Above-ground grazing affects floristic composition and modifies soil trophic interactions

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Abstract

There are few data on the functional inter-relationships between above- and below-ground components of soil ecosystems. Here, we report changes in below-ground soil invertebrate trophic relationships (manifested as alterations in stable isotope natural abundances, δ13C and δ15N) that arose in association with the removal of sheep grazing and from the resulting changes in above-ground floristic composition. Consequent to grazing removal, Lolium perenne L. (perennial rye-grass) was replaced as the dominant plant species in ungrazed treatments by Ranunculus repens L. (creeping buttercup), a species with more 13C-enriched foliage. Consequently, all invertebrate functional groups studied, but not whole soil, were more 13C-enriched in ungrazed treatments. Earthworms (detritivore) from grazed treatments were significantly 15N-enriched compared with earthworms from ungrazed treatments. In contrast, slug (herbivore) δ15N exhibited no treatment effect. Reasons for this are unclear but may be related to the effects of above-ground grazing on the composition of below-ground microbial/microfaunal communities. Omnivores/carnivores (beetles and spiders), were more 15N-enriched than primary producers in the grazed than in the ungrazed treatments (6 vs. 4‰) suggesting a longer below-ground foodchain in the grazed plots. The cessation of fertilizer application had no comparable effects on below-ground trophic relationships. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Ecosystem function; Grazing; Soil ecosystems; Stable isotopes; Trophic interactions

1. Introduction

The functioning of terrestrial ecosystems is affected by the composition of above-ground vegetation, where ‘function’ is defined in terms of, e.g. rates and amounts of resource processing (Hooper and Vitousek, 1997; Tilman et al., 1997; Wardle et al., 1997). Although links between the above- and below-ground components of soils are recognised, only a few studies have included the effects of changes in above-ground plant species composition on below-ground soil foodwebs (Bengtsson et al., 1996; Wardle, 1999; Wardle et al., 1999). In particular, the decomposer foodweb, which is a key contributor to overall ecosystem function via decomposition and nutrient mineralisation, has received little attention in this regard.

Above-ground grazing can alter the composition of plant communities. For example, the floristic composition of many temperate grasslands is maintained by the selective grazing of potential dominants (Harper, 1977). Similarly, contrasting grazing regimes alter the abundances and distributions of soil micro- and mesofauna (Bardgett et al., 1993a, 1997, 1998). It would be useful to know how changes above- and below-ground are coupled functionally. Essential, but so far missing, steps towards this aim are to detect and quantify the impacts of grazing and nutrient inputs on below-ground fauna.

Here, utilising stable isotope natural abundances, we show that plant community changes following the removal of grazing by a large herbivore (sheep) can alter soil–plant systems specifically trophic relationships among soil invertebrate functional groups (putative detritivore, herbivore, omnivore/carnivore).
2. Materials and methods

2.1. Experimental design and site description

The study site, located in central Scotland (Latitude, 55°49’N; Longitude, 03°50’W), is an upland pasture (245 m above msl) on poorly draining non-calcareous gley soil (Rowanhill Series; Ragg et al., 1976). Four treatments, each with two replicate plots were studied (Table 1). All treatments were imposed from 1990 onwards. As a consequence, of the difference in fertilizer application, grazing intensity in Treatment C was approximately 70% of that in Treatment A. In 1995, sheep grazed between 17 April and 1 November, and fertilizer was applied to the relevant plots as follows: N was applied on 13 April (50 kg N ha\(^{-1}\) ammonium nitrate), 31 May (40 kg N ha\(^{-1}\) as a compound fertilizer, including P and K) and 1 September (50 kg N ha\(^{-1}\) ammonium nitrate). \(\delta^{15}N\) of the fertilizer applied on 13 April, 31 May and 1 September was +1.1, +2.1 and 2.7\%e, respectively.

\(\textit{Lolium perenne}\) L. (44.8% cover), \(\textit{Poa annua}\) L. (17.7%) and \(\textit{Trifolium repens}\) L. (10.8%) were the dominant plant species in Treatments A and C, representing ca. 70% of the total vegetation cover. As a direct consequence of the removal of sheep grazing, these three species comprised <1% cover in Treatments B and D and were replaced by \(\textit{Ranunculus repens}\) L. (76.1% cover), \(\textit{Holcus lanatus}\) L. (1.4%) and \(\textit{Ranunculus acris}\) L. (1.4%) as the dominant species.

