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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.

Springtails that accumulated in the 75 μm sieve were rinsed and stored in ethanol, and then counted with a dissecting microscope to determine population growth over the 10-week period.

### 2.5. Statistical analyses

We used two-factor ANOVAs to determine the effects of $CO_2$, $O_3$, and their interaction on leaf litter chemistry and invertebrate consumption and production. Dependent variables included in the analyses were total carbon, total nitrogen, condensed tannin, acid-detergent fiber, lignin, carbon-to-nitrogen (C:N) ratio, lignin-to-nitrogen (L:N) ratio, individual earthworm consumption (g dry mass/6 wk), individual earthworm growth (Δ g dry mass/6 wk), earthworm growth efficiency (g biomass/g litter consumed), and springtail population growth (new individuals accrued/10 wk). We did not standardize earthworm consumption and growth rates for initial worm size because average initial masses did not differ significantly across treatments. Air-dried litter mass was multiplied by a conversion factor of 0.89 (derived by oven-drying a set of air-dried litter samples) to attain litter dry mass. Worm live mass was multiplied by 0.18 to attain worm dry mass (Satchell, 1971).

We used general linear modeling to determine how litter-chemistry variables were related to detritivore production. This process involved regressing all possible combinations of litter quality variables against earthworm consumption, earthworm individual growth, earthworm growth efficiency, and springtail population growth, individually (127 combinations per dependent variable). For each dependent variable, best models were determined as those with $\Delta AIC_c \leq 2$ (Burnham and Anderson, 1998). Results from these extensive analyses indicated that detritivore production was best explained by univariate litter-chemistry models. Thus, for simplicity, we illustrate relationships between litter chemistry and detritivore production variables in a correlation matrix.

For all analyses, the results of multiple subsamples per FACE ring were averaged prior to analysis, and ring was the unit of replication ($N = 12$ rings, 3 per $CO_2$ by $O_3$ treatment combination). Ring was used as the unit of replication in our analyses because it is the unit upon which the atmospheric treatments were administered, and to use subsample or experimental animal as the replicate for analyses would constitute pseudoreplication with respect to atmospheric treatments. Given the low replication at the Aspen FACE experiment, we follow the suggestion by Filion et al. (2000), that *P*-values should be considered significant at $P < 0.10$. All analyses were conducted using JMP, Version 7 software (SAS Institute Inc., Cary, NC, USA).

## 3. Results

Altered $CO_2$ and $O_3$ concentrations had a variety of effects on aspen leaf litter chemistry. The main effect of elevated $CO_2$ (averaged across $O_3$ treatments) was a minor reduction in total carbon concentrations, a 10% reduction in total nitrogen concentrations, a doubling of condensed-tannin concentrations, and a 10% increase in C:N ratios (Table 1). The main effect of elevated $O_3$ (averaged across $CO_2$ treatments) was a negligible reduction in total carbon concentrations, a 7% increase in fiber concentrations, a 15% increase in lignin concentrations, and a 17% increase in L:N ratios (Table 1). Interactions between $CO_2$ and $O_3$ were not common or pronounced, but were detectable for litter nitrogen concentrations and C:N ratios. In both cases, the effects of elevated $CO_2$ (i.e., reducing N concentration and increasing C:N ratio) were marginally stronger under ambient $O_3$ than elevated $O_3$ (Table 1).

Earthworm consumption was not influenced by $CO_2$ or $O_3$ treatments at the Aspen FACE site (Fig. 1a). Earthworm growth rates decreased by 38% when animals were fed litter from $CO_2$-enriched rings (Fig. 1b), but were unaffected by $O_3$ concentration and the interaction between $CO_2$ and $O_3$ (Fig. 1b). Because growth was related to $CO_2$ concentrations while consumption was not, earthworm growth efficiency decreased by 61% when worms were fed litter from rings with elevated $CO_2$ (Fig. 1c). As with growth, earthworm growth efficiency was not related to $O_3$ concentration or the interaction between $CO_2$ and $O_3$ (Fig. 1c).

