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Below ground carbon inputs to soil via root biomass and rhizodeposition of field-grown maize and wheat at harvest are independent of net primary productivity

Juliane Hirte[a,b,*], Jens Leifeld[a], Samuel Abiven[b], Hans-Rudolf Oberholzer[a], Jochen Mayer[a]

[a] Agroscope, Agroecology and Environment, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland
[b] University of Zurich, Department of Geography, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

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ABSTRACT

Below ground carbon (BGC) inputs to soil, i.e. root biomass and rhizodeposition carbon (C), are among the most important variables driving soil C dynamics in agroecosystems. Hence, increasing BGC inputs to deep soil is a proposed strategy to sequester C in the long term. As BGC inputs are inherently difficult to measure in the field, they are usually estimated from yield in order to supply soil C models with input data. While fertilization intensity considerably affects above ground biomass, its influence on BGC inputs is largely unclear, especially with respect to the subsoil. Therefore, we determined net root biomass and rhizodeposition C of field-grown maize and wheat at harvest in different farming systems (bio-organic, conventional) and fertilization treatments (zero, manure, mineral) along an intensity gradient in two Swiss long-term field trials. Plants in microplots were repeatedly pulse-labelled with ^{13}C-CO_2 throughout the growing seasons and shoots, roots, and soil to 0.75 m depth were sampled at harvest. Despite a strong increase of above ground biomass with increasing fertilization intensity, BGC inputs were similar among treatments on both sites irrespective of soil depth. However, the proportions of rhizodeposition C of BGC inputs averaged 54 to 63% and were, therefore, much larger than the widely adopted 40% for field-grown cereals. They increased with soil depth and were highest under sole organic fertilization. The shift in whole-plant C allocation towards above ground biomass with increasing fertilization intensity entailed 10% higher C allocation below ground in organic than conventional farming for both maize and wheat. Our findings imply that yield-independent values provide closer estimates for BGC inputs to soil of cereals in different farming systems than yield-based functions. We further conclude that fertilization has only little potential to alter absolute amounts of BGC inputs to deep soil in order to sequester C in the long term.

1. Introduction

Increasing carbon (C) storage in agricultural soils has been proposed as a viable means to reduce atmospheric C and mitigate climate change (Dignac et al., 2017; Paustian et al., 2016). Global agroecosystems could sequester 2–3 Gt C yr^{-1} if C stocks increase by 0.4% in the upper metre of soil, thereby offsetting 20–35% of global anthropogenic greenhouse gas emissions (Minasny et al., 2017). As plant photosynthesis and C allocation below ground is the primordial pathway for C to enter soil, promotion of crop root systems, i.e. more and deeper roots, may play a decisive role in soil C sequestration (Kell, 2011; Lynch and Wojciechowski, 2015; Maeght et al., 2013; Pierret et al., 2016).

Below ground C (BGC) inputs to soil are among the most important variables driving soil C dynamics in agroecosystems (Keel et al., 2017a). They account for 30–90% of total organic C inputs to agricultural soils (Kätterer et al., 2011) and reside in soil considerably longer than C derived from above ground crop residues and organic soil amendments (Rasse et al., 2005; Zhang et al., 2015). Moreover, they can be translocated deep into the subsoil (Canadell et al., 1996), where residence times might be longer than in the ploughed topsoil (Rumpel and Kögel-Knabner, 2011) due to less mechanical disturbance (Turkington et al., 2000) and lower decomposer abundance (Oehl et al., 2004; Sanaullah et al., 2016).

Plants allocate C below ground via root biomass and rhizodeposition (Kuzyakov and Domanski, 2000). They differ strongly in appearance, origin, and persistence in soil and, thus, require different means of determination (Kögel-Knabner, 2017; Kuzyakov and Domanski, 2000). Root biomass C mainly derives from long-chained polysaccharides (cellulose and hemicellulose) and lignin (Kögel-Knabner, 2002), while rhizodeposition C derives from a multitude of actively or passively

* Corresponding author at: Agroscope, Agroecology and Environment, Reckenholzstrasse 191, CH-8046 Zurich, Switzerland.
E-mail address: juliane.hirte@agroscope.admin.ch (J. Hirte).

