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Can earthworms simultaneously enhance decomposition and stabilization of plant residue carbon?

Ingrid M. Lubbers [a,*], Mirjam M. Pulleman [a,b], Jan Willem Van Groenigen [a]

[a] Department of Soil Quality, Wageningen University, PO BOX 47, 6700AA Wageningen, The Netherlands
[b] International Center for Tropical Agriculture (CIAT), Km 17 Recta Cali-Palmira, Apartado Aéreo 6713, Zip code: 763537 Cali, Colombia

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ABSTRACT

Earthworm activity can strongly influence soil structure and organic matter (OM) dynamics of agricultural soils. Several short-term studies (≤90 days) have shown that earthworms can increase incorporation of residue carbon (C) into soil aggregates, suggesting reduced decomposition in the longer term. In contrast, another body of short-term studies reported that earthworms can increase carbon dioxide (CO_2) emission from soils, thus suggesting increased decomposition in the longer term instead. To solve this controversy, we measured the effect of the epigeic *Lumbricus rubellus* (Hoffmeister) and the endogeic *Aporrectodea caliginosa* (Savigny) on the soil C balance in a unique 750-day mesocosm experiment, where loess soil was surface-applied with maize (*Zea mays* L.) residues every six months. Carbon inputs and outputs were strictly controlled: no soil C input through growing plants and no leaching of soil organic C. Flux measurements of CO_2 were taken regularly and aggregate size distribution and total C and residue-derived C in the aggregate fractions (using the natural $\delta^{13}C$ signature of maize) were measured after 185, 565 and 750 days. Both earthworm species increased cumulative CO_2 emissions by at least 25%, indicating a higher C loss compared to the no-earthworm control. Yet, both earthworm species also increased the amount of soil C associated with the macroaggregate fraction after 750 days. *L. rubellus* increased the amount of residue-derived C in the macroaggregate fraction after 565 and after 750 days, whereas *A. caliginosa* increased residue-derived C in all the measured soil fractions after 750 days. Our results show that earthworms can simultaneously enhance CO_2 emissions and C incorporation in aggregate fractions. However, over 750 days the presence of earthworms resulted in a lower total C content due to a higher overall OM decomposition rate. We therefore propose that under the most realistic incubation conditions so far (longer term and multiple residue applications), earthworms stimulate the mineralization of freshly added and older OM to a greater extent than that they stabilize residue-derived C inside biogenic aggregates. Future studies should focus on the balance between these processes in the presence of growing plants.

1. Introduction

Since Freeman Dyson (1977) first suggested the possibility of soil C sequestration, an enormous scientific effort has been made to determine the potential of, and prerequisites for, C sequestration in agricultural soils (Smith, 2004). For instance, management options such as no-tillage or reduced-tillage have often been recommended to stimulate C sequestration in agricultural soil (Lal, 2004; Ogle et al., 2012). The shift from conventional tillage (CT) to no-till (NT) management made by many farmers over the past decades has therefore been qualified as beneficial to climate change mitigation (Derpsch and Friedrich, 2009). However, it remains unclear whether NT management actually leads to increased soil C stocks throughout the soil profile and, if so, within what time frame (Baker et al., 2007; Gál et al., 2007; Govaerts et al., 2009; Ogle et al., 2012; Six et al., 2004b).

Changes in the role of biota when switching from CT to NT in relation to C dynamics are especially interesting. Soil invertebrate fauna and microbes interact in the regulation of soil carbon (C) cycling processes, thereby affecting soil organic carbon (SOC) dynamics and emissions of carbon dioxide (CO_2) (Binet et al., 1998; Wachendorf et al., 2014). It is currently debated whether in the

* Corresponding author.
E-mail address: Ingrid.Lubbers@wur.nl (I.M. Lubbers).

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long run earthworms increase or decrease SOC storage (Lubbers et al., 2013; Zhang et al., 2013). This question is especially relevant in agroecosystems, where earthworm communities and densities can be manipulated through management practices (Castellanos-Navarrete et al., 2012; Crittenden et al., 2014; Curry et al., 2002); where soil greenhouse gas (GHG) emissions are highest (IPCC, 2014); and where the potential to store C in the soil by restoring previously lost SOC is highest (Lal, 2004).

A major mechanism affecting soil C dynamics is the physical protection of C (Six et al., 2000). Through this mechanism, SOC is stabilized inside soil aggregates within which its accessibility to decomposer organisms is decreased. Particularly under NT, the turnover of aggregates is reduced, leading to better protection and a longer residence time of SOC in the soil (Jastrow et al., 2007; Schmidt et al., 2011Six et al., 2000). Beside soil tillage, bioturbation by soil fauna such as earthworms is known to be one of the key processes influencing aggregate turnover (Six et al., 2004a). Typically, earthworm presence is stimulated in NT systems with surface residue retention, where soil disturbance is minimal and food supply relatively constant (Castellanos-Navarrete et al., 2012; Chan, 2001). It could therefore be hypothesized that a role for earthworms in aggregation and C sequestration would be most strongly expressed in an NT system.

