Soil Biology and Biochemistry 123 (2018) 250–256

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

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

A Space-For-Time approach to study the effects of increasing temperature on leaf litter decomposition under natural conditions

Jenny Faber, Aline F. Quadros*[,1], Martin Zimmer[2]

FB Organismische Biologie, Paris-Lodron-Universität, Salzburg, Austria

ARTICLE INFO

Keywords:
Altitudinal gradient
Litter mass loss
Space-For-Time substitution
Detritivores
Mountain carbon stocks
Soil fauna
Temperature

ABSTRACT

Decomposition processes influence the formation of soil organic carbon stocks, and it is necessary to understand how both will respond to climate change. A Space-For-Time (SFT) substitution allows the comparison of litter decomposition under current and future conditions in the field, using a spatial gradient of environmental conditions. Here we used a SFT approach to study the effects of a difference in temperature similar to the predicted increase of 3.2–3.5 °C in Central Europe until 2100. To simulate this difference, we setup a five-fold replicated SFT substitution along mountain slopes and compared decomposition in two sites differing in ∿3.6 °C (600 *vs* 1200 m a.s.l). With this setup we compared the decomposition of high-quality (nettle) and low-quality (hay) litter, with and without fauna access, during summer, in five mountains in the Austrian Alps (Salzburg). Temperature loggers placed in one of the mountains indicated that the actual difference between the two altitudes was only ∿1.8 °C during summer. Nonetheless, decomposition of low-quality litter was 12% faster at 600 m than at 1200 m; altitude alone explained 19% of total variance. On the contrary, decomposition of high-quality litter was 9% faster at 1200 m. Fauna was the main driver of the high-quality litter decomposition at both altitudes and explained 26% of total variance, whereas altitude explained only 10%. Decomposition rates of the high-quality litter ($21.4 \pm 2.9\,mg\,g^{-1}\,d^{-1}$; ± s.d.) was much higher than that of the low-quality ($7.9 \pm 1.0\,mg\,g^{-1}\,d^{-1}$). Overall, the decomposition of the low-quality, slow-decomposing litter was more sensitive to warming and less influenced by the activity of detritivores, compared to a litter of higher quality. Through the use of the SFT substitution, we detected that a large part of the variance explained by the models was due to the variability between blocks and mountains, highlighting the important effect of spatial heterogeneity and the need for more replicated, field-based studies, to estimate the responses of decomposition processes to climate change.

1. Introduction

Soil carbon stocks are mainly driven by the interplay between the input of organic matter and its decomposition and decay rates. In temperate forests, litterfall provides the main input of organic matter, and it is the source of 70–80% of the total soil carbon (Liski et al., 2002). Litter decomposition rates are mediated by the interaction of climate, activity of detritivores and decomposers, and litter quality (Melillo et al., 1982; Aerts, 1997; Trofymow et al., 2002; Hättenschwiler and Gasser, 2005; Cotrufo et al., 2013). Litter quality, i.e. its chemical composition upon decomposition (Melillo et al., 1982), is usually indicated by traits such as nitrogen and lignin content, C:N ratio, toughness, and phenolic compounds (Melillo et al., 1982; Zhang et al., 2008). Earlier and recent studies have repeatedly demonstrated the control of nitrogen and lignin over decomposition rates (Mentemeyer, 1978; Aber et al., 1990; Preston and Trofymow, 2000; Cornelissen et al., 2004; Zhang et al., 2008), and lately the importance of other factors, such as water saturation capacity, magnesium (Makkonen et al., 2012), and calcium (García-Palacios et al., 2016) have also been shown. The traits that determine litter quality also determine decomposability (Zhang et al., 2008), digestibility (Cornelissen et al., 2004) and palatability to detritivores (Quadros et al., 2014). Detritivores, in turn, increase decomposition rates by processing the litter and producing a more easily degradable substrate (Wolters, 2000; Zimmer, 2002) and/or favouring the activity of microorganisms along the passage through the gut (Zimmer and Topp, 1998). Ultimately, climate, mainly temperature and precipitation, modulates both the activity of detritivores and microorganisms (Wall et al., 2008; García-

* Corresponding author. The Swire Institute of Marine Science, The University of Hong Kong, Cape d' Aguilar Road, Shek O, Hong Kong.
E-mail address: quadros.af@gmail.com (A.F. Quadros).
[1] Present address: School of Biological Sciences, University of Hong Kong, Hong Kong.
[2] Present address: Leibniz Centre for Marine Tropical Research, ZMT-GmbH, Bremen, Germany.

https://doi.org/10.1016/j.soilbio.2018.05.010
Received 12 February 2018; Received in revised form 21 April 2018; Accepted 13 May 2018

Palacios et al., 2013) and the physical degradation of litter through UV degradation and drying-rewetting cycles.