Elevated $CO_2$ and $O_3$ concentrations had opposite effects on springtail population growth. Population growth rate decreased by 31% when springtails were provided with litter from rings with elevated $CO_2$ (Fig. 2). In contrast, population growth increased by 56% when springtails were fed litter from elevated $O_3$ plots (Fig. 2). The opposing effects of elevated $CO_2$ and $O_3$ on springtail population growth roughly offset one another, and population growth was similar in the $aCO_2/aO_3$ and $eCO_2/eO_3$ treatments (Fig. 2).

There were few statistically significant relationships between aspen leaf litter chemistry and detritivore production variables (Table 2). However, a few general patterns in the data warrant mention. Earthworm growth, earthworm growth efficiency, and springtail population growth tended to be positively related to nitrogen concentrations and negatively related to condensed-tannin concentrations and C:N ratios of leaf litter. Earthworm growth and growth efficiency were also positively related with litter carbon concentrations, whereas springtail population growth was positively related to litter fiber and lignin concentrations.

## 4. Discussion

### 4.1. Leaf litter chemistry

Multiple chemical characteristics of aspen leaf litter were altered via changes in atmospheric composition at the Aspen FACE site (Table 1). First, litter nitrogen concentrations were considerably lower in rings with elevated $CO_2$, which agrees with results from several previous studies (Hättenschwiler et al., 1999; Norby et al., 2001; Parsons et al., 2004, 2008; Liu et al., 2005; Kasurinen et al., 2006; Liu et al., 2007). Second, litter condensed-tannin concentrations and C:N ratios were considerably higher in rings with elevated $CO_2$, which is also consistent with previous studies (Norby et al., 1986; Parsons et al., 2004, 2008; Kasurinen et al., 2007). Third, structural-carbon compounds, such as fiber and lignin, were notably higher in litter from rings with elevated $O_3$. This result agrees with those from other research sites (Norby et al., 2001), although it has not been observed previously at the Aspen FACE site (Parsons et al., 2004, 2008). The changes that we observed in litter chemistry were largely as expected, and we predicted that these changes would have implications for detritivore consumption and production.

### 4.2. Earthworm consumption and growth

Elevated $CO_2$ and $O_3$ concentrations did not influence litter consumption by earthworms, which consumed an average of 64% of the food provided (Fig. 1a). The fact that consumption rates did not vary across treatments indicates that the earthworms did not employ compensatory feeding to cope with food of low nutritional quality. We recognize that our measurements of consumption were only approximate, and are probably overestimates; some leaf litter fragments may have been small enough to pass through our sieves, and some of the litter mass loss was likely due to microbial respiration. Nonetheless, earthworm growth efficiencies calculated in this study were comparable to those of previous studies (e.g., Whalen and Parmelee, 2000).

**Table 1**
Summary statistics (mean ± 1 SD, $N = 3$) and ANOVA $P$-values for litter chemistry responses to Aspen FACE treatments. Superscripts denote statistically different means within a column where there is a significant interaction term.

| | Carbon (C) (% dry mass) | Nitrogen (N) (% dry mass) | Condensed tannin (% dry mass) | Fiber (% dry mass) | Lignin (L) (% dry mass) | C:N | L:N |
|---|---|---|---|---|---|---|---|
| FACE treatment combination | | | | | | | |
| Ambient $CO_2$/ambient $O_3$ | 49.3 ± 0.5 | 1.24 ± 0.02$^{a}$ | 0.6 ± 0.2 | 52.1 ± 2.5 | 29.4 ± 2.2 | 39.8 ± 0.4$^{a}$ | 23.7 ± 2.0 |
| Elevated $CO_2$/ambient $O_3$ | 48.7 ± 0.7 | 1.06 ± 0.09$^{b}$ | 1.7 ± 0.6 | 49.6 ± 3.5 | 28.0 ± 4.0 | 46.2 ± 3.3$^{b}$ | 26.4 ± 4.3 |
| Ambient $CO_2$/elevated $O_3$ | 48.9 ± 0.3 | 1.15 ± 0.02$^{ab}$ | 0.7 ± 0.3 | 54.2 ± 2.2 | 32.7 ± 1.5 | 42.6 ± 0.4$^{ab}$ | 28.3 ± 0.8 |
| Elevated $CO_2$/elevated $O_3$ | 48.0 + 0.2 | 1.09 ± 0.05$^{b}$ | 0.9 ± 0.5 | 54.6 ± 1.3 | 33.1 ± 1.3 | 44.3 ± 2.0$^{b}$ | 30.5 ± 2.3 |
| Two-way ANOVA source | | | | | | | |
| $CO_2$ | 0.028 | 0.004 | 0.040 | 0.470 | 0.740 | 0.007 | 0.153 |
| $O_3$ | 0.089 | 0.322 | 0.226 | 0.039 | 0.019 | 0.696 | 0.023 |
| $CO_2 \times O_3$ | 0.695 | 0.097 | 0.140 | 0.353 | 0.554 | 0.064 | 0.843 |