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released compounds from living roots, mainly low molecular weight solutes (short-chained sugars, amino and organic acids), high molecular weight polysaccharides (mucilage), border cells and senescent parts of the epidermis, and root symbionts (Jones et al., 2009). Net rhizodeposition C refers to the part of root-released C that remains in soil after immediate microbial respiration (Pausch and Kuzyakov, 2018) and will be the focus in this work from here on.

The determination of rhizodeposition C requires almost always the use of natural C isotopes, either in ^{13}C natural abundance or artificial labelling experiments (Jones et al., 2009; Pausch and Kuzyakov, 2018). While one-time pulse labelling does not provide information about rhizodeposition C that can be extrapolated to a whole growing season (Pausch and Kuzyakov, 2018), continuous labelling throughout the plant's life cycle is largely impossible in agricultural fields with small subpopulations designated for labelling. Hence, repeated pulse labelling in regular intervals over the entire growing season, either of the same (e.g. Martens et al., 2009) or different (e.g. Swinnen, 1994) subpopulations, serves as an adequate alternative to assess net rhizodeposition C at harvest (Kuzyakov and Domanski, 2000). However, only very few studies satisfy this requirement and, as a consequence, existing data on BGC inputs by crop plants into soil at harvest are largely limited to root biomass C.

Most work has been done with maize and wheat, which are two of the most important cereals and collectively cultivated on nearly 30% of the global arable land area (FAO, 2018). Root biomass C (assuming 45% C content) of field-grown maize ranges between 40 and 140 g m^{-2} (median of 13 studies: 90 g m^{-2}; Amos and Walters, 2006) and that of winter wheat between 40 and 125 g m^{-2} (median of 9 studies: 60 g m^{-2}; Hoad et al., 2001; Hu et al., 2018; Williams et al., 2013). The amount of additional C remaining in soil as rhizodeposition after one cropping season was found to be 30 g m^{-2}, or 30% of total BGC inputs, for maize (Balesdent and Balabane, 1992) and 2–70 g m^{-2}, or 5–70% of total BGC inputs, for wheat (median: 50 g m^{-2} or 45%; Gregory and Atwell, 1991; Keith et al., 1986; Martens et al., 2009; Swinnen, 1994). The recovery of BGC inputs as root biomass or rhizodeposition strongly depends on the method of separating roots from soil, e.g. sieve mesh size, and time of sampling, as finest roots and fragments of decaying roots inevitably add to the rhizodeposition pool when they are not recovered as root biomass (Pausch and Kuzyakov, 2018). Most data on BGC inputs refer to the topsoil as roughly two thirds of crop root systems concentrate in the upper 0.3 m of soil (Fan et al., 2016), prompting investigators to forgo the logistical challenges of studying subsoils (Campbell and Paustian, 2015). Hence, our knowledge about BGC inputs to deeper soil is extremely limited (Kögel-Knabner, 2017), which inevitably accounts for the use of undifferentiated proportions of rhizodeposition C in top- and subsoils in upscaling studies (e.g. Pausch et al., 2013).

Information on BGC inputs of field-grown crops at harvest is indispensable for soil C modelling (Keel et al., 2017b). Dynamic soil C models are increasingly used in national greenhouse gas inventories under the United Nations Framework Convention on Climate Change (Campbell and Paustian, 2015; Eggleston et al., 2006), e.g. in Australia (RothC; Skjemstad and Spouncer, 2003), Canada (CENTURY; VandenBygaart et al., 2008), Denmark (C-TOOL; Taghizadeh-Toosi et al., 2014), or Sweden (ICBM; Andrén et al., 2004). However, due to the scarcity of measured data, BGC inputs are usually estimated from net primary productivity (Campbell and Paustian, 2015; Kögel-Knabner, 2017) using some form of yield-based allometric function and associated C allocation coefficients for those plant C pools that are relevant for simulations of soil C stocks and changes (Keel et al., 2017b). Those include remaining straw, decaying roots, and rhizodeposits at the time of harvest; hence, the portion of already respired and lost root-derived C during the growing season is not accounted for. For example, the widely used approach established by Bolinder et al. (2007) for temperate crops assigns coefficients to the four C pools crop product, straw, root biomass, and extra-root material (i.e. rhizodeposition). These coefficients were derived from measured yield and published or assumed values for biomass C concentration, harvest index, root-to-shoot ratio, and rhizodeposition-to-root ratio. While yield is always determined at harvest, published data on root-to-shoot and rhizodeposition-to-root ratios most often refer to considerably earlier crop growth stages, namely flowering and the vegetative phase, respectively. In addition, the information on rhizodeposition used by Bolinder et al. (2007) was mainly derived from controlled experiments (Kuzyakov and Domanski, 2000; Kuzyakov and Schneckenberger, 2004). It is unclear, whether those data are applicable to field-grown crops at harvest. Further, allocation coefficients have been established for several functions for a wide range of crops or crop classes (Keel et al., 2017b) but are not differentiated by farming systems that differ in fertilization intensity. Hence, lower crop C inputs to soil via residues and rhizodeposition are expected from lower yields in organic than conventional farming (Lorenz and Lal, 2016).

