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Carbon transfer from maize roots and litter into bacteria and fungi depends on soil depth and time

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ABSTRACT

Plant-derived carbon (C) transfer to soil is one of the important factors controlling the size and structure of the belowground microbial community. The present study quantifies this plant-derived C incorporation into abiotic and biotic C pools in top- and subsoil in an arable field over five years. Stable isotope analysis was used to determine the incorporation of maize root and shoot litter C into soil organic C (SOC), extractable organic C (EOC), total microbial biomass (C_{mic}), ergosterol and phospholipid fatty acids (PLFAs). The following treatments were investigated: corn maize (CM), providing root- and shoot-derived C (without corncobs), fodder maize (FM), providing only root-derived C, and wheat plus maize shoot litter amendment (WL), providing only shoot-derived maize C. Wheat plants (W) without maize litter amendment served as control. Soil samples were taken each September directly before harvest from 2009 to 2013. During the experiment, the maize-derived C signal increased in SOC, EOC, C_{mic}, ergosterol, bacterial and fungal PLFAs in the topsoil (0–10 cm). Although total maize shoot C input was threefold lower than maize root C input, similar relative amounts of maize C derived from shoots and roots were incorporated into the different C pools in the WL and the FM treatments, indicating the importance of shoot-derived C sources for microorganisms in the topsoil. An additive effect of both C sources was found in the CM treatment with almost twice as much maize-derived C in the respective pools. Furthermore, the proportion of maize-derived C varied between the different pools with lower incorporation into the total SOC (17%) and total EOC (24%) pools and higher incorporation ratios of maize C into PLFAs of different microbial groups (29% in Gram-positive (Gr^+) bacterial PLFA-C, 44% in Gram-negative (Gr^-) bacterial PLFA-C, 69% in fungal PLFA-C and 78% in ergosterol) in the CM treatment in topsoil after five years. After the third and fifth vegetation periods, we also detected maize-derived C in the rooted zone (40–50 cm depth) and the root-free zone (60–70 cm depth). The maize-derived C incorporation was lower in subsoil C pools in comparison to topsoil C pools. In the root-free zone, the maize-derived C was found to be 2% in total SOC, 28% in total EOC, 9% in Gr^+ bacterial PLFA-C, 20% in Gr^- bacterial PLFA-C and 53% in fungal PLFA-C. Saprotrophic fungi incorporated maize-derived C in all soil depths to a greater degree than Gr^+ and Gr^- bacteria, indicating the importance of saprotrophic fungi in this agro-ecosystem.

1. Introduction

Soils contain a tremendous number of microorganisms and as primary decomposers they transform carbon (C) within the soil via decomposition, polymerization and immobilization of organic matter (Jastrow et al., 2007; Paterson et al., 2008). Generally, there are two main pathways of plant C input into the soil: first, via rhizodeposition by living plants and the decomposition of root litter after plant senescence; second, by incorporation of plant shoot material and its leachates (Gougoulias et al., 2014). Both pathways introduce C compounds of varying complexity into the soil, ranging from low molecular weight compounds, such as amino

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acids, sugars and peptides, to recalcitrant high molecular weight compounds, such as cellulose, hemicellulose, lignin or proteins (Brüggemann et al., 2011). During the early stage of plant residue decomposition, easily available and water-soluble C compounds are released into the soil (Bastian et al., 2009; Poll et al., 2010). After the depletion of these substrates, more complex plant-derived compounds are used and this is associated with more intensive interactions between microorganisms (Dilly et al., 2004; Fioretto et al., 2005). Previous studies have shown that labile and recalcitrant plant compounds are utilized by distinct microbial communities (Paterson et al., 2008). Gram-positive (Gr^+) bacteria use both easily available and recalcitrant compounds whereas Gram-negative (Gr^-) bacteria preferentially process low molecular weight compounds (Waldrop and Firestone, 2004; Kramer and Gleixner, 2006; Holtkamp et al., 2008). Saprotrophic fungi produce a wide range of extracellular enzymes, allowing decomposition of the recalcitrant ligno-cellulose matrix that other organisms are unable to degrade (de Boer et al., 2005).

The use of stable isotopes in combination with biomarker molecule analyses such as phospholipid fatty acids (PLFA) or ergosterol enables the determination of C incorporation into different groups of microorganisms (Butler et al., 2003; Treonis et al., 2004; Paterson et al., 2008). However, most research on C incorporation into soil microorganisms has been done as short-term laboratory incubations (Marx et al., 2007; Semenov et al., 2012; Yao et al., 2012) or within-season field studies (Treonis et al., 2004; Tavi et al., 2013). A ^{13}C pulse labeling experiment with maize plants showed that 20% of the C assimilated by plants was transferred into belowground C pools and the isotope label occurred in both bacteria and fungi only two days after the ^{13}C pulse labeling (Pausch et al., 2015). Furthermore, the authors showed that root-derived C was incorporated into the soil food web mainly via saprotrophic fungi rather than bacteria. In a longer term study, Kramer et al. (2012) found that ergosterol consisted of up to 76% maize-derived C after the second vegetation period, indicating an important role of saprotrophic fungi in plant C degradation.

