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Soil Biology & Biochemistry 39 (2007) 709–713

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Short communication

Introduced slugs and indigenous caterpillars as facilitators of carbon and nutrient mineralisation on a sub-Antarctic island

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Received 27 July 2006; received in revised form 11 September 2006; accepted 20 September 2006
Available online 27 October 2006

Abstract

Indigenous soil macroinvertebrates (moth larvae, weevil larvae, earthworms) are cardinal agents of nutrient release from litter on sub-Antarctic Marion Island (47°S, 38°/E). Their populations are threatened through predation by introduced house mice, which do not prey on an introduced slug *Deroceras panormitanum*. A microcosm study was carried out to explore whether slugs affect rates of carbon and inorganic nutrient mineralisation from plant litter differently to an indigenous caterpillar (larva of a flightless moth *Pringelophaga marioni*). Caterpillars stimulated N, Ca, Mg and K mineralisation from plant litter two to five times more than slugs did, whereas the two invertebrate types stimulated C and P mineralisation to the same degree. Consequently, ratios of C:N and N:P released from the litter were different for slugs and caterpillars. Such differences might affect peat nutrient quality and ultimately the peat accumulation-decomposition balance, an important driver of ecological succession. This suggests that slugs cannot simply replace caterpillars without consequences for ecosystem structure and functioning on the island.

Keywords: Sub-Antarctic; Moth larva; Slug; Soil fauna; Soil macroinvertebrate; Nutrient mineralisation; Nutrient cycling; Carbon mineralisation; Litter respiration; C:N ratio; Microcosm; Alien biota

Three features have important consequences for ecosystem functioning on sub-Antarctic Marion Island (47°S, 38°/E): (1) the island's hyperoceanic climate means there are no bitterly cold or dry periods and hence a long growing season and high annual primary production (Smith, 1987a, b), (2) the island evolved in isolation from the continents so there is an absence of important ecological functional groups such as vertebrate herbivores and predators, (3) soil macroinvertebrates occur at high densities in many of the island's habitats.

The lack of herbivores and predators means that most of the energy and nutrients incorporated in the primary production goes through a detritus-, rather than a grazing-, chain. However, the oceanic climate also results in slow decomposition since the consistently cool weather, high cloud cover and very high rainfall result in soils with continuously low temperature and excessive moisture, both of which restrict microbial activity. Decomposition, with the concomitant release of nutrients, is the main bottleneck in nutrient cycling (and hence a major limitation to primary production) for most of the island's plant communities (Smith, 1988). Soil-inhabiting macroinvertebrates feed on plant litter, peat and microorganisms and are cardinal facilitators of mineralisation of nutrients locked up in peat and plant litter (Smith and Steenkamp, 1992, 1993).

As is typical for oceanic islands, invasive alien organisms can substantially influence ecosystem structure and functioning at Marion Island. A particularly striking example is the introduced house mouse (*Mus musculus* L) which, by preying heavily on soil macroinvertebrates (Gleeson and van Rensburg, 1982), impacts severely on their population dynamics (Crafford and Scholtz, 1987; Chown, 1990). Mice daily consume up to 194 g (dry mass) macroinvertebrates per hectare, with between 1 and 6 times the average biomass of a particular prey species being consumed annually (Crafford, 1990; Smith et al., 2002).

Such heavy predation, by removing the cardinal agents of nutrient mineralisation, might have serious implications

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0038-0717/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2006.09.026

for ecosystem structure and functioning on the island, e.g. decreased rates of nutrient release might result in decreased nutrient quality of plant litter, slower decomposition and hence changed rates of peat accumulation. Peat accumulation, through its effects on the hydrological regime, is one of the most important factors controlling vegetation succession on the island, (Gremmen, 1981; Smith, 1987c).