Compared to forests of warmer regions, European cold temperate forests usually have the following combination of conditions: shorter growing seasons, lower abundance and/or activity of detritivores and microorganisms due to low temperatures, and abundant tree species that produce low-quality, lignin-rich and nutrient-poor litter (such as beech, spruce, and pine litter; Hättenschwiler and Gasser, 2005; Vesterdal et al., 2008). In combination, these conditions favour low litter decomposition rates and the stabilization and accumulation of carbon in the topsoil. For instance, there is a positive relationship between the total carbon in the forest floor and the C:N ratio of the leaf litter, a high C:N usually indicating low-quality litter (Vesterdal et al., 2008). It is not surprising, thus, that soils of old-grown temperate forests hold important carbon sinks (Luyssaert et al., 2008; Zhu et al., 2015). For the last two decades there has been an increasing concern about the stability of such soil carbon stocks upon climate change, and especially upon temperature increase (Goodale et al., 2002; Cornelissen et al., 2007; Luyssaert et al., 2008; Hagedorn et al., 2010b; Sarmiento et al., 2010). The average annual temperature in Europe is predicted to increase by 1–4 °C (B2 scenario) or 2.5–5.5 °C (A2 scenario) until 2100 (Christensen et al., 2007), and, due to the sensitivity of decomposition to temperature, increased temperatures can turn soil sinks into sources of CO_2 if decomposition rates increase (Davidson and Janssens, 2006; Hagedorn et al., 2010b; Spohn, 2015). Litter quality plays an important role in mediating these effects because the magnitude of temperature sensitivity depends on substrate quality ("carbon quality-temperature hypothesis"; Bosatta and Ågren, 1999; Fierer et al., 2005), increasing with decreasing litter quality. Low-quality substrates should have higher sensitivity to temperature because of a higher number of steps needed for its decomposition (Bosatta and Ågren, 1999). Coupled to that, relative more microbial CO_2 is produced (Spohn, 2015).

The effects of environmental changes on litter decomposition rates have been studied mainly under controlled conditions in microcosm experiments in the laboratory (Petchey et al., 1999; Hättenschwiler and Bretscher, 2001; Rouifed et al., 2010). Alternatively, there's the experimental manipulation of abiotic variables in the field (Luo et al., 2001; Dang et al., 2009), such as the warming of top soil layers using wires (Hagedorn et al., 2010a). Here we employed a third approach, the Space-For-Time (SFT) substitution (Pickett, 1989; Fukami and Wardle, 2005). The idea of SFT is to identify natural gradients, therefore "the space", representing two or more contrasting conditions that represent current and future scenarios, therefore "the time" (Pickett, 1989). Our SFT approach to study the effects of temperature increase used the natural environmental gradients of mountain slopes. Altitudinal gradients provide an excellent opportunity for addressing abiotic effects on ecological processes under field conditions: some abiotic factors change in a predictable way with increasing altitude, while biotic factors, such as fauna and plant communities, remain similar, at least within altitudinal ecotones (e.g. montane, alpine, nival) (Aerts, 2006). Temperature, for instance, is expected to decrease with increasing altitude, making *"Latitudinal and altitudinal gradients […] natural, long-term analogues for climate change"* (Aerts, 2006): air temperature decrease (or adiabatic rate) is, on average, 0.6 °C per 100 m elevation, with a range of 0.2–0.8 °C per 100 m (Nagy and Grabherr, 2009). Having this rate in mind, we used an altitudinal difference of 600 m, within the lower montane belt, to obtain a temperature difference of ∿3.6 °C between sites, attempting to simulate the predicted temperature increase in Central Europe (Christensen et al., 2007). Our aim was to quantify the effects of this small difference in temperature on litter decomposition rates in the field, but considering also the interactions between litter quality, soil fauna and microorganisms. Due to the know sensitivity of decomposition to temperature (Fierer et al., 2005) and according to previous studies along altitudinal gradients (Shanks and Olson, 1961; Coûteaux et al., 2002; Wang et al., 2010), we predicted that decomposition rates would be higher at the lower altitude (higher average temperature). Due to the expected decrease in abundance of soil fauna with increase in altitude (Hoover and Crossley, 1995; Wang et al., 2009), and to their known preference for high-quality litter (Quadros et al., 2014) and higher effects on its decomposition (Rouifed et al., 2010), we predicted that faunal effects would be stronger at the lower altitude and on the high-quality litter. We chose two litter types of contrasting quality and manipulated the fauna access into the mesocosms using different mesh sizes. We replicated the study on five closely situated mountains to account for the effects of habitat spatial heterogeneity and provide a realistic estimation of effects of temperature increase on litter decomposition rates.