In contrast to the concept of allometry, recent findings suggest that BGC inputs are not proportional to net primary productivity in agroecosystems and are rather a function of year, species, and farming system (Hu et al., 2018; Taghizadeh-Toosi et al., 2016). Root biomass in low-intensity systems was found to be similar as or even higher than that in high-intensity systems (Chirinda et al., 2012; Hirte et al., 2018; Lazicki et al., 2016), whereas rhizodeposition C seems to follow the opposite trend (Chowdhury et al., 2014; Liljeroth et al., 1994; Qiao et al., 2017; Swinnen, 1994). Type and amount of fertilization might have a considerable impact on plant C allocation; hence, it is questionable whether BGC inputs can be easily derived from yield. However, to our knowledge, comprehensive field studies that focus on the effect of fertilization intensity on below and above ground plant C allocation do not exist.

Our objectives were, therefore, to (i) quantify net BGC inputs of field-grown maize and wheat at harvest in the top- and subsoil in order to provide data for use in soil C models, (ii) evaluate the effect of soil depth and long-term fertilization intensity on BGC partitioning to root biomass and rhizodeposition C, and (iii) evaluate the effect of long-term fertilization intensity on C allocation coefficients for crop product, straw, root biomass, and rhizodeposition. Our hypotheses were that (i) current assumptions on the amounts of rhizodeposits are not applicable to field-grown crops at harvest, (ii) the proportion of rhizodeposition C of total BGC inputs is independent from soil depth but increases with increasing fertilization intensity, and (iii) whole-plant C allocation decreases with increasing fertilization intensity. To test these hypotheses, we conducted a comprehensive three-year field study with maize and wheat in different treatments with increasing long-term fertilization intensity on two sites and determined the remaining C in the four plant C pools product, straw, root biomass, and rhizodeposition at crop harvest.

2. Materials and methods

2.1. Sites, treatments, and crops

We conducted the study on two Swiss long-term field trials: DOK (47°30′09″ N, 7°32′21″ E; MAT 10.5 °C, MAP 842 mm; established in 1978) and ZOFE (47°25′36″ N, 8°31′08″ E; MAT 9.4 °C, MAP 1031 mm, established in 1949). In DOK, eight farming system treatments that differ by type and amount of fertilization and plant protection are compared in a strip-split-plot design with four field replications (Mayer et al., 2015). In ZOFE, 12 fertilization treatments that differ by type and amount of fertilization are compared in a systematic block design with five field replications (Oberholzer et al., 2014). The seven- (DOK) and eight-year (ZOFE) crop rotations include cereals, maize, grass-clover ley, potato, cover crops, and soybean (DOK only). The soil is ploughed to 0.2 m depth. On both sites, soil type is a haplic Luvisol with 12% sand, 72% silt, 16% clay, 1.2 Mg m^{-3} bulk density, and 1.3% organic C in DOK and 59% sand, 23% silt, and 18% clay, 1.6 Mg m^{-3} bulk density, and 0.9% organic C in ZOFE in the plough layer. We chose the treatments BIOORG1, BIOORG2, and CONFYM2 in DOK, which realistically

Table 1
Fertilization and plant protection in the chosen treatments of the long-term field trials DOK and ZOFE and recommended amounts of fertilizer nutrient inputs according to Swiss standard, amounts of applied fertilizer nutrients, stand densities at harvest, yields, and straw masses of maize (DOK and ZOFE: 2013) and wheat (DOK: 2015; ZOFE: 2014) in field plots of the chosen treatments (adapted from Hirte et al., 2018).

