



ELSEVIER

Soil Biology & Biochemistry 40 (2008) 1253–1258

**Soil Biology &
Biochemistry**

www.elsevier.com/locate/soilbio

Short communication

Slow-cycle effects of foliar herbivory alter the nitrogen acquisition and population size of Collembola

Mark A. Bradford^{a,*}, Tara Gancos^a, Christopher J. Frost^b

^a*Odum School of Ecology, University of Georgia, 517 BioSciences Building, Athens, GA 30602, USA*

^b*Department of Entomology, Pennsylvania State University, University Park, PA 16802, USA*

Received 22 August 2007; received in revised form 19 October 2007; accepted 2 December 2007

Available online 9 January 2008

Abstract

In terrestrial systems there is a close relationship between litter quality and the activity and abundance of decomposers. Therefore, the potential exists for aboveground, herbivore-induced changes in foliar chemistry to affect soil decomposer fauna. These herbivore-induced changes in chemistry may persist across growing seasons. While the impacts of such slow-cycle, ‘legacy’ effects of foliar herbivory have some support aboveground, such impacts have not been evaluated for soil invertebrates. Here, we investigate legacy effects on Collembola population structure and nitrogen acquisition. We collected foliar material (greenfall) from trees that had, in the preceding season, been exposed to insect herbivory by leaf-chewing Lepidoptera. Collembola populations were grown with the greenfall in soil microcosms across 16 weeks. While there were only modest effects of herbivory on the greenfall mass loss, Collembola abundance and biomass after 8 weeks of greenfall exposure were approximately 2.5-fold greater in the controls. Given that Collembola biomass

percentage nitrogen was relatively fixed, this translated to approximately 2.5-fold greater biomass nitrogen. The herbivore treatment decreased the absolute amount of Collembola biomass nitrogen derived from both greenfall and soil, and the relative contribution of litter nitrogen and soil nitrogen to Collembola biomass nitrogen was dependent on both the herbivory treatment and greenfall initial nitrogen. Our results show that slow-cycle, legacy effects of foliar herbivory may affect soil faunal population structure and nitrogen acquisition, demonstrating the potential for aboveground herbivory to influence belowground animal ecology and nitrogen cycling across multi-annual timescales.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Soil fauna; Decomposition; Greenfall; Aboveground; Belowground; Litter quality; Nitrogen mineralisation; Nitrogen immobilisation

There is increasing awareness that the relationships between aboveground and belowground foodwebs may structure communities and regulate ecosystem processes (Hooper et al., 2000; Wardle et al., 2004; Bardgett et al., 2005; Bezemer and van Dam, 2005). These relationships are often indirectly mediated via plant responses to aboveground and belowground herbivores (Bardgett and Wardle, 2003). A range of mechanisms may contribute to these modifications by herbivores (Hunter, 2001; Bardgett and Wardle, 2003), including slow-cycle (*sensu* McNaughton et al., 1988) changes in foliar chemistry (Choudury, 1988).

There is a well-established literature on the changes in foliar chemistry induced by invertebrate herbivores (Schultz and Baldwin, 1982; Agrawal et al., 1999; Nykanen and Koricheva, 2004; Hall et al., 2005) and the subsequent impacts of these changes on contemporary and later-season aboveground herbivory (Wold and Marquis, 1997; Boege, 2004). However, less is known about the 'after-life' effects of the chemical changes when leaves enter 'brown' foodwebs (Chapman et al., 2003; Schweitzer et al., 2005). Despite evidence that the changes in foliar chemistry in response to herbivory can both increase and decrease rates of soil nutrient cycling (Ritchie et al., 1998; Belovsky and Slade, 2000; Chapman et al., 2003; Fonte and Schowalter, 2005; Schweitzer et al., 2005), surprisingly little is known about how these changes impact the decomposer fauna (Mikola et al., 2001a, b; Bardgett and Wardle, 2003).

*Corresponding author. Tel.: +1 706 542 7829; fax: +1 706 542 3344.
E-mail address: markb@uga.edu (M.A. Bradford).