The limacid European slug *Deroceras panormitanum* (Lessona and Pollonera) is another invasive organism on Marion Island, inadvertently introduced there in the mid- to late-1960s (Smith, 1992; referred to there as *Deroceras caruanae*). In 1972, slugs were found only at the base station on the east side of the island. They have subsequently spread throughout the low altitude regions of the island and in some habitats occur in greater numbers than any indigenous macroinvertebrate. They feed on a wide variety of the island's vascular and cryptogamic plant species, are detritivores and probably also microbivores. Like the indigenous macroinvertebrates they markedly stimulate rates of nutrient release from plant litter (Smith and Steenkamp, 1992). Slugs do not appear to be preyed on regularly by mice since slug remains are seldom found in mouse stomach contents and captured starved mice refuse offered slugs but will readily eat indigenous invertebrates (Smith et al., 2002).

Potentially then, slugs can replace indigenous macroinvertebrates as nutrient recyclers in areas of high mouse density, according with suggestions based on modelling soil fauna–microorganism functional interactions that ecosystems could sustain the loss of some species or functional groups with little decline in functionality because of compensatory changes in the abundance of surviving species or functional groups (Hunt and Wall, 2002). However, that might not be the case if the slugs cause qualitative or quantitative differences in decomposition compared with indigenous soil macrofauna. For instance, they might cause inorganic nutrient release rates that, relative to rates of carbon release, are different to those caused by indigenous invertebrates, leading to different carbon:nutrient ratios in the decomposing substrate and ultimately affecting peat nutrient quality and hence primary production.

A microcosm study was carried out to explore whether slugs affect rates of carbon and inorganic nutrient mineralisation from plant litter differently to an indigenous caterpillar (larva of a flightless moth *Pringelophaga marioni* Viette). Sixteen microcosms similar to those described by Anderson and Ineson (1982) were used. The inner container (75 mm long, 65 mm diameter) closed at both ends with 400-mesh polyester netting contained 3 g air-dried *Agrostis magellanica* Lam. leaf litter cut into c. 2 cm pieces. *A. magellanica* is the most common vascular plant in mire communities and moth larvae and slugs both occur in mires. The microcosms were capped with lids fitted with a rubber "o-ring" that ensured an airtight fit. A 15 mm hole in the centre of the lid allowed air exchange between inside and outside the microcosm. A 5 ml inoculum of peat solution (100 g wet mass peat shaken up in 500 ml distilled water) was added to the litter in the microcosms and then 200 ml distilled water added. After 1 hour the microcosms were drained of water through the plastic tube. Another 200 ml water was added, left for 1 hour and drained. The litter of 4 microcosms was removed, oven-dried, weighed and kept for chemical analysis. The mean mass for the 4 samples (2.74 g) was taken as the oven-dried mass of litter in the rest of the microcosms, which were incubated at 10 °C for 5 days before again being leached with 200 ml water. After that leaching, one weighed slug was added to 4 of the microcosms and one weighed caterpillar to another 4. The 4 remaining microcosms without animals served as controls. Similar-sized, full-grown animals were chosen; mean slug (fresh) mass was 0.99 g and mean caterpillar mass was 0.84 g.

The microcosms were kept in the incubator at 10 °C for the duration of the experiment. Counting day 0 as the time when animals were added, the microcosm contents were leached with autoclaved distilled water on days 1, 3, 6, 8, 12 and 15. The leachates were analysed for inorganic forms of nutrients using standard methods (Mackereth et al., 1978).

The amounts of inorganic nutrients released per gram oven-dry mass of litter were calculated from the leachate concentrations. On days 1, 2, 3, 5, 7, 9, 11, 13 and 15, CO_2 efflux from the microcosms was measured as follows. The hole in the microcosm lid was fitted with a silicon rubber bung pierced by a glass tube. Each microcosm was flushed for about 30 min. with air taken from outside the laboratory and preconditioned to 10 °C. The microcosm was then connected to a gas exchange system that measured CO_2 efflux. The system was very similar to the one used for flushing except that the pump was regulated by a mass flow controller and the CO_2 concentrations in the inlet and outlet air streams were monitored by an ADC Series 225 III infrared CO_2 analyser (Analytical Development Corporation, Herts, UK). The difference between the inlet and outlet CO_2 concentrations were integrated over 30 min and used to calculate CO_2 efflux rate.

