available at www.sciencedirect.com

ScienceDirect

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

Microbial substrate preference and community dynamics during decomposition of *Acer saccharum*

Zachary L. RINKES[a], *Michael N. WEINTRAUB*[a,*], *Jared L. DEFOREST*[b], *Daryl L. MOORHEAD*[a]

[a]*Department of Environmental Sciences, University of Toledo, Toledo, OH 43606, USA*
[b]*Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA*

ARTICLE INFO

Article history:
Received 21 October 2010
Revision received 25 January 2011
Accepted 27 January 2011
Available online 17 March 2011
Corresponding editor: Petr Baldrian

Keywords:
Acer saccharum
Carbon sequestration
Decomposition
Extracellular enzyme
Incubation
Lignin
Litter
Microbial community
Nutrients
PLFA

ABSTRACT

The Guild Decomposition Model (GDM) hypothesized that temporal shifts in microbial "guilds," each with distinct substrate preferences, drive decomposition dynamics and regulate soil carbon (C) losses and sequestration. To test this hypothesis, we established a laboratory incubation of *Acer saccharum* litter and monitored respiration, microbial biomass and enzyme activities, inorganic nutrients and shifts in functional groups of decomposers using phospholipid fatty acid (PLFA) analysis. Biomass and respiration peaked within the first 2 d of incubation, and the Gram negative PLFA biomarker 18:1ω7c predominated during the first 5 d. Hydrolytic enzyme activities and two fungal biomarkers (18:2ω6,9c and 18:3ω6c) increased by 25 d and lignolytic enzyme activity was detected at 68 d. Our results suggest that decomposers preferentially use labile substrates and that shifts in decomposer groups occur in response to changes in available substrates, which supports the GDM.

Introduction

Globally, terrestrial soils represent a significant carbon (C) reservoir (Berg & McClaugherty 2008) and have the potential to be either a source or sink for atmospheric C (Schlesinger & Andrews 2000). Decomposition of plant litter is a key control on soil C sequestration and is mediated primarily by decomposer microorganisms. The trajectory of decay is regulated by complex interactions between the microbial community and litter substrate, each of which change through time in response to one another (Berg & Meentemeyer 2002; Moorhead & Sinsabaugh 2006). Therefore, litter chemistry and microbial activity jointly control the amount of C mineralized or metabolized at different stages of decay.

Litter chemistry changes predictably during decomposition (Aber *et al.* 1990; Moorhead & Reynolds 1993; Berg & McClaugherty 2008). Berg (2000) developed a three phase conceptual model of plant litter decay driven largely by the biological availability of different fractions of organic matter. Rapid decreases in water soluble compounds and unlignified holocellulose characterize Phase 1 with no decomposition of lignin (Berg 2000). Phase 2 is characterized by

* *Corresponding author.*
E-mail address: michael.weintraub@utoledo.edu (M.N. Weintraub).
1754-5048/$ – see front matter
doi:10.1016/j.funeco.2011.01.004

the mineralization of lignified carbohydrates and lignin decay regulating mass loss rates (Berg 2000). During Phase 3, the relative concentration of lignin increases to the point where mass loss is minimal and litter reaches its "limit of decomposition" (Berg *et al.* 2010).

Berg (2000) attributed this decrease in litter decomposability over time to chemical changes associated with the substrate and the succession of decomposers able to compete for recalcitrant, nutrient poor substrates. The primary mechanism by which decomposers mediate the transformation of detrital C, nitrogen (N) and phosphorus (P) compounds is the production of extracellular enzymes (Burns 1982; Sinsabaugh *et al.* 1993; Sinsabaugh 1994). Organic matter decomposition requires the synergistic interaction of several different classes of enzymes, which track Berg's (2000) predicted patterns of turnover in organic matter pools (Moorhead & Sinsabaugh 2000). For example, the various water soluble compounds and labile C substrates associated with fresh litter can be accessed by decomposers without the aid of extracellular enzymes (Frankland 1966; Linkins *et al.* 1990). As these labile substrates disappear, hydrolytic enzymes associated with cellulose decomposition, such as β-glucosidase, then increase (Dilly & Munch 1996; Sinsabaugh *et al.* 2002). Later stages of decay are closely associated with lignolytic enzyme activity, due to the high concentrations of recalcitrant compounds (Moorhead & Sinsabaugh 2000; Sinsabaugh *et al.* 2002).