2.2. Sampling of soil invertebrates, soil and vegetation

Three line-transects were laid out randomly in each plot. Above-ground plant biomass was harvested from three quadrats (0.3 m\(^2\), 13.5 m apart, deemed, using geostatistical techniques, to be the minimum distance required to ensure spatial independence of replicates; Marriott et al., 1997) along each transect, pooled to produce one sample per transect (three per plot), and subsequently separated into species before isotopic analysis. At each sampling date there was one pooled sample from each of three randomly placed transects in each duplicate plot per treatment, thus \(n = 6\) per treatment.

Soil cores (to 15 cm depth) were taken from each of the previously sampled quadrats, combined into a single sample for each transect and analysed for \(\delta^{13}C\) and \(\delta^{15}N\).

In each plot, adjacent to where the plant samples were taken, three quadrats (0.25 m\(^2\)), were sampled for soil invertebrates by the application of mustard solution (Gunn, 1992). In the field, invertebrates were placed in glass jars on ice and separated into major functional groups in the laboratory. In this study, omnivores/carnivores are represented by beetles and spiders (including \textit{Anura, Carabus} and \textit{Loricera} spp.), detritivores by earthworms (including \textit{Aporrectodea} and \textit{Lumbricus} spp.) and herbivores by slugs (including \textit{Arion} spp.).

Samples of plant shoots, whole soil and soil invertebrates were taken on eleven separate occasions approximately every 3 weeks from April 10 to September 26 1995 and thereafter monthly until November 27 1995.

2.3. Sample preparation for \(\delta^{13}C\) and \(\delta^{15}N\) analyses

Samples were prepared and analysed as described by Neilson et al. (1998). \(\delta\) values are expressed as the parts per thousand (\%/e) difference from a standard: \(\delta = ((R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}) \times 1000(\%/e)\), where \(R_{\text{sample}}\) is the ratio of heavy to light isotopes in the sample and \(R_{\text{standard}}\) is that of the reference standard. Analytical precision of \(\delta^{13}C\) and \(\delta^{15}N\) for soil invertebrates and vegetation was 0.2 and 0.4\%/e, respectively, and for whole soil \(\delta^{13}C\) and \(\delta^{15}N\), 0.2 and 1.0\%/e, respectively.

2.4. Data analysis

A percent cover-weighted-average (\(\delta_{\text{veg}}\)) of both \(\delta^{13}C\) and \(\delta^{15}N\) was calculated for the above-ground vegetation in each treatment (Neilson et al., 1998). A repeated measure analysis was done using the Arepmesures procedure in Genstat 5 (Payne et al., 1987) to check for any temporal correlations that may skew and an analysis of variance (ANOVA). No such correlations were found (data not shown) and soil invertebrate, whole soil and \(\delta_{\text{veg}}\) were subjected to a standard 3-way ANOVA to detect effects of sampling date, grazing regime and fertilizer applications using Genstat 5 (Payne et al., 1987).

3. Results

Fertilizer application had no effect on earthworm, slug or whole soil \(\delta^{15}N\) or \(\delta^{13}C\) during the experiment.
(Tables 2–4), nor were any fertilizer × grazing or fertilizer × month interactions found (data not shown). Consequently, only the effects of grazing and sampling date on below-ground trophic interactions are described here. Earthworms and slugs had smaller ANOVA mean square values for sampling date compared with grazing treatment for both isotopes. This is reflected in the significance levels of the ANOVA (Tables 2 and 3).

Earthworm $\delta^{15}N$ exhibited both sampling date ($p < 0.001$) and grazing ($p = 0.014$) effects (Table 2). Mean earthworm $\delta^{15}N$ from the grazed treatments were 1.5‰ more $^{15}N$-enriched than those from ungrazed treatments. In contrast, slug and whole soil $\delta^{15}N$ were not affected by grazing treatments, but varied with sampling date ($p < 0.001$) (Tables 3 and 4). During the sampling period, mean earthworm $\delta^{15}N$ from the grazed treatments generally became more $^{15}N$-enriched, peaking at +6.3‰ in early September, then declining to ca. 5‰ by the end of the sampling period (Fig. 1(a)). In contrast, mean earthworm $\delta^{15}N$ from the ungrazed treatments, became less $^{15}N$-enriched until mid June. Thereafter, within 3 weeks it became ca. 1.5‰ more $^{15}N$-enriched and remained relatively constant until the final month when it decreased from +4.5 to +2.2‰ (Fig. 1(a)). This divergence in earthworm $\delta^{15}N$ between grazed vs. ungrazed treatments during the sampling period produced a significant ($p = 0.007$) month × grazing interaction. Similarly, slug $\delta^{15}N$ exhibited a month × grazing interaction ($p < 0.001$) as $\delta^{15}N$ values remained constant throughout the sampling period in the ungrazed treatments but declined gradually throughout the sampling period in the grazed treatment (Fig. 1(a)). Although a month × grazing interaction ($p < 0.001$) existed, the difference in $\delta^{15}N$ was within analytical precision and not considered biologically significant.

