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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.

Key words: Nutrient fluxes in soil; Plant N uptake; Residue mineralization; Rhizodeposition; Soil organic matter decomposition

1.0 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 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

76 influences on native SOM decomposition are getting researchers' attention, no study
77 has yet investigated influences on the mineralization of other forms of C in soil,
78 especially recent dead roots in cropland, or plant residues returned to cropland to
79 improve soil fertility and reduce large use of chemical fertilizers. Suffice to say, we do
80 not know whether genotype-specific influences on the mineralization of these recent
81 plant residues in soil may lead to significant differences in nutrient uptake by crop
82 plants.

83 Where planted soils contain recent dead roots or residues from a previous
84 crop, the mechanisms of C mineralization and priming effects are likely to be
85 complex. In these systems, rhizodeposits may impact decomposition of old SOM and
86 the recent dead roots or crop residues, but the dead roots or crop residues
87 themselves may also impact SOM decomposition. For instance, Siciliano et al.
88 (2003) found that rhizodeposit C accelerated the decomposition of chemically
89 recalcitrant old SOM pools in the rhizosphere of tall fescue grass. On the other hand,
90 addition of plant-derived organic amendments (slurry of C3 or C4 plant materials) to
91 soil accelerated SOM decomposition (Kuzyakov and Bol, 2006) in unplanted soil. In
92 another study, Millar and Baggs (2004) observed increased emissions of N_2O and
93 CO_2 following addition of agroforestry residues to soil, with the magnitude of
94 emissions being influenced by residue chemical composition. Nonetheless, these
95 studies only accounted for the individual roles of plant residues or rhizodeposit C (i.e.
96 from a single plant type or contrasting plant species) on SOM mineralization, the
97 regulation of GHG emissions from soil and the release of nutrients essential for plant
98 growth. None of these studies was designed to consider the combined effects of
99 rhizodeposit C and crop residues or dead roots on SOM decomposition. A study to
100 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.

2.0 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 to 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^{o}C for 2 weeks. The soil had an organic matter content of 6.4% (muffle furnace, 450^{o}C, 24 hr), 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^{o}C for 15 min, then centrifugation at 1500 rpm for 10 min, x2) 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 X 10 cm X 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 22ºC, relative humidity of 70% and a 12 hr daily photoperiod with 512 µmol m^{-2} s^{-1} PAR. The soil water content was maintained at 65% WHC by adding deionized water on a mass basis. The plants were grown over 34 days to avoid other potential morphological differences, such as differences in heading dates, between the genotypes at later plant growth stages from impacting soil processes. Plants were grown without fertilizer addition to soil, and were labelled with ^{13}C depleted CO_2 throughout the growth period. The plant labelling was achieved by blending CO_2-free air routed via pressure swing adsorption CO_2 scrubber unit (Parker Balston, Haverhill, USA) with ^{13}C depleted CO_2 (-38‰) from a cylinder via Brooks thermal mass flow controllers (Flotech Solutions Ltd., Stockport, UK), supplied at 25 L min^{-1} with a CO_2 concentration of 367 µl/L (Paterson et al., 2006).

2.3 CO_2 sampling, partitioning and calculations

Soil CO_2 fluxes were sampled four times, at 20d, 23d, 27d and 33d after planting. To collect CO_2 samples, the gas collection chambers were flushed with CO_2-free air for 3 minutes, obtaining outlet airflow <10 µl/L CO_2 concentration, then sealed for 60 minutes using stopper end tubes to accumulate soil CO_2 efflux in the headspace. Thereafter, approximately 25 ml air was sampled from the headspace with a gas syringe connected to the outlet tubing. Gas chambers remained open except during collection of soil CO_2 efflux. Fifteen ml of the sampled air was injected into an infrared gas analyser (EGM-4, PP-Systems, Amesbury, USA) to obtain the CO_2 concentration. The remaining 10 ml was injected into a sealed N_2 flush-filled

glass vial (12 ml) (Labco Ltd, High Wycombe, UK) for $\delta^{13}C$-CO_2 analysis. The $^{12}C/^{13}C$ ratios of the air samples were determined on a DeltaPlus Advantage isotope ratio mass spectrometer via an interfaced Gas-bench II unit (all Thermo Finnigan, Bremen, Germany).

