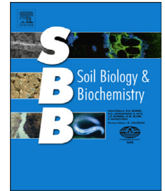
Soil Biology & Biochemistry xxx (2013) 1–7

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio



Trophic stability of soil oribatid mites in the face of environmental change

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ARTICLE INFO

Article history:
Received 27 June 2013
Received in revised form
13 September 2013
Accepted 18 September 2013
Available online xxx

Keywords:
^{15}N Stable isotope
N deposition
Oribatid mites
Stability
Q1 Trophic structure

ABSTRACT

A key issue in ecology is the degree to which trophic structure within communities responds to environmental change. Organisms with generalist diets are more flexible in their feeding habits than are specialists, and may be affected less in a changing environment. Soil fauna fulfill crucial ecosystem functions in terrestrial ecosystems and many are thought to have generalized diets. They may therefore be buffered from negative effects of environmental change. Here, we used ^{15}N isotope analysis to study trophic differentiation among 91 species of oribatid mites and their responses to chronic atmospheric N deposition. Combining our own measurements with published data, we established that the trophic positions of mite species were remarkably stable within and among forests, as well as between ambient and experimental N deposition. Trophic stability indicates a higher than expected level of feeding specialization, which may foster diversity, but limit the ability to switch food resources in a changing environment.

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1. Introduction

Soil animal communities are among the most species-rich components of terrestrial ecosystems (Giller, 1996). In one square meter of soil, there may reside ~200 species of arthropods and up to ~1000 species of soil animals (Anderson, 1975a). However, studies of the feeding biology of soil animals have revealed that many exhibit surprisingly similar behavior, with most apparently consuming a mixture of microbial and plant materials; accordingly, they have been classified as non-specialized feeders (Scheu et al., 2005). The existence of astonishingly high local diversity, with a low level of food resource specialization, is considered an ecological "enigma".

To explain the high diversity of soil animal communities, there has been speculation about finer-scale differences in food resource utilization among these generalist decomposers, which could go undetected using traditional methods, such as gut content analyses or food choice experiments (Anderson, 1975a). For instance, it is difficult to use gut content analyses to distinguish between what is ingested by soil animals and what is actually assimilated as food, unless egestion is also studied (Scheu, 2002). Similarly, observations of litter feeding do not exclude the possibility that the soil animals actually target microorganisms or other animals that colonize or dwell on the leaf litter. In this case, soil animals should be characterized as bacterial/fungal feeders (microbivores) or predators, rather than saprotrophic feeders that consume litter itself (Coleman et al., 2004).

In contrast to gut content analysis or food choice experiments, stable isotope ratios reflect the long-term trophic relationships of animals and are a powerful tool in evaluating the trophic structure of animal communities (Minagawa and Wada, 1984; Scheu and Falca, 2000). In general, there is discrimination against ^{15}N during catabolism, leading to an accumulation of ^{15}N in organisms relative to their food resource (Minagawa and Wada, 1984). Reviews of different food webs have demonstrated that there is an average increase of 3.4‰ of ^{15}N with each trophic level, although the enrichment levels may vary among different taxonomic groups or developmental stages (Post, 2002).

Describing the trophic structure of soil animals would not only provide insight into potential niche differentiation underlying their coexistence, but also substantially improve our ability to predict effects of global environmental change on soil food web structure and dynamics. If many soil fauna are indeed dietary generalists, they may be buffered to a greater extent from environmental change than are dietary specialists. Recent meta-analyses indicate that chronic atmospheric N deposition, a pervasive agent of global change, can reduce microbial biomass (−20%) and inhibit litter

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0038-0717/$ – see front matter © 2013 Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.soilbio.2013.09.019

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decay in many forests (Knorr et al., 2005; Liu and Greaver, 2010), thereby decreasing the flow of energy through soil food webs and reducing the population size of soil animals especially microarthropods (−44%, Gan et al., 2013). The decline of soil microarthropods in response to reductions in microbial biomass suggests that these animals are limited by food resources. Therefore, reduced energy flow from the microbial community could also alter the trophic structure of soil food webs, especially if microbivorous soil animals switch their diets to other food sources. The generalist feeding habits ascribed to most soil animals suggest that such a switch is plausible (Behan and Hill, 1978; Maraun et al., 2003; Scheu et al., 2005), but we have a limited understanding of how a reduced flow of energy, the result of chronic N deposition, may affect the trophic structure of soil food webs.

Our study focused on the trophic structure of soil oribatid mites, a major group of wingless microarthropods in many ecosystems; up to 170 species can coexist in the litter and soil of hardwood forests (Hansen, 2000). Recent studies of their $\delta^{15}N$ reveal that they occupy more than four trophic levels, which may, in part, contribute to their high local diversity (Schneider et al., 2004). However, estimating trophic differentiation among oribatid mites based on ^{15}N analysis requires additional empirical work (Maraun et al., 2011). By obtaining measurements of ^{15}N from oribatid mites dwelling in the forest floor and combining information from previous ^{15}N studies, the first aim of our study was to investigate the trophic structure of an oribatid mite community and determine the frequency of saprotrophic feeders compared to those with other feeding habits. We expected to find a low frequency of saprotrophic species, assuming a lack of co-evolution between consumers and dead plant material. Secondly, we investigated the stability of the trophic structure of soil oribatid mites in the face of environmental change, specifically chronic nitrogen deposition as well as variation among different forest types. Previous research at our field sites has revealed that chronic experimental N deposition has reduced plant litter decay and accelerated organic matter accumulation in forest floor and surface mineral soil (Zak et al., 2008). At the same time, microbial biomass has been reduced by 18% under experimental N deposition (DeForest et al., 2004). The lower microbial biomass and the slowing of litter decomposition has reduced the flow of energy into the detrital food web, reducing the abundance of microarthropods by 41% and shifting species composition within the oribatid mite community (Gan et al., 2013). We expected that, following the decrease in microbial biomass and slowing of litter decay under chronic nitrogen deposition (Zak et al., 2008), oribatid mites would feed more on plant litter leading to a decline in their trophic position from higher to lower trophic levels.