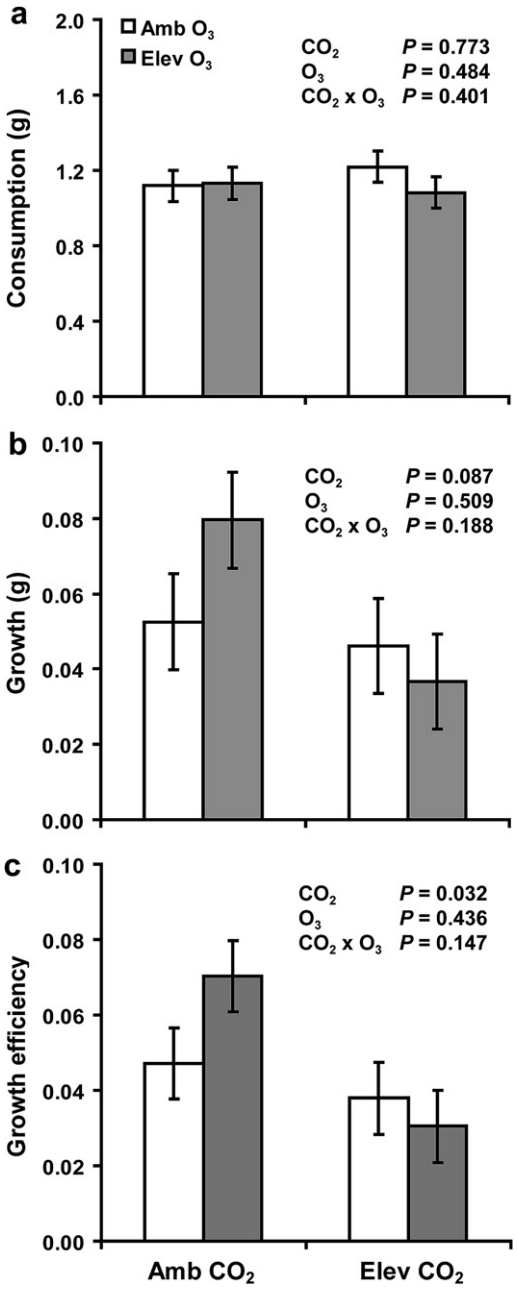


**Fig. 1.** Effects of elevated $CO_2$ and $O_3$ on (a) individual earthworm consumption (g dry mass/6 wk), (b) individual earthworm growth (g dry mass/6 wk), and (c) earthworm growth efficiency (g growth/g consumed). Error bars represent ± 1 SE.

Although consumption did not vary across atmospheric treatments, earthworms fed high-$CO_2$ litter exhibited markedly reduced growth (Fig. 1b). This growth reduction corresponded with low nitrogen concentrations in high-$CO_2$ litter (Table 1). When we related earthworm growth directly to litter nitrogen, we found a reasonably strong positive correlation ($r = 0.41$, Table 2). The relationship was not statistically significant; however, a power analysis revealed that a significant correlation would have been detected if our total sample size had been 18 rather than 12 replicates. Regardless, the overall patterns in our data are consistent with the suggestion by Kasurinen et al. (2007), that low mass gain by earthworms fed high-$CO_2$ litter is partly due to decreased litter nitrogen content. The patterns also agree with those from other studies that show positive correlations between the nitrogen content of food and earthworm mass gain (e.g., Shipitalo et al., 1988).