Calculation of total C respired for each treatment per sampling point was achieved using the CO_2-C concentration values. The total CO_2-C (C_{total}) was partitioned to two component sources (SOM- and barley root-derived C) or three component sources (SOM-, residue- and barley root-derived C) for residue-unamended soil and residue-amended soil, respectively, using $\delta^{13}C$ signatures. This was possible because plants were ^{13}C depleted while the residues incorporated in soil were ^{13}C enriched. In treatments with two C sources, the barley root-derived C (C_{plant}) and SOM-derived C (C_{soil}) were determined using the following equations (Garcia-Pausas and Paterson, 2011):

$$C_{plant} = C_{total}(\delta^{13}C_{control} - \delta^{13}C_{total})/(\delta^{13}C_{control} - \delta^{13}C_{plant}) \quad (1)$$

$$C_{soil} = C_{total} - C_{plant} \quad (2)$$

where $\delta^{13}C_{control}$ is the mean $\delta^{13}C$ value of CO_2 from SOM decomposition measured in the residue-unamended fallow soil, $\delta^{13}C_{total}$ is the measured $\delta^{13}C$ value of total soil respiration, and $\delta^{13}C_{plant}$ is the $\delta^{13}C$ value of plant tissue.

In treatments with three C sources, C partitioning was based on assumptions (i) that relative to the residue $\delta^{13}C$ signature (2534.44‰), SOM $\delta^{13}C$ signature measured in the residue-unamended control soil and plant $\delta^{13}C$ signature (section 3.1) were very similar and effectively a single source and (ii) that barley root-derived

respiration in the residue-amended soil was equal to the barley root-derived respiration in the residue-unamended soil. These assumptions then allowed us to test whether the combined effects of plant and residue were consistent with these effects being additive with respect to impacts on SOM mineralization. Therefore, in treatments with three C sources the average $\delta^{13}C$ value of soil and plant (-23.33‰) was used as control $\delta^{13}C$ value to calculate the residue-derived C ($C_{residue}$) as shown in the following equation:

$$C_{residue} = C_{total}(\delta^{13}C_{control} - \delta^{13}C_{total})/(\delta^{13}C_{control} - \delta^{13}C_{residue}) \quad (3)$$

where $\delta^{13}C_{control}$ is the mean $\delta^{13}C$ value of CO_2 from SOM plus plant and $\delta^{13}C_{residue}$ is the $\delta^{13}C$ value of the residue incorporated into soil. Thereafter, C_{soil} in the residue-amended treatments was calculated following the equation below:

$$C_{soil} = C_{total} - C_{plant} - C_{residue} \quad (4)$$

where C_{plant} is the barley root-derived CO_2-C calculated in the residue-unamended soil. Furthermore, based on these assumptions, it was possible to predict an expected isotopic signature of total soil respiration ($\delta^{13}C_{predicted\ total}$) following equation 5 (terms as described above), and to test whether the measured $\delta^{13}C$ value of total soil respiration was consistent with effects of plants and residues on SOM mineralization being additive. For all planted or residue-amended treatments, priming effects (C_{primed}) were quantified by subtracting C_{soil} of the fallow from those of the planted or residue-amended treatments (equation 6).

$$\delta^{13}C_{predicted\ total} = [(C_{plant} \times \delta^{13}C_{plant}) + (C_{residue} \times \delta^{13}C_{residue}) + (C_{soil} \times \delta^{13}C_{soil})] / C_{total} \quad (5)$$

$$C_{primed} = C_{soil\ (planted\ or\ residue\text{-}amended)} - C_{soil\ (residue\text{-}unamended\ fallow)} \quad (6)$$

