Soil Biology & Biochemistry 75 (2014) 102–112

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Warming alters potential enzyme activity but precipitation regulates chemical transformations in grass litter exposed to simulated climatic changes

Vidya Suseela [a,b,*], Nishanth Tharayil [b], Baoshan Xing [c], Jeffrey S. Dukes [a,d,e]

[a] Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA
[b] School of Agricultural, Forest and Environmental Sciences, Clemson University, Clemson, SC 29634, USA
[c] Stockbridge School of Agriculture, University of Massachusetts Amherst, MA 01003, USA
[d] Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA
[e] Department of Biology, University of Massachusetts Boston, Boston, MA 02125, USA

ARTICLE INFO

Article history:
Received 11 September 2013
Received in revised form
25 March 2014
Accepted 26 March 2014
Available online 13 April 2014

Keywords:
Litter decomposition
Warming
Extracellular enzyme activity
DRIFT
Drought
^{13}C NMR

ABSTRACT

Warming generally accelerates the decomposition of plant litter. However, changes in precipitation could alter the sensitivity of litter decomposition to warming, thereby affecting the formation of litter-derived soil organic matter. As grassland soils store ~20% of Earth's soil carbon, understanding the effect of climatic changes on the decomposition dynamics of grasses is important. However, little is known about how projected changes in climate would affect litter microbial communities and enzyme activities, and the consequences of these changes for the mass loss and compound-specific degradation of grass litter that possess complex lignocellulosic chemistry. Over a period of two years, using litter of the grass *Poa trivialis*, we studied how mass loss, microbial enzyme activity and fine-level litter chemistry responded to a factorial combination of 4 levels of warming (up to ambient +~4 °C) and three levels of precipitation [ambient, wet (+50%) and dry (−50%)] at the Boston-Area Climate Experiment (BACE), in Massachusetts, USA. After 393 days of decomposition, supplemental precipitation accelerated mass loss compared to the dry treatment, as a consequence of faster loss of hydroxycinnamates, which protect carbohydrates through cross-linkages with lignins. Only a third as much of the cell wall-bound ferulic and *p*-coumaric acids remained in litter from the supplemental precipitation treatment compared to the ambient controls. In contrast, the warming treatments did not affect mass loss until later, after 740 days, when the litter in the warmest treatment (+~4 °C) had lost the most mass. Although warming significantly affected mass loss after 740 days, there was also a trend in the warmest treatments toward greater mass loss in the wet (78% mass loss) and ambient (68%) plots compared to dry plots (61%), possibly due to the higher activity of β-glucosidase. Though mass loss at this final time point varied with both warming and precipitation treatments, the compound-specific degradation of litter captured by diffuse reflectance infra-red Fourier transform (DRIFT) and ^{13}C Nuclear Magnetic Resonance (NMR) spectroscopy revealed that only the precipitation treatments significantly altered the chemistry of carbon compounds in the decomposed tissue. Litter that decomposed in the dry treatment had a higher proportion of carbohydrates remaining than litter in the wet and ambient treatments. Similarly, although ergosterol content and potential activity of phenol oxidase decreased in the warmer treatments, the consequences of this response were not observed in the degradation of specific compounds in litter, which varied only with precipitation treatments. Our results suggests that mass loss and enzyme activities may not accurately capture the complexity of compound-specific degradation of litter during decomposition. Our results also identified non-linear responses of β-glucosidase and N-acetyl-β-D-glucosaminidase (NAG) activities to warming. These results thus emphasize the complexities of litter decomposition and suggest that similar changes in decomposition across other grass species could alter the carbon budget of grasslands.

1. Introduction

Grassland ecosystems store ~20% of Earth's soil carbon and occupy ~30% of its land surface (Asner et al., 2004; FAO, 2010), and

* Corresponding author. 105 Collins Street, Clemson University, Clemson, SC 29634, USA. Tel.: +1 864 656 4453; fax: +1 864 656 0274.
E-mail address: vsuseel@clemson.edu (V. Suseela).

http://dx.doi.org/10.1016/j.soilbio.2014.03.022
0038-0717/

thus strongly influence terrestrial carbon cycling. Rates of grassland carbon cycling respond to warming and changes in precipitation. For instance, the projected 4–6 °C increase in temperature by the turn of this century and associated changes in precipitation patterns (IPCC, 2007) would alter soil temperatures and moisture balances, changing the rates of litter decomposition (Adair et al., 2008; Suseela et al., 2013). Any associated increase in nutrient mineralization might help to sequester more atmospheric CO_2 through higher ecosystem productivity (Melillo et al., 2011), leading to a negative feedback to climate change. However, an accelerated release of CO_2 during litter decomposition would positively feed back to climate change. The magnitude and direction of any feedback effects would depend largely on the changes in climate, on litter chemistry, and on their interaction (Erhagen et al., 2013; Suseela et al., 2013).

