcareous forest soil in our study was, however, nutrient-rich (Bader et al., 2009) and received substantial atmospheric N deposition, leading to higher-than-average nitrate concentrations in the soil solution. Further, the availability of nitrate in the soil was found to increase with the CO_2 treatment (Schleppi et al., 2012), so that a limitation due to the availability of inorganic N can be ruled out. On the contrary, the increased nitrate concentration may even have had a depressing effect on Collembola abundances, as shown earlier in an N-addition experiment (Xu et al., 2009). With increased nitrification (Schleppi et al., 2012), there is also the risk of nitrate and base-cation leaching, which can accelerate soil acidification. These factors are known to affect Collembola negatively (Matson et al., 2002; Rusek and Marshall, 2000).

At the Swiss Canopy Crane site, 5–6 years of CO_2 enrichment did not affect the quantity of leaf litter, but it did reduce the biomass of living fine roots (<1 mm diameter) by approximately 30% (Bader et al., 2009). This reduction in fine roots was no longer measurable in year 7 of the experiment, when our study took place. All the same the decrease of fine roots may explain the reduced abundance of Collembola that we observed. The exudation and decomposition of fine roots supply energy and other resources to the soil biota, and most biotic activity in soil occurs in the rhizosphere (Fitter and Garbaye, 1994). This was confirmed by a study conducted earlier at the Hofstetten site, which demonstrated (on the basis of the organisms' ^{13}C signature) that the majority of soil invertebrates obtained their carbon from roots (Pollierer et al., 2007). Another

possible reason for the decreases in Collembola individuals may be that the soil environment changed with the long-term CO_2 treatment. The top soil of the experimental area is finely textured (loamy clay) and has thus a good water-holding capacity, but the soil is relatively shallow. In the CO_2-enriched area, it was found to have a higher water content than the control area (Bader et al., 2009). In moderately dry periods, the reduced transpiration of CO_2-treated trees (Leuzinger and Körner, 2007) led to the soil remaining moister than in the control (Bader and Körner, 2010). The increased soil water content reduced the gas diffusion, and caused consistently significantly higher soil air CO_2 concentrations under CO_2-enriched trees during the growing season, amounting to, on average, 52% more than under control trees in year 7 of the experiment (Bader and Körner, 2010). Such changed soil conditions are likely to have affected some of the Collembola, especially those living deeper in the soil.

The classification of Collembola species into three life-strategy groups corresponds to a vertical stratification of habitats and diet sources. In an agro-ecosystem, hemiedaphic species were more affected by elevated CO_2 than euedaphic species, perhaps because the CO_2-induced, plant-mediated impacts reached hemiedaphic species sooner and affected them more directly than species occurring deeper in the soil (Sticht et al., 2008). In our study, in contrast, euedaphic species were more drastically affected by the CO_2 treatment than hemiedaphic species. This discrepancy may arise from differences in the distribution of plant roots. The roots of crops (wheat and sugar beet in this case) have a relatively shallow distribution compared to those of the mature trees in our study, which can even grow between rocks down into the calcareous sub-soil. We suspect that the euedaphic species in our study were more closely linked to the rhizosphere than hemiedaphic species and

Table 3
Average length (L. in mm) and proportion in the population (P. in %) of the common and abundant Collembola species (abundance > 1% of the total) under control or elevated CO_2 concentrations in the Free Air CO_2 Enrichment experiment at Hofstetten.

Treatment		Thalassaphorura alborufescens	Mesaphorura krausbaueri	Marcuzziella tripartite	Isotomiella minor	Isotomiella sp.	Folsomides parvulus	Parisotoma notabilis	Lepidocyrtus cyaneus
Control	L.	0.65 (0.12)[a]	0.30 (0.01)	0.67 (0.04)	0.54 (0.01)	0.32 (0.01)	0.58 (0.10)	0.50 (0.03)	0.79 (0.07)
	P.	1.01	27.64	10.55	19.60	18.09	2.51	3.02	3.02
Elevated CO_2	L.	0.74 (0.05)[a]	0.31 (0.01)	0.58 (0.20)	0.58 (0.03)	0.31 (0.02)	0.69 (0.03)	0.54 (0.04)	0.97 (0.35)
	P.	2.63	21.93	10.53	13.16	14.91	9.65	7.90	1.75
Change (%)[b]		15.07	1.53	−14.05	7.53	−1.75	18.55	8.27	22.88