2.4 Plant and soil harvesting, analysis and isotope partitioning of C and N

Plants were harvested as shoot and root fractions. The shoots were harvested by cutting off at the soil surface. Roots with adhering soil were gently shaken off from bulk soil, and the roots were washed in deionized water. The bulk soil was thoroughly mixed by hand and a sub-sample was taken for freeze-drying, as were harvested shoots and roots. Further sub-samples (described below) of fresh bulk soil were immediately stored at 4^{o}C for soil microbial biomass C (MBC) and mineral N determination after the harvesting was completed. Weights of freeze-dried root and shoot fractions were used to quantify plant (root and shoot) biomass. Sub-samples (15 g) of freeze-dried bulk soil were used to determine the relative distribution of rhizodeposition- and residue-derived C and N in SOM fractions at the end of the experiment. To achieve this, a particle-size physical soil fractionation procedure used by Garcia-Pausas et al. (2012) was performed. In this procedure, whole soil was separated into three size fractions of coarse sand (2000-250 μm), fine sand (250-53 μm), and silt plus clay (<53 μm) by wet sieving. The fractions were oven dried to constant weight at 60^{o}C. Dried samples (roots, shoots and soil particle-size-fractions) were ball milled and analysed for total C, total N, $\delta^{13}C$ signature and $\delta^{15}N$ signature on a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a DeltaPlus XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen,

Germany). For soil samples, their $\delta^{13}C$ values were used to partition total C into the component sources of SOM-, rhizodeposition- or residue-derived C applying similar models to those described in section 2.3. The $\delta^{15}N$ values of the harvested plant materials (root and shoot tissues) were used to calculate the residue-derived N (released through residue mineralization in soil) uptake by plants using a two source model analogous to equation 1 (terms replaced accordingly).

The soil microbial biomass C was determined by the chloroform fumigation-extraction method according to Vance et al. (1987), where fresh fumigated and non-fumigated soil samples (equivalent 12.5 g dry soil) were extracted with 50 ml of 0.5 M K_2SO_4 solution. Organic C of the extracts was analysed on a TOC Analyser 700 (Corporation College Station, TX), and MBC was calculated as the difference between organic C in the paired fumigated and non-fumigated extracts using a conversion factor k_{EC} of 0.45 (Joergensen, 1996). Thereafter, the $\delta^{13}C$ values of MBC were determined using the method described by Garcia-Pausas and Paterson (2011) and fractions of MBC derived from rhizodeposition, residue and SOM were calculated in similar way to two-source or three-source C partitioning equations described in section 2.3. Mineral N (NH_4^+ and NO_3^-) concentrations of the harvested soil samples were determined using an autoanalyser (Technicon Traaks 800, Saskatoon, Canada) following extraction of 10 g fresh soil with 50 ml of 1 M KCl solution (Mitchell et al., 2000).

2.5 Statistical analyses

Two-way analysis of variance (ANOVA) was used to assess the effects of barley genotype and ryegrass residue amendment to soil on soil respiration rates (i.e. total C, SOM-derived C, barley root-derived C and ryegrass residue-derived C respired as CO_2) sampled at different dates, and on soil mineral N (NH_4^+ and NO_3^-) and C and N partitioning in soil particle-size fractions at harvest. For each soil treatment (i.e. with or without residue amendment), one-way ANOVA was used to test for differences between genotypes in soil respiration at each sampling date and soil mineral N and amount-C or amount-N (SOM-, rhizodeposition- and/or residue-derived) in particle-size soil fractions at harvest date. One-way ANOVA was also used to evaluate differences between genotypes in plant uptake of residue-derived N and in rhizodeposition-, SOM- and residue-derived proportions of MBC. Where significant (P<0.05) treatment effects were found, least significant differences (LSD) were used to assess differences between individual means. In addition, simple linear regression (all genotypes, 95% confidence limit) was used to determine the relationship between residue-derived N uptake by plants and residue-derived soil CO_2-C flux rates across genotypes. The software package GenStat (Eighteenth Edition, VSN International Ltd) was used for all statistical analyses.

