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Effect of litter quality and soil fungi on macroaggregate dynamics and associated partitioning of litter carbon and nitrogen

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ABSTRACT

We investigated the effect of plant residue decomposability and fungal biomass on the dynamics of macroaggregate (250–2000 μm) formation in a three months' incubation experiment and determined the distribution of residue-derived C and N in the microbial biomass and in aggregate size fractions (250–2000 μm, 53–250 μm and <53 μm) using ^{13}C and ^{15}N data. A silty loam soil (sieved <250 μm) was incubated with and without addition of ^{15}N labelled maize leaves (C/N = 27.4) and roots (C/N = 86.4). Each treatment was carried out with and without fungicide application. The addition of maize residues enhanced soil respiration and microbial biomass C and N and resulted in increased macroaggregate formation with a higher and more rapid maximum macroaggregation in the soil amended with maize leaves than in that with addition of roots. Fungicide application led to a significant decline of microbial biomass C and mineralization of the added residues compared to untreated soils, which demonstrates a successful suppression of part of the active microbial biomass by the fungicide. However, this was not confirmed by a generally lower ergosterol concentration. Consequently, ergosterol was no reliable fungal biomarker in periods of rapid decline of the fungal biomass. A single addition of fungicide was insufficient for continued inhibition of the fungal biomass. Yet, a significant delay (28–42 days) in macroaggregation in fungicide treated compared to untreated samples highlighted the importance of the fungal biomass in macroaggregate formation. Macroaggregates were enriched in maize-derived ^{13}C and ^{15}N compared to microaggregates or the fraction < 53 μm. They turned over rapidly with decreasing substrate availability, which entailed a transfer of maize-derived C and N stored within macroaggregates during the first weeks of incubation to microaggregates with proceeding incubation time. Our results indicate that this transfer happened within macroaggregates, because no considerable amount of free particulate organic matter (POM) was released upon macroaggregate breakdown. We conclude that substrate decomposability and fungal activity are key factors determining extent and dynamics of macroaggregation during decomposition processes. Macroaggregate formation implied rapid incorporation and thereby short-term protection of maize-derived C and N. Moreover, macroaggregates allowed a transfer of maize-derived organic matter into microaggregates within macroaggregates, which prevented the release of significant amounts of free POM upon macroaggregate breakdown. Consequently, macroaggregates constitute to the transfer of recently added C into more stable soil organic matter fractions.

1. Introduction

Soil aggregation mediates many of the soil's biological, chemical and physical properties (e.g. aeration or water infiltration); it contributes to soil fertility, and it reduces soil erosion, because water infiltration and the resistance to raindrop impact or wind action are supported (Oades, 1984; Degens, 1997). In addition, aggregate formation physically protects soil organic matter (SOM) from biodegradation due to reduced accessibility of SOM by enzymes when SOM is located within soil aggregates (Besnard et al., 1996; Golchin et al., 1994; Sollins et al., 1996).

Aggregate formation and stabilization are affected by several factors, e.g. the clay content, the mineralogy of the clay fraction and the type and amount of organic material (Lynch and Bragg, 1985). Several workers have noted that the addition of easily decomposable substrate to soil causes a rapid stimulation of the soil microflora accompanied by a significant increase in aggregate stability

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(e.g. Schlecht-Pietsch et al., 1994; Martens, 2000; De Gryze et al., 2005; Abiven et al., 2007).

For soils with SOM as the major binding agent, Tisdall and Oades (1982) proposed a conceptual model of soil aggregation, according to which soil microaggregates (<250 μm) are bound together by organic compounds of different origin to form stable macroaggregates (>250 μm). The binding agents are supposed to be mainly young organic materials such as roots or fungal hyphae. This hypothesis was supported by the observation that aggregate stability can be increased by the addition of readily decomposable C (e.g. Martens, 2000; Bossuyt et al., 2001; De Gryze et al., 2005; Abiven et al., 2007). The young, organic nature of the binding materials was confirmed by several field studies which reported that water-stable macroaggregates are enriched in young organic matter compared to microaggregates (e.g. Puget et al., 1995; Jastrow et al., 1996; Monreal et al., 1997; Six et al., 2000; John et al., 2005; Yamashita et al., 2006). Few studies stressed the importance of the fungal and bacterial biomass to soil aggregation (e.g. Chantigny et al., 1997; Bossuyt et al., 2001; Denef et al., 2001; De Gryze et al., 2005). Bossuyt et al. (2001) and Denef et al. (2001) found a vital importance of soil fungi to soil macroaggregation. However, Guggenberger et al. (1999) reported that the decline of fungal and bacterial biomass was not reflected by a decrease in the yield of macroaggregates. They concluded that living filamentous organisms may have created macroaggregates, but other factors seemed to be involved in the stabilization of the aggregates. De Gryze et al. (2005) suggested that aggregate formation relates to microbial activity rather than the number of living fungi and bacteria, since their activity influences the production of exudates and hyphae, which in turn act as binding materials. The quality of plant residues is a key factor determining the composition and activity of the soil microbial biomass (Wardle and Lavelle, 1997; Bardgett and Shine, 1999) and thus it can also affect the processes included in soil aggregation (Bossuyt et al., 2001; Denef et al., 2001; Abiven et al., 2007). However, there is little information of how the quality of plant residues influences the short-term dynamics of aggregate formation and about the partitioning of recently added C and N within aggregate size fractions during the course of decomposition.