C fluxes and the contribution of microorganisms are often investigated only for the topsoil (tilled layer), while C inputs into deeper soil horizons receive less attention. Generally, microbial abundance and diversity declines with increasing depth due to lower nutrient and C supply as well as larger separation of microbes from substrates (Salomé et al., 2010). Kramer and Gleixner (2008) reported a shift in the isotopic signature of different C pools in two soil profiles to a depth of 60 cm at one time point 40 years after a vegetation change from C3 to C4 crops. In this study, the contribution of C4-derived C to the soil organic matter (SOM) C in 40–60 cm was only 3%. However, the incorporation of maize C into PLFA biomarkers was 34%, suggesting faster turnover of microbial biomass C compared to bulk SOM C in subsoil.

To the best of our knowledge, a continuous determination of root- and shoot-derived C incorporation into different groups of soil microorganisms in an agriculturally managed ecosystem has not yet been reported for time periods longer than two years. Furthermore, the C incorporation into the subsoil microbial community is entirely lacking for a continuous time series. Therefore, a field experiment was set up on arable land in 2009 to determine the incorporation of root- and shoot-derived maize C into soil organic C (SOC), extractable organic C (EOC), microbial biomass (C_{mic}), Gr^+ bacteria, Gr^- bacteria and fungi in the topsoil (0–10 cm) as well as into two subsoil layers, one representing the lower rooting zone (40–50 cm), the other the almost root-free zone (60–70 cm).

We hypothesized that (i) the incorporation of plant-derived C in the different C pools in topsoil (SOC, EOC, C_{mic}, Gr^+ bacteria, Gr^- bacteria and fungi) depends on C origin, (ii) shoot litter application fosters the incorporation of maize-derived C in the microbial pools due to higher total C input, and (iii) root-derived C is more important than shoot-derived C for the subsoil microbial decomposer organisms due to spatial proximity.

2. Materials and methods

2.1. Study site

The experiment was established on an agricultural field located in Holtensen (51°33′N, 9°53′O, 158 m a.s.l.) north-north-west of the city of Göttingen (Lower Saxony, Germany). The site has a temperate climate with mean air temperature of 7.9 °C and mean annual precipitation of 720 mm (Fig. S1). According to IUSS (2007), the dominant soil types are Cambisols (Braunerden, KA5, 2005) and Luvisols (Parabraunerden, KA5, 2005) with partially stagnic properties (Pseudogley, KA5, 2005). Due to long-term agricultural use, two plough layers at 20 and 30 cm depths were found and a strong compaction in and below the second plough layer (below 30 cm) occurs with a bulk density of 1.6 g cm^{-3} (Table S1). Before the start of the experiment, the isotopic signature of SOC in the Ap horizon was −27.4 ± 0.01‰ and the isotopic ^{13}C value increased with depth (−25.5 ± 0.03‰ at 60–70 cm depth). More detailed information about the soil properties are given in Table S1 and in Kramer et al. (2012).

The experiment was set up in 2009 with maize (*Zea mays* L.) and wheat (*Triticum aestivum* L.) in a strip design of two rows. Ten plots (24 × 24 m) were arranged in a factorial design within each row. Four different treatments with four replicates per treatment were established, differing in the source of maize C input. The corn maize (CM) treatment introduced the $\delta^{13}C$ signal belowground by rhizodeposition during the growing season and decomposition of dead root material after harvest and aboveground by maize litter decomposition. In the fodder maize (FM) treatment the $\delta^{13}C$ signal derived only from belowground input via roots and rhizodeposition, because aboveground shoot biomass was removed after harvest. Maize litter was applied to wheat plots (WL) to introduce the C4 signal into the soil via aboveground maize shoot decomposition only. Wheat plots (W) were used as reference to maintain habitat function for soil organisms without changing the isotopic signature. To establish the CM and FM treatments, hybrid maize "Ronaldino" (34 kg ha^{-1}) was sown in 2009, "Fernandez" in 2010 (26 kg ha^{-1}) and "Cordisco" from 2011 to 2013 (2011: 21 kg ha^{-1}, 2012: 21 kg ha^{-1}, 2013: 23 kg ha^{-1}). In the WL and W plots winter wheat "Julius" (224 kg ha^{-1}) was grown in 2009 and spring wheat "Melon" (2010: 224 kg ha^{-1}; 2011: 180 kg ha^{-1}; 2012: 204 kg ha^{-1} and 2013: 189 kg ha^{-1}) was sown in the following four vegetation periods. For fertilization and herbicide application see Tables S2 and S3. To establish the CM and WL treatments, maize shoots (without corncobs) were chopped into 1 cm^2 pieces, dried, and applied at 0.8 kg dry weight m^{-2} (equivalent to 0.35 kg C m^{-2}) annually in autumn on half of both maize and wheat plots. In April of each year, all experimental plots were tilled with a chisel plough to a depth of 12 cm.

2.2. Soil sampling

Soil samples were taken yearly in September from 2009 to 2013 shortly before maize harvest. Ten soil cores (diam. 2.5 cm) were taken down to 70 cm depth randomly from each plot between the maize rows. Three soil horizons were investigated: topsoil (0–10 cm) within the plough layer, rooted subsoil below the plough layer (40–50 cm) and the deep almost root-free subsoil (60–70 cm). Samples from each layer per plot were mixed and homogenized by hand. Samples were transported in a cooling box to the laboratory and stored at 4 °C until sieving