3.0 Results

3.1 Plant growth and ^{13}C and ^{15}N enrichment

All plants were at tillering stage on harvest date, 34d after planting, and no significant differences in root and shoot biomass were found between the genotypes

(mean 0.66 ± 0.02 g and 0.63 ± 0.03 g root dry weight per plant, and 1.03 ± 0.03 g and 1.02 ± 0.05 g shoot dry weight for residue-amended and residue-unamended treatments, respectively, Figure S1). The plants showed no signs of pathogen or pest infestation, nor nutrient or water deficiency. At harvest, plant tissue $\delta^{13}C$ enrichment (average -35.05‰) and $\delta^{15}N$ enrichment from the residue-amended treatments (average 225.08‰) did not significantly differ between genotypes.

3.2 Soil CO_2-C efflux

Total CO_2-C flux rates from the unplanted soils (residue-amended and residue-unamended fallow soils) were always smaller than planted treatments throughout the experiment period (Figure 1a). Similarly, the total CO_2-C efflux rate from the residue-unamended fallow soil was consistently smaller than that from the residue-amended fallow soil. Furthermore, total CO_2-C efflux rates from both fallow treatments slightly declined over the experiment period, but the $\delta^{13}C$ signature of the CO_2 evolved from the residue-unamended fallow did not change while the $\delta^{13}C$ signature of the CO_2 evolved in the residue-amended fallow also declined over time (370.39‰ at 20d to 190.03‰ at 33d). For the planted soils, the $\delta^{13}C$ signature of CO_2 emitted from the residue-unamended treatments did not change over time, while in the residue-amended planted treatments the $\delta^{13}C$ signature of the CO_2 emitted declined (a mean of 217.57‰ at 20d to a mean of 46.84‰ at 33d). The measured $\delta^{13}C$ values of the CO_2 effluxes from the residue-amended planted soils were not significantly different from their predicted $\delta^{13}C$ values (Table 1).

In the residue-amended soil, total CO_2-C efflux rates were significantly (P<0.05) different between genotypes at 20d, 23d and 27d but not at 33d (Figure 1a), and the greatest genotype difference between the largest and smallest total respiration rate of 14% was observed at 20d. In the residue-unamended soil, the total CO_2-C fluxes varied between genotypes at all sampling dates (Figure 1a), with the greatest genotypic variation between the largest and smallest total respiration rate of 12% observed at 27d. During the first sampling dates (i.e. at 20d, 23d and 27d), total CO_2-C fluxes were larger (by 26% average) in the residue-amended soil relative to the residue-unamended soil for all genotypes and increased over time. At the last sampling (33d), however, the largest total CO_2-C flux rates were from residue-unamended planted treatments (Figure 1a).

Residue amendment in soil alone increased SOM mineralization (positive priming) at all sampling dates (20d, 23d, 27d and 33d) (Figure 1b), with significant (P<0.05) increases in SOM mineralization in the residue-amended fallow treatment of 6% (relative to the residue-unamended fallow soil) observed at 20d and 33d. SOM mineralization was to a greater extent influenced by barley plant roots throughout the experiment period (Figure 1b). For the residue-amended soil and residue-unamended soil, presence of plants increased SOM mineralization by up to 16% at 20d and up to 86% and 114%, respectively, at 33d (relative to respective fallow treatments), while the combination of plants and residue amendment in soil increased SOM mineralization by up to 22% at 20d and up to 95% at 33d (both relative to the residue-unamended fallow treatment). SOM mineralization in the residue-amended soil planted with RCSL 124 and RCSL 144 was consistently greater at the first three sampling dates (20d, 23d and 27d). For these treatments and sampling dates, the primed C (resulting from the combination of plants and

residue amendment in soil) was not significantly different from the sum of primed C induced by residue amendment in soil alone and that induced by presence of plants alone. In contrast, at 33d SOM mineralization was greater (P<0.05) in the residue-unamended soil compared to the residue-amended soil for all three genotypes (Figure 1b). While the presence of plants or residue incorporation into soil generally increased SOM mineralization, for one genotype (RCSL 44) the combination of plants and residues reduced SOM mineralization relative to control soils (negative priming) at the first sampling (20d) (Figure 1b). All in all, SOM priming significantly (P<0.05) varied between the three barley genotypes regardless of soil treatment.