Carbon and nutrient mineralisation rates were estimated as the slopes of the linear regressions of the cumulative totals of C or nutrients released against time. The rates (nmol C or nutrient released g^{-1} litter h^{-1}) were subjected to Anova testing to assess the between-treatment differences in mineralisation rate. Subtracting the mean rate for the 4 control microcosms from the rates for individual animal microcosms gave an estimate of how much the slug or caterpillar enhanced mineralisation rate in a particular microcosm. Dividing that value by the wet mass of the added animal yielded mass-normalised release rates (μmol C or nmol nutrient released g^{-1} litter g^{-1} animal h^{-1}), which accounted for between-microcosm differences due to the fact that the animals used had different masses. Differences between the effects of caterpillars and slugs on C and nutrient release were assessed by Anova testing of the mass-normalised rates.

For control microcosms 88–92%, and for animal microcosms 93–97% (difference, $P<0.001$), of the inorganic N was released as ammonium and the rest as nitrate. Here, I report the combined amounts of NH_4–N and NO_3–N released. Fig. 1 shows the cumulative amounts of inorganic C, N and P released in the 12 microcosms during the 15 days incubation, with mean regression lines fitted per treatment. Release curves for K, Ca and Mg are not shown but exhibit a similar pattern to those in Fig. 1, with the slope of the regression lines being steeper for microcosms containing animals than for control microcosms. Treatment-mean mineralisation rates derived from the regression slopes are given in Table 1 and show that mineralisation of C and all the nutrients was stimulated by the presence of slugs or caterpillars, although the effect of slugs on Mg release was not significant at $P\leqslant 0.05$. Normalising the mineralisation rates using animal masses (the animal-mass specific release rates in Table 1) showed that caterpillars caused a significantly greater enhancement of N, Ca, Mg and K release than did slugs but that there were no differences in mass-specific C or P release rates between the two invertebrate types.

