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Response of soil biota to elevated atmospheric CO_2 in poplar model systems

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Abstract We tested the hypotheses that increased belowground allocation of carbon by hybrid poplar saplings grown under elevated atmospheric CO_2 would increase mass or turnover of soil biota in bulk but not in rhizosphere soil. Hybrid poplar saplings (*Populus* × *euramericana* cv. Eugenei) were grown for 5 months in open-bottom root boxes at the University of Michigan Biological Station in northern, lower Michigan. The experimental design was a randomized-block design with factorial combinations of high or low soil N and ambient (34 Pa) or elevated (69 Pa) CO_2 in five blocks. Rhizosphere microbial biomass carbon was 1.7 times greater in high-than in low-N soil, and did not respond to elevated CO_2. The density of protozoa did not respond to soil N but increased marginally ($P < 0.06$) under elevated CO_2. Only in high-N soil did arbuscular mycorrhizal fungi and microarthropods respond to CO_2. In high-N soil, arbuscular mycorrhizal root mass was twice as great, and extramatrical hyphae were 11% longer in elevated than in ambient CO_2 treatments. Microarthropod density and activity were determined in situ using minirhizotrons. Microarthropod density did not change in response to elevated CO_2, but in high-N soil, microarthropods were more strongly associated with fine roots under elevated than ambient treatments. Overall, in contrast to the hypotheses, the strongest response to elevated atmospheric CO_2 was in the rhizosphere where (1) unchanged microbial biomass and greater numbers of protozoa ($P < 0.06$) suggested faster bacterial turnover, (2) arbuscular mycorrhizal root length increased, and (3) the number of microarthropods observed on fine roots rose.

Key words Atmospheric CO_2 · Roots · Arbuscular mycorrhizas · Microbial biomass · Microarthropods

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Introduction

Rising atmospheric CO_2 is expected to increase disproportionally the flow of C to the belowground biota because most plants allocate relatively more carbon belowground than aboveground when grown under elevated atmospheric CO_2. In a survey of the responses of 161 plant species to elevated CO_2, Rogers et al. (1994) found that 87% increased root growth, and that of these, 59% responded with relatively more belowground than aboveground growth, as suggested by increased root-to-shoot ratios. Increased belowground C under elevated atmospheric CO_2 will be in the form of larger root systems and possibly increased rates of exudation (Rogers et al. 1994). Additional belowground C is important because C is a major limitation on the activities of belowground biota (Paul and Clark 1989).

An increase in belowground C will affect both the bacterial-based food chain of bacteria, protozoa, and nematodes, as well as the fungal-based food chain of fungi, collembola, and mites. Organisms in the bacterial-based food chain are concentrated in the rhizosphere where bacteria are supported by root exudates and dead tissue, in turn supporting protozoa, nematodes, and predatory mesostigmatid mites. In contrast, biota of the fungal-based food chain occur both in rhizosphere and bulk soil. Saprophytic fungal hyphae occur in rhizosphere and bulk soil. Arbuscular mycorrhizal (AM)

fungi produce runner hyphae and hyphal bridges in the rhizosphere and absorptive hyphal networks in bulk soil (Friese and Allen 1991). These fungi support fungivorous collembola and mites, and mesostigmatid mite predators (Curl 1988).

In past research on soil biota, when C input alone was experimentally increased through addition of straw (Schnürer et al. 1985) or glucose (Bääth et al. 1978), biomass C as well as numbers of bacteria, amoebae, and hyphae increased. The results of Bääth et al. (1978) further suggested that the response would be strongest in the soil with the highest N content. In the present experiment, elevated CO_2 resulted in larger coarse-root biomass and increased production and mortality of fine roots (Pregitzer et al. 1995). For this reason, we hypothesize that (1) the density of biota in the rhizosphere (microbial biomass C, protozoan density, and percentage of roots that are mycorrhizal) will be unchanged by elevated CO_2 although there will be more rhizosphere biota overall because root systems will be larger. We also hypothesize that (2) the density of biota in bulk soil (extramatrical hyphae, microarthropods) will increase because larger root systems will raise the C in bulk soil.