	Fertilization			Plant protection		Fertilizer N_{min} (N_{tot}) - P - K[c] [kg ha^{-1}]		Density [# m^{-2}]		Yield[d] [Mg ha^{-1}]		Straw[e] [Mg ha^{-1}]	
Recommended[f]	type	dosage[a]	intensity[b]	pests	weed	maize	wheat	maize	wheat	maize	wheat	maize	wheat
— DOK —													
BIOORG1	FYM[g], slurry	half	0.4	biological	mechanical	18(91)-23-183	30(79)-22-198	8.5	553	12.5	4.2	–	9.1
BIOORG2	FYM, slurry	full	0.8	biological	mechanical	36(182)-47-365	59(157)-43-396	8.8	549	13.2	4.8	–	9.7
CONFYM2	FYM, slurry, mineral[h]	full	1.2	chemical	chemical	202(335)-40-299	125(125)-26-33	8.9	595	18.6	5.9	–	10.4
— ZOFE —													
CONTROL	none	zero	0	chemical	chemical	0	0	7.1	344	2.9	1.8	2.8	2.1
MANURE	FYM (biannual)	full	0.5	chemical	chemical	1(13)-3-23	0	7.7	341	5.0	2.5	4.4	2.8
N2P1K1[i]	mineral	full N, half P, K	0.7	chemical	chemical	145(145)-21-91	150(150)-13-33	7.6	444	6.9	5.8	5.0	6.3
N2P2K2Mg	mineral	full N, P, K, Mg	1.1	chemical	chemical	145(145)-41-183	150(150)-26-66	7.6	466	8.2	5.8	5.2	6.7

[a] according to Swiss standard (Richner and Sinaj, 2017).
[b] average long-term fertilizer N-P-K input relative to recommended N-P-K amounts, mineral N only (Hirte et al., 2018).
[c] fertilizer input of mineral N, i.e. total N in mineral fertilizers, ammonium- and nitrate-N in organic fertilizers, (total N), P, and K.
[d] dry matter; DOK maize (silage): whole plant, ZOFE maize (grain): kernel, winter wheat: grain.
[e] dry matter; excluding stubble mass.
[f] Swiss standard (Richner and Sinaj, 2017).
[g] farmyard manure.
[h] maize: organic fertilization plus mineral N (110 kg ha^{-1}), wheat: mineral fertilization only.

reflect Swiss agricultural practice (Mayer et al., 2015), and CONTROL, MANURE, N2P1K1, and N2P2K2Mg in ZOFE, which represent conditions with distinct nutrient insufficiencies (Table 1) and therefore allow for a clearer interpretation of the results. The treatments were also chosen with regard to a pronounced fertilization intensity gradient on both sites (Table 1; Hirte et al., 2018).

Maize (Zea mays) was grown from end of May to end of September 2013 in DOK (silage maize, var. Colisée) and from beginning of May to beginning of October 2013 in ZOFE (grain maize, var. Birko). On both sites, row distance was 0.75 m and sowing density was 10.5 seeds m^{-2}, apart from CONFYM in DOK where it was 9.5 seeds m^{-2}. Winter wheat (*Triticum aestivum*) was grown from end of October 2014 to mid-July 2015 in DOK (var. Wiwa) and from mid-November 2013 to end of July 2014 in ZOFE (var. CH-Claro). Row distance was 0.17 m on both sites and sowing density was 450 (BIOORG) and 425 seeds m^{-2} (CONFYM) in DOK and 400 seeds m^{-2} in ZOFE. Sowing densities differed between treatments in DOK to compensate for differences in sprouting success and to ensure similar stand densities at harvest. Fertilization details and harvest parameters are given in Table 1 and soil chemical properties in Supplementary Table 1. Further information on yields and climate conditions during the respective growing seasons is presented and discussed in Hirte et al. (2018).

Subpopulations of one individual maize plant or approximately 40 wheat plants in two adjacent rows were grown in microplots within field plots. At the beginning of each growing season, one stainless steel cylinder (0.55 m length, 0.35 m diameter) per treatment and field replication was driven into soil to 0.5 m depth. All four field replications in DOK and four of five field replications in ZOFE (blocks I to IV) were included in this study.