Herbivore-induced shifts in foliar chemistry can initiate feedback mechanisms between aboveground and belowground organisms (Bardgett and Wardle, 2003), which may operate across multi-annual timescales. Aboveground, legacy effects of herbivory have been shown to reduce the fitness of invertebrate foliar herbivores in years following severe defoliation (Haukioja et al., 1985) and even, to a certain extent, explain the population dynamics of these aboveground fauna (Zvereva et al., 1997). This led us to ask whether legacy effects of foliar herbivores might affect the population dynamics and resource acquisition of soil invertebrate decomposers. We examined legacy effects of foliar herbivory on Collembola population abundance, biomass and nitrogen (N) acquisition. Since we focused on investigating potential legacy effects of aboveground herbivory on belowground organisms, we used greenfall as opposed to senesced litter. Greenfall (i.e. fallen green leaves) is an important input to the decomposer system with distinct temporal dynamics relative to senesced litter, and its input rate can itself increase with increasing herbivory (Risley and Crossley, 1988; Fonte and Schowalter, 2004). Foliar material was collected from oak trees that had, in the preceding season, been exposed to early-season, insect herbivory by leaf-chewing Lepidoptera. Collembola, which are a dominant component of the soil decomposer mesofauna (Petersen and Luxton, 1982), were then grown with the collected foliar material in soil microcosms across 16 weeks. Given

Greenfall was prepared from a field mesocosm study conducted in Athens, Georgia, USA, where *Quercus rubra* L. (red oak) saplings were exposed in June 2003 to the larvae of the herbivore *Orgyia leucostigma* Fitch. (white-marked tussock moth). Herbivore damage removed $21.2 \pm 5.71\%$ leaf area, compared with $5.9 \pm 1.52\%$ under control conditions (mean ± 1 SD). Saplings were grown in individual containers, which each received 60 gm^{-2} ^{15}N -enriched frass, an ecologically relevant deposition that was in proportion to the level of damage inflicted by *O. leucostigma* (Frost and Hunter, 2007). Trees were maintained into the next growing season (2004), when the foliage was harvested mid-season, prior to senescence. Herbivore damage rates in 2004 were at background levels for trees that had been assigned to either the control or herbivore-damage treatments in 2003 (mean ± 1 SD across both treatments in 2004: $3.9 \pm 1.35\%$ leaf area). Greenfall from individual trees was kept separate and their $\delta^{15}\text{N}$ signatures and total N and carbon (C) concentrations determined (see below). We had ^{15}N -labelled greenfall from four control trees and from four herbivore-treated trees. This greenfall spanned a range of initial N concentrations (see Table 1), a variable which was unaffected by the herbivore treatment (Frost and Hunter, 2007).

Microcosms (88 mm dia., 57 mm deep) were established using soils collected from a mixed-deciduous woodland under an oak-dominated stand. The soils, from the upper 5 cm of the surface mineral (A) horizon, were passed

foliar material in soil microcosms across 16 weeks. Given established relationships between secondary chemical concentrations in leaves and differences in their decomposition rates (e.g., Cornelissen et al., 1999), and the expectation that oaks increase foliar secondary chemical concentrations in response to folivory (Hunter, 2001), we established the following hypothesis: slow-cycle, legacy effects of foliar herbivores will reduce Collembola population abundance and biomass, and lead to greater N acquisition from sources other than litter.

5 cm of the surface mineral (A) horizon, were passed through a 2 mm sieve to remove stones and roots and then placed at -20°C for 76 h, thawed at room temperature and then placed at -20°C for a further 24 h. This freezing routine killed soil mesofauna and macrofauna, but not the microbial community required for litter colonisation. Prior to being introduced into microcosm units, soils were gently leached with DI water for 10 days to remove the nutrient pulse associated with partial soil sterilisation (Bradford et al., 2002). Following leaching, soil was air-dried to 60%