Materials and methods

The experiment was conducted at the University of Michigan Biological Station near Pellston, Mich. (45°34′ N, 84°40′ W). Root boxes were laid out in five rows of four boxes each. The four treatments (low soil N-ambient CO_2, low soil N-elevated CO_2, high soil N-ambient CO_2, high soil N-elevated CO_2) were replicated in the five rows that constituted blocks in our randomized-block design.

Five cuttings of a single genotype of the hybrid poplar *Populus* × *euramericana* cv. Eugenei were planted on 21 May 1992 in 20 open-bottom root boxes (0.5 m^2 × 1.3 m deep) lined with plastic. Cuttings were obtained from stock propagated at Michigan State University. The mean dry weight of the cuttings was 5.2 g. Cuttings were planted in either high-N soil (100% Kalkaska series topsoil), or low-N soil (homogenized 80% Rubicon sand and 20% Kalkaska series topsoil). In the high- and low-N soils, total nitrogen was 15.1 and 4.55 g kg^{-1}, acid-extractable P was 65 and 110 mg kg^{-1}, and percent organic matter was 2.7 and 1.0, respectively. Since plants were well watered and P was not limiting, the major difference between soils was N content.

Open-top chambers made of polyethylene film supported by PVC tubes were placed over the root boxes, and CO_2 was delivered and monitored with the system described by Curtis and Teeri (1992) and Curtis et al. 1995. Analysis of hourly atmospheric samples recorded during the experiment showed that mean seasonal daytime CO_2 partial pressures were 69.3 (±4.5) Pa inside elevated chambers, and 34.5 (±1.5) Pa inside ambient chambers. Water stress was avoided by adding 3 l water to each box every third day. The 1992 summer was cool in northern lower Michigan: temperatures averaged 1.5° lower than 30-year averages during the growing season.

Mycorrhizal inoculum and invertebrate populations were primarily from the high-N soil. At the start of the experiment, there were 1 and 5.1 AM spores per gram of soil in low- and high-fertility soil, respectively, as determined by sugar flotation (Brundrett 1995). Root length and invertebrate numbers were recorded with video cameras inserted in minirhizotron tubes (20.2 cm^2 × 2 m long) in each root box. Two tubes in each box extended from the top of one side to the bottom of the other side of the root box at a 30° angle. Images of 130, 1.17-cm^2 frames on the side of the 40 minirhizotron tubes were made biweekly. Because it was possible to see about 2.5 mm into the soil, the volume of soil censused for invertebrates in each frame was considered to equal 0.29 cm^3. Invertebrate density was calculated by dividing the number of invertebrates observed by the product of the frame volume × 130 × number of minirhizotron tubes sampled.

Plants were harvested on 16 October 1992. Bulk and rhizosphere soil samples from each root box were collected, mixed by root box and stored at 5°C. Root boxes were disassembled and large roots were excavated. Fine roots were collected by passing all of the soil from each root box through a 3-mm sieve.

Microbial biomass C data was supplied by Donald R. Zak and was measured using methods described in Zak et al. (1993). Total protozoan density (active and encysted) was determined with a most-probable-number protocol (Ingham 1994). Five grams of soil was diluted serially (1:10) in root/soil extract media (2% dried aspen roots ground to pass a no. 40 mesh plus 5% soil extract, strained and autoclaved). One milliliter portions of the dilutions were plated in 24-well culture plates (6.0 ml, Corning). The solution in each well was augmented with 1 ml of nutrient broth (Bacto) containing a 24-h-old culture of *Pseudomonas fluorescens*. Dilutions were sampled after 5 days at room temperature, and presence or absence of protozoa was determined with phase-contrast microscopy. Most probable numbers were calculated with the computer program written by Clark and Owens (1983).