The most direct effect of earthworm activity on C cycling is through their feeding, burrowing and casting behaviour (Curry and Schmidt, 2007). In this manner, earthworms can promote C stabilization in macroaggregates and microaggregates formed in their casts (Bossuyt et al., 2005; Pulleman et al., 2005a, 2005b). Under organic management, Fonte et al. (2007) found an increase of 35% of new C incorporated in biogenic aggregates, compared to a conventional system. This indicates that agroecosystem management greatly influences the magnitude and direction of the effect of earthworms on C dynamics (Hedde et al., 2013). The feeding behaviour of earthworms based on the ecological strategies describing their feeding and burrowing activities: epigeic, anecic and endogeic (Bouché, 1977) can differentially affect incorporation of fresh organic matter (OM) into biogenic aggregates. This might have important consequences for the protection of C and long term SOC storage (Bossuyt et al., 2006).

However, next to facilitating C stabilization, earthworms also stimulate and accelerate OM decomposition by enhancing microbial respiration (Binet et al., 1998; Wachendorf et al., 2014), and by fragmentizing, ingesting, disintegrating and transporting fresh plant material into the soil (Edwards, 2004; Nieminen et al., 2015). A quantitative literature review studying the influence of earthworm presence *vs*. earthworm absence on soil CO_2 emissions showed an overall enhancing effect of 33% (Lubbers et al., 2013). This analysis was based on data from mostly short-term studies that showed either increased or unaffected CO_2 emissions in the presence of earthworms, despite claims that physical protection of SOC incorporated into casts could lead to C sequestration in the longer term. A longer-lasting field study concluded that, after 5 months, treatments with earthworms had a lower C content of the total soil than without earthworms (49.3 *vs.* 50.3 g C kg^{-1}, $P = 0.004$) (Coq et al., 2007). Simultaneously, a higher proportion of large macroaggregates and casts enriched in C in the presence of earthworms was found. Yet, 16.5% higher CO_2 emissions for earthworm casts than for non-ingested soil was measured in a 28-day follow-up study, suggesting a net positive effect of earthworm activity on C mineralization (Coq et al., 2007).

Many of the above-mentioned studies emphasized the importance of time scale when assessing the effect of earthworms on SOC dynamics, and call for longer duration studies in order to improve our understanding of short *vs.* longer term effects of earthworms on soil C dynamics. In an effort to approach the time-scale issue, Zhang et al. (2013) recently explored the controversy of earthworm-facilitated C stabilization and mineralization by coining the concept of an earthworm-mediated ‘carbon trap’ (Zhang et al., 2013). This concept is described as “earthworm-mediated unequal amplification of C stabilization compared with mineralization,” meaning that, over time and compared to systems without earthworms, earthworms may stabilize a greater proportion of plant residue C inside biogenic aggregates than they mineralize as CO_2. Zhang et al. (2013) raised three main points that need to be overcome in future studies:

1) due to the large background of soil C, an increase in C stabilization is difficult to observe. Therefore, the magnitude of C stabilization has to be estimated indirectly by resultant effects on C mineralization;
2) the short duration of most experimental studies to date makes it difficult to detect possible C stabilization; and
3) most studies have restricted soil depths (up to a few centimeters) and re-distribution of earthworm-stabilized C throughout the soil profile has not been quantified.

Here, we present a study that addresses these three concerns. In a 750 day incubation study, we quantified the effect of the epigeic *Lumbricus rubellus* (Hoffmeister) and the endogeic *Aporrectodea caliginosa* (Savigny) on the top- (0–10 cm) and subsoil C (10–25 cm) budget of a simulated NT maize system. We measured earthworm effects on cumulative CO_2 emissions, aggregate size distribution, and total C and ^{13}C in the aggregate size fractions of two soil layers (i) as it develops over time; and (ii) as mediated by two common earthworm species with different feeding strategies and life histories.

2. Materials and methods

2.1. Experimental design

In a 750-day mesocosm study, we quantified the effects of two earthworm species on CO_2 emissions, soil aggregation and SOC dynamics in a simulated NT system where we applied maize residue on the soil surface. For the entire experimental time span C inputs and outputs were strictly controlled: no soil C input through growing plants and no leaching of soil organic matter through drainage. The experimental timeline, treatment codes and mesocosm design are shown in Fig. 1a, b and c, and the entire setup is presented in detail by Lubbers et al. (2015). In short, the study was set up as a full 2 × 2 factorial design, with *L. rubellus* (presence or absence) and *A. caliginosa* (presence or absence) as independent variables. A separate treatment without residue nor earthworms was included as a control (Fig. 1b). Treatments were laid out in a randomized block design with five blocks, each block containing three mesocosms of each treatment. The total number of mesocosms in this experimental setup thereby accumulated to 75. To enable destructive soil analyses and determine earthworm survival during the 750-day span of the experiment, one mesocosm of each treatment per block was harvested at three separate harvest dates: after 185 days, 565 days and after 750 days (Fig. 1a).

2.2. Soil and earthworm collection

The soil was collected from the 0–25 cm depth layer of a minimum tillage loess soil (Gleyic Luvisol, with 20% sand, 61% silt and 19% clay) and was air-dried and sieved through an 8 mm screen. The loess soil originates from a field that has been under arable cropping for more than 50 years. The past 15 years were under