Soil Biology & Biochemistry 36 (2004) 1521–1524

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Short communication

Elevated CO_2 and O_{3t} concentrations differentially affect selected groups of the fauna in temperate forest soils

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Received 10 October 2002; received in revised form 26 March 2004; accepted 5 April 2004

Abstract

Rising atmospheric CO_2 concentrations may change soil fauna abundance. How increase of tropospheric ozone (O_{3t}) concentration will modify these responses is still unknown. We have assessed independent and interactive effects of elevated [CO_2] and [O_{3t}] on selected groups of soil fauna. The experimental design is a factorial arrangement of elevated [CO_2] and [O_{3t}] treatments, applied using Free-Air CO_2 Enrichment technology to 30 m diameter rings, with all treatments replicated three times. Within each ring, three communities were established consisting of: (1) trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*) (2) trembling aspen and sugar maple (*Acer saccharum*) and (3) trembling aspen. After 4 yr of stand development, soil fauna were extracted in each ring. Compared to the control, abundance of total soil fauna, Collembola and Acari decreased significantly under elevated [CO_2] (−69, −79 and −70%, respectively). Abundance of Acari decreased significantly under elevated [O_{3t}] (−47%). Soil fauna abundance was similar to the control under the combination of elevated [$CO_2 + O_{3t}$]. The individual negative effects of elevated [CO_2] and elevated [O_{3t}] are negated upon exposure to both gases. We conclude that soil fauna communities will change under elevated [CO_2] and elevated [O_{3t}] in ways that cannot be predicted or explained from the exposure of ecosystems to each gas individually.

Keywords: Arthropods; Elevated CO_2; FACE technology; Global change; Northern forests; Ozone

Over the past 150 yr, atmospheric CO_2 concentration has increased from about 280 $\mu l\, l^{-1}$ to the current 360 $\mu l\, l^{-1}$, mainly due to the burning of fossil fuels and deforestation (Schimel et al., 2000). Coincident with the rise in atmospheric [CO_2], the ambient concentration of tropospheric ozone (O_{3t}) has more than doubled, to the current 30–40 $nl\, l^{-1}$ (Hough and Derwent, 1990). Therefore, to understand future forest productivity, biodiversity and biogeochemistry in regions that will experience increases in both atmospheric [CO_2] and [O_{3t}], experiments should explicitly examine the joint effect of these two gases.

The invertebrate community influences soil fertility by participating in organic matter decomposition and nutrient cycling (Coleman and Crossley, 1996). To fully understand important soil-mediated mechanisms underlying ecosystem responses to changing environmental conditions, it is necessary to study responses of the soil fauna.

The direct effects of elevated [CO_2] on soil fauna should be negligible because the organisms are already adapted to the high [CO_2] in the soil (Van Veen et al., 1991). However, indirect effects such as through the quantity and quality of litter produced, and altered physical conditions are expected to affect soil fauna (Coûteaux and Bolger, 2000). Because elevated [CO_2] usually increases plant biomass and litter production, we hypothesized that soil fauna abundance would increase under elevated [CO_2]. To the extent elevated [O_{3t}] diminished plant responses to elevated [CO_2], we expected similar dampening of soil fauna responses.

We collected soil fauna at the FACTS-II Aspen FACE Project (Karnosky et al., 1999; Dickson et al., 2000) located at the USDA Forest Service, near Rhinelander, Wisconsin, USA. This project uses Free-Air CO_2 Enrichment (FACE) technology (Hendrey et al., 1999) to maintain elevated concentrations of CO_2 and O_{3t} around intact, developing forest stands. The site is an old agricultural field that was

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doi:10.1016/j.soilbio.2004.04.022

Table 1
P-values, df and *F* ratio (ANOVA tests) for responses of soil animal to the experimental treatments at the Aspen FACE project in Rhinelander, WI

	Elevated $[CO_2]$ (df = 1)	Elevated $[O_{3t}]$ (df = 1)	Plant community (df = 2)
Soil fauna abundance			
Total	$F = 16.3$, $P < 0.001$	$F = 2.9$, $P = 0.09$	$F = 7.1$, $P = 0.005$
Collembola	$F = 9.8$, $P = 0.002$	$F = 0.2$, $P = 0.697$	$F = 2.8$, $P = 0.07$
Total Acari	$F = 22.6$, $P < 0.001$	$F = 12.1$, $P = 0.001$	$F = 3.3$, $P = 0.04$
Acari: Oribatida	$F = 11.1$, $P = 0.001$	$F = 4.1$, $P = 0.045$	$F = 3.1$, $P = 0.048$