In general, graminoids decompose much more slowly than forbs (Cornwell et al., 2008), largely because these two plant functional types differ in the chemical composition of their litters (Carpita, 1996). In the primary cell walls of grasses, aromatic heteropolymers such as lignin cross-link with proteinaceous compounds and polysaccharides such as cellulose to form a strong structural framework. During decomposition of grass litter, this structural framework makes the polysaccharides and proteins less accessible to microbes, ultimately slowing C and N mineralization. Most previous studies on the effect of climate on litter decomposition have focused on forest ecosystems, using foliar litter from trees (Gholz et al., 2000; Liski et al., 2003). As the chemistry of grass litter is substantially different from other herbaceous plants and trees, focusing on the effects of multiple climate factors on grass litter decomposition can provide new insights into carbon cycling in grassland ecosystems. To our knowledge, none of the previous studies on the effects of climate on grass litter have assessed the degradation of specific compounds, thus limiting our knowledge of the chemical transformations during decomposition that facilitate soil organic matter formation. Addressing this knowledge gap would provide a more complete understanding of the contribution of litter to soil organic matter formation (Wickings et al., 2012).

Warming generally increases the metabolic activity of microbes (Schindlbacher et al., 2011) and the rate of litter decomposition (Fierer et al., 2005). However, changes in precipitation regimes could alter the response of the microbial community to warming, affecting the rate and magnitude of litter decomposition. For example, in a long-term warming experiment, during normal precipitation years the population size of soil bacteria increased with warming, whereas under dry conditions warming led to significant reduction in bacterial population (Sheik et al., 2011). Similarly, in an annual grassland system, water additions enhanced the activity of phenol oxidase and peroxidase, which degrades lignin in plant litter (Henry et al., 2005). Although these studies suggest the significance of moisture in driving the responses of soil microbial communities and their functional activity, little is known about the concerted effects of warming and altered precipitation on the compound-specific degradation of litter via changes in microbial activity. Also, most studies that have measured responses of extracellular enzyme activities to climate manipulations have used only two levels of each climatic factor (Allison and Treseder, 2008; Bell et al., 2010; Kardol et al., 2010). However, microbial activity is known to respond to distinct moisture and/or temperature thresholds leading to non-linear responses (Suseela et al., 2012; Suseela and Dukes, 2013). To characterize any non-linear response of the extracellular enzyme activity (EEA) we need climate experiments that manipulate each factor at multiple levels (Henry, 2012). Although few studies have measured the EEA in soils exposed to multiple climatic factors (Brzostek et al., 2012; Steinweg et al., 2012), to our knowledge none of the previous studies have characterized EEA in litter decomposing at multifactor climatic conditions.

To test in unprecedented detail the degree to which changes in precipitation and temperature affect the rate and compound-specific degradation of grass litter, we decomposed stem litter of *Poa trivialis* for 740 days in 12 different combinations of warming and precipitation treatments at the Boston-Area Climate Experiment (BACE). We hypothesized that addition and removal of precipitation would alter the temperature responses of litter decomposition and enzyme activities. Specifically, we predicted that moisture stress induced by precipitation removal and/or warming would slow litter decomposition, but that warming would accelerate mass loss under ambient and wet precipitation treatments (i.e., conditions with less water stress). We also predicted that extracellular enzyme activity would respond non-linearly to climate treatments, as microbial activity would exhibit distinct temperature and/or soil moisture thresholds.

2. Materials and methods

2.1. Site description and experimental design

The litter decomposition experiment was conducted at the Boston-Area Climate Experiment (BACE), located at the University of Massachusetts Agricultural Experiment Station in Waltham, Massachusetts (42°23.1′N, 71°12.9′W). This mesic old-field system with ~40 species of grasses and forbs is comparable to temperate grasslands in plant community composition (Hoeppner and Dukes, 2012). Mean annual precipitation and temperature in nearby Boston are 1063 mm and 10.3 °C, respectively. The study site has a loamy topsoil (Mesic Typic Dystrudept; Haven series) with 45% sand, 46% silt and 9% clay (gravel content: 7%) and a gravelly sandy loam subsoil. BACE is a factorial split-plot experiment with three levels of precipitation [ambient (A), dry (D) and wet (W)] as main treatments and four levels of warming [unwarmed (0), low (L), medium (M) and high warming (H)] as subplot treatments (Suseela et al., 2012). There are three experimental blocks. The soil around each 2 × 2 m plot had been trenched to 60 cm and lined with polyethylene sheets to prevent the movement of water and nutrients between plots. The precipitation treatments were applied using rainout shelters and a sprinkler system. The dry section of each block was located under clear polycarbonate slats that intercepted 50% of the ambient rainfall, which was then diverted to storage tanks and applied immediately to the wet section using sprinklers. We used infrared heaters of different wattages (200 W for low, 600 W for medium and 1000 W for high warming) to apply the warming treatments. Heaters were mounted 1 m above each corner of each plot. Infrared radiometers above the ambient and high warming plots measured canopy temperatures every 10 s. The difference in canopy temperature readings within each group of four plots was used to achieve feedback control (target difference of 4 °C; Suseela and Dukes, 2013). Volumetric soil moisture (10 cm depth) was measured weakly using time-domain reflectometry (TDR) waveguides installed in each plot. In each plot, we also monitored soil temperature (2 cm depth) every 30 min using custom-made linear temperature sensors (Auyeung et al., 2013).

2.2. Litter placement, harvest and processing

We started the decomposition experiment at the BACE in October 2008, using the senesced litter of the grass *Poa trivialis* (hollow stem litter) collected from the old-fields adjacent to the BACE plots. Chemical analysis of initial undecomposed tissues showed that *P. trivialis* litter had a C:N ratio of 107. We put 2 ± 0.03 g of air-dried stem of *P. trivialis* in each 5-cm-diameter