The barley root-derived CO_2-C flux rates varied between the three genotypes at all four sampling dates (20d, 23d, 27d and 33d), with the average difference of 25% between the largest and smallest barley root-derived CO_2-C flux rates (Figure 1c). For each genotype, the barley root-derived soil respiration rate did not change over the experiment period.

Mineralization of ryegrass root residues mixed in soil also significantly (P<0.05) varied between genotypes at all four sampling dates, and rates of residue-derived CO_2-C fluxes continuously declined over time (Figure 2a). On average, residue-derived CO_2-C efflux rate in planted treatments declined by 61.9% between 20d and 33d, which was higher compared with the unplanted soil in which residue-derived CO_2-C efflux rate declined by 55.9% over the same period (data not shown). The largest variation in residue mineralization in soil between the genotypes was observed at the first sampling (20d), where residue-derived CO_2-C efflux in the RCSL 124 treatment was 11% larger (P<0.05) relative to that in the RCSL 44 treatment.

3.3 Plant ^{15}N uptake

Residue-derived N uptake by plants, calculated as mg N incorporated into biomass (root + shoot biomass), is shown in Figure 2b. The differences between genotypes in residue-derived N uptake were not significant, but their pattern positively corresponded with that of the genotypes impacts on residue mineralization. For example, the largest residue-derived N uptake (Figure 2b) was measured in genotype RCSL 124, the same treatment where the largest residue mineralization rate (Figure 2a) in soil was consistently observed. This relationship between residue-derived N uptake by plants and residue mineralization in soil, as calculated using regression analysis (95% confidence limit) (Figure 3), was significant (P<0.05) at all time points and was strongest at 27d (P=0.002). On average, 12% of the total residue N added to soil was recovered in the harvested plant tissues, which was approximately 2.2% of the total plant biomass N.

3.4 Soil microbial biomass C and soil mineral N

The incorporation of ryegrass root residue in soil did not significantly affect the total MBC. Furthermore, neither the residue-amended soil nor the residue-unamended soil significantly differed between genotypes in total MBC and SOM-derived MBC (Table 2). Likewise, in the residue-amended soil, the proportion of residue-derived MBC did not significantly differ between genotypes. However, the

rhizodeposition-derived MBC significantly (P<0.05) varied between genotypes (Table 2).

For soil mineral N at harvest, there were no significant differences in ammonium (NH_4^+) and nitrate (NO_3^-) concentrations (average 0.43 μg NH_4^+-N and 0.98 μg NO_3^--N g^{-1} dry soil) between the genotypes in both soil treatments. The presence of plants, however, greatly reduced the NO_3^- concentration in soil (from a mean of 30.22 μg NO_3^--N g^{-1} dry soil in unplanted controls), but did not significantly alter the NH_4^+ concentration. Comparing the fallow treatments, residue incorporation in soil also did not significantly alter the NH_4^+ and NO_3^- concentrations.

3.5 Distribution of C and N in soil particle-size fractions

At harvest (34d), there were no significant differences between genotypes in total organic C remaining in soil and its component fractions of rhizodeposition- and SOM-derived C (for the residue-unamended soil) or rhizodeposition-, residue- and SOM-derived C (for the residue-amended soil) recovered in each soil particle-size fraction, i.e. coarse sand, fine sand or silt plus clay. Total organic N also did not vary between genotypes in all three soil particle-size fractions, nor residue-derived N in the residue-amended treatments (Table 3). For all genotypes, the largest proportions of total organic C, total organic N and their component fractions of SOM- and residue-derived C or N were recovered in the silt plus clay fraction, while there were no significant differences in the recovered amounts of rhizodeposit C between soil particle-size fractions (Table 3).