$N = 3$. No significant effect were found for elevated $[CO_2 + O_{3t}]$. The interactions (elevated $[CO_2] \times$ community, $[O_{3t}] \times$ community and $[CO_2 + O_{3t}] \times$ community) were not significant.

farmed for potatoes and small grains. Trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and sugar maple (*Acer saccharum* Marsh.) were planted in mixed communities in early June 1997. These species provide about 70% of the pulpwood harvest in the upper Midwest region of the USA (Piva, 1996). The 32 ha facility consists of 12 individual FACE rings (plots) of 30 m diameter. Treatments include three control rings (ambient air), three elevated $[CO_2]$ rings, three elevated $[O_{3t}]$ rings, and three elevated $[CO_2 + O_{3t}]$ rings. Each ring is divided by a walkway into three parts. In one-half of each ring is planted trembling aspen. The other ring half is divided into two-quarters. One quarter is planted with trembling aspen and birch, and the other with trembling aspen and maple. Elevated $[CO_2]$ is added at 200 $\mu l\, l^{-1}$ over ambient (average 522.7 ± 76.1 $\mu l\, l^{-1}$ in 2000) and elevated $[O_{3t}]$ is maintained at approximately 1.5 times ambient (average 54.5 ± 8.4 nl l^{-1} in 2000). Soils at the site are classified as mixed, frigid, coarse loamy Alfic Haplorthods.

Soil fauna were sampled in the 12 rings over 2 d during late May 2001, well after snowmelt. This single sampling was considered to be representative because the soil fauna communities had been exposed to the experimental treatments for 4 yr, and represented an 'equilibrated' response. In each ring, soil invertebrates were sampled along a transect within each of three plant communities. Four regularly spaced cores, 10×10 cm^2 in cross-section and 10 cm in depth including the litter layer, were taken along the transects for a total of 144 samples. Soil invertebrates were extracted within a week using large funnels and 5×5 mm^2 mesh screens (dry funnel method, modified from Macfadyen, 1957).

The data were tested with analyses of variance (ANOVA). The statistical model was set up as a randomized complete-block design with factorial combinations of CO_2 and O_{3t}, replicated three times. Effects due to plant community type were evaluated as a split-plot source of variation. Data were log transformed to normalize the variance across treatments. Tukey HSD multiple comparisons tests (matrix of pairwise comparison probabilities) were calculated a posteriori.

There was a strong decrease in total soil animal abundance under elevated $[CO_2]$ (Table 1, Fig. 1). This decrease corresponded mainly to a depletion in Collembola and Acari in enhanced CO_2 plots (Table 1). Acari abundance also decreased under elevated $[O_{3t}]$. The number of Oribatid mites (mainly microbial feeders)

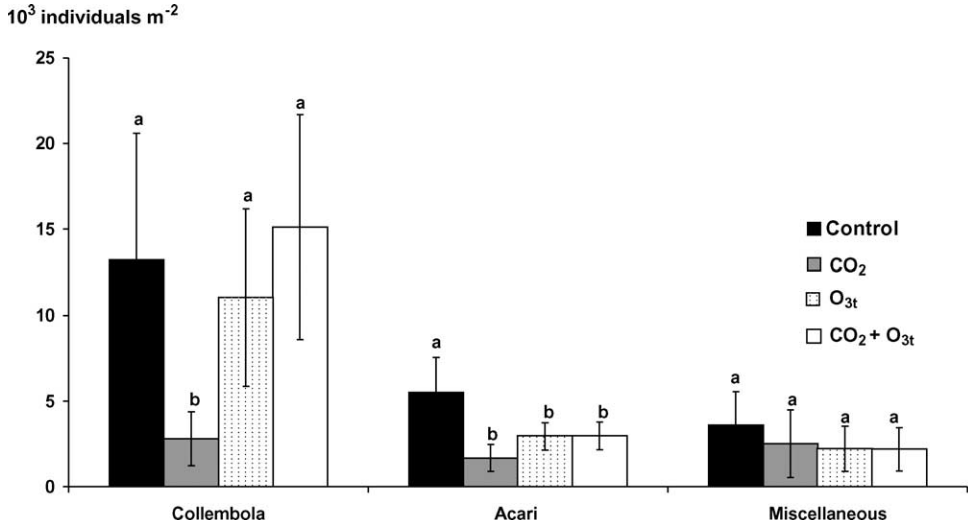

Fig. 1. Soil animal abundance (main groups) under different atmospheric treatments (ambient control, elevated $[CO_2]$, elevated $[O_{3t}]$ and elevated $[CO_2 + O_{3t}]$). Values are means ($N = 3$) and bars are SEs. For each group, means with the same letter are not significantly different according to the Tukey HSD test. Miscellaneous: Insect larvae, Heteroptera, Homoptera, Myriapoda, Hymenoptera, Coleoptera, Dermaptera, Protura, Diplura, Terrestrial Turbellaria.