2. Materials and methods

2.1. Site description

We collected soil oribatid mites from a long-term study of experimental N deposition consisting of four sugar maple (*Acer saccharum* Marsh.)-dominated northern hardwood forests in the Great Lakes region of North America. These four sites are denoted as Site A (46:51N; 88:52W), Site B (45:32N; 84:51W), Site C (44:22N; 85:49W) and Site D (43:40N; 86:08W) spanning from north to south in the state of Michigan, USA. The sites are floristically and edaphically matched (>80% sugar maple on sandy soils), but they differ in climate along a north-south latitudinal gradient. These hardwood forests are underlain by slightly acid soils (pH 4.41–4.70) that are well-drained sandy typic Haplothords of the Kalkaska series. Within each study site, six 30-m × 30-m plots were established in 1994; 3 plots receive ambient N deposition and the remaining 3 plots receive an additional 30 kg $NO_3^- - N\ ha^{-1}\ y^{-1}$. The additional NO_3^- is delivered over the growing season in six equal applications of solid $NaNO_3$ pellets; an additional 10-m wide buffer surrounds each plot, and it also receives the experimental treatments.

2.2. Oribatid mite collections

Forest floor (including Oi and Oe/a horizons) samples were first collected in late May 2011 as in Gan et al. (2013). Within each plot, a 10-cm × 10-cm PVC frame was randomly placed on the forest floor, and any organic substrate above the mineral soil was collected and placed into a plastic bag. At each site, a total of 6 samples were collected from each plot receiving either ambient (n = 3) or experimental N deposition (n = 3), resulting in a total of 144 samples (4 sites × 6 plots × 6 samples). All of the samples were transported to the lab in coolers and each sample was placed on a modified Tullgren funnel within 48 h to extract microarthropods (Crossley and Blair, 1991). After the 5-day extraction, litter was placed in a 60 °C oven for 24 h for subsequent determination of dry mass. A second microarthropod collection was conducted in early June 2012 in all four study sites, but from ambient N plots only (4 sites × 3 plots × 6 samples = 72 samples total).

The extracted microarthropods were preserved in 70% ethanol, which does not influence the $\delta^{15}N$ of soil animals (Fábián, 1998). The major group, oribatid mites, were enumerated under a microscope and further identified to genus or species based on the keys written by R.A. Norton and V.M. Behan-Pelletier (*unpublished*) for use at the Ohio State University Summer Acarology Program.

2.3. Stable isotope analysis

Dominant oribatid mite species from each site were removed from ethanol and placed into pre-weighed tin capsules. For each species, 10–150 individuals from the same site and sampling date were composited to generate enough mass for stable isotope analysis, which also ensured that we had a representative sample of individuals from a particular species. The tin capsules with oribatid mites were weighed again, after they were oven-dried at 60 °C for 24 h, to obtain the dry weight of mites. Each species composite ranged from 0.40 mg to 1.50 mg. For each study site, we selected the dominant species to ensure enough mass for isotope analysis. In total, we were able to analyze 23 species of oribatid mites, each with 1–4 composite replicates from the ambient N plots at our four study sites. In addition, nine of the 23 species were also sufficiently abundant in the experimental N deposition plots for analysis. These 9 species were paired for comparisons with the same species from adjacent ambient N plots, with 5 species pairs from Site A, 3 pairs from Site C and 1 pair from Site B from the same sampling trip (May 2011).

A total of 24 ground litter samples were also analyzed for ^{15}N abundance, which we used as background to adjust the $\delta^{15}N$ of mites. The litter samples collected on May 2011 were oven dried at 60 °C for 24 h, following microarthropod extraction. The dried litter from each N deposition treatment (ambient vs. elevated) was composited and homogenized for each site. A subsample of 5 g from each of the litter composites was ground. Two replicates (5 mg) from the ground samples, together with mite samples collected in June 2012, were sent for stable isotope analysis at the Stable Isotope Facility at the University of California, Davis. The mite samples collected in May 2011 were analyzed in the Terrestrial Ecology Stable Isotope Lab at the University of Michigan. In both facilities, the $^{15}N/^{14}N$ ratios of animals and litter were determined by a coupled system of an elemental analyser (UC Davis: NA 1500, Carlo Erba, Milan; U of Michigan: NC2500, CE Elantech, NJ) and stable isotope mass spectrometer (UC Davis: MAT 251, Thermo Finnigan, CA; U of Michigan: Delta Plus, Thermo Finnigan, CA).

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