Soil Biology & Biochemistry 72 (2014) 19–25

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Change the menu? Species-dependent feeding responses of millipedes to climate warming and the consequences for plant–soil nitrogen dynamics

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ARTICLE INFO

Article history:
Received 29 July 2013
Received in revised form
18 January 2014
Accepted 21 January 2014
Available online 1 February 2014

Keywords:
Climate change
Ecosystem engineer
Functional traits
Ectotherm
Indirect effect
Soil macrofauna
Plant-soil linkage

ABSTRACT

Although the direct effects of global warming on carbon and nutrient cycling between vegetation and soil have received much research attention, little is known about the indirect effects that occur through trophic interactions. The combined effects of air warming (+3.3 °C) and millipedes on plant–soil nitrogen cycling and the millipede species dependency of the warming effects were assessed for two millipede species in a laboratory microcosm experiment. Warming accelerated cast production derived both from leaf litter and also probably soil, by millipedes, which resulted in an increase in inorganic nitrogen in the soil. However, the changes in millipede feeding and cast production due to warming did not have any significant effects on plant properties. Furthermore, the effects of warming on the cast production by millipedes and coincidental changes in soil inorganic nitrogen were similar for both of the evaluated millipede species. Interestingly, however, warming altered the way of food consumption differently for the two species: litter consumption by *Parafontaria tonominea* was increased, whereas that by *Parafontaria laminata* decreased under the warmer regime. Such species-specific consequences of warming on food consumption may cause a change in the structure and function of the organic horizon and surface soil. To predict the consequences of a warming climate on plant–soil nutrient feedback via millipedes, it is suggested that attention should be given to the relationship between behavioral traits, such as species-specific feeing behavior and environmental changes.

1. Introduction

Understanding the effects of increasing temperature on the quantity and quality of primary production is crucial for predicting future forest ecosystem services (Millennium Ecosystem Assessment, 2005). However, when compared to the direct abiotic effects of warming on plants (e.g., Zhao and Running, 2010), the indirect effects on plants mediated through organisms associated with the plants are poorly understood (Rouifed et al., 2010) because of the complex interactions between the responses of such organisms and the responses of plant performance.

The soil macrofauna, such as earthworms and millipedes, attains a large biomass in forest soil (e.g., Hopkin and Read, 1992; Toyota et al., 2006) and enhance nitrogen cycling in plant–soil systems by feeding on litter and/or soil (Anderson et al., 1983; Setälä et al., 1996; Callaham and Hendrix, 1998; Fujimaki et al., 2010; Kawaguchi et al., 2011; Sylvain and Wall, 2011). Indeed, the soil macrofauna facilitates nitrogen dynamics via litter comminution and their digestive activity, thereby promoting nitrogen release and litter utilization by soil microbes through detritivore casts (Cárcamo et al., 2000). As primary production is often limited in forest ecosystems by the nitrogen availability (LeBauer and Treseder, 2008), the feeding activity of the soil macrofauna can be linked to primary production through the nitrogen available in the soil (Osler and Sommerkorn, 2007).

Temperature increases influence the metabolism of the soil macrofauna and its feeding behavior (Read, 1985; David and Gillon, 2009; Ott et al., 2012). In fact, a temperature increase from 15 to 23 °C was reported to enhance the consumption of pine needle litter by a millipede species in temperate forests (Coûteaux et al., 2002). Nonetheless, the effects of warming-induced changes in the feeding behavior of the soil macrofauna on soil nitrogen cycling and primary production have not been well investigated to date (but see Eisenhauer et al., 2012). The increase in the litter and/or soil feeding of the soil macrofauna by warming is expected to

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0038-0717/$ – see front matter © 2014 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.soilbio.2014.01.016

enhance available N in soil for plants through the increase of cast production, which could lead to the increase of primary production (Hypothesis 1).

Millipedes species exhibit great variation in morphological, physiological, and behavioral traits (see examples in Hopkin and Read, 1992; David and Handa, 2010), which may help response of the soil fauna to changes in climate conditions (Sheridan and Bickford, 2011; Bokhorst et al., 2012; Dias et al., 2013; Krab et al., 2013). In central Japan, two millipede species, *Parafontaria laminata* and *Parafontaria tomominea* have been intensively investigated to play an important role for litter decomposition and soil N dynamics (Hashimoto et al., 2004; Toyota et al., 2006; Fujimaki et al., 2010; Iwashima et al., 2011; Iwashima, 2013). Traits such as body size and temperature range of the main habitat are different between the two species, which lead to the expectation that alterations in feeding behavior and the associated nitrogen dynamics in a plant–soil system under a warming climate are specific for the two millipede species inhabiting in the system (Hypothesis 2).

To test these hypotheses, we conducted a microcosm experiment to determine the effects of warming on plant–soil N dynamics and species dependency of these effects. To our knowledge, this is the first study that explicitly unravels the interactions of global warming, interspecific variation in detritivore behavioral traits, and nutrient dynamics between plants and soil.