decreased in plots enriched with CO_2 and in plots enriched with O_{3t}. There was a significant effect of plant community on total soil invertebrate and Acari abundances (Table 1). Sub-plots with aspen supported a lower soil animal density than sub-plots with aspen plus birch (Tukey HSD multiple comparisons test, $P < 0.05$).

Contrary to our hypothesis, soil fauna abundance decreased under elevated [CO_2]. However, at the FACTS-II experiment, photosynthesis of aspen was stimulated 7–58% under elevated [CO_2] leading to increased plant biomass (Noormets et al., 2001). Thus, the decrease of soil animal abundance might be due to some other property of the organic matter, such as its chemical composition.

In support of this hypothesis, decrease of *N* concentrations and increase of condensed tannin were observed in leaf litter under elevated [CO_2] (King et al., 2001a,b; Lindroth et al., 2001). This change in tissue quality could decrease the rate of consumption of litter by soil invertebrates or decrease assimilation efficiency (Cotrufo et al., 1998).

The decrease in soil fauna abundance under elevated [CO_2] has been observed for other soil animal groups (Markkola et al., 1996; Yeates et al., 1999; Hansen et al., 2001), suggesting the effects of elevated [CO_2] propagate through multiple components of the soil food web. Likewise, a recent study at the FACTS-II site demonstrated that elevated [CO_2] increased the concentration of phenolic glycosides in trembling aspen leaves (Percy et al., 2002). These phenolic glycosides are of singular importance as protective agents against pests (Lindroth and Hwang, 1996). Enhanced CO_2, through changes in leaf chemical quality, then reduced female pupal mass of the leaf-chewing forest tent caterpillar *Malacosoma disstria* (Percy et al., 2002).

Coûteaux and Bolger (2000) reported that although elevated atmospheric CO_2 induces changes in several attributes of the soil fauna, no generalized pattern of response has yet been identified. These contradictory effects could be due to differences in soil fertility. On more fertile soils, the main below-ground effect is an increase in the production of organic matter, which has a stimulatory effect on soil microflora and thus indirectly on microbial feeders and saprophagous fauna. On the contrary, on less fertile soil, nutrient depletion and soil acidification overcome the positive effects of increasing plant productivity.

Ozone impairs stomatal function and decreases net photosynthesis and water use efficiency of plants (Reich et al., 1985). Several studies have shown that elevated [O_{3t}] had negative effects on tree growth (Karnosky et al., 1999; Dickson et al., 2001; Isebrands et al., 2001). Booker et al. (1996) and Lindroth et al. (2001) have also reported that elevated [O_{3t}] decreases foliage and litter quality (increase of secondary metabolites and phenols and decrease of *N* concentrations). This would be expected to decrease Acari abundance.

After 4 yr, the abundance of soil invertebrates are similar between ambient control and elevated [$CO_2 + O_{3t}$] plots. This indicates that the individual negative effects of elevated [CO_2] and elevated [O_{3t}] on soil fauna are somehow negated upon exposure to both gases. These responses may result from (1) the decrease of stomatal conductance by elevated [CO_2] which can decrease the influx of O_{3t} into leaves; and (2) the possible competition between O_{3t} and CO_2 molecules for plasma membrane receptors, which can decrease the influx of O_{3t} and CO_2 into leaves. The interaction of these air pollutants in the future may affect C cycling in terrestrial ecosystems in ways that are unpredictable based on studies of these gases individually.

Acknowledgements

Thanks are due to Professor Jean-François Ponge (National Museum of Natural History, France) for comments on an earlier draft of this manuscript. We thank Becky Ketterer, Kim Larsen, Dan Moore, Elisabeth Nauertz, and Matt Porter for their help in the field and in the laboratory. Dave Karnosky, Judd Isebrands, Jak Sober and Wendy Jones provided logistical support by maintaining the FACTS-II field site. Financial support for this study was provided by the US Department of Energy and US Forest Service Northern Global Change Program. Base funding for the FACTS-II experiment is provided by the US Department of Energy Office of Biological and Environmental Research.

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