Table 1

Variation in initial litter N concentrations and biomass N variables of Collembola juveniles grown with leaf litter produced in the 2004 growing season by trees exposed to control conditions or foliar herbivory in the 2003 growing season

| Treatment | Litter initial N (%) | Biomass (mg) | Biomass N (μg) | Litter-derived N (μg) | Soil-derived N (μg) | Litter-derived N (%) |
|-----------|----------------------|------------------|-----------------------------|------------------------------------|----------------------------------|----------------------|
| Control | 1.25 | 0.85 ± 0.224 | 97 ± 22.3 | 78 ± 15.9 | 20 ± 6.9 | 81 ± 2.1 |
| | 1.36 | 0.83 ± 0.110 | 102 ± 11.1 | 81 ± 9.7 | 21 ± 2.6 | 79 ± 1.8 |
| | 1.42 | 1.15 ± 0.285 | 123 ± 25.9 | 92 ± 17.7 | 31 ± 8.5 | 76 ± 2.4 |
| | 1.78 | 1.39 ± 0.270 | 151 ± 27.7 | 109 ± 19.4 | 43 ± 8.6 | 71 ± 1.8 |
| Herbivore | 1.26 | 0.51 ± 0.118 | 58 ± 10.5 | 40 ± 6.8 | 18 ± 4.2 | 70 ± 3.2 |
| | 1.38 | 0.59 ± 0.084 | 69 ± 9.2 | 48 ± 7.2 | 21 ± 2.9 | 69 ± 2.3 |
| | 1.46 | 0.69 ± 0.126 | 83 ± 15.1 | 59 ± 12.2 | 24 ± 3.4 | 69 ± 2.9 |
| | 1.64 | 0.64 ± 0.074 | 71 ± 8.3 | 56 ± 6.4 | 15 ± 2.5 | 79 ± 2.0 |

For all the variables, except the proportion of N derived from greenfall, there were significant main effects of initial litter N (biomass— $F_{1,4} = 8.47$, $P < 0.05$; biomass N— $F_{1,4} = 10.2$, $P < 0.05$; litter N— $F_{1,4} = 8.44$, $P < 0.05$; soil N— $F_{1,4} = 9.20$, $P < 0.05$) which were independent of time and herbivore treatment ($P > 0.05$ for all the interactions that initial N was involved in). For the relative proportion of N derived from greenfall litter there was a significant initial N \times treatment interaction ($F_{1,4} = 12.0$, $P < 0.05$), which arose because of the negative relationship between initial N and this variable for the control greenfall and the absence of a similar relationship for the herbivore-treated greenfall. Data are means \pm 1 SE (pooled across time: $n = 10$ for greenfall with initial N contents of 1.25%, 1.38%, 1.46% and 1.78% and $n = 6$ for contents of 1.26%, 1.36%, 1.42% and 1.64%; see text).

water holding capacity (WHC), which is within the range deemed favourable for microbial activity, and added to each microcosm to a depth of 1 cm. Soils were maintained at this WHC through addition of DI water and units were kept at 20 °C in the dark.

Greenfall was cut into 1 cm² pieces and ~1 g (air dry wt) encased into 2 mm mesh nylon litterbags. One litterbag was placed into each microcosm, on top of the soil surface. For greenfall from each tree, we established between 9 and 15 microcosms, depending on how much greenfall was available. For the ¹⁵N natural abundance greenfall (from two trees treated as controls but with unlabelled frass) we established six microcosms each.

Collembola were introduced once litter had been exposed to the soils in the microcosms for 14 days. Each microcosm contained 10 adult individuals of the Collembolan (Entomobryidae) *Sinella curviseta* Brook, a species widely used in soil microcosm studies (e.g., Sjursen and Holmstrup, 2004). These 10 individuals were introduced to establish a population, and were not the expected 'carrying-capacity' of the microcosms. No mesofauna, other than the introduced Collembola, were recovered from the microcosms, indicating that the partial-sterilisation procedure was effective.

Microcosms were harvested 4, 8 and 16 weeks after Collembola were added. At each of these times, between three and five (per tree) control and herbivore microcosms were harvested. Collembola were separated from decom-

S-Plus 7.0 (Insightful, Seattle, USA). Due to a power failure, samples collected at the 4-week harvest rotted in the oven and so these data were not analysed. Also, we present data for Collembola juveniles because they comprised the majority of the population abundance and biomass (on average 97.4% of the individuals and 92.1% of the biomass); the adult mass we recovered was too small to obtain accurate C, N and $\delta^{15}\text{N}$ values.