The reduced earthworm growth rates observed in this study also corresponded with high condensed-tannin concentrations in high-$CO_2$ litter (Table 1). When we related earthworm growth directly to litter condensed tannins, we found a reasonably strong negative correlation ($r = -0.44$, Table 2). Again, the relationship was not statistically significant, although power analysis indicated that a significant relationship would have been detected if our samples size had been 15 rather than 12 replicates. Mechanisms by which dietary tannins can reduce growth include feeding deterrence (not observed in this study), chemical binding of dietary proteins or digestive enzymes, increases in costly excretory processes, formation of gut lesions, and inhibition of gut microbial activity (discussed in Simpson and Raubenheimer, 2001). A full exploration of

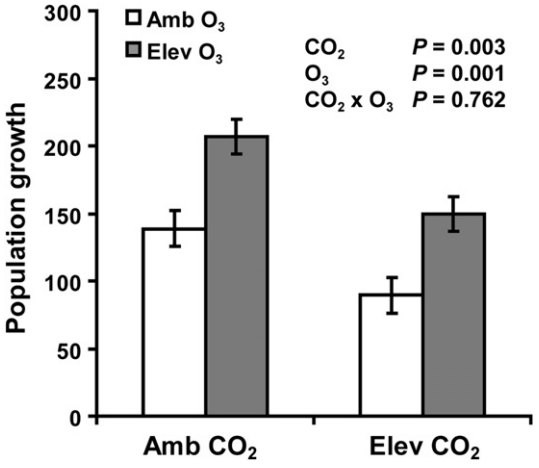


**Fig. 2.** Effects of elevated $CO_2$ and $O_3$ on the growth of springtail populations (Δ abundance/10 wk). Error bars represent ± 1 SE.

**Table 2**
Correlations between litter chemistry and invertebrate consumption and production variables. $^{*}P < 0.10$, $^{**}P < 0.05$, $^{***}P < 0.01$.

| | Carbon | Nitrogen | Condensed tannin | Fiber | Lignin | C:N | L:N |
|---|---|---|---|---|---|---|---|
| Nitrogen | 0.74*** | | | | | | |
| Condensed tannin | −0.05 | −0.61** | | | | | |
| Fiber | 0.02 | 0.13 | −0.17 | | | | |
| Lignin | −0.07 | −0.02 | −0.04 | 0.96*** | | | |
| C:N | −0.62** | −0.98*** | 0.68** | −0.19 | −0.03 | | |
| L:N | −0.46 | −0.59** | 0.35 | 0.70** | 0.82*** | 0.54* | |
| Earthworm consumption | 0.18 | 0.15 | −0.10 | −0.39 | −0.38 | −0.11 | −0.43 |
| Earthworm growth | 0.42 | 0.41 | −0.44 | 0.16 | 0.14 | −0.37 | −0.16 |
| Earthworm growth efficiency | 0.54* | 0.45 | −0.36 | −0.01 | −0.08 | −0.40 | −0.35 |
| Springtail population growth | 0.00 | 0.22 | −0.54* | 0.38 | 0.40 | −0.26 | 0.18 |

these mechanisms was beyond the scope of this study, and could be the topic of future research.