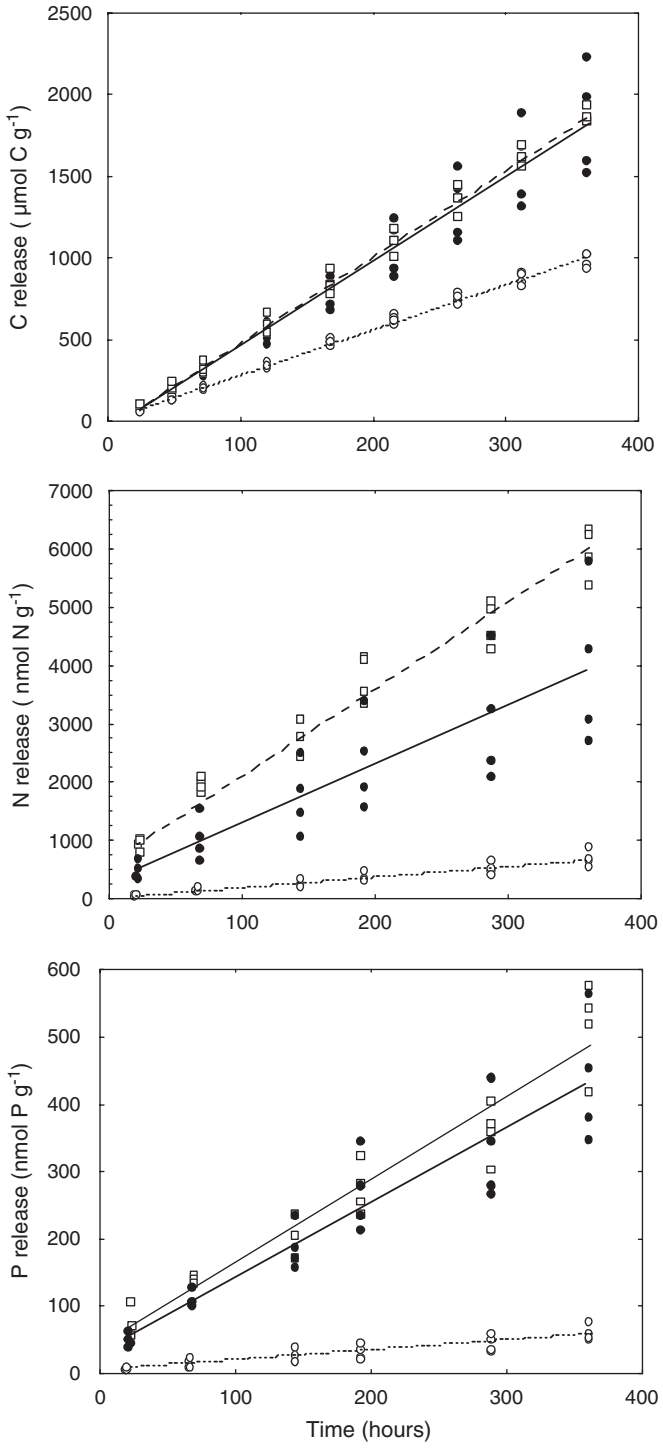

Fig. 1. Cumulative amounts of C, N and P release from microcosms containing only litter (open circles), litter plus a slug (solid circles), and litter plus a caterpillar (open squares). Mean linear regression lines are fitted for each treatment.

Patten and Witkamp (1967) were the first to use microcosms to reduce decomposition and nutrient mineralisation processes to a realistic level of complexity, where the parameters can be compartmentalised and the direct and indirect effects on nutrient mineralisation related to simple, first-order variables. That study, and many subsequent ones (see Coleman et al., 1984; Anderson and Ineson, 1984 for reviews), showed that in the presence of soil fauna CO_2 output increases over that without fauna, but by a proportionately smaller amount than the increase in nutrient mineralisation. The C, N, P and K results presented here agree; C mineralisation was increased 2-fold, but N, P and K mineralisation 3- to 8-fold, by slugs or caterpillars. Ca and Mg mineralisation was only about twice as high in animal-containing microcosms than in the controls, approximately the same as for C.

The direct contribution of soil fauna (respiration of ingested C, excretion of ingested nutrients) to decomposition/mineralisation is generally thought to be less important than the indirect effects of the fauna on microbially-mediated mineralisation (Anderson et al., 1981; Ingham et al., 1985). Indirect effects include substrate comminution and breakdown of recalcitrant high molecular weight compounds to molecules that can more easily be assimilated by microbes (Anderson and Ineson, 1984; Ji and Brune, 2001), inocula dispersal (Swift and Boddy, 1984; Rantalainen et al., 2004), a change in bacterial:fungal ratio of the decomposer population (Ingham et al., 1985; Mamilov et al., 2001) and microbivory (Aira et al., 2006). The latter, although it may decrease the density of the decomposer microorganisms, often leads to increased microbial turnover rate and activity through removal of density-dependent limitations on microbe growth and increased nutrient availability (Bååth et al., 1981; Schroter et al., 2003). Soil fauna can also cause an increase in microbial density on the decomposing substrate, due to enhanced growth of both ingested and endogenous gut microbiota during the passage of materials through the animal gut. (Reyes and Tiedje, 1976; Bardgett et al., 1998; Tiunov and Scheu, 2000). Mucous excretion by slugs has also been shown to significantly increase microbial

Table 1
Carbon and nutrient release from litter in microcosms containing litter only (controls), litter plus a slug or litter plus a caterpillar

	C	N	P	Ca	Mg	K
(a) *Release rate (nmol g^{-1} litter h^{-1})*						
Control	2759 ± 134^{a}	1.80 ± 0.040^{a}	0.15 ± 0.03^{a}	4.65 ± 0.54^{a}	6.49 ± 0.40^{a}	1.44 ± 0.49^{a}
Slug	5189 ± 969^{b}	10.03 ± 3.62^{b}	1.11 ± 0.28^{b}	7.02 ± 1.48^{b}	8.77 ± 0.82^{a}	5.03 ± 2.41^{b}
Caterpillar	5282 ± 146^{b}	14.25 ± 1.08^{b}	1.23 ± 0.19^{b}	9.67 ± 1.21^{c}	15.32 ± 3.19^{b}	8.02 ± 1.73^{b}
(b) *Animal mass-specific enhancements of release rate (nmol g^{-1} litter g^{-1} animal h^{-1})*						
Slug	2416 ± 581^{a}	8.16 ± 2.36^{a}	0.97 ± 0.17^{a}	2.24 ± 1.16^{a}	2.29 ± 0.50^{a}	3.47 ± 1.88^{a}
Caterpillar	3056 ± 423^{a}	15.27 ± 3.73^{b}	1.31 ± 0.34^{a}	6.16 ± 2.05^{b}	11.04 ± 2.63^{b}	7.80 ± 1.31^{b}