Slow-cycle, legacy effects of herbivory on greenfall decomposition rate were marginally significant ($F_{1,4} = 5.04$, $P = 0.088$), and independent of time and initial N. Despite evidence that slow-cycle effects of herbivory influence soil nutrient dynamics (Findlay et al., 1996; Ritchie et al., 1998; Belovsky and Slade, 2000; Chapman et al., 2003; Schweitzer et al., 2005), herbivory only resulted in a slight reduction in rate of greenfall mass loss (ca. 2.5% difference). Means \pm 1 SE (% mass loss) for the control and treatment greenfall were 48.58 ± 0.586 and 46.45 ± 0.747 , respectively ($n = 32$, pooled across time and initial N).

While herbivore treatment effects on the amount of initial N lost from the litterbags, and the amount of N immobilised from the soil by the greenfall, were not significant ($P > 0.05$), C:N ratios of the decomposing greenfall were affected. These effects were dependent on time (time \times treatment: $F_{1,52} = 4.50$, $P < 0.05$) and initial N (initial N \times treatment: $F_{1,4} = 10.8$, $P < 0.05$), but the interaction between the three factors was not significant ($P > 0.05$). The interaction with time most likely occurred

were harvested. Collembola were separated from decomposing greenfall under a dissecting microscope. To collect those Collembola remaining in the soils, microcosm units were flooded above a 53 μm sieve with DI water; live Collembola were collected from the surface of the water, separated into adults and juveniles, enumerated and then placed into pre-weighed, 9 \times 5 mm tin capsules. After drying at 65 $^{\circ}\text{C}$ for 24 h, tin capsules were weighed, and along with greenfall, which had been dried at 65 $^{\circ}\text{C}$, weighed and then finely milled, analysed for total C and N, and $\delta^{15}\text{N}$ signatures, using elemental analysis and CF-IRMS (Thermo Scientific, Waltham, USA). Analytical precision was $\pm 0.1\%$. Working gas and solid standards were calibrated to atmospheric N_2 . Initial $\delta^{15}\text{N}$ values for greenfall ranged between 506.4‰ and 886.3‰. We used these enrichments to partition N acquisition by Collembola from the soils and greenfall using isotope mixing models (Coleman and Fry, 1991). Similar mixing models were used to estimate N immobilisation and loss for the control and herbivore greenfall.

For the statistical analysis we used linear mixed effects models, where time, greenfall initial N concentration (both continuous variables), and the herbivore treatment (discrete variable) were all treated as fixed effects and permitted to interact. Tree identity was included as a random effect to account for the fact that replicates containing greenfall of the same initial N were derived from the greenfall from a single tree. When heteroscedasticity occurred, data were square-root (proportion, count) or \log_e (mass) transformed. Analyses were performed in

because the treatment effect on C:N ratio was more pronounced at 16 than 8 weeks (mean \pm 1 SE pooled across litter initial N, $n = 16$, control vs. treatment; 8 weeks: 15.8 ± 0.69 vs. 16.5 ± 0.26 ; 16 weeks: 20.3 ± 0.49 vs. 22.3 ± 0.24). The interaction with litter initial N most likely occurred because, for control litters, there was a positive relationship between initial N concentration of the greenfall and the narrowness of the C:N ratio of the decomposing greenfall (i.e. C:N ratios were smaller when the initial N concentration of the greenfall was higher). However, no such relationship was apparent for herbivore-treated greenfall (data not shown). Whether these differences in decomposing greenfall chemistry and mass loss are of ecological significance for plant–soil nutrient dynamics remains to be tested.