### 4.3. Springtail population growth

As with earthworm individual growth, springtail population growth was considerably lower when populations were given litter from rings with elevated $CO_2$ (Fig. 2). Springtails, in general, are flexible consumers that can ingest leaf litter and the microbes that live on or within leaf litter (Chen et al., 1996; Ponge, 2000). The feeding habits of *S. curviseta*, in particular, are not well documented for wild populations, although the population used in this study had subsisted on fungi (baker's yeast) for approximately 50 years. Given uncertainty about the feeding habits of the springtails in our experiment, we do not know exactly how altered atmospheric chemistry affected springtail population growth; this will be a subject of further study. Reduced population growth might have followed the causal chain described above for earthworms, i.e., elevated $CO_2$ led to litter or litter-associated microbes with low nitrogen and high condensed-tannin concentrations, which led to slow springtail growth, low fecundity, or high mortality (e.g., Booth and Anderson, 1979). It is also possible that litter with low nitrogen and high condensed-tannin concentrations yielded low microbial biomass (Harrison, 1971; Swift et al., 1979), which, in turn, caused a shortage of resources for springtail population growth. A third potential explanation is that litter chemistry may have elicited a shift in microbial community composition (e.g., Chung et al., 2006), such that microbes dominating high-$CO_2$ litter were not consumed by springtails. We did not monitor microbial biomass or community structure, so we cannot evaluate these mechanisms.

We did not expect to see increased springtail population growth in microcosms receiving litter from rings with elevated $O_3$, especially because litter from these rings had relatively high concentrations of structural carbohydrates such as fiber and lignin (Table 1). Increased population growth rates associated with elevated $O_3$ may have resulted from chemical changes in leaf litter that were not measured. Growth rates of leaf-chewing herbivores show a similar unexplained increase under elevated ozone (Valkama et al., 2007). A second possible explanation for increased population growth is that the $O_3$-induced changes in litter chemistry led to a change in microbial community composition (e.g., Chung et al., 2006) that was favorable for springtail production.

### 4.4. Scaling up

Our study showed that earthworm individual growth and springtail population growth are negatively affected when animals are fed aspen leaf litter grown under elevated $CO_2$. If all other factors were equal, this result would imply that productivity of these organisms will be reduced under predicted increases in atmospheric $CO_2$ in aspen-dominated forests of the Great Lakes region. We also found that increases in $O_3$ have a stimulating effect on springtail population growth. Thus, if atmospheric concentrations of both $CO_2$ and $O_3$ increase at rates similar to those employed in this study, we would expect a net-negative effect on earthworm productivity, but a net-neutral effect on springtail productivity.

To better understand the implications of our results, it is necessary to consider environmental temperature, an additional environmental factor that will change with increased $CO_2$ and affect invertebrate productivity (David and Gillon, 2009). Climate models predict that, under likely emission scenarios, elevated $CO_2$ will cause a 2 °C increase in average annual temperature in the Great Lakes region by 2050 (IPCC, 2007). Assuming minor temperature acclimation and a $Q_{10}$ temperature coefficient between 1.5 and 3 for production rates (Savage et al., 2004; Frazier et al., 2006), a temperature increase of 2 °C would increase the production rates of litter invertebrates by approximately 10–25%. In the present study, we found that $CO_2$-induced changes in litter quality decreased invertebrate productivity by approximately 35%. If we further assume that the effects of temperature and litter quality are additive (e.g., David and Gillon, 2009), we can hypothesize that projected increases in $CO_2$ alone will have an overall negative effect on invertebrate productivity (+10 to +25% temperature effect, combined with a −35% litter quality effect, yields a −10 to −25% overall effect). Using the same logic, we hypothesize that projected increases in both $CO_2$ and $O_3$ will have a net-negative effect on earthworms (as above), but a net positive effect on springtails (+10 to +25% temperature effect, combined with no litter quality effect, yields a +10 to +25% overall effect). Thus, taxon-specific effects of elevated $CO_2$ and $O_3$ could lead to shifts in detritivore community structure. Changes in detritivore community structure could lead to changes in ecological patterns and processes in aspen-dominated forests of the Great Lakes region. A fuller understanding of the effects of elevated $CO_2$ and $O_3$ on detritivore community structure and function will be attained when assumption-laden projections, like those above, can be replaced with empirical results from experiments that simultaneously manipulate resource quality and environmental temperature (e.g., David and Gillon, 2009) for a wide variety of functionally important taxa.

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