[a] Values are the means (standard error).
[b] Relative changes with the CO_2 enrichment as compared to the control.

were therefore more affected by the decrease in the fine root biomass arising from the CO_2 enrichment. Atmobiont species, on the other hand, depend more on litter as a feeding source. As the litterfall did not change significantly with the CO_2 treatment (Bader et al., 2009), the abundance of atmobiont Collembola also remained largely unaffected. In addition, as mentioned above, the increased soil water content and the following higher soil air CO_2 concentration in the mature forest soil were also sure to affect euedaphic species in deeper soil more than atmobiont species.

In spite of the significant decrease in Collembola abundance in the CO_2-enriched area, the biomass of the Collembola community was unaffected. Community biomass depends on abundance, individual biomass and community structure. The community biomass may be balanced by an increase in individual body size (= individual biomass) or by an increase in the relative abundance of large species. We did not detect a clear increase in the contribution of large species, but we did find a general increase in individual body size. This was the case for the community in general and for most of the common species in particular (Fig. 2, Table 3). Makkonen et al. (2011) reported that larger Collembola species were more abundant in open-top chambers subjected to a drought treatment. They proposed that larger species are more tolerant to drought as they have a smaller surface-to-volume ratio. In another study, however, drought was found to cause the Collembola and soil mite community to be smaller in individual size (Xu et al., 2012). Discrepancies between these studies can be explained by the fact that Makkonen et al. (2011) did not measure individual body sizes but used reference values per species, only assessing the interspecific changes in the community. This approach does not take intrapecific size changes into account. Xu et al. (2012), in contrast, used individual measurements, assessing changes including intra- and interspecific drought effects. They could thus verify the general rule that, for a given species, a small body size is advantageous during drought (Rhind and Bradley, 2002; Jones, 1987; Danthanarayana, 1975). In our study, the body size of Collembola was also individually measured. While we found no clear contribution of large species, we did detect a general intraspecific increase in body size in the CO_2-treated, wetter area. This fits to the same pattern, namely larger body sizes in wet conditions and smaller body sizes in dry conditions. To sum up, even if we cannot definitely conclude which were the mechanisms leading to the reduced Collembola abundances and increased individual sizes, the combination of reduced fine root growth and increased soil moisture certainly played a major role.

Previous studies have shown atmospheric CO_2 enrichment to have positive, neutral, or negative effects on other soil fauna groups. Loranger et al. (2004) found that elevated CO_2 concentrations led to a significant decrease in the total soil animal abundance compared to that under control conditions. As mentioned above, Hansen et al. (2001) reported that the mean microarthropod abundance was reduced by the CO_2 enrichment. However, enchytraeids were found to be 50–100% more abundant and the cumulative earthworm surface cast production 35% greater with increased CO_2 concentrations (Newton et al., 1995; Zaller and Arnone, 1997). Although microbial-feeding nematodes have been reported to increase significantly in many studies (Klironomos et al., 1996; Markkola et al., 1996; Yeates et al., 1997), Freckman et al. (1991) found that the density of nematodes did not change after 2 years exposure to elevated CO_2 concentrations (see also Runion et al., 1994). The results published so far are, however, mostly based on short-term experiments conducted in artificial plantations or under more-or-less artificial conditions (Coûteaux and Bolger, 2000). The lack of long-term *in situ* data means that it is difficult to conclude or predict how soil fauna will respond to future global climate changes. To our knowledge, the Swiss web-FACE experiment is unique in having mature trees growing in a near-natural forest stand and being exposed to higher CO_2 concentrations for a relatively long period (7 years in our study). Our results can only be interpreted by considering many aspects of the soil ecology, including root life, plant nutrients, water status, and niches of soil biota. The Hofstetten experiment thus provides a unique opportunity to obtain insight into the complexity of the long-term effects of CO_2 enrichment on a natural forest ecosystem, including its soil biota.

Acknowledgments

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