(a) Mean release rates ($\pm$standard deviation, $N = 4$), (b) Invertebrate mass-specific stimulation of release rate ($\pm$standard deviation, $N = 4$). Different superscripts indicate that the treatment means differ at $P \leqslant 0.05$, from Anova and Tukey's Honest Significant Difference tests.

biomass, respiration and release of C, N and P from leaf litter (Theenhaus and Scheu, 1996).

The degrees to which the slugs or caterpillars directly or indirectly stimulated microbial carbon mineralisation in this study can be estimated on the assumption that at the start of the experiment (day 1) the difference in CO_2 evolution between control and animal-containing microcosms was due to animal respiration, whereas at the end (days 13 and 15) it was due to animal respiration plus the stimulatory effect of the animals on microbial respiration. On day 1 the difference in CO_2 efflux between animal and control microcosms, ascribed to animal respiration, was 1.26 μmol CO_2 g^{-1} h^{-1} for slugs and 1.43 μmol CO_2 g^{-1} h^{-1} for caterpillars. By days 13/15, the mean difference in CO_2 efflux rate between slug-containing microcosms and control microcosms was 3.14 μmol'CO_2 g^{-1} h^{-1}, 40% of this due to slug respiration and 60% to the slug's stimulation of microbial respiration. The mean difference between caterpillar-containing microcosms and control microcosms on days 13/15 was 2.98 μmol CO_2 g^{-1} h^{-1}, 48% due to caterpillar respiration and 52% to the stimulation of microbial respiration. These proportions of enhanced CO_2 evolution due to slug- or caterpillar respiration (40% and 48%, respectively) are larger than those reported from other microcosm studies, where the invertebrates account for 13% or less of total CO_2 evolution (Anderson et al., 1981; Schroter et al. 2003), probably due to the large size of the slugs and caterpillars compared with the protozoa, collembola and nematodes considered in the other studies.

Considering the argument made at the start of this paper—that a decline of indigenous macroinvertebrate populations through mouse predation might be compensated for by an increase in the abundance of slugs so that nutrient cycling processes are minimally affected, the most significant finding of this study is that caterpillars stimulated N, Ca, Mg and K mineralisation 2–5 times more than did slugs, whereas C and P mineralisation was enhanced to the same extent by the two invertebrate types. Average C:N ratio released in control microcosms was 1580 ± 296 (1580 mol carbon released per mol N). For slug microcosms, C:N released was 541 ± 89 and for caterpillar microcosms it was 372 ± 30 (between-invertebrate difference, $P = 0.011$). Similarly, the C:P ratio released in control microcosms ($18\,683 \pm 2491$) was lowered by slugs (4735 ± 298) and caterpillars (4380 ± 649) but the slug–caterpillar difference was not significant at $P \leqslant 0.05$. Leachate N:P ratio was 9 ± 1 for slugs and 12 ± 1 for caterpillars ($P = 0.016$). These differences in the relative rates of C, N and P release are possibly related to differences in feeding strategies of the two invertebrate types and a consequent effect on the size and activity of the decomposing microorganisms. Mucous production by slugs is almost certainly another cause, also related to its effect on microorganisms.

It is qualitative and quantitative differences during decomposition such as these that can result in changes in peat nutrient quality, altered density and diversity of soil microbial populations, and a shifted balance between primary production and decomposition. Although this study considered only one of Marion Island's indigenous soil macroinvertebrate species, the results do suggest that the substitution, or partial substitution, of indigenous macroinvertebrates by slugs as facilitators of decomposition and nutrient cycling is unlikely to be inconsequential for ecosystem structure and functioning on the island.

This research was supported by the National Research Foundation under Grant number 2068303 and by the University of Stellenbosch. The South African Department of Environmental Affairs and Tourism provided logistic support for the research.

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