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Comparing the effects of litter quantity and quality on soil biota structure and functioning: Application to a cultivated soil in Northern France

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ABSTRACT

Plant litter is the main carbon (C) source of belowground communities, influencing the functioning of terrestrial ecosystems. In cultivated systems, litter varies quantitatively (restitution or exportation of aerial plant parts) and qualitatively (crop rotation) throughout the year. The effects of litter quantity and quality on the soil biota structure and their relative contributions at different trophic levels have rarely been simultaneously assessed in agricultural soils. To evaluate the role of litter quality and quantity on soil food webs, we incorporated two litter types (labile or recalcitrant) and two litter quantities (low or high) in a long-term experimental site studying the impact of different cultural practices in Northern France. After 7 months, we measured the litter mass loss, enzymatic activities (hydrolytic and oxidative), nitrogen (N) content and biomass of the soil biota: microorganisms, nematodes, Acari, Collembola, earthworms and macro-arthropods. Litter quantity and quality had distinct effects on the structure and functions of soil communities.

Doubling the quantity of added litter caused deep changes in the composition of detritivorous fauna by promoting the largest-sized group of detritivores (anecic earthworms) to the detriment of the smaller-sized groups (Collembola), which in turn led to higher litter consumption for a similar amount of soil biota biomass and hydrolytic enzyme activities after seven months of decomposition. In contrast, low litter quality stimulated the fungal energy channel, with an increase in the relative proportion of fungi, fungal feeding nematodes and euedaphic and hemiedaphic collembolans. This food web was characterized by a shift towards nitrogen acquisition that decreased the C:N ratio of enzymatic activities. Litter management is a central factor to consider for influencing ecosystem services such as soil fertility and nutrient cycling through the promotion of specific functional groups in soil.

1. Introduction

Plant residue decomposition is an essential process that drives carbon (C) and nutrient cycling in soils (Wardle et al., 2004). Because of their capacity to produce extracellular enzymes, bacteria and fungi are the main contributors to litter decay, explaining approximately 85–90% of litter mineralization in a variety of ecosystems (reviewed by Ekschmitt et al., 2008). In addition to the key role of microorganisms, soil fauna participates actively through direct (fragmentation, burying) and indirect (alterations of microbial communities and their activities) effects during the decomposition of plant residues (Coleman et al., 2004). For instance, microbial feeders, such as nematodes or micro-arthropods, reportedly stimulate microbial activities and nutrient recycling through their grazing activities (Lussenhop, 1992; A'Bear et al., 2014; Trap et al., 2015), whereas macrofauna, such as earthworms, generally increase litter decomposition through comminution and bioturbation (Lavelle et al., 1997; Bertrand et al., 2015). Despite the number of studies demonstrating the predominant role of soil organisms in litter degradation (Swift et al., 1979; Cadisch and Giller, 1996; Coleman et al., 2004), little is

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known about how litter management shapes the structure of soil biota and whether it can generate positive feedbacks for sustaining crop production with massive exportation of biomass. Indeed, litter management in cultivated systems drives both the quantity of litter restituted through the exportation or restitution of crop residues and the quality of litter through the selection of the plant included in the cultural rotation.

Litter quantity and quality are two major factors that can influence the activity and composition of soil organisms. Higher resource quantity and quality usually support the development of opportunistic bacterial taxa that increase with the greatest quantity of labile C compounds (Nemergut et al., 2010; Pascault et al., 2010). In contrast, decreasing litter quality usually stimulates oligotrophic microbial communities, mainly dominated by fungi that are better suited to address recalcitrant litter compounds, such as lignin, or litters with high litter C:N ratios (de Boer et al., 2005). At higher trophic levels, litter quantity controls the abundance and biomass of soil arthropods mainly because of the concomitant increase in the supply of food and habitat space in natural ecosystems (Kaspari and Yanoviak, 2009; Sayer et al., 2010). However, litter quality is rather related to the structure and diversity of decomposers mainly because of the distinct feeding preferences of detritivorous taxa (Brown et al., 2000; Wolters, 2000) and modifications of resource availability (Kaspari and Yanoviak, 2009; Sayer et al., 2010). Thus, increasing litter quantity should theoretically favour the total biomass of belowground biota and, in particular, organisms better suited to address the greater availability of C compounds *via* exploitative resource strategies (Nemergut et al., 2010), whereas decreasing litter quality should favour the fungal energy channel that is better suited to address recalcitrant litter degradation *via* acquisitive resource strategies (de Vries et al., 2012). However, the relative effects of litter quantity and quality on the soil food web structure have rarely been assessed at several trophic levels, and to our knowledge, there are no studies disentangling the effects of these two factors on ecosystem processes in agricultural soils. This assessment is important for the new schemes of agricultural management that aim to promote ecosystem services such as soil biodiversity or biogeochemical cycles through modifications of the quantity and quality of crop residues entering the soil.