2. Methods

2.1. Study sites

In order to find appropriate mountains to replicate our study, we analysed hiking track maps of the vicinities of Salzburg, Austria, searching for mountains that had 1) an accessible north slope; 2) minimum elevation of 1200 m; 3) forests dominated by *Fagus sylvatica* with the presence of *Picea abies*. Through this search, and based on previous personal experience, we chose five mountains: Gaisberg (47°48′N, 13°06′W; 1287 m), Untersberg (47°41′N, 12°59′W; 1973 m), Tristkopf (47°32′N, 13°07′W; 2110 m), Wirreck (47°34′N, 13°12′W; 1473 m), and Kleiner Göll (47°35′N, 13°07′W; 1752 m). The soil types are Calcaric Leptosols (WRB classification; IUSS Working Group WRB, 2015). Besides *Fagus sylvatica* and *Picea abies*, other woody trees in these mountains were *Abies alba*, *Acer platanoides*, *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Ulmus glabra*. A more detailed list of species can be seen in Schwap et al. (2000). The most common macrodetritivores seen in our study sites were diplopods *Glomeris pustulata* (Fabricius, 1781) and *Cylindroiulus* spp., woodlice *Armadillidium versicolor (Stein 1859), Trachelipus rathkii* (Brandt, 1833), *T. ratzeburgii* (Brandt, 1833), and land snails.

On each mountain we established two sites, one at 600 m a.s.l. and another at 1200 m a.s.l., totalling 10 sites (Fig. 1). Exceptionally, due to difficult access, on Untersberg the lower site was located at 750 m a.s.l. and the upper one at 1240 m a.s.l. According to the classification of Körner et al. (2011), both the 600 m and 1200 m sites belong to the Lower Montane thermal belt, a mountain thermal zone characterized by growing seasons with mean temperatures between 10 and 15 °C. To estimate the actual mean air temperature (at the soil surface) during the field study, we placed temperature loggers (HOBO) at 450, 750, 1040 and 1240 m a.s.l. along one of the five altitudinal transects (Untersberg,

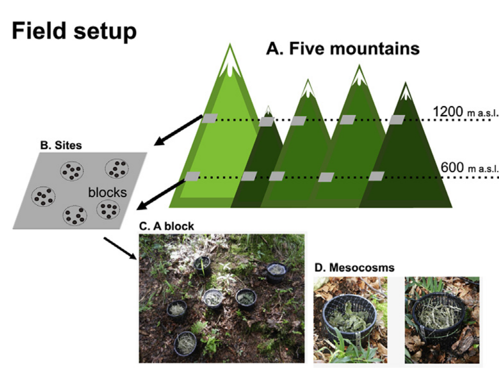

Fig. 1. Schematic representation of the field setup. A) We chose five mountains, in the surrounding of Salzburg, Austria, ranging from 1287 to 2110 m altitude; B) Along the northern slopes we stablished one site at 600 m a. s. l. and one at 1200 m a. s. l. (except for Untersberg, see text), totaling 10 sites; C) Each site had five blocks. Each block had six mesocosms (i. e. three types of mesocosms for different faunal access for each litter type), with 300 in total; D) Examples of mesocosms with high-quality litter (*Urtica dioica* leaves) in the left, and low-quality litter (hay leaves), in the right.