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Differential priming of soil carbon driven by soil depth and root impacts on carbon availability

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ABSTRACT

Enhanced root-exudate inputs can stimulate decomposition of soil carbon (C) by priming soil microbial activity, but the mechanisms controlling the magnitude and direction of the priming effect remain poorly understood. With this study we evaluated how differences in soil C availability affect the impact of simulated root exudate inputs on priming. We conducted a 60-day laboratory incubation with soils collected (60 cm depth) from under six switchgrass (*Panicum virgatum*) cultivars. Differences in specific root length (SRL) among cultivars were expected to result in small differences in soil C inputs and thereby create small differences in the availability of recent labile soil C; whereas soil depth was expected to create large overall differences in soil C availability. Soil cores from under each cultivar (roots removed) were divided into depth increments of 0–10, 20–30, and 40–60 cm and incubated with addition of either: (1) water or (2) ^{13}C-labeled synthetic root exudates (0.7 mg C/g soil). We measured CO_2 respiration throughout the experiment. The natural difference in ^{13}C signature between C_3 soils and C_4 plants was used to quantify cultivar-induced differences in soil C availability. Amendment with ^{13}C-labeled synthetic root-exudate enabled evaluation of SOC priming. Our experiment produced three main results: (1) switchgrass cultivars differentially influenced soil C availability across the soil profile; (2) small differences in soil C availability derived from recent root C inputs did not affect the impact of exudate-C additions on priming; but (3) priming was greater in soils from shallow depths (relatively high total soil C and high ratio of labile-to-stable C) compared to soils from deep depths (relatively low total soil C and low ratio of labile-to-stable C). These findings suggest that the magnitude of the priming effect is affected, in part, by the ratio of root exudate C inputs to total soil C and that the impact of changes in exudate inputs on the priming of SOC is regulated differently in surface soil compared to subsoil.

1. Introduction

Root derived soil carbon (C) inputs, the soil microbial community, and the soil C cycle are intrinsically linked, because roots supply soil microbes with highly assimilable C-rich substrates that drive microbial decomposition processes (Lynch and Whipps, 1990; Kong and Six, 2010). As such, roots exert significant control on the rate at which C cycles between plants, soils and the atmosphere, making them an important component of the global C cycle (Norby and Jackson, 2000; Lal, 2004). Environmental perturbations, such as climate change and increasing atmospheric CO_2 concentrations can change the relative allocation of C to belowground organs in plants, and increase the production of fine roots (Meier and Leuschner, 2008; Iversen et al., 2008; Iversen, 2009; Phillips et al., 2011). Such changes enhance root-derived soil C input, and the availability of C to soil microbes (Drake et al., 2011; Carillo et al., 2011; Phillips et al., 2009, 2011, 2012). Despite a general consensus that root-derived C inputs are a key component of the soil C cycle, the effect of changes in root-derived C release on soil C cycling remains highly uncertain.

Greater root C inputs to soil, for example as a result of elevated atmospheric CO_2 concentrations, may not lead to measurable increases in soil C (Langley et al., 2009; van Kessel et al., 2006), although increased soil C sequestration has been observed in some cases (Jastrow et al., 2005; Hoosbeek and Scarascia-Mugnozza, 2009). One explanation for a lack of soil C accrual in response to greater root C inputs, is that increased C inputs can promote soil organic carbon (SOC) turnover rates (Hoosbeek et al., 2004; Phillips

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et al., 2012) via the priming effect (Kuzyakov et al., 2000). Priming is defined as the stimulation of microbial activity and overall decomposition rates by the addition of labile plant-derived substrates (Dalenberg and Jager, 1989; Kuzyakov et al., 2000). Indeed, increases in root-C inputs, such as observed under elevated atmospheric CO_2 concentrations, are predominantly driven by increased input of labile plant-derived substrates such as root exudates (i.e., the passive continuous release of low molecular weight organic compounds from living roots [Merckx et al., 1986]) and root turnover (Drake et al., 2011; Carillo et al., 2011; Phillips et al., 2009, 2011, 2012). This C is a preferred "food-source" for soil microbes and can stimulate microbial decomposition processes (Joslin et al., 2006; Rasse et al., 2005), including decomposition of native SOC (Phillips et al., 2012). A priming effect can be positive (increase in SOC decomposition) or negative (slowdown of SOC decomposition) and can vary in magnitude from very small to rather large (Cheng et al., 2003; Cheng and Kuzyakov, 2005; Hamer and Marschner, 2005; Blagodatskaya et al., 2007; De Graaff et al., 2010). Although priming appears to mediate climate change impacts on ecosystem C dynamics in important ways, the direction and magnitude of priming effects are highly variable among experiments, and the mechanisms responsible for these diverse responses are uncertain.

The variability in magnitude and direction of the priming effect observed in different experiments is likely caused by a myriad of factors, including the quantity and quality of short-term substrate input to soil, the active microbial community, C quality and availability in soil, and interactions among all of these factors (Hamer and Marschner, 2002; Fierer et al., 2003; Fontaine et al., 2003; De Graaff et al., 2010; Salome et al., 2010). Root characteristics that control the rate and quality of root-C input to soil over longer time periods may be key factors in regulating how short-term increases in exudation impact the magnitude and direction of SOC priming. Namely, in the long-term roots regulate C quality and availability across the soil profile through: (1) rooting depth, which controls soil C availability at corresponding depths, and (2) root branching, because increased root branching increases root exudation rates (Groleau-Renaud et al., 1998) and may promote fine root turnover rates (Guo et al., 2008b) thereby increasing soil C availability. Thus, root system characteristics including rooting depth and root architecture may be important traits that control soil C availability, the soil microbial community, and the response of SOC cycling to climate-induced changes in rhizodeposition.