A random subsample of 0.5 g of roots <1 mm in diameter was prepared for counts of AM fungi. Roots were placed in a tissue cassette, cleared by autoclaving in 10% KOH for 15 min, bleached in alkaline 3% H_2O_2 for 10 min, acidified in 1% HCl, and autoclaved in a trypan blue-lactic acid-glycerol solution. Total lengths of root and colonized root were determined for each subsample with the gridline-intersect method (Giovannetti and Mosse 1980). Lengths of extramatrical AM hyphae in bulk soil were determined with the membrane-filter method of Miller and Jastrow (1992). Hyphal widths and the lengths and widths of vesicles were measured with phase contrast microscopy. Biomass carbon in extramatrical hyphae from soil was estimated using the formula: hyphal biomass carbon = $\pi \times r^2 \times$ length × density × moisture, using average values of r for each slide, buoyant density = 1.03 g cm^{-3} and dry matter content = 0.21 (Bakken and Olsen 1983). Fungal mass in roots was not estimated, but length and width of vesicles was measured and their volume calculated with the formula for an ellipsoid of revolution = $4/3\pi$ length × $width^2$.

Analysis of variance tests were performed using the general linear models procedure (SAS 1989). Mixed-model analyses were used for percent mycorrhizal infection, extramatrical hyphae, protozoa, and microbial biomass where root boxes were the units of analysis. In the ANOVA, soil and CO_2 were fixed, and blocks were random effects; main effects were tested against the effect × block interaction. Invertebrate numbers were analyzed using repeated-measures ANOVAs with time as the within-subject factor, and soil, CO_2 and blocks as between-subject factors. The arcsin transformation was used for percent mycorrhizal infection, the log + 1 transformation for mycorrhizal root length and protozoa, and the square root transformation for soil hyphae and microarthropods. The Mann-Whitney U-test (Siegel 1956) was used to test differences in mycorrhizal root length, and confidence intervals for proportions (Agresti 1996, p. 11) were used to test differences in proportions of microarthropods on fine roots.

Results

Microbial biomass carbon in the rhizosphere was greater in high-N soil, but was not affected by CO_2 treatment (Table 1). The protozoa were almost entirely amoebae and flagellates; there were few ciliates. Protozoa numbers were double in high- compared with low-N soil and 2.5 times greater in elevated compared with ambient CO_2 ($P < 0.06$, $F_{1,12} = 4.02$, Table 1). There was no interaction between soil N and CO_2 for protozoa. Numbers of

Table 1 Response of soil consumers to 158 days of exposure to ambient or elevated CO_2 at low or high soil N. Means (SD) in the same row followed by different letters are significantly different by ANOVA (a, b: $P \leq 0.10$; c, d: $P \leq 0.05$; e, f: $P < 0.001$), the Mann-Whitney U-test (g, h: $P \leq 0.028$), or confidence limits for proportions (i, j: $P < 0.05$) . In no case did soil N and CO_2 interact

	Observations per cell	Low soil N		High soil N	
		Ambient CO_2	Elevated CO_2	Ambient CO_2	Elevated CO_2
Rhizosphere microbial biomass C, (mg C g^{-1} soil)	20	1,281 (659)^{c}	1088 (212)^{c}	3,879 (4937)^{d}	2542 (421)^{d}
Rhizosphere protozoa (individuals g^{-1} soil)	20	12,104 (6,031)^{a}	78,450 (49,118)^{b}	57,075 (97,483)^{a}	143,088 (104,193)^{b}
Mycorrhizal root mass (g g^{-1} root)	60	0.27 (0.19)^{a}	0.19 (0.10)^{a}	0.32 (0.26)^{g}	0.67 (0.36)^{h}
Extramatrical hyphae (cm g^{-1} soil)	60	2.56 (1.88)^{e}	2.92 (1.75)^{e}	6.18 (2.74)^{f}	6.90 (3.32)^{f}
Extramatrical hyphae (μg g^{-1} soil)	60	8.66 (6.35)^{e}	9.87 (5.83)^{e}	20.89 (9.30)^{f}	23.30 (11.22)^{f}
Microarthropods (individuals cm^{-3} soil)	20	0.13 (0.15)^{c}	0.18 (0.18)^{c}	0.42 (0.42)^{d}	0.32 (0.29)^{d}
Microarthropods, proportion on roots	22–66	0.17 (0.07)^{i}	0.07 (0.04)^{i}	0.10 (0.03)^{i}	0.23 (0.05)^{j}

amoebae and flagellates were positively correlated with microbial biomass ($r = 0.452$, $P < 0.0001$) on a root box basis.