2.2. ^{13}C-CO_2 labelling

We used multiple-pulse labelling with ^{13}C-CO_2 during the time period of most active plant development to assess net rhizodeposition C at the end of the cropping season (Kuzyakov and Domanski, 2000). Between tillering and ripening, maize and wheat were labelled for 4 h between mid-morning and early afternoon during 8–12 weekly labelling campaigns (Supplementary Table 2). Mobile height-adjustable Plexiglas®-chambers (400 mm diameter; Supplementary Fig. 1) were set up on the soil surface over the microplots and voids were tightly closed with soil. The CO_2-concentration in each chamber was monitored using a portable infrared CO_2-analyser (LI-820; LI-COR). When it dropped below 150 ppm, a dose of ^{13}C-CO_2 (99 atom-%; Cambridge Isotope Laboratories) was injected with a super syringe (1.5 L; 20 mL precision; Hamilton) to raise it to approximately 800 ppm. Depending on chamber size and assimilation rate of the subpopulation, 5–8 doses of 40–200 mL ^{13}C-CO_2 were applied during each labelling campaign (details in Supplementary material).

2.3. Sampling

We sampled the above ground parts of the entire subpopulations just before crop harvest directly above the soil surface (i.e. including stubbles to 0.15 m height) and separated them into crop product (silage maize: above ground biomass; grain maize: cob; wheat: grain) and straw. Stubbles were cleansed from adhering soil particles with tap water. We sampled roots and soil in the microplots immediately after crop harvest in three layers: top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m). The maize microplots were vertically divided in halves to 0.5 m depth and the top and intermediate layers were one-sidedly sampled as monoliths. Two soil cores were taken from the deep layer with a Riverside auger (50 mm diameter; Eijkelkamp). The wheat microplots were sampled as whole monoliths in the top layer, root-stocks were separated from soil, the soil was thoroughly mixed and subsampled (2.5 kg; 10% of soil mass), and the remaining portion was discarded. Four soil cores (two within and between rows, respectively)

were taken with a Riverside auger from the intermediate and deep layer, respectively. In addition, unlabelled roots and soil were sampled with a Pürckhauer gouge auger (four cores per field plot and layer; 30 mm diameter; Eijkelkamp) at a distance of at least 5 m from the microplots. Labelled and unlabelled samples from the same layer and position were separately pooled and stored at 4 °C for a maximum of four weeks.

2.4. Separation of roots and soil and ^{13}C analysis

We separated roots and soil in a three-step procedure: 1) Field-fresh soil was 2 mm sieved and the sieve residue was separated into coarse roots and mineral remains by hand. Roots and remains were cleansed under running tap water and collected and the 2 mm sieved soil was oven dried at 40 °C for 48 h. 2) A subsample of 720 g dried soil was mixed with deionized water (ratio 1:1.25) on an overhead shaker for 20 min, the suspension was 0.5 mm sieved, and the sieve residue was cleansed under running tap water, transferred into a plastic bowl, and separated into fine roots (including extraneous organic matter; Hirte et al., 2017) and mineral remains by repeated decantation. Roots and remains were collected and the 0.5 mm sieved soil was discarded. 3) Parallel to step 2, a subsample of 120 g dried soil was mixed with deionized water (ratio 1:1.25) on an overhead shaker for 20 min, the suspension was 0.5 mm sieved, and the sieve was rinsed with 300 mL deionized water while soil aggregates were carefully squashed through the mesh with a rubber spatula. The sieve residue was discarded and the 0.5 mm sieved soil suspension was collected in a glass dish and spiked with 0.5 mL 4.5 mM silver solution (redispersed polyvinylpyrrolidone-coated nanopowder, particle size < 100 nm; Sigma Aldrich) to inhibit microbial activity (Gajjar et al., 2009; Swarnavalli et al., 2011). This procedure was identical for labelled and unlabelled samples except for the separation of fine roots and soil, which were simultaneously collected in a combined step using 240 g dried soil of unlabelled samples.

All plant parts and mineral remains were oven dried at 60 °C for 48 h (except maize cobs: 7 days) and weighed. The soil suspension was oven-dried at 80 °C for 12–18 h until constant weight. Roots were cut (scissors) and soil was ground (RM 200; Retsch) before thoroughly homogenized subsamples were milled (MM 200; Retsch). Total C and ^{13}C abundance ($\delta^{13}C$ relative to V-PDB) of coarse and fine roots and soil were simultaneously analysed by isotope ratio mass spectrometry (EA 1110; Carlo Erba; coupled with Delta S; Thermo Finnigan).