Earthworm and slug $\delta^{13}C$ were affected by sampling date (earthworm, $p = 0.014$; slug, $p < 0.001$) and grazing treatment (earthworm, $p < 0.001$; slug, $p = 0.009$) (Tables 2 and 3). Earthworms and slugs from the ungrazed treatments were ca. 2‰ more $^{13}C$-enriched than those from the grazed treatments. In contrast, whole soil $\delta^{13}C$ was not affected by sampling date or grazing treatment (Table 4).

Both invertebrates had a month × grazing interaction (earthworm, $p = 0.003$; slug, $p = 0.013$). Earthworms and slugs from ungrazed treatments were 2.3 and 1.9‰, respectively, more $^{13}C$-enriched than equivalent samples taken from the grazed treatments. During the sampling period, within the different grazing treatments, $\delta^{13}C$ of both invertebrates differed by only ca. 0.5‰, except for slugs from the grazed treatment which became ca. 3‰ more $^{13}C$-depleted between September and the end of November (Fig. 1(b)).

Comparing seasonal means, slug $\delta^{15}N$ was 0.9 and 0.7‰ $^{15}N$-enriched relative to $\delta_{\text{veg}}$ in the grazed and ungrazed treatments, respectively (Table 5). Earthworms were similarly $^{15}N$-enriched relative to $\delta_{\text{veg}}$ in the ungrazed treatments (Table 5) but those from grazing treatments were 3.2‰ more $^{15}N$-enriched than $\delta_{\text{veg}}$ (Table 5). Mean earthworm $\delta^{15}N$ across all treatments was +4.5‰ compared with +3.2‰ for slugs. Earthworms from grazed treatments had the same $\delta^{15}N$ values to that of whole soil (Table 5) but, in contrast, $\delta^{15}N$ of earthworms from the ungrazed treatments and of slugs from both grazing regimes were, respectively, 1.4 and 1.8‰ less $^{15}N$-enriched relative to whole soil (Table 5).

In the ungrazed treatments, beetle and spider (i.e. omnivores/carnivores) $\delta^{15}N$ was 3.3 and 3.7‰ more

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Table 2
Summary analysis of variance of the main effects on earthworm $\delta^{15}N$ and $\delta^{13}C$

<table>
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<th>SS</th>
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<td>6.3</td>
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<tr>
<td>$\delta^{13}C$</td>
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<td>11.6</td>
<td>1.2</td>
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<td></td>
<td>M × G</td>
<td>14.8</td>
<td>1.5</td>
<td>10</td>
<td>3.54</td>
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Table 3
Summary analysis of variance of the main effects on slug $\delta^{15}N$ and $\delta^{13}C$

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<td>$\delta^{15}N$</td>
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<td>$\delta^{13}C$</td>
<td>Month (M)</td>
<td>53.3</td>
<td>5.3</td>
<td>10</td>
<td>9.33</td>
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<td></td>
<td>Fertilizer (F)</td>
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<td>26.5</td>
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<td></td>
<td>M × G</td>
<td>16.8</td>
<td>1.9</td>
<td>9</td>
<td>3.27</td>
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Table 4
Summary analysis of variance of the main effects on whole soil $\delta^{15}N$ and $\delta^{13}C$