In contrast to decomposition processes, the herbivore treatment markedly reduced Collembola abundance and biomass, but only at the 8-week sampling (Fig. 1). There were no effects of herbivory, time nor initial N on Collembola biomass percentage N, C or C:N ratios (data not shown) presumably because, like herbivores, the stoichiometric ratios of decomposer fauna are relatively fixed (Elser et al., 2000). This meant that the approximately two-fold greater juvenile biomass with control litters at 8 weeks (Fig. 1a) translated to approximately two-fold greater total C (data not shown) and N masses (Fig. 1b). As for Collembola biomass, the herbivore treatment effect on the absolute and relative amounts of Collembola biomass N derived from both litter and soil were dependent

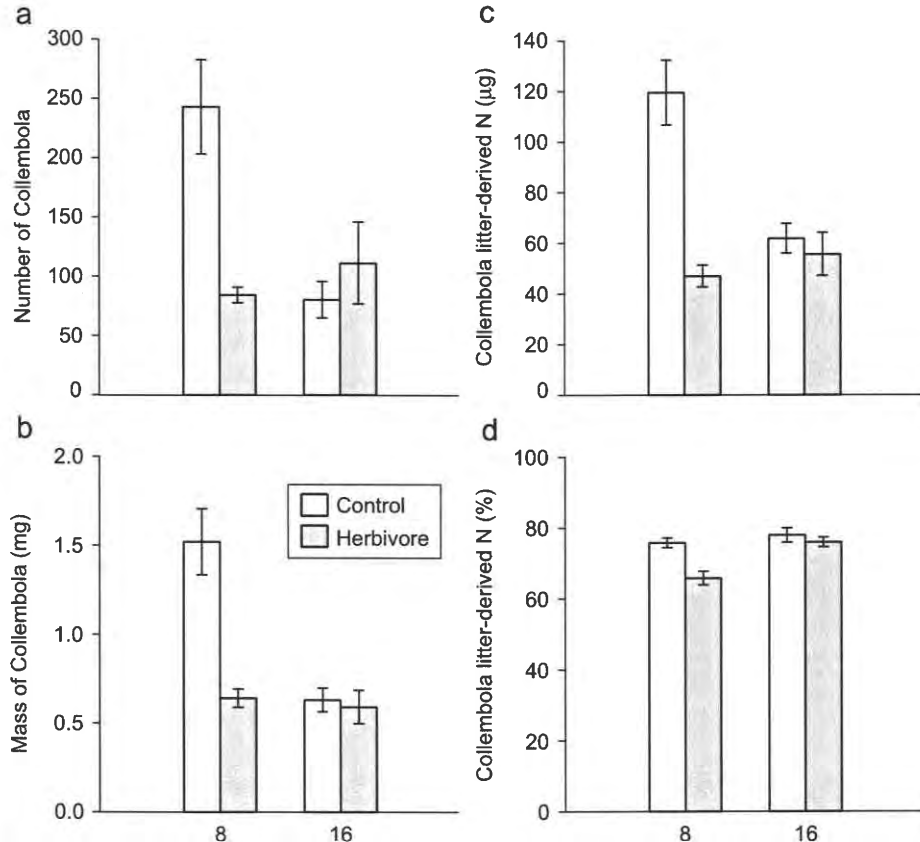


Fig. 1. Abundance (a), biomass (b), and the absolute (c) and proportional (d) biomass of N derived from greenfall for Collembola juveniles exposed to greenfall produced in the 2004 growing season by trees exposed to control conditions (white bars) or foliar herbivory (grey bars) in the 2003 growing season. All absolute units are numbers or mass per microcosm. There was a significant time \times treatment interaction for all variables: abundance— $F_{1,52} = 9.35$, $P < 0.01$; biomass— $F_{1,52} = 6.36$, $P < 0.05$; N mass— $F_{1,52} = 13.1$, $P < 0.001$; percent N mass— $F_{1,52} = 15.2$, $P < 0.001$. Data are means \pm 1 SE, and, because greenfall initial N concentration did not affect the time \times treatment interaction (i.e. the three-way interaction was not significant), are pooled across initial N ($n = 16$). The time \times treatment interactions most likely occurred because the legacy effects of herbivory decreased (relative to the controls) the measured variables at the 8-week harvest but not at the 16-week harvest.