2.5. Calculations and statistics

To obtain root biomass C, we corrected the amount of C in the labelled fine root samples for the proportion of C derived from extraneous organic matter (Hirte et al., 2017, 2018) and summed coarse and fine root C. To obtain rhizodeposition C, we corrected ^{13}C abundance (expressed as ^{13}C atom fraction, $x(^{13}C)$; Coplen, 2011) of all labelled root samples for the proportion of ^{13}C in adhering soil (Janzen et al., 2002) and that of labelled fine root samples for the proportion of ^{13}C derived from extraneous organic matter. We then calculated rhizodeposition C (g kg^{-1}) from ^{13}C excess (Coplen, 2011) based on the concept by Janzen and Bruinsma (1989):

$$Rhizodeposition\ C = \frac{x^E(^{13}C)_{soil}}{x^E(^{13}C)_{roots}} * C_{soil} * (1 - f_{min}) \quad (1)$$

where $x^E(^{13}C)_{soil}$ and $x^E(^{13}C)_{roots}$ are excess ^{13}C atom fraction in soil and roots, respectively, C_{soil} is the C concentration in soil (g kg^{-1}), and f_{min} is the mass proportion of mineral remains (> 0.5 mm) in the soil. To calculate $x^E(^{13}C)_{soil}$, we used $x(^{13}C)$ of labelled soil (for each subpopulation individually) and $x(^{13}C)$ of unlabelled soil (averaged per treatment). To calculate $x^E(^{13}C)_{roots}$, we used the weighted average of $x(^{13}C)$ of labelled coarse and fine roots with respect to their mass ratio (for each subpopulation individually) and $x(^{13}C)$ of unlabelled coarse roots (averaged across treatments per site; differences between treatments not significant). The concept by Janzen and Bruinsma (1989) relies on two major assumptions. First, the ^{13}C enrichment of root biomass is homogeneous and, second, root biomass and rhizodeposition have the same ^{13}C enrichment.

Plant C (crop product and straw: g subpopulation^{-1}; root biomass and rhizodeposition: g kg^{-1} soil) was extrapolated to field scale (g m^{-2}; Hirte et al., 2018) and relative C allocation coefficients for crop product, straw, root biomass, and rhizodeposition were expressed as proportions of whole-plant C (Bolinder et al., 2007).

For each site individually, we fitted different data subsets for (i) the entire profile (0–0.75 m) and the three soil layers (0–0.25, 0.25–0.5, 0.5–0.75 m) individually and (ii) the three soil layers together to mixed effects models with (i) treatment*crop as fixed factors and plot as random factor and (ii) treatment*crop*layer as fixed factors and plot/crop as random factors. The explained variables were (i) BGC inputs, root biomass C, rhizodeposition C, proportion of rhizodeposition C of BGC inputs, above ground C, product C, straw C, and C allocation coefficients for product, straw, root biomass, and rhizodeposition and (ii) BGC inputs, root biomass C, rhizodeposition C, and proportion of rhizodeposition C of BGC inputs. Differences between means of (i) treatments and crops and (ii) treatments, crops, and layers were determined by analysis of variance (ANOVA) with a significance level of $p < 0.05$ and subsequent simultaneous multiple comparison of least squares means of group pairs with Tukey-adjustment of p-values. All analyses were performed on untransformed data except for absolute values of BGC inputs, root biomass C, and rhizodeposition C, which were log-transformed for (ii) the evaluation of depth effects. Treatments were handled as independent levels due to the limited treatment selection on each site, which did not reflect the field designs. Statistical analyses and data visualization were done with the software R version 3.4.2 (R Core Team, 2017) and the R packages “lme4” (Bates et al., 2015), “lmerTest” (Kuznetsova et al., 2016), “pbkrtest” (Halekoh and Højsgaard, 2014), “emmeans” (Lenth, 2017), and “ggplot2” (Wickham, 2009).

3. Results

3.1. Net below ground carbon inputs

In DOK and ZOFE, respectively, total BGC inputs (root biomass plus rhizodeposition C) in the entire investigated (0–0.75 m) profile averaged 220 and 93 g m^{-2} for maize and 134 and 110 g m^{-2} for wheat, of which rhizodeposition C was 140 and 53 g m^{-2} for maize and 73 and 63 g m^{-2} for wheat (Fig. 1). BGC inputs were similar among treatments for both crops on both sites, whereas root biomass C of wheat in ZOFE was higher in N2P1K1 than in CONTROL ($p < 0.05$) and MANURE ($p < 0.01$; N2P2K2Mg intermediate) and rhizodeposition C of maize in DOK was higher in BIOORG2 than in BIOORG1 ($p < 0.01$) and CONFYM2 ($p < 0.05$; Fig. 1, Table 4).