We conducted a soil incubation experiment with and without the addition of ^{15}N labelled maize residues of different decomposability (leaf and root materials) and with and without fungicide addition to obtain more detailed information about the controls of macroaggregate formation during litter decomposition and the role of newly formed macroaggregates for the storage of maize-derived C and N. The objectives of our study were (i) to determine the effect of plant residue decomposability on the short-term dynamics of soil macroaggregation, (ii) to examine the role of fungi in the formation of water-stable macroaggregates and (iii) to determine the distribution of maize-derived C and N among size classes of water-stable aggregates using ^{13}C and ^{15}N data.

2. Material and methods

2.1. Experimental design

Soil from the Ap horizon (0–30 cm) of a field with long-term wheat cropping of the Höhere Landbauschule in Rotthalmünster (Stagnic Luvisol) was collected in September 2005. The soil was air-dried and sieved <250 μm to break all macroaggregates. The coarse sand >250 μm was discarded. The soil used for incubation was a silty loam with a low amount (~5%) of sand particles >250 μm (Ludwig et al., 2005). One hundred and fifty grams of dry, sieved soil were filled into 250-ml pots, adjusted to a bulk density of 1 g cm^{-3} and brought to 60% of the maximum water holding capacity using distilled water. The relatively low bulk density refers to the state of field soils following mechanical incorporation of plant material. During incubation, the water content of the soil was controlled by weight and corrected when necessary.

The following six treatments were applied with four replicates each: (1) "Control" (soil without incorporation of maize residues, without fungicide), (2) "Control + Captan" (soil without incorporation of maize residues, with addition of fungicide), (3) "Soil + Leaf" (soil with incorporation of maize leaf residues, without fungicide), (4) "Soil + Leaf + Captan" (soil with incorporation of maize leaf residues, with fungicide), (5) "Soil + Root" (soil with incorporation of maize root residues, without fungicide), and (6) "Soil + Root + Captan" (soil with incorporation of maize root residues, with fungicide).

For the treatments with incorporation of maize residues, 150 g of dry and sieved soil were thoroughly mixed with 0.75 g (dry weight) of maize leaves (2.1 mg C g^{-1} soil; C/N 27.4) or maize roots (2.1 mg C g^{-1} soil; C/N 86.4) and then filled into pots and adjusted to 60% of the maximum water holding capacity. Maize leaves and roots were chosen due to their different composition and decomposability and because it was possible to trace the fate of maize-derived C during the decomposition experiment. The biochemical composition of the maize litter was determined using the Van Soest method (Goering and Van Soest, 1970) and the Weende method (Naumann and Bassler, 1988). The maize roots had considerably larger C/N and lignin/N ratios than the maize leaves. Further, they contained lower amounts of polysaccharides and proteins and higher amounts of more recalcitrant components. General properties of the soil and plant materials used for the incubation experiment are given in Table 1.

The added residues were derived from maize plants that were grown in pots with coarse sand during the vegetation period 2005. The maize plants were watered with a nutrient solution which contained 10% labelled ammonium nitrate ($^{15}NH_4$ $^{15}NO_3$) in order to obtain two isotope tracers for the incubation experiment (^{15}N in maize biomass originating from the labelled nutrient solution and ^{13}C natural abundance). Leaf and root materials were harvested separately and oven-dried at 40 °C. Before application to the soil, plant materials (maize leaves and coarse maize roots (>2 mm)) were milled <500 μm.

The fungicide application for treatments 2, 4 and 6 was carried out as described by Denef et al. (2001) and Bossuyt et al. (2001) by adding 0.3 g fungicide (Captan 50W wettable powder, 89% active ingredient) per 100 g soil. To ensure homogeneous mixing of the fungicide with the soil, it was dissolved in the water used for wetting the soil.

The incubation was run for 84 days at 15 °C. At each sampling date (days 14, 28, 56 and 84 after the start of the incubation), four pots of each treatment were harvested destructively. In addition, the initial soil properties were determined from the control with and without fungicide (treatments 1 and 2) at day 0. Based on the

Table 1
General properties of the soil and plant materials (leaves and roots of ^{15}N labelled maize) used for the incubation experiment (means standard and deviation ($n = 4$), or $n = 1$)

	Soil	Leaf material	Root material
C (g kg^{-1} DW)	12.6 (0.1)	421 (0.7)	422 (1.8)
C/N ratio	8.9 (0.1)	27.4 (0.7)	86.4 (1.6)
$\delta^{13}C$ (‰ V-PDB)	−26.5 (0.1)	−12.7 (0.2)	−11.9 (0.2)
^{15}N (atom%)	0.37 (0.0)	7.4 (0.4)	7.9 (0.5)
Ergosterol (mg kg^{-1} DW)	0.41 (0.0)	8.2 (1.7)	5.5 (1.9)
Ash (% of dry matter)		11.4	18.4
Crude protein (% of dry matter)		15.5	5.6
Crude fibre (% of dry matter)		26.3	29.9
Cellulose (% of dry matter)		26.5	10.0
Hemicellulose (% of dry matter)		28.0	29.5
Lignin (% of dry matter)		6.2	32.0
Lignin/N ratio		0.4	6.6