Stoichiometric linkages between plant litter, trophic interactions and nitrogen mineralization across the litter–soil interface

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ABSTRACT

The common notion for describing N mineralization in models is that it results from decomposer organisms trying to meet their stoichiometric demands based on their own elemental composition and that of the resource. However, in addition to influencing C and nutrient availability, plant litter also influences the composition of both the litter and mineral soil community — importantly not in the same manner — resulting in altered trophic interactions. Since decomposer groups and their consumers vary in their elemental composition and demands, a change in composition and abundance of soil functional groups may result in a change in the stoichiometry of the whole soil food web, thus altering their stoichiometric relations with the available resource with potential functional consequences. We use experimental data and quantitative food web modeling to investigate the impact of the changes in the litter and soil food webs brought about by the differing stoichiometry of plant litter on (a) N mineralization, (b) the contribution of different functional groups to mineralization, and (c) the stoichiometric flexibility of the system, assessed as the ability to mineralize materials with different stoichiometry. Our simulations suggested that the effects of litter stoichiometry on trophic interactions, their impacts on N mineralization and the relative contribution of functional groups may not behave as a continuum across the litter and soil interface. Further, changes in food webs associated with variation in plant stoichiometric traits can influence the relative importance of functional groups, which given their particular stoichiometric demands may affect ecosystem-level N cycling. Our results suggested that litter materials of intermediate N contents, or litter mixtures encompassing materials with different nutrient contents and thus resulting in mixtures of intermediate stoichiometry, may promote food webs that are better suited to deal with changing substrate stoichiometry.

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1. Introduction

As temporal and spatial scales decrease, the importance of resource chemical composition and the decomposer community as regulators of decomposition processes increases (Lavelle et al., 1993; Adair et al., 2008; Wall et al., 2008). The effects of the interactions of these two factors are not well understood. Strong relationships between the stoichiometric composition of substrates and their decomposition rates have been demonstrated (Meentemeyer, 1978; Aerts, 1997; Manzoni et al., 2008) and result from the degree of stoichiometric imbalance between decomposers and their resources (Hessen et al., 2004; Manzoni et al., 2008). The impact of the soil community composition on decomposition and mineralization rates is also amply supported (Setälä et al., 1991; Bradford et al., 2002; Heemsbergen et al., 2004; Carrillo et al., 2011). Experimental evidence of interactive effects between plant litter elemental composition and the structure of the soil community is scarce, however, these interactions may be responsible for unexplained variability observed when exploring the general patterns of decomposition and elemental composition (Parton et al., 2007; Manzoni et al., 2008; Ågren et al., 2013). For example, Carrillo et al. (2011) experimentally demonstrated that the relationship between litter nitrogen (N) and phosphorus content with N mineralization was dependent on the structure of the soil community. Similarly, Buchkowski et al. (2014) demonstrated that the role of the microbial biomass in controlling decomposition was

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determined by the relation of microbial and available resource stoichiometries. Understanding these types of interactions is key to increasing our ability to predict nutrient dynamics and decomposition in the face of changes in plant and soil community composition. In order to understand substrate quality–community interactions, however, separately considering the litter and the soil layer is important, yet very rarely done. It is becoming increasingly clear that a disconnect between the regulation of processes in the litter layer and in the underlying soil exists (Parton et al., 2007; Adair et al., 2008). Recent studies are challenging the notion of the litter–soil continuum, and suggesting that how carbon (C) and nutrient availability regulate decomposer function and vice versa may vary for the litter and soil layer (Fanin et al., 2012; Ball et al., 2014; Mooshammer et al., 2014a).

The common notion used for describing N mineralization in C and N models is that it results from decomposer organisms trying to meet their stoichiometric demands based on their own elemental composition and that of the resource (Manzoni and Porporato, 2009). More recent advances consider various microbial physiological mechanisms to deal with the stoichiometric imbalances (Mooshammer et al., 2014b). For the most part the decomposer organisms are described as acting in isolation or as a single group, but not functioning as a community comprised of various functional groups. However, in addition to determining C and nutrient availability, plant litter elemental composition also influences the composition of both the litter and mineral soil community, including microbes and fauna. Such changes in composition result in altered community interactions, including competitive, facilitative, and trophic interactions, which in turn, could affect the outcome of the decomposition process (Wardle, 2002; Kaiser et al., 2014). In this study, we focus on trophic interactions in the soil and litter food webs as major drivers of C and nutrient mineralization (Moore et al., 2003; Bardgett and Wardle, 2010). C mineralization is affected by the grazing-driven turnover activity and respiration of consumed populations (Bardgett et al., 1993; Mikola and Setala, 1998), while N mineralization occurs mainly due to excretion of excess N (Bardgett and Chan, 1999; Bonkowski, 2004). In addition, top-down control of microbial decomposer populations by members of the soil fauna regulates decomposer demand for C and nutrients, and subsequently, their role as consumers and prey (Hedlund and Ohrn, 2000). While trophic interactions are an important component of the role of the soil community in the decomposition process, they have been given little attention when trying to understand the regulation of decay by resource chemical composition.