on time: negative effects of herbivory were pronounced at 8 weeks but not at 16 weeks (Fig. 1c). Further, when we corrected for the differences in biomass between treatments, we found support for our hypothesis that the Collembola feeding on the herbivore-damaged litter derived less of their N from the litter than did those in the control microcosms, but only at 8 weeks (Fig. 1d). Notably, Collembola biomass and N variables were relatively unchanged between 8 and 16 weeks when grown with herbivore-treated greenfall (Fig. 1). This suggests that the population decline between 8 and 16 weeks in the control microcosms (Fig. 1) was not an artefact of the experimental design. Instead, it may indicate that herbivore-damaged litters are initially a poorer resource, but through the decomposition process quite rapidly (16 weeks in our study) become of equivalent resource value to undamaged litters.

There were significant positive relationships between greenfall initial N concentration and a range of variables. These were: Collembola biomass, biomass N, and the

absolute amount of biomass N derived from both greenfall and soil (Table 1). While these effects of initial N concentration were independent of time and treatment (Table 1), the effects of initial N on the relative amount of N derived from greenfall (as opposed to soil) were dependent on the herbivore treatment (Table 1). Specifically, the amount of Collembola biomass N derived from greenfall, relative to soil, was negatively related to initial N for control greenfall, but seemingly unrelated for herbivore-treated greenfall (Table 1).

We cannot elucidate whether the influence of the herbivore treatment on the relationship between initial N and relative N acquisition arose through a direct alteration in the foraging for (or assimilation of) N sources by the Collembola or whether it occurred indirectly through alterations in the feeding ecology of soil microbes, such as saprotrophic fungi, upon which Collembola feed (Gange, 2000). The latter possibility is plausible: oak defoliation is known to increase foliar tannin concentrations (Hunter and Schultz, 1995), which can in turn

influence microbial community structure as well as soil N dynamics and litter decomposition (Kraus et al., 2003; Schweitzer et al., 2004). To evaluate this possibility, we determined initial concentrations of total phenolics, and condensed and hydrolysable tannins, using the methods described in Frost and Hunter (2008), but found none of these variables were significantly affected by the herbivory in the previous growing season (data not shown). Whatever the mechanism(s), slow-cycle, legacy effects of herbivory should be considered when using natural abundance $\delta^{15}\text{N}$ ratios to investigate soil foodweb structure (Ponsard and Arditi, 2000; Scheu and Falca, 2000), as well as relationships between soil nutrient dynamics and decomposer communities per se.

While there is a well-established precedent for using microcosms to study short-term population dynamics of soil mesofauna (Coleman et al., 2004), they cannot substitute for field research. For example, the Collembola we used is found in forested systems (Battigelli and Marshall, 1993) but has not been reported in soils below the oak species we studied. Our results, however, demonstrate the potential for slow-cycle, legacy effects of foliar herbivores to affect soil decomposer community structure and N dynamics. Field research is now required to assess whether these potential effects manifest in nature. Indeed, mechanisms such as interannual (Hall et al., 2005), interspecific (Schweitzer et al., 2005), or intraspecific (Madritch and Hunter, 2002) variability in foliar quality

foliar herbivores can affect soil decomposer population structure and N acquisition.

The Analytical Chemistry Laboratory (University of Georgia) performed element and isotope analyses. Thanks to Christian Davies, Mike Strickland and Jaya Srivistava for technical comments. Our research was supported by grants from the National Science Foundation, Coweeta LTER Programme.

References

- Agrawal, A.A., Tuzun, S., Bent, E., 1999. Induced Plant Defenses Against Pathogens and Herbivores: Biochemistry, Ecology and Agriculture. APS Press, Saint Paul, MN.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. *Trends in Ecology and Evolution* 20, 634–641.
- Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84, 2258–2268.
- Battigelli, J.P., Marshall, V.G., 1993. Relationships between soil fauna and soil pollutants. In: Marshall, V.G. (Ed.), *Proceedings of the Forest Ecosystem Dynamics Workshop*, BC Ministry of Forests, Victoria, Canada, pp. 31–34.
- Belovsky, G.E., Slade, J., 2000. Insect herbivory accelerates nutrient cycling and increases plant production. *Proceedings of the National Academy of Sciences USA* 97, 14412–14417.
- Bezemer, T.M., van Dam, N.M., 2005. Linking aboveground and belowground interactions via induced plant defenses. *Trends in*