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<th>P</th>
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<td>$\delta^{15}N$</td>
<td>Month (M)</td>
<td>23.6</td>
<td>2.36</td>
<td>10</td>
<td>16.35</td>
</tr>
<tr>
<td></td>
<td>Grazing (G)</td>
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<td>0.4</td>
<td>1</td>
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<td></td>
<td>Fertilizer (F)</td>
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<td>0.1</td>
<td>1</td>
<td>0.18</td>
</tr>
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<td>M × G</td>
<td>6.1</td>
<td>0.6</td>
<td>10</td>
<td>4.22</td>
</tr>
<tr>
<td>$\delta^{13}C$</td>
<td>Month (M)</td>
<td>372.0</td>
<td>37.2</td>
<td>10</td>
<td>1.05</td>
</tr>
<tr>
<td></td>
<td>Grazing (G)</td>
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<td>13.6</td>
<td>1</td>
<td>0.36</td>
</tr>
<tr>
<td></td>
<td>Fertilizer (F)</td>
<td>44.6</td>
<td>44.6</td>
<td>1</td>
<td>1.17</td>
</tr>
<tr>
<td></td>
<td>M × G</td>
<td>353.7</td>
<td>35.4</td>
<td>10</td>
<td>1.00</td>
</tr>
</tbody>
</table>


15N-enriched than earthworms and slugs, respectively (Table 5). In the grazed treatments, beetle and spider δ15N was 2.8‰ more 15N-enriched than earthworms and 5.1‰ more 15N-enriched than slugs (Table 5).

After 4 years of grazing removal earthworms and putative omnivores/carnivores (beetles and spiders) were, respectively, 1.5 and 1.0‰ 15N-depleted whereas, both slugs and δveg were slightly (0.5‰) 15N-enriched (Fig. 2).

When data from all treatments were combined, earthworm and slug δ13C were not significantly different. With the exception of whole soil, δ13C of earthworms, slugs, beetles and spiders and δveg from the ungrazed treatments were 1.6–2.3‰ more 13C-enriched than similar samples from the grazed treatments (Fig. 2). Whole soil δ13C values from both grazing treatments varied little after grazing removal (Fig. 2).

4. Discussion

Our data demonstrate that above-ground changes in plant species composition, consequent to the removal of sheep grazing had an effect on below-ground soil invertebrate trophic relationships at the functional group level. In contrast, removing fertilizer applications caused no detectable change in below-ground trophic relations, as measured by δ15N and δ13C.

Our primary objective was targeted at the overall soil–plant system level and to that end we chose to study soil invertebrates at the functional group level. Thus identifying fauna to species was not made, as the study did not demand such a degree of precision. However, isotopic information at the species level is a necessary pre-requisite for studies of, e.g. intra-generic trophic relationships (Schmidt et al., 1997; Briones et al., 1999, 2001; Neilson et al., 2000) or detailed food web and feeding studies (Scheu and Falca, 2000; Tayasu et al., 2002).

Previous ecological studies, which integrated above- and below-ground components of the soil ecosystem, used soil invertebrate abundance and biomass, in addition to microbial biomass, to measure treatment effects (Bardgett et al., 1993a, 1997, 1998; Laakso and Setälä, 1999; Wardle et al., 1999; Stark et al., 2000). From our study, it is evident that subtle changes in trophic relationships (e.g. earthworm cf. slug) within an ecosystem can be detected using stable isotopes.

Earthworm abundances are highly unresponsive to floristic changes (Wardle et al., 1999), however, earthworm δ15N from the grazed treatments was significantly more

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**Table 5**

<table>
<thead>
<tr>
<th></th>
<th>Grazed</th>
<th>Ungrazed</th>
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<tbody>
<tr>
<td></td>
<td>δ15N (‰)</td>
<td>δ13C (‰)</td>
</tr>
<tr>
<td>Slugs</td>
<td>3.0 (0.35)</td>
<td>27.4 (0.29)</td>
</tr>
<tr>
<td>Earthworms</td>
<td>5.3 (0.18)</td>
<td>27.6 (0.12)</td>
</tr>
<tr>
<td>Beetles and spiders</td>
<td>8.1 (0.50)</td>
<td>28.0 (0.25)</td>
</tr>
<tr>
<td>Whole soil</td>
<td>5.3 (0.15)</td>
<td>28.2 (0.09)</td>
</tr>
<tr>
<td>δveg</td>
<td>2.1</td>
<td>29.6</td>
</tr>
</tbody>
</table>

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\[ ^{15}\text{N-enriched than those from the ungrazed treatments. } \]

There are several possible explanations for this effect, inter alia.

