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Combined effects of rhizodeposit C and crop residues on SOM priming, residue mineralization and N supply in soil

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ABSTRACT

Fluxes of rhizodeposit carbon (C) to soil stimulate microbial activity affecting soil organic matter (SOM) decomposition and, in turn, nutrient fluxes in soil. In agricultural soils, residues from previous crops also have major impacts on SOM and nutrient cycling, and their turnover by microbes is likely to be indirectly impacted by rhizodeposition. However, the combined effects of rhizodeposit C and inputs of C from dead plant materials in soil on native SOM decomposition are unclear. In this study, we assessed (i) the individual and combined effects of barley rhizodeposition and ryegrass root residue inputs (as a model for residue input from previous crop) on SOM mineralization, (ii) the intraspecies variation within barley in impacting residue mineralization, and (iii) whether genotypes that stimulate high mineralization rates of plant residues in soil also directly benefit through increased nutrient uptake from these residues. We continuously applied ^{13}C depleted CO_2 to selected barley recombinant chromosome substitution lines (RCSLs) to trace the flow of barley root-derived C in surface soil CO_2 efflux, soil microbial biomass and soil particle-size fractions. In addition, ^{13}C and ^{15}N enriched ryegrass root residues were mixed into soil to trace the mineralization of residue-derived C and the residue-derived nitrogen (N) uptake by plants. Our results show (i) genotype-specific variation in impacting total soil CO_2 efflux and its component sources: SOM-derived C, barley root-derived C and/or ryegrass residue-derived C, (ii) residue effects on total C and SOM-derived C respired as CO_2, (iii) genotype-residue combined effects on SOM primed C, that were very similar to the sum of primed C caused by planting or residue addition alone (except for the last sampling date), and (iv) that plant uptake of residue released N between genotypes was linked to genotype impacts on residue mineralization. These results suggest that impacts of plant rhizodeposition and residue inputs had additive effects on SOM priming. Furthermore, these results demonstrate, for the first time, genotype differences in impacting the mineralization of recent plant-derived organic materials in soil, and reveal that this process directly contributes to plant nutrition.

1. Introduction

Soil organic matter (SOM) decomposition affects nutrient fluxes in soil and contributes to plant nutrition and greenhouse gas (GHG) emissions from soil (Zancarini et al., 2012; Li et al., 2013). Therefore, increased understanding of SOM decomposition processes could help to improve strategies for sustainable agriculture production. The magnitude of SOM decomposition is determined by several factors that include plant type, soil type and nutrient availability in soil (Cheng et al., 2003; Rasmussen et al., 2007; Chen et al., 2014; Datta et al., 2015), but actual mechanisms of SOM decomposition are less understood.

In planted systems, one key factor impacting SOM decomposition is inputs of labile carbon (C) from rhizodeposition, in the form of root exudates and other rhizodeposits, that microbes utilize as C sources to derive energy for their activity (Paterson, 2003; Cheng and Kuzyakov, 2005). Indeed, Cheng et al. (2003) reported that plant roots increase SOM decomposition by up to 3.8 fold relative to

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unplanted soil. This stimulation of SOM decomposition resulting from inputs of labile C substrates is defined as the priming effect (Jenkinson et al., 1985; Kuzyakov et al., 2000). Other studies have found strong variation in priming effects between plant species (Zhu et al., 2014; Shahzad et al., 2015). Recently, there has been increased demonstration of differences in rhizodeposit C and priming effects between genotypes within a single plant species (Zhu and Cheng, 2012; De Graaff et al., 2014; Mwafulirwa et al., 2016; Pausch et al., 2016), that may promote variety selection to control GHG emissions from soil and nutrient release from SOM, thereby supporting sustainable agricultural production. While the genotype-specific influences on native SOM decomposition are getting researchers' attention, no study has yet investigated influences on the mineralization of other forms of C in soil, especially recent dead roots in cropland, or plant residues returned to cropland to improve soil fertility and reduce large use of chemical fertilizers. Suffice to say, we do not know whether genotype-specific influences on the mineralization of these recent plant residues in soil may lead to significant differences in nutrient uptake by crop plants.

Where planted soils contain recent dead roots or residues from a previous crop, the mechanisms of C mineralization and priming effects are likely to be complex. In these systems, rhizodeposits may impact decomposition of old SOM and the recent dead roots or crop residues, but the dead roots or crop residues themselves may also impact SOM decomposition. For instance, Siciliano et al. (2003) found that rhizodeposit C accelerated the decomposition of chemically recalcitrant old SOM pools in the rhizosphere of tall fescue grass. On the other hand, addition of plant-derived organic amendments (slurry of C3 or C4 plant materials) to soil accelerated SOM decomposition (Kuzyakov and Bol, 2006) in unplanted soil. In another study, Millar and Baggs (2004) observed increased emissions of N_2O and CO_2 following addition of agroforestry residues to soil, with the magnitude of emissions being influenced by residue chemical composition. Nonetheless, these studies only accounted for the individual roles of plant residues or rhizodeposit C (i.e. from a single plant type or contrasting plant species) on SOM mineralization, the regulation of GHG emissions from soil and the release of nutrients essential for plant growth. None of these studies was designed to consider the combined effects of rhizodeposit C and crop residues or dead roots on SOM decomposition. A study to investigate the combined effects of labile and recalcitrant C on short term availability of nitrogen (N) was conducted by San-Emeterio et al. (2014), but the investigators used additions of model C substrates of glucose, phenols and an extract from ryegrass. As such, the combined effects of rhizodeposit C and other recalcitrant plant-derived inputs in soil, such as dead roots and plant residues from a previous crop, on microbial mediated C mineralization in planted systems remain unclear.