(Wardle and Tilman, 2002) variability in foliar quality may obscure slow-cycle effects of insect herbivores on decomposer communities. Future research should use both green and senesced litterfall given that changes in foliar chemistry in the former, while often transferred to senesced litter, do not necessarily influence decomposition dynamics (Norby et al., 2001). Further, while we reasoned that herbivore effects on secondary chemistry might mediate legacy effects, those secondary chemical variables we measured were not affected by the herbivory in the preceding growing season. Potential mechanisms such as secondary chemistry, and altered fungal activity and/or community composition, need to be established if we are to understand better linkages between aboveground and belowground ecology. Such mechanisms, as well as potential slow-cycle effects of foliar herbivory on decomposer fauna in the same year as the herbivory occurs, should be explored in future work.

Slow-cycle, legacy effects on foliar chemistry have been shown to affect invertebrate fitness and population dynamics in aboveground 'green' foodwebs (Haukioja et al., 1985; Zvereva et al., 1997). As far as we are aware, we are the first to demonstrate that slow-cycle legacy effects may also affect invertebrate organisms within belowground 'brown' foodwebs. Our results provide experimental evidence for a potential linkage between aboveground and belowground ecology that occurs across multi-annual timescales (Wardle et al., 2004; Bardgett et al., 2005; Bezemer and van Dam, 2005). Specifically, they show that slow-cycle, legacy effects of

- belowground herbivory on aboveground decomposition. *Ecology and Evolution* 20, 617–624.
- Boege, K., 2004. Induced responses in three tropical dry forest plant species—direct and indirect effects on herbivory. *Oikos* 107, 541–548.
- Bradford, M.A., Jones, T.H., Bardgett, R.D., Black, H.I.J., Boag, B., Bonkowski, M., Cook, R., Eggers, T., Gange, A., Grayston, S.J., Kandeler, E., McCaig, A.E., Newington, J.N., Prosser, J.I., Setälä, H., Staddon, P.L., Tordoff, G.M., Tscherko, D., Lawton, J.H., 2002. Impacts of soil faunal community composition on model grassland ecosystems. *Science* 298, 615–618.
- Chapman, S.K., Hart, S.C., Cobb, N.S., Whitham, T.G., Koch, G.W., 2003. Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology* 84, 2867–2876.
- Choudury, D., 1988. Herbivore induced changes in leaf-litter resource quality: a neglected aspect of herbivory in ecosystem nutrient dynamics. *Oikos* 51, 389–393.
- Coleman, D.C., Fry, B., 1991. *Carbon Isotope Techniques*. Academic Press, Inc., San Diego.
- Coleman, D.C., Crossley Jr., D.A., Hendrix, P.F., 2004. *Fundamentals of Soil Ecology*, second ed. Elsevier Academic Press, Burlington.
- Cornelissen, J.H.C., Perez-Harguindeguy, N., Diaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F., Cerabolini, B., 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* 143, 191–200.
- Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H., Sterner, R.W., 2000. Nutritional constraints in terrestrial and freshwater food webs. *Nature* 408, 578–580.
- Findlay, S., Carreiro, M., Krischik, V., Jones, C.G., 1996. Effects of damage to living plants on leaf litter quality. *Ecological Applications* 6, 269–275.
- Fonte, S.J., Schowalter, T.D., 2004. Decomposition of greenfall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* 36, 474–482.