Decomposers vary in their abilities to use different litter substrates, and shifts in functional groups of microorganisms occur as different resources become available (Waldrop & Firestone 2004; Hanson *et al.* 2008). For instance, a typical fungal succession includes zygomycetes, which are commonly associated with the availability of sucrose and cellulose early in decay, followed by ascomycetes and finally basidiomycetes that decompose lignin in later stages (Frankland 1998; Torres *et al.* 2005). Therefore, it has been shown that the predicted patterns of substrate loss during decay are driven by a succession of microorganisms capable of exploiting various organic matter fractions. A recent theoretical model by Schimel & Weintraub (2003) proposed that enzyme production by decomposers is controlled by relative demands for C and nutrients, and that different substrates yield different C and nutrient returns. This suggests that microbial preferences for various substrates are based on their return on investment in enzyme production.

More recently, the Guild Decomposition Model (GDM) coupled activities of specific microbial functional groups, or guilds, to a changing litter substrate, and included decomposer organisms and their enzyme kinetics as integral drivers of decomposition (Moorhead & Sinsabaugh 2006). This theoretical model hypothesizes regulation of microbial activities within guilds of decomposers and is consistent with the conceptual model proposed by Berg (2000). The GDM partitioned the microbial community into three ecological guilds, each with different physiologies, life history traits and enzymatic capabilities, and linked these guilds to three C substrate pools with varying substrate affinities (Moorhead & Sinsabaugh 2006). In brief, they hypothesized that opportunist organisms capable of invading quickly and thriving on soluble carbohydrates and other labile C forms (C1) would be first to colonize freshly deposited litter due to their fast growth rate. As soluble substrates disappear, opportunists are replaced by a decomposer guild with the ability to decompose holocellulose (C2) through the release of hydrolytic and oxidative enzymes. As unlignified cellulose is consumed, lignocellulose (lignin encrusted cellulose) predominates in the remaining litter. At this phase a lignin (C3) decomposing miner guild establishes, but grows very slowly due to the relatively low C and nutrient return on oxidative lignin decomposition.

Most traditional predictive models of litter decay are largely driven by changes in litter quality and environmental conditions (Meentemeyer 1978; Gholz *et al.* 2000), but pay little attention to the activities of decomposers as explicit drivers of decay. Although useful under equilibrium conditions, these models do not sufficiently describe C cycling under variable conditions or fully predict the behavior of soil C flow and microbial dynamics, especially following disturbance (Schimel & Weintraub 2003). Traditional models also fail to capture changes in microbial community composition and function, which could have substantial impacts on C losses and gains when the entire time-course of decay is considered. Recent mechanistic models of decay, such as the GDM, have incorporated more ecological interactions between the microbial community and litter substrate and should be better able to predict ecosystem responses to perturbations (Schimel & Weintraub 2003; Moorhead & Sinsabaugh 2006; Ingwersen *et al.* 2008). However, high resolution empirical studies are needed to fully test the hypotheses set forth in these theoretical models, as data for many of the parameters are lacking.

The first goal of this study was to evaluate microbial substrate preferences to determine if the conceptual model of litter decay based on litter chemistry (Berg 2000) is supported. Activities of different extracellular enzymes were used as proxies for specific substrate use (e.g. β-glucosidase and phenol oxidase are indicative of cellulose and lignin breakdown, respectively).

Our second goal was to determine if changes in litter chemistry due to decay correlates with shifts in microbial community composition and if different functional groups of decomposers correlate with microbial function. This would test the pattern of succession hypothesized by the GDM, and attempt to resolve microbial behaviors that track dynamic litter substrate pools.

We hypothesized that shifts in functional groups of microorganisms, each with different enzymatic capabilities and substrate preferences, would occur over the time course of decomposition due to changes in substrate quality and nutrient availability (N and P). To accomplish our goals and test this hypothesis, we established a laboratory incubation of *Acer saccharum* leaf litter and monitored microbial respiration, extracellular enzyme activities, phospholipid fatty acid (PLFA) biomarkers and soil inorganic nutrient availability over 500 d.

Materials and methods

Sample collection

Freshly senesced *Acer saccharum* leaves were collected in litter traps during the fall of 2008 at The University of Toledo's R. A. Stranahan Arboretum (N 41°42′, W 83°40′) in Northwest