Soil Biology & Biochemistry xxx (2013) 1–8

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

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

Reduction in snow depth negatively affects decomposers but impact on decomposition rates is substrate dependent

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ARTICLE INFO

Article history:
Received 6 February 2013
Received in revised form
8 March 2013
Accepted 10 March 2013
Available online xxx

Keywords:
Acari
Collembola
Litter
Mass loss
Snow
Soil respiration
Winter

ABSTRACT

Decomposition of organic matter in high latitude biomes makes a significant contribution to global fluxes of nutrients and carbon and is expected to accelerate due to climate change. The majority of studies have focused on decomposition during the growing season, but winter climate is expected to change dramatically. Furthermore, knowledge of the drivers of organic matter decomposition, such as litter chemical composition, has primarily been tested across the growing season so it is unknown whether these drivers are also important during the winter. Given that the depth of snow cover insulates the subnivean climate from the much colder air, it is an important control on winter decomposition and is expected to be influenced by climate change, we experimentally manipulated snow cover to simulate impacts of different winter precipitation scenarios on soil processes. Our results show that despite snow reduction negatively affecting decomposer abundance (by 99%) and bulk soil respiration (by 47%), litter decomposition rates showed little to no response. Furthermore, variation in winter decomposition rates among litter types was unrelated to nutrient status, indicating that our current understanding of drivers of litter decomposition may not hold during winter months. Despite very large reductions in decomposer fauna due to snow removal, litter decomposition rates were not consistently responsive, indicative of decoupled responses of soil organisms and soil processes to winter climate change.

1. Introduction

Decomposition of organic material is highly dependent on climatic factors, the quality of the material and the activity of soil organisms (Melillo et al., 1982; Seastedt et al., 1983; Aerts, 2006). Decomposition during winter at high latitudes is typically slow due to lower temperature and reduced activity of soil organisms. Despite these restrictions there is often considerable litter mass loss during the cold season from the start of litter fall in autumn until snow melt in spring (Hobbie and Chapin, 1996). However, this mass loss does not necessarily decline in a simple manner throughout the cold season. As such, stochastic events can cause significant litter mass loss, and this is apparent through the high amounts of dissolved organic carbon in river systems following the spring flush (Kawahigashi et al., 2004), and the leaching of soluble compounds from freshly fallen litter in late autumn (Kučera, 1959; Nykvist, 1961). The cold period between leaf fall and snow melt can include periods of significant snow cover which has an insulating effect on the soil, given that air temperatures in winter are often considerably lower than soil temperatures. As such, the thickness of this cover can strongly regulate underlying soil temperature dynamics and therefore the rate of decomposition (Schimel et al., 2004).

The small number of studies on winter litter decomposition in ecosystems with significant winter snow cover and freezing have reported litter mass loss rates of approximately 20% between autumn and spring (Bleak, 1970; Abouguendia and Whitman, 1979; Moore, 1983; Hobbie and Chapin, 1996), but Bokhorst et al. (2010) found that this mass loss could occur through leaching in the autumn and with very little decomposition occurring throughout the rest of winter. However, eco-physiological activity of soil organisms does not cease when winter begins and can continue through the winter under snow cover (Grogan and Jonasson, 2006). Microbial activity measured through soil respiration is highly responsive to changes in ambient air temperatures if the snow cover is insufficient (Grogan and Jonasson, 2006; Larsen et al., 2007; Bokhorst et al., 2011). In contrast, decomposition of freshly fallen litter during winter has been shown to be unresponsive to extreme winter warming events in combination with multiple freeze–thaw cycles (Bokhorst et al., 2010). Such differences in responsiveness to winter temperatures between decomposition of fresh litter and microbial activity in soil organic matter suggests

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http://dx.doi.org/10.1016/j.soilbio.2013.03.016

that either the freshly fallen litter does not decompose during winter or that the presence and activity of litter decomposers differs between fresh litter and more degraded organic matter (Pflug and Wolters, 2001).

Soil arthropods play a major role in determining decomposition rate by fragmenting litter and through grazing pressure on saprotrophic fungi (Seastedt, 1984; Filser, 2002; Heemsbergen et al., 2004). However, they also show a vertical stratification down the soil profile (Daniel, 1965; Wood, 1967; Berg et al., 1998a; Krab et al., 2010), meaning that they are not always in the proximity of freshly fallen litter (vanderDrift, 1951; Seastedt et al., 1983). This is especially true during colder periods when the animals may migrate downwards to avoid adverse temperature conditions (Leather et al., 1995). For this reason, snow thickness plays a key role in maintaining a suitable sub-nivean microclimate for soil arthropods, and reductions in the winter snow pack will alter their community composition and distribution through the soil profile, and negatively affect their abundance (Bokhorst et al., 2012), which could in turn influence their impact on decomposition rates.