All of the fungi observed in roots were AM. An average of 2.5% of roots were mycorrhizal at final harvest, and percent infection showed no response to soil N or CO_2. But since the root systems were longer in high N-elevated CO_2 than in low N-ambient CO_2, the total length of mycorrhizal roots was also longer. In high-N soil, AM root length was twice as long under elevated as under ambient CO_2 ($P < 0.028$, Mann-Whitney U test). In low-N soil there was no change in mycorrhizal root length under elevated CO_2. Neither the density of vesicles in the root cortex nor their volume were changed by soil N or CO_2 treatments (data not shown).

Extramatrical hyphae in bulk soil responded to soil N and CO_2 in a similar pattern to that observed for mycorrhizal. The length of extramatrical hyphae was 2.3 times greater in high- compared with low-N soil ($F_{1,4}$, $P < 0.001$s), and 12% greater in soil under elevated as under ambient CO_2 ($P < 0.08$, Mann-Witney U-test, Table 1). Hyphal diameters were measured in order to convert lengths to mass. Treatments did not affect hyphal diameters which averaged 4.4 μm. In terms of mass, in the low N-ambient CO_2 treatment, there was an average of 8.6 μg g^{-1} of extramatrical hyphae in bulk soil, with an additional 12.8 μg g^{-1} in high-N soil and 1.8 μg g^{-1} more in elevated CO_2. Fungal mass in roots was not estimated.

Invertebrates observed in minirhizotrons included collembola (*Folsomia* sp., *Neilus* sp., *Onychiurus* sp.), prostigmatid mites (*Tydeus* sp.), protura (*Eosentomon* sp.), pauropods, and juvenile earthworms. Populations of these species probably originated from eggs and some adults which survived soil excavation, transport, mixing, and placement in root boxes. Microarthropod numbers did not respond over the 5 months to either soil N or CO_2. The initial threefold higher density in high- compared with low-N soil was maintained throughout the experiment (repeated-measures ANOVA, $F_{1,16} = 10.56$, $P < 0.01$). The depth distribution of microarthropods did not change as a result of soil N or CO_2, but two other responses suggested a response to food. First, microarthropod density was weakly correlated with density of extramatrical hyphae ($r = 0.41$, $P < 0.06$) and fine-root biomass ($r = 0.29$, $P < 0.06$) on a root box basis. Second, in high-N soil, microarthropods were more often observed on roots in elevated than in ambient treatments. When microarthropods were observed in minirhizotron frames, we recorded whether roots were in the same frames and, if so whether microarthropods were on roots. In high-N soil, when roots were present in a minirhizotron frame, twice as many microarthropods were on the roots in elevated compared with ambient CO_2 treatments (Table 1).

Earthworms observed in minirhizotrons were juveniles. Earthworm density was not affected by soil N or CO_2, and declined throughout the 5-month experiment in all treatments (repeated-measures ANOVA, $F_{1,3} = 4.50$, $P < 0.005$). Earthworm depth distribution in the soil did not respond to CO_2, and the association of earthworms with roots in minirhizotron frames was not changed by soil N or CO_2 treatments.

Discussion

Elevated CO_2 determined the response of the bacterial-based food chain independently of soil N, but in the case of the fungal-based food chain, soil N determined the response to elevated CO_2. We will discuss the effect of soil N on the response of the soil organisms to additional C inputs separately for each food chain.