448

449 ## 4.0 Discussion

450

451 ### 4.1 Effects of plant rhizodeposits, residue addition to soil or their combination
452 ### on SOM priming

453

454 This study showed that the presence of plants, residue incorporation into soil
455 or their combination all induced positive SOM priming, except for one residue-
456 amended planted treatment that induced negative SOM priming at the first sampling.
457 Importantly, this study showed that during the first three sampling dates priming
458 effects induced in the residue-amended planted soil were very similar to the sum of
459 priming effects induced by residue amendment in soil alone and that caused by
460 presence of plants alone for the respective genotypes. At the last sampling,
461 however, the combination of plants and residues induced smaller priming effects
462 than plants alone. These results provide a clear demonstration of the dynamic
463 combined effects of plant and residue on SOM priming, and that these effects were
464 additive during the first three sampling dates. The measured and the predicted $\delta^{13}C$
465 signatures of the CO_2 efflux from soil (in treatments with three C sources), that were
466 very similar, are also consistent with the effects of plant and residues on SOM
467 priming being additive.

468 The positive SOM priming caused by presence of plants, residue
469 incorporation into soil or their combination was likely due to increased microbial
470 activity resulting from inputs of labile C as rhizodeposit C or residue C (i.e. the
471 microbial activation hypothesis, Cheng and Kuzyakov, 2005), considering that there
472 were no significant differences in total MBC between genotypes or residue

473 treatments. Indeed, because we did not apply fertilizer to soil, and plant growth may
474 have caused nutrient limitation in soil, we suggest that microbes used the
475 rhizodeposits or the labile fraction of residue C to release nutrients from SOM (i.e.
476 microbial N mining, Fontaine et al., 2011). The large C/N ratio of the residue (35.8)
477 also supports the assumption of microbial N mining of SOM. Others have attributed
478 the increase in SOM mineralization caused by plants (Dijkstra et al., 2009, 2013;
479 Frank and Groffman, 2009; Bengtson et al., 2012; Kumar et al., 2016; Wang et al.,
480 2016) or crop residues returned to soil (Li et al., 2013; Thangarajan et al., 2013;
481 Moreno-Cornejo et al., 2014) to microbial activation by inputs of labile C.
482 Furthermore, we propose that greater positive SOM priming caused by the
483 combination of plants and residues during the first three sampling dates, compared
484 to that caused by plants alone, was due to an overall increase in labile C input from
485 the two C sources combined. On the other hand, at the last sampling the smaller
486 positive SOM priming caused by the combination of plants and residues, compared
487 to plants alone, could be due to temporary microbial adjustment when the easily
488 decomposable fraction of the residues was significantly reduced (discussed
489 underneath), thereby altering the overall labile C input. The negative SOM priming
490 observed in one planted treatment at the first sampling date is consistent with the
491 soil containing sufficient nutrients initially (section 3.4), and that microbes
492 preferentially switched from decomposing SOM to using the labile C from
493 rhizodeposition or the residue (Cheng, 1999). This negative SOM priming found in
494 one planted treatment at the first sampling (20d) is also in line with previous findings
495 (Mwafulirwa et al., 2016) where all barley genotypes induced negative SOM priming
496 at 19d and positive SOM priming thereafter.

Irrespective of soil treatment (i.e. residue-amended soil or residue-unamended soil), there were significant differences in SOM priming between the barley genotypes. This result also corroborates earlier findings (Mwafulirwa et al., 2016) where differences in SOM mineralization between barley genotypes were linked to potential differences in the quality (composition) of rhizodeposits between the genotypes. This result was expected when taking into account that the barley genotypes used in this study were selected for their potential variations in rhizodeposit C and their respective impacts on SOM mineralization (section 2.1). As such, the differences in SOM priming between genotypes observed here were also likely caused by variations in rhizodeposit quality between genotypes, especially that other plant factors such as phenology and root or shoot biomass production, known to affect gross rates of rhizodeposition (Kuzyakov and Domanski, 2000), did not differ between genotypes.

