



Litter chemistry influences earthworm effects on soil carbon loss and microbial carbon acquisition



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ABSTRACT

Earthworms could affect soil C and N cycling process to balance their energy and nutrients requirements, and they could also regulate soil microbial community structure and microbial acquisition for C and N. However, the connection between faunal and microbial stoichiometry in the coupling soil C and N cycling remains poorly understood. In a controlled laboratory experiment, we amended soil with five litters differing in litter chemistry (clover, maize stover, wheat straw, *Rumex* and bagasse fiber) including a no litter control and treated them without or with earthworms (*Metaphire guillelmi*). After 90 d incubation, we examined changes in earthworm tissue and microbial stoichiometry and different soil C and N fractions. Earthworm tissue C content was rather stable compared with the fluctuation in tissue N, implying that C is under stronger control and associated with higher demand than N. The presence of earthworm significantly enhanced CO₂ emissions and decreased particulate organic carbon (POC) and soil organic carbon (SOC) contents in the low lignin litter species clover, maize stover and wheat straw. Meanwhile, earthworm presence increased N₂O cumulative emissions but exerted negligible effects on particulate organic nitrogen (PON) and soil total nitrogen (TN) contents irrespective of litter species. Correspondingly, earthworm regulated microbial C and N acquisition as C to N-degrading enzyme activity ratio were nearly doubled in the low lignin litter species clover, maize stover and wheat straw, while it was decreased in the high lignin litter species *Rumex* and bagasse fiber. However, the structural equation modeling indicated C loss induced by earthworms was mainly attributed to their effects on soil fungi and bacteria abundance, while much less related to C-degrading enzyme activities. In conclusion, litter species controlled earthworm effects on soil C and N loss and associated microbial acquisition for C and N, highlighting the pivotal role of resource chemistry in the regulation of soil fauna impact on soil functioning and ecosystem services.

1. Introduction

Litter is an important resource providing one of the main sources of energy and nutrients for the soil food web (Wardle et al., 2004). Litter chemistry regulates growth and metabolism of soil biota and associated energy flows and nutrient cycling in terrestrial ecosystems (Scheu and Schaefer, 1998; Cornwell et al., 2008; Ott et al., 2014; Bradford et al., 2016; Cesarz et al., 2016). Litter species with high concentration of accessible organic compounds could significantly stimulate microbial activities and accelerate C and N mineralization (Hobbie, 2015). Therefore, soil fauna are likely to be most beneficial for the

decomposition of litter species with high recalcitrant compounds. Nevertheless, earlier studies have indicated that higher resource availability litters could favor soil fauna utilization (Yatso and Lilleskov, 2016). So far, the interactions between soil fauna and litter chemistry and the consequences for C and N turnovers are not well understood.

It is well-known that burrowing, feeding and casting activities of earthworms affect C and N cycling by regulating soil microbial and biochemical process (Lavelle, 1988; Edwards, 2004; Blouin et al., 2013; van Groenigen et al., 2014; Bertrand et al., 2015). Earthworms can stimulate a small proportion of C and N gaseous loss by their respiration

Abbreviations: NL, no litter; CL, clover; MA, maize stover; WH, wheat straw; RU, *Rumex*; BA, bagasse fiber; DOC, dissolved organic carbon; DON, dissolved organic nitrogen; POC, particulate organic carbon; PON, particulate organic nitrogen; SOC, soil organic carbon; TN, total nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen

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and gut-associated process (Scheu, 1991; Horn et al., 2003; Edwards, 2004). More importantly, earthworms facilitate microbial mineralization of labile organic substrates and greenhouse gas emissions by releasing C and N locked away in plant litter and soil organic matter (Bernard et al., 2012; Lubbers et al., 2013). Besides, earthworms showed stoichiometric invariability according to an investigative research conducted on different experimental plantations (Marichal et al., 2011). To balance their requirements for C and N, earthworms might have distinct strategies for C or N mining. Few studies applied stoichiometric principles when interpreting the combined effects of earthworms and microorganisms on biogeochemical cycling (Tiunov and Scheu, 2004; Marichal et al., 2011; Fahey et al., 2013). Understanding the role of soil faunal stoichiometry would improve our knowledge about the functional roles of earthworm in soil C and N cycling.

Soil microbes produce extracellular enzymes to break down complex organic matter compounds and acquire bioavailable C and N (Sinsabaugh et al., 2002; Waring et al., 2013). The relative abundance of enzymes involved in C and N cycling reflects the biogeochemical equilibrium between microbial biomass stoichiometry as well as the quantity and quality of organic matter (Sinsabaugh and Follstad Shah, 2012). Recently, Hoang et al. (2016) described distinct strategies of earthworms for re-allocating C- and N-related enzyme activities in order to acquire the resource in the shortest supply relative to their requirements. However, there are still two seemingly contradictory mechanisms explaining how earthworms affect microbial enzyme activities. As higher demand for the product can promote enzyme activities (Bell et al., 2013; Manzoni et al., 2017), earthworm could utilize available C and/or N, therefore increase microbial C- and/or N-mining activities to compensate for earthworm competition. On the other hand, earthworms could enhance substrate availability, hence stimulate microbial C-mining activities, as Allison et al. (2014) indicated low substrate availability could suppress the production of an enzyme. So far, there is still a lack of knowledge regarding how earthworms influence microbial stoichiometry and the linkage with earthworm-induced C and N changes.