- Fonte, S.J., Schowalter, T.D., 2005. The influence of a neotropical herbivore (*Lamponius portoricensis*) on nutrient cycling and soil processes. *Oecologia* 146, 423–431.
- Frost, C.J., Hunter, M.D., 2007. Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia* 151, 42–53.
- Frost, C.J., Hunter, M.D., 2008. Insect herbivores and their frass affect *Quercus rubra* leaf quality and initial stages of subsequent litter decomposition. *Oikos* 117, 13–22.
- Gange, A., 2000. Arbuscular mycorrhizal fungi, Collembola and plant growth. *Trends in Ecology & Evolution* 15, 369–372.
- Hall, M.C., Stiling, P., Hungate, B.A., Drake, B.G., Hunter, M.D., 2005. Effects of elevated CO₂ and herbivore damage on litter quality in a scrub oak ecosystem. *Journal of Chemical Ecology* 31, 2343–2356.
- Haukioja, E., Soumela, J., Neuvonen, S., 1985. Long-term inducible resistance in birch foliage: triggering cues and efficacy on a defoliator. *Oecologia* 65, 363–369.
- Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., van der Putten, W.H., de Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M., Wolters, V., 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience* 50, 1049–1061.
- Hunter, M.D., 2001. Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agricultural and Forest Entomology* 3, 77–84.
- Hunter, M.D., Schultz, J.C., 1995. Fertilization mitigates chemical induction and herbivore responses within damaged oak trees. *Ecology* 76, 1226–1232.
- Kraus, T.E.C., Dahlgren, R.A., Zasoski, R.J., 2003. Tannins in nutrient dynamics of forest ecosystems—a review. *Plant and Soil* 256, 41–66.
- Madritch, M.D., Hunter, M.D., 2002. Phenotypic diversity influences ecosystem functioning in an oak sandhills community. *Ecology* 83, plant species combinations in an experimental grassland community. *Soil Biology & Biochemistry* 33, 205–214.
- Norby, R.J., Cotrufo, M.F., Ineson, P., O'Neill, G.E., Canadell, J., 2001. Elevated CO₂, litter chemistry, and decomposition: a synthesis. *Oecologia* 127, 153–165.
- Nykanen, H., Koricheva, J., 2004. Damage-induced changes in woody plants and their effects on insect herbivore performance: a meta-analysis. *Oikos* 104, 247–268.
- Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos* 39, 287–388.
- Ponsard, S., Ardit, R., 2000. What can stable isotopes (delta 15N and 13C) tell about the food web of soil macro-invertebrates? *Ecology* 81, 852–864.
- Risley, L.S., Crossley Jr., D.A., 1988. Herbivore-caused greenfall in the southern Appalachians. *Ecology* 69, 1118–1127.
- Ritchie, M.E., Tilman, D., Knops, J.M.H., 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79, 165–177.
- Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia* 123, 285–296.
- Schultz, J.C., Baldwin, I.T., 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science* 217, 149–151.
- Schweitzer, J.A., Bailey, J.K., Rehill, B.J., Martinsen, G.D., Hart, S.C., Lindroth, R.L., Keim, P., Whitham, T.G., 2004. Genetically based trait in a dominant tree affects ecosystem processes. *Ecology Letters* 7, 127–134.
- Schweitzer, J.A., Bailey, J.K., Hart, S.C., Wimp, G.M., Chapman, S.K., Whitham, T.G., 2005. The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos* 110, 133–145.
- Sjursen, H., Holmström, M., 2004. Direct measurement of ammonium excretion in soil microarthropods. *Functional Ecology* 18, 612–615.

- 2084–2090.
- McNaughton, S.J., Ruess, R.W., Seagle, S.W., 1988. Large mammals and process dynamics in African ecosystems. *Bioscience* 38, 794–800.
- Mikola, J., Yeates, G.W., Barker, G.M., Wardle, D.A., Bonner, K.I., 2001a. Effects of defoliation intensity on soil food-web properties in an experimental grassland community. *Oikos* 92, 333–343.
- Mikola, J., Yeates, G.W., Wardle, D.A., Barker, G.M., Bonner, K.I., 2001b. Response of soil food-web structure to defoliation of different
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between above-ground and belowground biota. *Science* 304, 1629–1633.
- Wold, E.N., Marquis, R.J., 1997. Induced defense in white oak: effects on herbivores and consequences for the plant. *Ecology* 78, 1356–1369.
- Zvereva, E.L., Kozlov, M.V., Niemelä, P., Haukioja, E., 1997. Delayed induced resistance and increase in leaf fluctuating asymmetry as responses of *Salix borealis* to insect herbivory. *Oecologia* 109, 368–373.