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Soil characteristics determine soil carbon and nitrogen availability during leaf litter decomposition regardless of litter quality

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ABSTRACT

Climate and litter quality have been identified as major drivers of litter decomposition, but our knowledge of how soil characteristics (e.g. microbial community and chemical properties) determine carbon (C) and nitrogen (N) availability derived from the decomposition of litter of different qualities is still scarce. We conducted a microcosm experiment to evaluate how soils with contrasting microbial communities and soil properties (denoted Soils A and B hereafter, where Soil B has higher bacterial and fungal abundance, fungal:bacterial ratio, and organic C than Soil A) determine the availability of soil C (carbohydrates, proteins, amino acids and phenols) and N (dissolved organic and inorganic N, microbial biomass N and available N) during the decomposition of litter of contrasting quality (C:N ratios ranging from 20 to 102). We also evaluated the relative importance of soil characteristics and litter quality as drivers of C and N inputs to the soil during this process. Overall, higher soil C and N availability after litter decomposition was found in Soil B than in Soil A. Soil characteristics had a higher positive effect on soil C and N contents than litter quality during litter decomposition. We also found that changes in N availability and organic matter quality registered after litter decomposition, linked to different soil characteristics, were able to promote dissimilarities in the potential mineralization rates. In conclusion, our study provides evidence that soil characteristics (e.g. microbial communities and chemical properties) can be more important than litter quality in determining soil C and equally important for N availability during the decomposition of leaf litter.

1. Introduction

Litter decomposition is one of the main processes controlling the availability of carbon (C) and nitrogen (N) in terrestrial ecosystems (Schlesinger, 1996). Identifying the main factors controlling this process has been a major topic in ecological research over the last decades (Meentemeyer, 1978; Cleveland et al., 2014). Climate and litter chemistry have been traditionally considered as the main drivers of litter decomposition (Meentemeyer, 1978; Hättenschwiler et al., 2005; Cornwell et al., 2008; García-Palacios et al., 2013a), with soil playing a minor role in this process (Schimel, 1995; Reed and Martiny, 2007; Green et al., 2008). However, a growing number of studies are showing that soil with different characteristics (e.g. different microbial communities) have different functionalities ("functional breadth" *sensu* Keiser et al., 2013), and thus differentially affect ecosystem processes such as litter decomposition (Strickland et al., 2009; Wallenstein et al., 2010; Keiser et al., 2013; Cleveland et al., 2014). For example, it is well known that litter decomposes faster with its local soil microbial community than when it is exposed to a non-native soil (Ayres et al., 2009; Strickland et al., 2009; Wallenstein et al., 2010; Keiser et al., 2011, 2013). In addition to their direct effects on litter decomposition, soil microbial communities largely determine the availability of C and N in soils through a number of mechanisms. For instance, fungal-dominated microbial communities use N more

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efficiently, and thus accelerate mineralization, than bacterial-dominated ones, enhancing N availability in the soil (Paul and Clark, 1996; Austin et al., 2004). In addition, complex processes, such as the depolymerization of large organic molecules into dissolved organic N (DON), require the cooperation of diverse groups of microorganisms (Schimel et al., 2005; Delgado-Baquerizo et al., 2013a). This is not the case for processes such as nitrification, which is carried out by specific groups of microorganisms (Schimel et al., 2005; Delgado-Baquerizo et al., 2013a).

Soil microbes interact with litter and soil chemistry to determine soil C and N availability. For example, a lower C:N ratio in the microbial substrate and/or a higher soil N availability have been related to a higher N mineralization and lower relative dominance of DON (Austin et al., 2004; Schimel and Bennett, 2004). The interplay between litter quality and microbial communities can have important implications on the total soil C and N storage in response to global change impacts (Wallenstein et al., 2010; Keiser et al., 2013). In this direction, litter quality is shifting in multiple biomes due to changes in plant community composition and/or phenotypic responses to global changes (Murphy et al., 2002; Kurokawa et al., 2010; Sardans et al., 2012). Similarly, climate change drivers, such as warming and drought, are shifting the soil microbial communities by promoting a higher fungal:bacterial ratio in many ecosystems worldwide (Zhang et al., 2005; Jung Kwon et al., 2013; Maestre et al., 2013), while increasing N deposition has been found to reduce the abundance of fungi relative to bacteria (Wallenstein et al., 2006; Strickland and Rousk, 2010). Improving our knowledge of how different soil characteristics (e.g. microbial and chemical properties) modulate the availability of soil C and N during litter decomposition in response to different litter qualities is of importance for understanding nutrient cycling in soils, and to predict how it will evolve with ongoing global environmental change (Cleveland et al., 2014). For example, a shift in the microbial community structure from fungal-dominated to bacterial-dominated communities may decrease N depolymerization and subsequent mineralization in soils with low quality litter inputs, which are expected to occur with global change (e.g. high litter C:N ratio as a consequence of increasing atmospheric CO_2, Sardans et al., 2012). Changes in the availability of nutrients linked to different microbial communities during litter decomposition may influence future decomposition and mineralization processes for a particular soil, as a consequence of the previous nutrient legacy (Keiser et al., 2011). Despite the importance of C and N cycles on ecosystem functioning and services (Schlesinger, 1996; Wardle, 2002; Robertson and Groffman, 2007), our understanding of how soil characteristics control soil C and N dynamics during leaf litter decomposition is still scarce (Bradford et al., 2013; Keiser et al., 2013).