With this work, we evaluated how subtle versus large differences in soil C availability, as induced by differences in root architecture and rooting depth, affect microbial processing of simulated root exudate inputs and the decomposition of SOC via the priming effect. To create subtle differences in soil C availability, we collected soil from beneath monocultures of six *Panicum virgatum* (hereafter: switchgrass) cultivars with a wide range of root architectures (De Graaff et al., 2013) as defined by specific root length (SRL). In addition, by sampling to a depth of 60 cm below each cultivar, we obtained soils at different depth increments with stark differences in C availability. These differences were due to a significant decline with depth in the abundance of roots and, thus, root-C inputs under switchgrass and throughout the site's preceding land-uses. We hypothesized that exudate-C inputs would have a greater effect on SOC decomposition (1) at greater depth and (2) in soil from cultivars with coarser root systems. In both cases, we inferred that a decrease in particulate or otherwise uncomplexed organic matter and microbial biomass resulting from a decline in root mass with depth (Fierer et al., 2003; Fontaine et al., 2007) would limit C availability to soil microorganisms and, therefore, that the addition of C-rich substrates would lead to greater increases in microbial biomass, microbial activity and SOC decomposition.

To evaluate how differences in soil C availability, as induced by differences in root architecture and soil depth, affect SOC decomposition following an increase in exudation, we applied a ^{13}C-labeled synthetic exudate cocktail to soils collected from beneath the six switchgrass cultivars. Our previous work has shown that the switchgrass cultivars used for this study have different root architectures to a depth of 15 cm, where three of the cultivars have coarse root systems, whereas the other three have finely branched root systems (De Graaff et al., 2013). The switchgrass cultivars (C_4 plants) were established on soils that supported a stand of C_3 grasses for 36 years, which enabled us to use the natural abundance C isotope ratio technique to (1) estimate the contribution of new root-derived C to the available SOC pool, (2) test whether differences in the architecture of the root systems were accompanied by differences in soil C availability, and (3) evaluate how differences in C availability among cultivar-soils and soil depth affect microbial processing of simulated root exudates and decomposition of SOC.

2. Materials and methods

2.1. Sample collection

We collected soils in October 2010 from field plots supporting six switchgrass cultivars grown as monocultures at the Fermilab National Environmental Research Park in Batavia, IL. The experimental field plots in this research facility were established in June 2008 on Grays silt loam (fine-silty, mixed, superactive, mesic Mollic Oxyaquic Hapludalfs) that previously supported a stand of perennial, cool-season Eurasian pasture grasses for 36 years. In the experimental area, switchgrass cultivars originating from different latitudes were grown in 2 × 3 m or 2 × 1 m replicated field plots ($n = 4$). The cultivars were (1) Alamo, (2) Kanlow, (3) Carthage, (4) Cave-in-Rock, (5) Forestburg, and (6) Blackwell. A single soil core (4.8-cm diameter) was collected to a depth of 60 cm from on top of the crown of one individual in each of the four replicate plots of each cultivar (total cores = 24).

Upon collection, the cores were divided into six depth increments of 10 cm. For the incubation study we used the following depth increments: 0–10 cm, 20–30 cm and 40–60 cm. These depth increments were selected for the incubation study because of their observed general correspondence to three soil horizons. On the basis of the United States Department of Agriculture, Natural Resources Conservation Service (NRCS) official soil series description for Grays silt loam (https://soilseries.sc.egov.usda.gov/OSD_Docs/G/GRAYS.html), the 0–10 cm depth increment lies within the Ap horizon (0–20 cm depth; silt loam), the 20–30 cm depth increment roughly corresponds to the BE horizon (20–28 cm depth; silt loam), and the 40–60 cm increment occurs within the Bt horizon (28–86 cm depth; silty clay loam). Representative distributions of sand-, silt- and clay-sized particles given in the NRCS Web Soil Survey, Soil Report (http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm) for the Grays soil series vary minimally across these horizons: 9%, 70%, and 21% (Ap), 9%, 71% and 20% (BE), and 9%, 61% and 30% (Bt). Measured dry-combustion soil C concentrations (mean ± SE, $n = 6$) for each depth increment were: 2.6% ± 0.1 (0–10 cm), 1.3% ± 0.1 (20–30 cm), and 0.6% ± 0.03 (40–60 cm).

The soil cores were shipped to Boise State University and kept at 6 °C until further processing. The field-moist soils were sieved (2 mm), rhizomes were removed, and all visible roots were hand-picked from the soil. Soils were kept at 6 °C until further analyses. A subsample of sieved, root-free soil was dried (100 °C for 48 h), ground to a fine powder using a ball mill, and analyzed for total C, N and stable C isotope ratios ($^{13}C/^{12}C$) using a Thermo Delta V Plus isotope ratio mass spectrometer (IRMS) coupled with a Costech Elemental Analyzer in continuous flow mode. Analysis of root samples for C and N was conducted previously (De Graaff et al., 2013).