4.2 Barley genotype-specific impacts on residue mineralization

The three barley genotypes also varied in affecting the mineralization of ryegrass root residues incorporated in soil, suggesting that the differential activation of soil microbes resulting from differences in rhizodeposit quality between the genotypes also influenced residue mineralization. Our study therefore also demonstrates that intraspecies variation on the decomposition of plant materials in soil, such as roots from a previous cropping cycle or plant-derived organic amendments, also impacts nutrient release from those plant materials (section 4.4). The decline in residue-derived CO_2-C over time was expected considering that there

was a single addition of residues at the start of the experiment, meaning that the residue amount, or its labile fraction, would decline over the experimental period. Another laboratory incubation experiment that used single additions of plant residues in unplanted soil (Majumder and Kuzyakov, 2010) also observed that the easily decomposable part of ryegrass residue mineralized strongly at the initial phase of incubation, and the residue impact on soil respiration declined following the depletion of the labile residue fraction.

4.3 Recovery of C and N pools in soil

For all genotypes, largest proportions of total organic C, total organic N and their component fractions of SOM- and residue-derived C or N were recovered in the silt plus clay fraction, while there were no significant differences in the recovered amounts of rhizodeposit C between soil particle-size fractions. It is known that the fine soil particle-size fraction (i.e. the silt plus clay fraction) is associated with protected SOM pools relative to SOM within coarse soil fractions that is associated with less protected and labile pools (Gregorich et al., 1988; Six and Jastrow, 2002; Von Lutzow et al., 2007). Therefore, in this study the recovery of large proportions of SOM-derived C and N in the silt plus clay fraction relative to the coarse soil fractions was as expected. However, the recovery of large proportions of residue-derived C and N in the silt plus clay fraction may mean that a large proportion of the initial ryegrass root residue incorporated into soil was turned over by microbes over the experiment period, considering that most of the products of decomposition remaining in soil would accumulate within the fine soil fraction (Vogel et al., 2015).

Neither rhizodeposit C recovered in each soil particle-size fraction of coarse sand, fine sand or silt plus clay, nor residue-derived C and N recovered in each soil particle-size fraction, significantly varied between the genotypes. This result is consistent with our previous study (Mwafulirwa et al., 2016) where the three genotypes used in this recent work also did not significantly vary in amounts of rhizodeposit C recovered in each soil particle-size fraction, although in that study other genotypes showed variation in the allocation of rhizodeposit C to the silt plus clay fraction after 40 days, inferring differential stabilization of rhizodeposit C in soil between those genotypes.

4.4 Relationship between mineralization of residue N and plant N uptake

Linear regression demonstrated that the residue-derived N taken up by plants was positively correlated with residue mineralization rates in soil although residue-derived N uptake by plants did not significantly differ between genotypes. This reveals a direct positive relationship between plant-influenced residue decomposition in soil and uptake of the residue released N by the growing plants, and thus the possibility of selecting crop varieties for greater use efficiency of organic sources of nutrients. The plant-influenced priming of SOM (section 4.1) may also have functioned to supply N, which is in line with the findings of Murphy et al. (2015) who showed that SOM priming is a response mechanism to increase soil N supply.

As reviewed by Tilman et al. (2002), crop plants take up about 30-50% of N applied in inorganic form. Availability of residue N is slower (Beare et al., 2002), and the proportion taken up by plants will vary, for example with soil mineral N and SOM