To explore whether faunal and microbial stoichiometry help to explain the mechanisms of earthworm-driven soil C and N turnover, we performed a factorial experiment with different litter species combined with or without earthworms. Different C and N fractions as well as the CO₂ and N₂O flux were measured. Particulate organic C and N which are characteristic of intermediately decomposed plant litter, were used to express earthworm-induced litter C and N losses as they are much more sensitive than total soil organic C and N (Cambardella and Elliott, 1992; Benbi et al., 2014). Microbial biomass, microbial community structure and enzyme activities were also determined to explore the stoichiometric mechanisms underlying the effects of earthworms on soil C and N changes. The C-degrading enzyme activities including α -1,4-glucosidase (AG), β -1,4-glucosidase (BG), and β -D-cellobiohydrolase (CB) and N-degrading enzyme activities including β -1,4-N-acetylglucosaminidase (NAG) and leucine aminopeptidase (LAP) were measured. The ratio of C- to N-degrading enzyme activities was used as indicators of microbial resources demand between C and N (Waring

et al., 2013). We hypothesized that (i) earthworm effects on C and N pools vary with plant chemistry, for example high resource availability litters (low C:N ratio, low lignin content and high soluble compounds) could favor earthworms utilization compared to the high recalcitrant compounds litters (high C:N ratio, high lignin content and low soluble compounds), therefore reinforce earthworm effects on C and N cycling process; (ii) increased microbial mining for C (or N) will be reflected by shifts in the relevant enzyme activities as well as shifts in microbial community structure to favor bacteria over fungi (or vice versa).

2. Materials and methods

2.1. Experimental set-up

The endogeic earthworm *Metaphire guillelmi* was collected from an arable field rotated with soybean, maize and different kinds of vegetables each year in Rudong county (32°33'N, 121°15'E), Jiangsu, China. To avoid the earthworm cast from diminishing the effects of earthworms in the following experiment, soil was collected from the top 5–20 cm layer. The background soil properties were soil pH (water:soil 2.5:1) 6.5, 30.0% sand, 63.5% silt, 6.5% clay, 13.9 g of organic C kg⁻¹ and 0.7 g of total N kg⁻¹. The soil was sieved (< 2 mm) and all visible debris and fauna were removed before the incubation experiment.

This experiment was set up with a two-way factorial design (earthworm \times litters), with five litters including residues of clover (*Trifolium repens* L.), maize stover (*Zea mays* L.), wheat straw (*Triticum aestivum* L.), *Rumex* (*Rumex japonicus* Houtt.), bagasse fiber (*Saccharum officinarum*) and a control (no litter input) and across earthworm treatments (with or without earthworms). Litters are abbreviated as following: clover (CL), maize stover (MA), wheat straw (WH), *Rumex* (RU) and bagasse fiber (BA). Each treatment had five replicates leading to 60 experimental units in total. The selected litters spanned a gradient of litter chemistry (Table 1). Litters were collected from the same location as earthworms and subsequently dried at 60 °C for 24 h and milled and sieved (1 mm mesh). Each litter was added at a rate equivalent to 10.0 g litter C kg⁻¹ dry soil. Litters were homogeneously mixed with soil to separate the litter-mixing effect of earthworms from the stoichiometric effects. After 10 d of pre-incubation, three adult earthworms with a total fresh weight of 7.5 g were added to each microcosm. Litter C and N concentrations were determined by potassium dichromate oxidation-ferrous sulphate titration and the Kjeldahl digestion with sulfuric acid and hydrogen peroxide, respectively (Sparks et al., 1996). Litter soluble C and N were obtained by extracting 3.0 g air-dried litter in 30 mL distilled water (20 °C, 30 min), then centrifuged (3500 rpm, 20 min) and filtered through 0.45- μ m cellulose nitrate membrane filter (Ghani et al., 2003), then determined using a TOC analyzer (Elementar, Germany) and a continuous flow analyzer (Skalar, Breda, The Netherlands), respectively. Cellulose and lignin were determined using a Fibertec System 2021 FiberCap (Foss Tecator, Höganäs, Sweden) following the procedures described by Soest and Wine (1967).

The microcosms were incubated in a climate chamber at 25/15 °C

Table 1

Initial properties of different litters used as soil amendments in the experiment (Mean \pm standard error, n = 5). Litters are presented in the order of increasing C:N ratio.

	Clover	Maize stover	Wheat straw	Rumex	Bagasse fiber
Total C (%DM)	35.3 (\pm 0.3)	37.5 (\pm 0.5)	36.3 (\pm 0.6)	35.4 (\pm 0.7)	38.0 (\pm 0.4)
Total N (%DM)	1.75 (\pm 0.02)	0.84 (\pm 0.02)	0.67 (\pm 0.01)	0.56 (\pm 0.02)	0.25 (\pm 0.01)
Total C:N	20.4 (\pm 0.3)	44.2 (\pm 1.3)	54.6 (\pm 2.1)	63.4 (\pm 1.4)	150.8 (\pm 7.7)
Soluble C (g kg ⁻¹)	23.88 (\pm 0.95)	8.46 (\pm 0.29)	7.29 (\pm 0.33)	9.22 (\pm 0.23)	2.31 (\pm 0.10)
Soluble N (mg kg ⁻¹)	276.4 (\pm 11.0)	90.9 (\pm 3.0)	42.4 (\pm 0.6)	43.7 (\pm 0.8)	25.3 (\pm 2.2)
Soluble C:N	87.0 (\pm 6.9)	93.4 (\pm 5.9)	180.5 (\pm 11.8)	216.6 (\pm 8.3)	95.2 (\pm 6.8)
Cellulose (g kg ⁻¹)	89.2 (\pm 6.8)	103.8 (\pm 5.1)	226.7 (\pm 11.3)	195.0 (\pm 5.9)	385.4 (\pm 11.2)
Lignin (g kg ⁻¹)	44.8 (\pm 5.9)	187.9 (\pm 8.2)	152.6 (\pm 10.2)	233.2 (\pm 4.1)	250.6 (\pm 14.5)

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