García-Palacios et al. (2013b) used a litter decomposability assay to show that soils with higher levels of organic C, microbial abundance, microbial functional diversity and fungal:bacterial ratio accelerated litter decomposition in response to a wide variety of litter species. Here we used the experimental set up of García-Palacios et al. (2013b) to: i) evaluate changes in C and N availability in soils with contrasting characteristics (organic C, total N and microbial communities) during the decomposition of litters differing in its quality; ii) determine the relative importance of soil characteristics and litter quality as predictors of soil C and N availability; and iii) assess how changes in the nutrient availability derived from litter decomposition can distinctively affect potential net N mineralization and transformation rates in soils with contrasting soil characteristics. We hypothesized that soils with higher microbial functional diversity, bacterial and fungal abundance and fungal:bacterial ratio will increase C and N availabilities during litter decomposition (Austin et al., 2004). Additionally, we expected that changes in the N availability of the soil linked to different microbial communities would have a direct legacy effect on processes such as potential N mineralization rates (Schimel and Bennett, 2004).

2. Methods

2.1. Study site and soil sampling

Soils for this study were collected during Spring 2011 from two semiarid roadside grasslands from central Spain (Fig. S1). The first site was a 2- year-old roadside grassland, and represents an early-successional stage (39° 47′ N, 3° 12′ W, 731 m a.s.l.); the other was a >20-year-old roadside grassland representing a late-successional stage (40° 22′ N, 03° 53′ W; 615 m a.s.l.). For the top 10 cm, soil pH ranged between 7.2 and 8.3, organic C between 0.8% and 2.3%, total N between 0.08% and 0.24%, and total P between 0.03% and 0.07%, for the early- and late-successional grasslands, respectively (Table 1). We selected roadside grasslands for our study because they show rapid structural and compositional changes in their microbial communities, following a similar trajectory to that recorded during secondary succession in old fields (Harris, 2009; García-Palacios et al., 2011a,b), and thus represent a valid study system to investigate the functional role of soils with contrasting characteristics.

Thirty soil cores (0–10 cm depth) were randomly sampled at each grassland. Soil samples were bulked by site to get a representative microbial community, homogenized, and kept cold in the field until laboratory preparation. In the laboratory, the samples were sieved (2-mm mesh), and one fraction was immediately frozen at −80 °C for microbial analysis. The other fraction was kept at 4 °C for 1 day before conducting the decomposability assay. Before this assay, we characterized the microbial communities from both the early- and late-successional grasslands. The abundance of bacterial 16S and fungal 18S rRNA genes was obtained using qPCR as described by Evans and Wallenstein (2011). We calculated the fungal: bacterial ratio from these data. Additionally, the microbial functional diversity was measured by using Microresp (Campbell et al., 2003), as described in García-Palacios et al. (2011b). The

Table 1
Main characteristics of the studied soils. Data are means (SE), $n = 5$.

Variable	Soil A	Soil B
pH	8.31 (0.29)	7.15 (0.02)
Total N[a]	0.08 (0.01)	0.24 (0.02)
Organic C[a]	0.77 (0.07)	2.30 (1.28)
Total P[b]	0.03 (0.01)	0.06 (0.02)
Microbial functional diversity[b]	1.88 (0.51)	2.63 (0.84)
Bacteria[c]	$1.36 \cdot 10^8$ ($8.52 \cdot 10^7$)	$3.56 \cdot 10^9$ ($1.31 \cdot 10^9$)
Fungi[c]	$9.24 \cdot 10^6$ ($3.71 \cdot 10^6$)	$9.27 \cdot 10^8$ ($4.40 \cdot 10^8$)
Fungal:bacterial ratio	0.07 (0.01)	0.26 (0.02)
Dissolved inorganic N (DIN)[d]	18.61 (1.36)	20.18 (1.38)
Dissolved organic N (DON)[d]	31.17 (7.59)	17.42 (1.85)
Available N[d]	49.78 (6.55)	37.60 (1.60)
Microbial biomass N[d]	22.72 (7.60)	23.16 (3.47)
Carbohydrates[e]	34.42 (2.04)	33.22 (2.69)
Amino acids[e]	6.46 (0.01)	3.36 (0.24)
Proteins[e]	20.76 (2.03)	19.84 (1.26)
Phenols[e]	8.22 (0.44)	7.15 (0.30)
DIN: DON	0.83 (0.28)	1.24 (0.21)
Pentoses: hexoses ratio	0.63 (0.15)	1.04 (0.08)
Carbohydrates: phenols ratio	4.42 (0.39)	4.59 (0.57)
Potential net mineralization[f]	2.39 (0.29)	1.94 (0.28)
Potential net N transformation[f]	1.02 (0.35)	1.57 (0.23)

[a] %.
[b] Decits.
[c] DNA copies g^{-1} soil.
[d] mg N kg^{-1} soil.
[e] mg C kg^{-1} soil.
[f] mg N kg^{-1} soil day^{-1}.