572 concentrations. Here plant uptake of the residue-derived N of 12% (relative to initial
573 total residue N) was measured at the end of the experiment, and we expect that
574 comparatively more residue-derived N would have been recovered in plant tissue if
575 unextracted residue with a smaller C/N ratio (relative to the C/N ratio of the hot water
576 extracted residue) was used. Indeed, according to Mancinelli et al. (2013), the plant
577 material used as organic amendments in form of green manure have a small C/N
578 ratio to ensure rapid biomass decomposition and avoid microbial immobilization of N
579 that would decrease available N in soil. Nevertheless, use of the insoluble fraction in
580 our experiment better represents previous crop inputs remaining in soil and enabled
581 accurate measurement of the decomposition-derived residue N. Use of the insoluble
582 fraction avoided causing major impacts on soil processes that could have subdued
583 the genotypes impacts, taking into consideration the findings from a microcosm
584 incubation study by McMahon et al. (2005) where the soluble fraction (leachate) of
585 ryegrass straw strongly influenced decomposer communities in soil compared to
586 unleached and leached straw.
587
588
589 **5.0 Conclusions**
590
591 We have shown the combination of presence of plants and residue
592 incorporation into soil to result in greater positive SOM priming than the presence of
593 plants alone at 20d, 23d and 27d, but smaller positive SOM priming than the
594 presence of plants alone at the last sampling (33d) when the residue amount in soil
595 was significantly reduced. These results demonstrate dynamic combined effects of
596 rhizodeposit C and other recalcitrant plant-derived inputs in soil (such as dead roots

or plant residues from previous crop) on SOM mineralization in a planted system. Our results are consistent with the effects of plants and residue additions on priming of SOM being additive, in that (except for the last sampling) SOM priming induced by the combination of plants and residues was very similar to the sum of priming effects caused by plants alone and residues alone. Besides the observed genotype-specific influences on SOM mineralization, our work also revealed genotype-specific influences on the mineralization of other recalcitrant sources of C in soil, such as dead root material or plant residues from a previous crop. In addition, we show for the first time that plant uptake of the residue released N was linked to plant influence on residue mineralization in soil, suggesting that it is possible to select for crop varieties that have greater use efficiency of organic sources of nutrients, that may benefit farmers the most in parts of the world where crop production is limited by inadequate application of chemical fertilizers. These findings provide the first step towards helping improve current strategies, or define new strategies, for sustainable management of C and N dynamics in agricultural soils which next need to be considered across crop species and under field conditions.

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781 **Figure legends**
782
783 **Figure 1**: Total CO_2-C (a), SOM primed CO_2-C (b) and barley root-derived CO_2-C (c)
784 efflux rates for residue-amended and residue-unamended soils planted with 3 barley
785 genotypes (RCSL 124, RCSL 144 and RCSL 44) and from unplanted control soils.
786 PE represent priming effect. Values are means (n=4), ± 1SEM.
787
788 **Figure 2**: Residue-derived CO_2-C efflux rates from the residue-amended soil (a) and
789 total residue-derived N uptake by barley plants (b) for three barley genotypes (RCSL
790 124, RCSL 144 and RCSL 44). Significant (P<0.05) differences between the

genotypes are indicated by different lowercase letters. Values are means (n=4), ± 1SEM.

Figure 3: Relationship (95% confidence limit) between total residue-derived N uptake by plants at harvest and residue-derived soil CO_2-C flux rates at 20d, 23d, 27d and 33d for three barley genotypes (RCSL 124, RCSL 144 and RCSL 44). Values are individual treatment measurements (n=4).

Table legends

Table 1: Measured and predicted* $\delta^{13}C$ signatures of CO_2 effluxes from residue-amended soils planted with three barley genotypes (RCSL 124, RCSL 144 and RCSL 44). Values are means (n=4), ± 1SEM.

Table 2: Concentrations of rhizodeposition-derived MBC in soil, residue-derived MBC in residue-amended soil and SOM-derived MBC in residue-amended or residue-unamended soil for three barley genotypes (RCSL 124, RCSL 144 and RCSL 44). Different lowercase letters indicate significant (P<0.05) differences between genotypes. Values are means (n=4), ± 1SEM.

Table 3: Accumulation of SOM-derived C, rhizodeposit C, residue-derived C, residue-derived N and total N in soil particle-size fractions of coarse sand (CS), fine sand (FS) and silt plus clay (S+C) for three barley genotypes (RCSL 124, RCSL 144 and RCSL 44) planted in residue-amended and residue-unamended soil. Different

816 lowercase letters within columns and within rows indicate significant (P<0.05)
817 differences between soil fractions and genotypes, respectively. Values are means
818 (n=4), ± 1SEM.