

Short communication

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

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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.

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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).

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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 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.

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 \pm 1 SD). Saplings were grown in individual containers, which each received 60 g m^{-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 \pm 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 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).

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