With the objective of disentangling the effects of litter quantity and quality on soil community structure and function, we hypothesized that (i) litter quantity should increase the biomass of soil organisms, whereas litter quality should shape the composition of soil communities; and that (ii) the increase of biota biomass by litter quantity should increase litter degradation and C enzymatic activities, while the change in community composition by litter quality should change C and N enzymatic activities. We tested these hypotheses in a field experiment by adding two different crop residue quantities (5 t ha^{-1} or 10 t ha^{-1}) and qualities (pea and barley) plus a control treatment to agricultural soil in Northern France. We determined during litter decomposition the enzymatic activities (hydrolytic and oxidative), soil mineral nitrogen (Nmin), and soil biota biomasses (micro-organisms, nematodes, Acari, Collembola, earthworms and macro-arthropods) in the amended and non-amended treatments.

2. Materials and methods

2.1. Study site and experimental design

The study was conducted in a long-term French experiment based at the Estrées Mons station in Northern France (49°873′N, 3°032′E). The experimental site was established in 2010 to study the impact of different cultural practices such as tillage, residue exportation and N fertilization on soil physicochemical properties, biological activities and environmental impacts (Coudrain et al., 2016). We established plots in a field with the same history of cropping management: since 2010, the field has been cultivated in a six-year rotation (spring pea – winter wheat – rapeseed – spring barley – maize – winter wheat) with shallow tillage (8 cm depth) and crop residues restitution. The soil was classified as a Luvisol Orthique (FAO classification) or a Typic Hapludalf (USDA classification). The soil texture was characterized by 16.8% clay, 76.3% silt and 3.8% sand, with a mean pH (soil H_2O) of 7.8 in the topsoil. The average soil C content was 8.7 g C kg^{-1}, and the soil nitrogen mineral content was 2.8 mg N kg^{-1} at the beginning of the experiment. To test the effects of resource quantity and quality on the structure and functions of the soil food web, three treatments were set-up in situ, corresponding to litter additions of 5 t ha^{-1} pea *(Pea $^1/_2$)*, 10 t ha^{-1} pea *(Pea 1)* and 10 t ha^{-1} barley *(Barley 1)*. Two weeks prior to the beginning of the experiment, the soil was prepared by shallow tillage (8 cm depth) and weeded with Glyphosate to remove any living plants from the site. Hand weeding was performed regularly thorough the experiment in order to keep the soil in the plots bare during the time of the experiment. The three treatments plus a control without litter addition (*No litter*) were applied to 8 m^2 plots that were repeated randomly within four blocks distributed in our experimental zone, with litter buried manually in the 0–15 cm layer. The plots within the blocks were separated by at least 2 m of distance. To prevent a "border effect", only the central 4 m^2 of each plot were sampled. The experiment started in October 2013 by mixing the litter vigorously with the top soil layer (0–15 cm) with spades. Each plot was delimited by wood pieces to form a square of 2 m length, 2 m width and 25 cm high, which was placed on the soil surface. To evaluate the litter mass loss, we buried litterbags at 8 cm depth (20 × 20 cm, 5 mm mesh size) in each plot at the beginning of the experiment. Litterbags contained 5.0 g C of litter corresponding to the treatment (i.e pea-filled litterbags in *Pea 1* and *Pea $^1/_2$* plots and barley-filled litterbags in *Barley 1* plots), corresponding respectively to 11.1 and 11.0 g DM of barley or pea. Litterbags were collected in each plot in spring and autumn 2014 (i.e 7 and 11 months after litter addition). Litter quality was characterized before the experiment (see paragraph 2.2). Measurements of soil biota and abiotic parameters were performed during three main measurement campaigns: in autumn 2013, spring 2014 and autumn 2014, corresponding respectively to 0, 7 and 11 months after litter addition. The time scale between the sampling dates was determined in order to follow simultaneously the response of functional groups of heterogeneous life spans (microorganisms to earthworms) and to perform biota sampling at its optimal seasonal development stages (spring and autumn). For the three campaigns, we collected soil samples (0–10 cm) to determine the mineral nitrogen content, microbial biomass, dissolved organic C, ergosterol, enzymatic activities, nematodes, micro-arthropods and macrofauna communities.

2.2. Initial litter quality and litter mass loss

To assess the initial quality of litters, pea and barley were analyzed using four replicates of 1.2 g DM of litter. Total C and N contents were measured by elemental analysis (NA 2000, Fisons Instruments, Milan, Italy). The soluble and cell wall contents were determined by neutral detergent fibre (NDF) extraction, according to the method described by Goering and Van Soest (1970). Polysaccharide analyses were performed as previously described (Machinet et al., 2011). Briefly, ten mg of litter was placed to swell in 125 ml of 12 M H_2SO_4 for 2 h at 20 °C and then subjected to acid hydrolysis with 1 M H_2SO_4 for 2 h at 100 °C. The monosaccharides released by the acid were then separated by high performance anion-exchange chromatography (HPAEC) on a CarboPac PA-1