Above- and below-ground grazing increases root exudation (Bokhari and Singh, 1974; Dyer and Bokhari, 1976; Holland et al., 1996; Denton et al., 1999; Schuman et al., 1999). Exudation is an important soil microbial substrate in grasslands (Bardgett et al., 1998; Holland et al., 1996; Mawdsley and Bardgett, 1997). Resulting microbial growth can support a greater abundance of other soil microfauna, e.g. nematodes (Freckman et al., 1979). Conversely, the removal of grazing reduces the abundance of soil microfauna such as nematodes and Collembola (Bardgett et al., 1993a, 1997). Therefore, the \(^{15}\text{N-enrichment of earthworms from the grazed treatments may reflect the ingestion of a wider range of microfauna and/or omnivory. That would imply a longer soil foodchain under grazing, a possibility supported by the larger difference (6%\(\delta \)) between omnivores/carnivores (beetles and spiders) and primary producers (\(\delta_{\text{veg}}\)) in the grazed than in the ungrazed treatments (4%\(\delta \)) (Cabana and Rasmussen, 1994).}

Removal of grazing from temperate grasslands can produce a decomposer community dominated by fungi rather than a bacteria-dominated community found in grazed plots (Bardgett et al., 1993a,b, 1996, 1997; Bardgett and Leemans, 1995). This change has concomitant ‘cascade’ effects on the species composition of other soil microfauna. For example, within nematode assemblages under grazed sites, microbivorous (bacterial feeding) nematodes predominate (Freckman et al., 1979; Ingham and Detling, 1984; Merrill et al., 1994), whereas in ungrazed sites fungivorous nematodes prevail (Freckman et al., 1979). These varying food sources may propagate different \(\delta^{15}\text{N}\) values through the trophic levels.

Slug \(\delta^{15}\text{N}\) provides further evidence that above-ground grazing by sheep altered below-ground trophic relations. Contrary to earthworm \(\delta^{15}\text{N}\), slug \(\delta^{15}\text{N}\) did not differ between grazing treatments. Slugs are herbivores (Swift et al., 1979) and \(\delta_{\text{veg}}\) differed little between treatments (Fig. 2). Although slugs take refuge from dry conditions by moving into soil, they essentially remain and feed at the soil surface (Port and Port, 1986) and would not have access, as earthworms do, to the below-ground dietary sources—microfauna or microbes. Equally, slugs have access to invertebrate-derived N only after it has been taken up by plants. Earthworms, by contrast have access to invertebrate-derived N from a number of sources including the microbes and dissolved organic N (Whalen et al., 1999).

Unlike \(\delta^{15}\text{N}\), slug \(\delta^{13}\text{C}\) differed between grazed and ungrazed treatments, with specimens from the ungrazed treatments (B and C) being 1.9%\(\delta \) more \(^{13}\text{C-enriched than those from grazed treatments (A and D). This difference also existed for earthworms. The ca. 2%\(\delta \) difference is consistent with the difference found between \(\delta_{\text{veg}}\) in the same treatments (Fig. 2), suggesting that both earthworms and slugs assimilate plant-derived C. The difference in \(\delta_{\text{veg}}\) \(\delta^{13}\text{C}\) was associated with the removal of sheep grazing and the replacement of \textit{L. perenne} with \textit{R. repens} as the dominant plant species. The foliar \(\delta^{13}\text{C of } \textit{R. repens was more }^{13}\text{C-enriched than all other sampled plant species (Neilson et al., 1998). This difference was reflected in }\delta^{13}\text{C values for slugs, earthworms and putative omnivores/carnivores in the soil system, but not for whole soil (Fig. 2).}

N fertilizer application had no measured effects on soil invertebrates or on their trophic relationships, as evaluated by \(\delta^{13}\text{C and }\delta^{15}\text{N}\). It was not possible (nor was it intended) to directly trace fertilizer N into the fauna because the fertilizer \(\delta^{15}\text{N}\) is known to be quickly transformed and lost as a distinct signal in soil microbial processes (Hauck et al., 1972).

The \(\delta\) values of fresh or decaying plant material change temporally (Farquhar and Richards, 1984; Stewart et al., 1995; Wedin et al., 1995; Handley and Scrimgeour, 1997; Handley et al., 1999). As measured here, the isotopic values of soil organisms feeding on plant material track these changes. In contrast, Ponsard and Arditi (2000) noted no temporal shifts of invertebrate \(\delta^{15}\text{N}\) in studies from temperate deciduous forests.

In conclusion, changes in above-ground grazing which altered plant species composition were propagated through the soil food web to detritivores, herbivores and omnivores/carnivores, and were manifested as changes in \(\delta^{13}\text{C and }\delta^{15}\text{N}.

Acknowledgments

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