



## Barley genotype influences stabilization of rhizodeposition-derived C and soil organic matter mineralization



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### ABSTRACT

Rhizodeposition is an important source of substrate for microbial communities, supporting activities including soil organic matter (SOM) and nutrient cycling. Therefore, it is a potential trait of interest for crop plants, particularly in the context of variety selection for sustainable production systems. However, we do not have a good understanding of (i) whether there is significant variation in root-C deposition between varieties of important agricultural crops and (ii) whether variation in C deposition between varieties leads to major differences in C cycling in soil. In two experiments, we assessed variations in C deposition amongst barley genotypes and their respective impacts on microbial activity and SOM dynamics. In experiment 1, we applied <sup>13</sup>C–CO<sub>2</sub> labelling to selected barley recombinant chromosome substitution lines (RCSLs) and traced root-derived C in surface soil CO<sub>2</sub> efflux, soil microbial biomass-C (MBC), soil solution, and soil particle-size fractions. In experiment 2, we conducted MicroResp analysis using 15 ecologically relevant C substrates to assess the impacts of barley genotypes on microbial activity. Soil respiration measurements (partitioned into plant- and SOM-derived components) revealed genotype-specific effects on plant-derived C, SOM-derived C and total C respired as CO<sub>2</sub>. For particle-size fractionation, we found that incorporation of plant-derived C to the silt-and-clay fraction varied between genotypes, indicating differences in relative stabilization of root-derived C as a result of barley genotype. Our data did not indicate genotype effects on total MBC size or dissolved organic-C (DOC) in soil solutions, but significant differences in plant-derived MBC and DOC were observed. MicroResp analysis showed differential utilization of 7 substrates (glucose, trehalose, lignin, arabinose, alanine, aminobutyric acid and lysine) revealing variation in community level physiological profiles (CLPPs) of soil microbes as impacted by barley genotypes. Furthermore, we found significant clustering of microbial CLPPs as a function of RCSLs and parent lines (Caesarea 26-24 and Harrington) suggesting a strong plant genetic control of the barley microbiome, and that this genetic control is heritable. Our results demonstrate barley genotype-specific effects on soil processes, revealing the potential for germplasm selection and variety improvement in barley to support sustainable production systems.

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### 1. Introduction

The world's largest terrestrial C stock (around 1500 Pg) is held in organic matter in the top metre of soils (Batjes, 1996; Smith, 2004; IPCC WGI, 2007), and is about twice the amount of C contained in the atmosphere as CO<sub>2</sub> (Poeplau et al., 2011; Powlson et al., 2011).

Therefore, shifts in the balance of C exchange across the soil-atmosphere interface have potential to strongly impact feedbacks to the global C cycle. Agricultural soils are important in this respect because (i) they are currently net sources of greenhouse gases (GHG) (Carney et al., 2007; Smith et al., 2010; Smith, 2012; Reinsch et al., 2013), (ii) they are thought to have depleted C stocks (Lal, 2011) creating potential to increase their storage of C (Smith et al., 2013), and (iii) their active management potentially allows implementation of measures to enhance C accumulation. Rhizodeposition (the release of organic substrates from living roots to soil) is an important component of the C cycle because it

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contributes C to soil through the transfer of photosynthates from plants (Helal and Sauerbeck, 1984; Bardgett et al., 2005), and it is a substrate for microbial communities impacting soil organic matter (SOM) decomposition (priming effect) and C loss from soil (Kuzyakov, 2002). This was stressed by Schimel (1995) who reported that rhizosphere processes contribute almost half of the total CO<sub>2</sub> emissions from terrestrial ecosystems to the atmosphere at a global level.

We know that around 5–25% of total photosynthetically fixed C in plants is transferred into the rhizosphere through root exudates (Helal and Sauerbeck, 1984; Derrien et al., 2004) and that there is variation in rhizodeposition-derived C inputs into soil between plant species (Zagal et al., 1993 in Jin et al., 2013; Kuzyakov and Domanski, 2000; Derrien et al., 2004). This variation in root-C deposition is particularly interesting considering that even small amounts of labile C inputs, less than supplied by root exudates, can significantly affect SOM mineralization (Nobili et al., 2001). Isotope labelling approaches have been used to quantify the impact of root exudates on native SOM mineralisation (Kuzyakov, 2002; Paterson, 2003; Cheng and Kuzyakov, 2005; Cheng et al., 2014), and assays of microbial activity have been used to demonstrate functional responses to rhizodeposition (Berg and Steinberger, 2008; Yan et al., 2008; Marshall et al., 2011). However, to our knowledge, there are only limited studies investigating SOM priming effects among plant species (Zhu et al., 2014; Shahzad et al., 2015) and even less is known about the intra-species variation in root exudation and the associated impact on priming. As such, there is limited understanding of whether there is significant variation in root-C deposition between crop varieties and whether variation in C deposition between varieties leads to significant differences in C cycling.