The CO_2 response of the rhizosphere microbial biomass C and protozoa suggested a response of prey and predator to increased carbon flow. We interpret constant microbial biomass C and higher protozoan density as reflecting increased bacterial turnover in response to higher rates of grazing by a larger protozoan population under elevated CO_2. Similar to the present experiment, microbial biomass carbon or bacterial plate count colonies showed no change under twice ambient versus ambient CO_2 in six studies (O'Neill et al. 1987; Runion et al. 1994; Newton et al. 1995; Schenk et al. 1995; Klironomos et al. 1996; Niklaus and Körner 1996). Microbial biomass increased in association with elevated CO_2 in three other experiments (Diaz et al. 1993; Zak

et al. 1993; Rice et al. 1994), but protozoa were not counted.

The proportion of AM roots was not affected by soil N or elevated CO_2 for yellow poplar (O'Neill et al. 1987), cotton (Runion et al. 1994), white clover (Jongen et al. 1996), and C_3 grasses (Monz et al. 1994), but increased in response to both soil N and elevated CO_2 in *Artemisia tridentata* (Klironomos et al. 1996). However, as O'Neill et al. (1987) pointed out, since root system mass increased, mycorrhizal mass increased proportionally. For this reason, an increase in extramatrical hyphae was expected, and a statistically insignificant trend of increased extramatrical hyphae in the high N-elevated CO_2 treatment was observed. The mass of extramatrical hyphae was 15.9% of the fine-root mass reported for the present experiment by Pregitzer et al. (1995), and was larger relative to fine-root mass in ambient than in elevated CO_2 treatments. AM spore density was quite low in soils used in the present experiment. In nature, spore density would be higher, a greater proportion of roots would be mycorrhizal, and extramatrical hyphae might be a larger proportion of fine-root mass.

The invertebrate response to elevated CO_2 was determined by soil N. The density response of microarthropods matched that of fine-root mortality in the present experiment (Pregitzer et al. 1995): both were highest in high-N soil regardless of CO_2 treatment. The positive (though marginal) correlation between microarthropod density and both fine-root biomass and extramatrical hyphal length was stronger than that reported in a minirhizotron study of collembola and soybean roots (Snider et al. 1990).

Microarthropod density increased in response to elevated CO_2 only in high-N soil in a study using *A. tridentata* (Klironomos et al. 1996). Similarly, it was also in the high N soil-elevated CO_2 treatment that microarthropods were more frequently present on fine roots. Since this was the treatment with by far the greatest fine-root turnover (Pregitzer et al. 1995), the collembola may have been attracted to fine roots because a larger proportion of them were decaying than in other treatments. Earthworm density declined during the experiment, possibly because of insufficient surface litter and soil organic matter. Similarly, earthworm populations in soil monoliths collected from pastures, and subjected to ambient or twice-ambient CO_2 for 149 days showed no density change (Yeates and Orchard 1993). Larger species of soil fauna may require more time and more natural conditions to respond to elevated CO_2.

In summary, the bacterial-based food chain responded directly to elevated CO_2 by increased microbial turnover and protozoan grazing, not supporting the first hypothesis. The fungal-based chain responded to elevated CO_2 only in high-N soil. In high-N soil, the hypothesis that density of rhizosphere biota would be unchanged was not supported: AM root length and microarthropod association with fine roots both increased. The second hypothesis, that bulk soil biota density would increase, was also unsupported. In high-N soil, biota in bulk soil did not increase, although extramatrical hyphae showed a strong increasing trend. The implication of the present experiment is that increased belowground C flux will raise fine-root mortality (Pregitzer et al. 1995), and that this in turn will increase processing rates by microbes and invertebrates. The microarthropod response suggests that high C/N ratios will not slow processing rates, supporting the work of Coûteaux et al. (1991). Thus, compensatory responses of soil food chains to increased belowground carbon flux observed in the present study suggest that the additional carbon fixed by plants growing under elevated atmospheric CO_2 will be metabolized by organisms in the bacterial-based and fungal-based food chains.

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