Here the individual and combined effects of rhizodeposit C from barley and ryegrass root residues (that may represent dead roots or residues from a previous crop) on C and N cycling in soil were assessed. We continuously applied ^{13}C depleted CO_2 to selected barley recombinant chromosome substitution lines (RCSLs) to trace the flow of barley root-derived C in surface soil CO_2 efflux, soil microbial biomass and soil particle-size fractions. These RCSLs have genetically tractable exotic diversity (Close et al., 2009; Comadran et al., 2012), and have demonstrated variation in rhizodeposit C inputs and subsequent mineralization of SOM (Mwafulirwa et al., 2016). In addition, ^{13}C and ^{15}N enriched ryegrass root residues mixed into soil allowed tracing of residue-derived C in soil pools and CO_2 efflux, and plant uptake of residue-derived N. We hypothesized that (i) rhizodeposit C and plant residue inputs to soil individually affect native SOM mineralization, but the rate of SOM mineralization would increase when sources of C from rhizodeposition and plant residue in soil are combined, (ii) the variation in rhizodeposit C between barley genotypes would affect rates of the plant residue mineralization in soil and (iii) genotypes that stimulate high rates of residue mineralization in soil will directly benefit through increased uptake of the residue released N.

2. Materials and methods

2.1. Plants and soil

Three barley RCSLs were used in this experiment. These RCSLs were selected based on (i) differences in rhizodeposit C and the respective impacts on SOM mineralization, as observed in previous work (Mwafulirwa et al., 2016), and (ii) consistency in aboveground plant morphological traits of height and heading date in order to limit potential confounding influences of plant growth rate and phenology. These RCSLs were derived from a cross between an accession of *Hordeum vulgare* subsp. *spontaneum* from a dry and saline region in Israel (Caesarea 26-24) as a donor and North American malting *Hordeum vulgare* subsp. *vulgare* (Harrington) as the recurrent parent (Matus et al., 2003).

The soil was collected from a depth of 0–10 cm from a conventionally managed field at Balruddery farm (56°N, 3°W) near Dundee, Scotland. At time of collection, the field was cropped with barley (tillering stage), having been planted with potato in the previous year. The soil was a sandy loam of Balrownie Series, Balrownie Association (as identified by Bell et al. (2014), unpublished), and was sieved to <6 mm onsite before storing at 4 °C for 2 weeks. The soil had an organic matter content of 6.4% (muffle furnace, 450 °C, 24 h), pH of 6.0 (H_2O) and water content (w/w) of 22.3%.

2.2. ^{13}C and ^{15}N labelling and experimental setup

Before planting, the soil was mixed with ^{13}C and ^{15}N enriched ryegrass root residues. These residues were uniformly labelled from previous work under continuous ^{13}C and ^{15}N enriched CO_2 and KNO_3 solution, respectively. Furthermore, these residues were hot water extracted (80 °C for 15 min, then centrifugation at 1500 rpm for 10 min, ×2) to remove the soluble and readily available C and N fractions, producing the insoluble material with isotopic enrichment of 3.83 ^{13}C-atom% and 3.81 ^{15}N-atom% and C/N ratio of 35.8. The C/N ratio of the root residues before hot water extraction was 29.6. Use of the insoluble fraction of the root material was preferred in this experiment as it better represents plant material remaining in soil from a previous crop, such as dead roots. One gram (dry weight) of the insoluble ryegrass root residues was thoroughly mixed in 1225 g fresh soil that was packed in a 1 L pot (10 cm × 10 cm × 10 cm), representing a C input rate of 0.01 mg residue C per gram soil C, and 16 pots were prepared in this way. A further equal number of pots were packed with soil to which no residue had been applied. All pots were prepared to a soil bulk density of 1 g cm^{-3}, adjusted to 65% water holding capacity (WHC) and left to stabilize over 7 days, after which gas chambers (210 ml headspace) were inserted to the middle of pots for trapping CO_2 efflux from soil. The gas chambers had inlet and outlet stopper end tubes for controlled gas flow. The complete system was also left to stabilize to conditions used in the experiment for 5 days before planting.

Each pot, with or without residue incorporation in soil, was planted with one of the 3 genotypes (2 seeds were planted and thinned to 1 at 5 days from planting) and fallow pots of both soil treatments were included providing no plant controls. These were arranged in a randomized complete block design with four replications in a controlled environment growth chamber (Conviron CG90; Winnipeg, Canada) set to a temperature of 22 °C, relative humidity of 70% and a 12 h daily photoperiod with 512 μmol m^{-2}