Wild accessions (progenitors of major crop species) are believed to possess beneficial traits for soil microbial interactions affecting soil C content and the availability of key nutrients for plants. In contrast, for modern crop varieties their development through selection for yield and other beneficial traits (such as tolerance to biotic and abiotic stresses), usually under intensive chemical fertilizer applications to soil, is believed to have resulted in the loss of the genetic variation in plant–soil interactions (Wissuwa et al., 2009). In view of this, it is not surprising that there are few studies that have investigated root-C deposition and SOM priming, especially amongst individual varieties of major agricultural crops. However, recent work by Aira et al. (2010), Bouffaud et al. (2012) and Peiffer et al. (2013) suggest that rhizosphere microbial community composition under maize is related to plant genotype. Whereas Tyree et al. (2014) observed that contrasting genotypes of *P. taeda* forest trees affected total and SOM-derived surface soil CO<sub>2</sub> fluxes differently. However, we are not aware of comparable observations of the genotype impacts on root- or SOM-derived soil CO<sub>2</sub> fluxes in agricultural crops. Therefore, concrete links between soil CO<sub>2</sub> emissions, root-derived C stabilization in soil and the genetic variation between plant varieties remain limited. As such, there is untapped potential to control C dynamics through plant breeding approaches that value root–soil interactions and microbial processes, especially in agriculture. Exploring this would complement the recently expanding efforts to increase or retain C stocks in agricultural soils through management practices in the context of sustainable crop production.

Many studies on plant–soil interactions in the context of soil C dynamics have been focussed on the role of root exudates as drivers of soil processes and SOM decomposition, rather than on the stabilization of the rhizodeposition-derived C in soil. This may be justified considering that root exudates are largely a labile form of C (Paterson, 2003) and rapidly processed by microbes

(Kuzyakov and Domanski, 2000; Paterson et al., 2011). However, an important component of root-derived C may be released as more recalcitrant organic material, and to trace that more recalcitrant organic material it is necessary to isotopically label plants over relatively long periods. Furthermore, the decomposition rate of root-derived compounds and, subsequently their loss or incorporation in soil, is dependent on both chemical properties and physical protection from microbes (De Deyn et al., 2008; Jin et al., 2013). Therefore, when exploring the potential of breeding for root–soil interactions to lower CO<sub>2</sub> emissions from agriculture or enhance C sequestration, studies that consider whole rhizodeposition and that account for C stabilization in soil are needed.

Several soil fractionation procedures (chemical, physical, and combinations of chemical and physical methods) can be used to isolate SOM pools that provide information on C stabilization (Paul et al., 2006). Amongst these methods, physical fractionation techniques (particle-size and density fractionation) are increasingly reported to provide a vital contribution to the understanding of SOM turnover and SOM as an important element of agricultural systems (Leifeld and Kogel-Knabner, 2005). For instance, Puget and Drinkwater (2001) applied a combined density and particle-size physical fractionation approach to determine the fates of root-derived C and shoot-derived C using <sup>13</sup>C-labelled hairy vetch. In their experiment, a greater proportion of root-derived C was found as occluded particulate organic matter and associated with the silt-and-clay fraction, unlike shoot-derived C where only a small proportion was still present in soil at the end of the growing season. Research on the turnover or stabilization of rhizodeposition-derived C in soil, however, remains insufficient. Physical fractionation methods are based on the understanding that SOM association with soil particles affects its stabilization or protection against microbial decomposition through physical protection within aggregates and chemical protection through interactions with mineral surfaces. SOM within the sand fraction is therefore considered to be a relatively labile pool, in comparison with more stable silt and clay fractions (Von Lutzow et al., 2007).

Here we applied <sup>13</sup>CO<sub>2</sub>–C labelling and particle-size SOM fractionation methods to assess net root-C deposition amongst barley genotypes and their respective impacts on soil processes. Additionally, we conducted MicroResp analysis using ecologically relevant C substrates to evaluate the impacts of barley genotypes on microbial activity. We used a set of Recombinant Chromosome Substitution Lines (RCSLs) developed using a wild barley donor (Caesarea 26–24 from Israel) and an elite cultivar (Harrington, a North American malting variety) as recipient parent via an advanced backcrossing strategy (BC2F9) (Matus et al., 2003). These lines represent the wild barley genome by carrying small introgressions in the predominantly elite background and have been used previously to dissect tolerance to drought stress and other complex important agronomic traits (Inostroza et al., 2009; Schmalenbach et al., 2009; Sato et al., 2011).

We hypothesized that (i) closely related barley genotypes, but that have genetically tractable introgressed exotic diversity, would vary in root-C deposition in soil, (ii) the variation in root-C deposition between barley genotypes would determine rates of SOM decomposition, (iii) the contribution of rhizodeposits to individual labile and recalcitrant SOM pools would vary between barley genotypes, and (iv) the variation in root-C deposition between barley genotypes would be reflected in the functional response of soil microbial communities in terms of the utilization of ecologically relevant C substrates in MicroResp assays.

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