Despite increasing knowledge of the driving factors of decomposition during the growing season, relatively few studies have considered decomposition during the cold season. Yet knowledge of this is essential for understanding how northern communities and the global carbon cycle will respond to climate change, especially given that considerable shifts are expected for winter climate (ACIA, 2005; Lemke et al., 2007). Notably the duration and depth of the snow cover may undergo significant change (Johansson et al., 2011; Liston and Hiemstra, 2011) which will have major implications for both the sub-nivean temperature conditions and those organisms active in the decomposition process. To address the issue of changing winter snow conditions for decomposers and the decomposition process, we conducted a field experiment in which we experimentally reduced winter snow depth. We studied leaf litters of contrasting nutrient content because litter quality is a fundamental control of litter decomposability during the growing season (Cornwell et al., 2008) and we wanted to explore whether this is also true during the cold season. Because a decrease in snow depth is likely to inhibit soil organisms, the response of the decomposers should contribute to driving the response of litter decomposition rates to this decrease. As such, older and more recalcitrant litters may be affected more because they tend to have a higher level of microbial colonization (Berg et al., 1998b). For this reason we studied the response of litter decomposition to snow removal both for fresh litter and for older litter that had already been decomposing for a year. In addition we quantified the response to snow removal of soil microbial activity (i.e., bulk soil respiration), and of the abundance of soil micro-arthropods. Finally, we repeated measurements through the summer following snow removal to assess the longer-term consequences of changes in snow-pack depth. Specifically, we hypothesized that a) plant litter decomposition and soil respiration will be lower when snow is removed as a result of less insulation and therefore lower soil temperatures inhibiting decomposer activity. b) The relative response of litter decomposition to snow removal will be greater for low-quality litters that had already been decomposed for a year due to the build-up of decomposers (Hasegawa and Takeda, 1996; Moorhead and Sinsabaugh, 2006). c) Soil decomposer animals will be reduced in number and will occur abundantly only at greater depths when snow is removed. d) These changes in micro-arthropods will coincide with reduced decomposition rates due to snow removal, because of the role of microarthropods in the decomposition process. The experimental testing of these four hypotheses will provide valuable insights into how soil processes leading to litter breakdown and C sequestration may be altered as a result of changes in winter snow regimes.

2. Materials and methods

2.1. Site description and snow manipulation

The snow manipulation treatments were set in a mixed boreal forest stand dominated by birch (*Betula pubescens*), aspen (*Populus tremula*) and pine (*Pinus sylvestris*) close to the Swedish University of Agricultural Sciences campus in Umeå (63°49′ N, 20°15′ E). The mean annual temperature for Umeå is 5 °C with mean temperatures of −8 °C and 16 °C for January and July respectively. The understory vegetation was dominated by *Vaccinium myrtillus*, *Vaccinium uliginosum*, *Calluna vulgaris* and *Ledum palustre*, and the mosses *Polytrichum commune* and *Sphagnum* spp. The experiment consisted of 6 blocks with 3 plots (1 m × 1 m) each which were least 20 cm apart. The treatments consisted of ambient control plots (C), snow reduction to half that of the ambient plots (HS) and low snow cover (<5 cm) (LS). Assignment of treatments within each block was random and plots were established during September 2011. Snow reduction was achieved by manually shoveling snow away following each major (>5 cm snow deposition) precipitation event. Snow height for the HS treatment was determined by measuring snow depth using a ruler in four places in the control plots of each block. The snow removal treatments may have affected the insulating properties of the snow pack due to interrupted snow metamorphosis compared to undisturbed plots but these effects are considered minor compared to the absolute effects of the treatments. Hourly temperature measurements of the soil were performed by loggers (Tiny Tag Aquatic 2, Gemini Data Loggers, Chichester, West Sussex, UK) in 3 plots of each treatment for the duration of the experiment (September 2011–October 2012). The temperature recordings integrated the top 1–4 cm of the soil profile, because the loggers were placed just below the moss surface and the logger casing had a diameter of 4 cm and was 3 cm high.

2.2. Litter decomposition

All litters were collected from forests near (hundreds of meters) the University campus. One year old litter (intact leaves only) of birch (*B. pubescens*) and aspen (*P. tremula*) was collected during the last week of August 2011 before leaf fall (which begins in early September). Freshly fallen litter from the same species was collected from the ground during the first week of September 2011. Freshly fallen pine (*P. sylvestris*) litter was collected from the forest floor during September 2009. These five litter types represent contrasting qualities with differing nutrient status; 'fresh' birch N content = 1.080% P content = 0.217%, 'old' birch N: 1.323%, P: 0.140%, 'fresh' aspen, N: 0.88% P: 0.168%, 'old' aspen N: 1.327%, P: 0.142% and pine N: 0.532%, P: 0.041%. Although N and P are two major drivers of litter decomposition, other litter traits such as lignin may be relevant but were not included in this initial assessment of the relative role of litter quality for winter decomposition rates. Litter material was air dried at room temperature for 7 days after which it was placed in litterbags (8 cm × 8 cm with 2.0 mm mesh size). This type of mesh allows access of all micro-arthropods but may restrict the larger macro-detritivores such as earthworms and insect larvae. A total of 990 litterbags were placed across the 18 plots (55 in each), with 11 bags allocated to each of the 5 litter types. All air dried litter mass (1.000 g) was corrected to oven dry weight (70 °C for 48 h) by oven drying a weighed subsample of each litter type. Litterbags were placed on the moss surface on the 29 September 2011. Each set of litterbags was marked and attached to a long thin plastic pole to ease locating the litterbags without having the dig up the snow pack across the plot. One set of five litterbags (one of each litter type) was then collected

Please cite this article in press as: Bokhorst, S., et al., Reduction in snow depth negatively affects decomposers but impact on decomposition rates is substrate dependent, Soil Biology & Biochemistry (2013), http://dx.doi.org/10.1016/j.soilbio.2013.03.016