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Impacts of elevated CO_2 and O_3 on aspen leaf litter chemistry and earthworm and springtail productivity

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ABSTRACT

Human alteration of atmospheric composition affects foliar chemistry and has possible implications for the structure and functioning of detrital communities. In this study, we explored the impacts of elevated carbon dioxide and ozone on aspen (*Populus tremuloides*) leaf litter chemistry, earthworm (*Lumbricus terrestris*) individual consumption and growth, and springtail (*Sinella curviseta*) population growth. We found that elevated carbon dioxide reduced nitrogen and increased condensed-tannin concentrations in leaf litter. These changes were associated with decreases in earthworm individual growth, earthworm growth efficiency, and springtail population growth. Elevated ozone increased fiber and lignin concentrations of leaf litter. These changes were not associated with earthworm consumption or growth, but were associated with increased springtail population growth. Our results suggest that changes in litter chemistry caused by increased carbon dioxide concentrations will have negative impacts on the productivity of diverse detritivore taxa, whereas those caused by increased ozone concentrations will have variable, taxon-specific effects.

1. Introduction

Tropospheric concentrations of carbon dioxide and ozone are increasing at rates unparalleled in human history (Marenco et al., 1994; Vingarzan, 2004; IPCC, 2007). These increases are expected to alter the chemical characteristics of tree foliage and leaf litter (Norby et al., 2001; Valkama et al., 2007; Bidart-Bouzat and Imeh-Nathaniel, 2008; Lindroth, 2010). Changes in leaf litter chemistry will likely lead to changes in soil carbon and nutrient dynamics, as litter chemistry reflects resource quality for organisms that are responsible for decomposition (Cotrufo et al., 1995; Hättenschwiler et al., 1999; Parsons et al., 2004, 2008; Lindroth, 2010).

Soil invertebrates play important roles in litter decomposition. Although the fraction of litter carbon respired by soil invertebrates is fairly small, invertebrate exclusion studies have shown that litter processing by soil animals causes disproportionately large increases in decomposition rates, especially in temperate and tropical regions (Seastedt, 1984; Wall et al., 2008; Powers et al., 2009). Earthworms and springtails are major components of the detritivore community in many ecosystems. In temperate hardwood forests, earthworm biomass can reach 1 Mg ha^{-1}, and springtails often reach densities of 100,000 individuals m^{-2} (Coleman et al., 2004). Furthermore, both taxa are known to have important impacts on soil processes (Lavelle et al., 1998; Filser, 2002). These impacts are clearly demonstrated in forests of the Great Lakes region, where introduction of earthworms, in particular, has resulted in the complete elimination of the litter layer, development of topsoil, and marked changes in soil carbon, nitrogen, and phosphorus dynamics (Alban and Berry, 1994; Bohlen et al., 2004; Hale et al., 2005; Madritch and Lindroth, 2009). Invertebrate-mediated changes in soil processes, in turn, have had cascading effects on plant establishment and community structure (Hale et al., 2006, 2008).

Despite the importance of soil invertebrates for decomposition and nutrient cycling, relatively few studies have considered how CO_2- and O_3-induced changes in litter quality will affect their activities. In short-term feeding trials, Cotrufo et al. (1998) found that isopods (*Oniscus asellus*) avoided consuming litter from trees grown under high CO_2. They suggested that this result was due to a decrease in nitrogen and an increase in lignin concentrations in high-CO_2 leaves. In long-term feeding trials, Hättenschwiler et al. (1999) found that isopods (*O. asellus and Porcellio scaber*) increased their consumption rates of litter from trees grown under high CO_2. These authors suggested that consumption was increased

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over the long-term to compensate for low nitrogen concentrations in high-CO_2 leaves. Kasurinen et al. (2007) reported a limited and variable influence of atmospheric chemistry and leaf litter quality on isopod (*P. scaber*) consumption and growth. However, these authors also found that earthworm (*Lumbricus terrestris*) growth rates were reduced when worms were fed leaves from trees grown under increased CO_2 or O_3. Reduced growth rates were attributed to the relatively high concentrations of condensed tannins and lignin, and low concentrations of nitrogen, in leaf litter. Altogether, previous studies suggest that increases in atmospheric CO_2 and O_3 reduce food quality for soil invertebrates by increasing concentrations of structural-carbon and phenolic compounds and decreasing concentrations of nitrogen. Reductions in resource quality presumably cause a decrease in individual growth, with possible implications for detritivore community structure and function.

In this study, we collected leaf litter from the Aspen Free Air CO_2 Enrichment (Aspen FACE) facility and conducted a laboratory microcosm experiment to determine how atmosphere-induced changes in litter quality affect the individual growth of earthworms (*L. terrestris*) and the population growth of springtails (*Sinella curviseta*). We predicted, based on previous studies using litter from greenhouses (Cotrufo et al., 1998) and open-top chambers (Hättenschwiler et al., 1999; Kasurinen et al., 2007), that 10 years of exposure to increased CO_2 and O_3 at the Aspen FACE facility would lead to leaf litter of lower quality, and that reduced leaf litter quality would have direct (via leaf quality) and indirect (via litter microbes) negative effects on earthworm growth and springtail populations.