Soil and litter communities and thus their food web structures are very responsive to changes in resource chemistry (Carrillo et al., 2012) with potential impacts on function. The functional consequences of the changes in food web structure associated with changes in plant litter chemistry may be mediated by its impacts on the stoichiometric relations among food web members and the detritus available. These relations may vary for litter and soil, given the dramatic difference in C and nutrient stoichiometry in these two environments (Cleveland and Liptzin, 2007). It has been suggested that the result of trophic transfers between the members of the soil food web can depend on the quality of resources (Herlitzius, 1983; Wardle, 2002; Bardgett, 2005). In one of the few studies to address this question, Hanlon (1981) found that the influence on fungal respiration exerted by a collembolan grazer depended on the nutrient concentration of the growth medium. Such dependency may result from the fact that decomposer groups and their consumers vary in their elemental composition and demands and thus their stoichiometric relations depend on the trophic groups involved and the particular C and nutrient sources available (Hessen et al., 2004; Fanin et al., 2013; Kaiser et al., 2014). Thus, a

change in composition and abundance of soil functional groups as a response to variation in substrate may result in a change in the stoichiometry of the whole soil food web with potential functional consequences. For instance, the resulting food web could vary in its ability to process substrates of differing stoichiometry thus altering the system's stoichiometric flexibility, which is defined as the system's ability to modify the balance of elements while maintaining function (Sistla and Schimel, 2012).

The inherently complex nature of these interactions makes them difficult to assess via experimental means as this would require isolating the effect of the soil populations from that of litter quality, making modeling approaches not just desirable but necessary. Organism-oriented models, which explicitly incorporate soil organisms and their interactions with the biophysical environment, have a high explanatory value and permit the evaluation of the effects of intervention and management (Paustian, 1994; Smith et al., 1998). The quantitative food-web modeling approach initiated by Hunt et al. (1987) has been applied to several natural and agricultural systems and has proven useful in simulating C and N mineralization rates and in explaining rates in terms of the relative contribution of groups of organisms and particular trophic interactions (Hassink et al., 1994; de Ruiter et al., 1994; Berg et al., 2001; Schroter et al., 2003; Bezemer et al., 2010). In this approach food webs are constructed by aggregating species into functional groups and N and C cycling are analyzed in relation to the structure and functioning of the food webs.

We used this approach to simulate N mineralization from surface applied litter of differing N contents and from mineral soil based on observed population sizes and the trophic interactions among the members of the soil and litter food webs. With simple modifications our model could further describe mineralization as being regulated not only by trophic interactions or litter elemental composition, but by the interplay of both, in both the litter and soil. In order to do this, we added simple features to describe differential composition of the litter and differential abilities of fungi and bacteria to degrade organic matter fractions. This approach allowed us to isolate the effects of the changes in soil food web structure prompted by the added litter from the effects of the quality of litter on trophic transfers. In a field experiment we assessed the abundances of soil and litter microbial detritivores, protozoa, nematodes and microarthropods and measured N mineralization over the course of six months after the surface application of six plant materials of contrasting chemical compositions (Carrillo et al., 2011; Ball et al., 2014). We calibrated the model using the measured soil populations and N mineralization after the application of one substrate. We then used the model to investigate the impact of the changes in the litter and soil food webs brought about by the differing stoichiometry of plant litter on: (a) N mineralization, (b) the contribution of different functional groups to mineralization, and (c) the stoichiometric flexibility of the system, assessed as the ability to mineralize materials with different stoichiometry.

2. Methods

Net N mineralization rates and abundances of trophic groups in soil and litter from a field study in the Piedmont region of Georgia USA and previously published in Carrillo et al. (2011) and Ball et al. (2014) were used to calibrate and validate the trophic transfer N mineralization model. Briefly, the field approach involved using a 100-m^2 site divided into 24 2 × 2 m aluminum flashing enclosed plots arranged in four blocks and cleared of vegetation and litter. Mineral soil from the top 5 cm of 6 separate 25 × 50 cm areas within these plots was removed, sieved, frozen (to kill fauna) and placed back in the field enclosed in 5 mm wire mesh. Before application of treatments, soils were left bare for 6 weeks to allow