2. Materials & methods

2.1. Collection of litter, soil, animals, and seedlings

We studied the effects of air temperature and the presence of two related species of millipedes on decomposition, soil properties, and plant growth characteristics. Adult individuals of two millipede species, *Parafontaria tonominea* Attems and *P. laminata* Attems (Xystodesmidae), were collected in the spring of 2012. Because the adult individuals of the two species emerge periodically (i.e., every three years for *P. tonominea* (Kaneko and Hashimoto, 2010) and every eight years for *P. laminata* (Niijima, 1984)), it is often difficult to locate these two species at the same sites within the same season. Therefore, we hand-collected the two species from two locations under different climate conditions in central Japan: *P. tonominea* from Mt. Okusu at 240 m a.s.l. (35°15′00″N, 139°37′41″E) and *P. laminata* from Mt. Kumotori at 1100 m a.s.l. (35°51′19″N, 138°56′37″E). The mean body mass of each species was as follows: male *P. tonominea*, 0.99 ± 0.03 g individual^{-1}; female *P. tonominea*, 1.09 ± 0.05 g individual^{-1}; male *P. laminata*, 0.29 ± 0.02 g individual^{-1}; and female *P. laminata*, 0.41 ± 0.01 g individual^{-1}.

The top 20 cm of soil under the litter layer was collected for the experiment from a Japanese oak (*Quercus crispula* Blume) forest in Yatsugatake Forest, University of Tsukuba in central Japan (35°57′N, 138°27′E). The soil type is Andosol according to the FAO-UNESCO classification. Because the soil profile does not have a distinct humus layer, the collected soil mainly included organic-rich mineral soil. It is reported that the geographical origin and species of leaf litter does not affect the feeding behaviors of these two millipedes (Iwashima et al., 2011; Iwashima, 2013; unpublished Ph.D. thesis).

We collected the over-wintered litter of Japanese oak in the same forest; the litter was placed in a plastic bag to avoid desiccation and transported to the laboratory for the experiment described below. We used current-year Japanese oak seedlings, the seeds of which were collected in 2011 from the same region and pre-grown in a nursery. Japanese oak is one of the most dominant species in cool-temperate forests in Japan and is predicted to expand further with the continuing decline of *Fagus crenata* Blume due to temperature warming in central Japan (Matsui et al., 2004).

2.2. Microcosm

The microcosms were prepared to represent the forest floor habitats of the two millipede species in central Japan. The soil was passed through a 4.75-mm sieve for homogeneity and to remove roots and stones, and 1500 g of fresh soil was placed in a PVC cylinder of 15.5 cm diameter and 15 cm depth (Fig. 1). The density of the soil in the cylinder was standardized by compression to approximately 1.6 g fresh soil cm^{-3}, which was the average value in the forest where we obtained the samples. After planting one Japanese oak seedling in the center of each cylinder, 5.5 g of Japanese oak litter, representing the litter pool at the sampling site (12.0 g litter within 0.04 cm^{-2}), was placed on the soil surface. A pair (one male and one female) was introduced into each cylinder, resulting in a density of approximately 121 individuals m^{-2}, which was within the range observed during the swarming of *P. laminata* in the Yatsugatake region (Hashimoto et al., 2004). The present design does not take into account “biomass effects” (two individual of the two species have different biomass), because this study aims to clarify the response of millipede at individual level. Each cylinder was then covered with 2-mm nylon mesh to prevent the millipedes from escaping (Fig. 1).

2.3. Experimental design

We arranged three microcosm millipede treatments: without millipedes, with *P. tonominea*, and with *P. laminata*. The microcosms were incubated at two temperature regimes (Low, 20 °C during the day and 15 °C at night; High, 23.3 °C during the day and 18.3 °C at night) from the beginning of July to the end of September in the Earthtron climate chamber at Yokohama National University (for details, see Kamitani and Kaneko, 2006). The “Low” temperature regime is in the range of mid-summer temperatures in the central mountain range of Japan where we

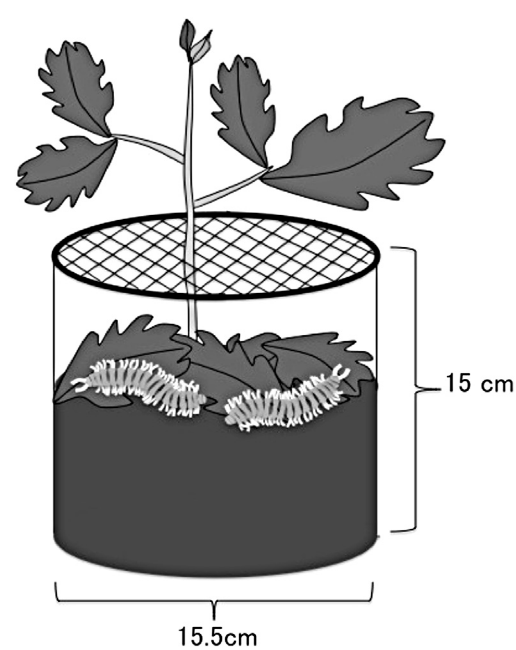

Fig. 1. Schematic presentation of a microcosm used in the study.