2. Methods

2.1. Leaf litter collection

Our study was conducted using leaf litter from the Aspen FACE facility, which is located near Rhinelander, WI, USA (N 45.678, W −89.628). The facility is comprised of 12, 30-m diameter, open-air, circular plots (rings). In these rings, two factors, CO_2 concentration and O_3 concentration, are maintained at one of two levels: current ambient concentrations and elevated concentrations forecasted for the middle of this century. The 12 rings are divided into 3 rings per 4 treatment combinations: aCO_2/aO_3 rings have ambient concentrations of CO_2 and O_3 (monthly averages for daytime concentrations ranged from 365 to 406 ppm for CO_2 and 32–48 ppb for O_3 during the 2007 growing season); eCO_2/aO_3 rings have elevated CO_2 (454–556 ppm) and ambient O_3 concentrations; aCO_2/eO_3 rings have ambient CO_2 and elevated O_3 concentrations (37–57 ppb); and eCO_2/eO_3 rings have elevated concentrations of both CO_2 and O_3.

Each ring is partitioned into three community types, including interplanted aspen genotypes (*Populus tremuloides*), aspen and birch (*Betula papyrifera*), and aspen and maple (*Acer saccharum*). Trees were planted at the site in 1997; atmospheric treatments were begun in 1998 and have continued to present. For our study, four litter samples were collected during the last two weeks of September 2007 from the mixed aspen genotype portion of each ring, using laundry baskets placed on the forest floor. Baskets had an opening of 57 × 41 cm and had holes drilled into the bottom to provide drainage of precipitation. Collected leaf litter, representing a mix of five genotypes, was air-dried in the lab and stored for approximately 1 month under ambient conditions until chemical analyses and microcosm studies were begun.

2.2. Litter chemical analyses

A portion of the leaf litter from each basket was freeze-dried, ground, and assayed for total carbon, total nitrogen, condensed tannin, acid-detergent fiber, and lignin concentration (% dry mass). Carbon and nitrogen analysis was performed with a Thermo Finnigan Flash 1112 elemental analyzer (Thermo Finnigan, San Jose, CA, USA). Condensed tannins were extracted with 70% acetone and assayed by the acid-butanol method of Porter et al. (1986) using purified aspen standards. Acid-detergent fiber and lignin were estimated gravimetrically using an Ankom 2000 fiber analyzer (Ankom Technology, Macedon, NY, USA).

2.3. Earthworm consumption and growth

Young earthworms were obtained from a fishing supply company (Knutson's Recreational Sales, Brooklyn, MI, USA). Upon arrival to our laboratory, individuals were placed in petri dishes with moist paper towels and fasted for 24 h to eliminate residual digestive material before determining initial live masses.

Forty-eight earthworm microcosms (corresponding with 12 FACE rings × 4 litter basket subsamples) were prepared by placing 800 mL of silt loam topsoil in 1 L plastic containers. Soil was collected from the Eagle Heights Community Garden in Madison, WI, USA during November 2007, passed through a 2 mm sieve, and then defaunated by three rounds of rapid freezing and thawing.

Each of the microcosms received 2 g of leaf litter, cut into 1-cm^2 pieces, from a single litter-collection basket. We then added one fasted and weighed earthworm to each microcosm, moistened litter with a spray of distilled water, covered microcosms with a perforated plastic lid, and placed them into a growth chamber (Percival Scientific, Perry, IA, USA) set to a 12:12 h day (20 °C) to night (15 °C) cycle. Volumetric water content of microcosm soil was monitored with a soil moisture meter (HydroSense Soil Water Measurement System, Campbell Scientific, Logan, UT, USA) and kept at 20% throughout the duration of the experiment.

After six weeks in the growth chamber, earthworms and unconsumed leaf litter fragments were extracted from microcosms using soil sieves. Worms were again fasted for 24 h and reweighed to attain a final live mass. Litter fragments were air-dried and weighed to give a rough estimate of the amount of litter consumed during the 6-week period.

2.4. Springtail population growth

A population of *S. curviseta* was obtained from a laboratory culture established by D. A. Crossley, Jr., University of Georgia. Springtails were propagated in 1 L plastic containers on a moist 2:1 plaster/charcoal substrate and fed baker's yeast for one month until the beginning of the experiment.

Forty-eight springtail microcosms were prepared as described above for earthworms. Each of these microcosms received 800 mL of silt loam topsoil and 2 g of leaf litter, cut into 1-cm^2 pieces, from a single litter-collection basket. We then transferred 10 adult springtails to each microcosm and moistened the litter with a spray of distilled water. Microcosms were then covered with a perforated plastic lid and placed into a growth chamber set to the same light and temperature parameters as described above. Volumetric water content of soil was kept at 20% throughout the duration of the experiment.

After 10 weeks in the growth chamber, springtails were extracted from microcosms using a modified salt-floatation method (Edwards and Fletcher, 1971). First, microcosms were placed in a freezer at −20 °C for 1 h to immobilize springtails. Then the top 6 cm of litter and soil from each microcosm was transferred to another 1 L container and soaked in 700 mL of saturated NaCl solution to separate springtails and litter from soil. The salt solution, along with floating material, was decanted through stacked 1500 μm and 75 μm sieves. The 1500 μm sieve was rinsed with tap water to dislodge any remaining springtails from organic material.