BGC inputs decreased with soil depth (Fig. 2) and accounted for roughly 80, 12, and 8% in the top, intermediate, and deep layer, respectively, of the inputs in the entire profile. However, the distributions varied between crops: BGC inputs of maize on both sites differed between all layers ($p < 0.001$ each), while those of wheat differed between top- and subsoil layers only ($p < 0.001$ each) and were similar below 0.25 m depth (Fig. 2, Table 5). Consequently, absolute amounts of BGC inputs differed between crops in the individual layers: Compared to wheat, maize allocated 1.7- and 2-times more C to the top and intermediate layer, respectively ($p < 0.001$ each), but similar C amounts to the deep layer in DOK and similar C amounts to the top and intermediate layer, respectively, but only 0.4-times as much C to the deep layer ($p < 0.05$) in ZOFE (Fig. 2, Table 5). Root biomass and rhizodeposition C followed the same distributions as BGC inputs (Fig. 2, Table 5).

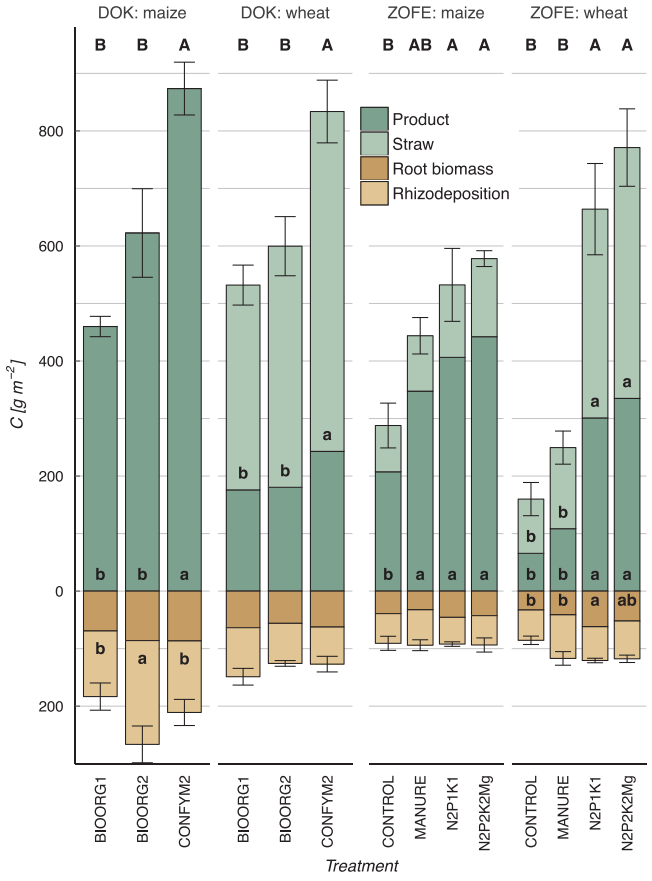

Fig. 1. Below and above ground plant C of field-grown maize and wheat at harvest in different treatments of the DOK and ZOFE long-term field trials. Product refers to total above ground biomass of silage maize (DOK) or grain yield of grain maize (ZOFE) and wheat. Error bars: SEs of total below and above ground C (4 field replications). Different letters (lower case: root biomass, rhizodeposition, product, and straw C; upper case: total below and above ground C) denote significant ($p < 0.05$) differences in least squares means of C pools between treatments within crops and sites (missing letters: no differences).

In the top layer, maize in DOK allocated more C to soil as BGC inputs in BIOORG2 (230 g m^{-2}) than in BIOORG1 (150 g m^{-2}; $p < 0.05$; CONFYM2: 171 g m^{-2}) and as rhizodeposition C in BIOORG2 (149 g m^{-2}) than in BIOORG1 (89 g m^{-2}; $p < 0.01$) and CONFYM2 (89 g m^{-2}; $p < 0.01$). Wheat in ZOFE allocated more C to soil as root biomass in N2P1K1 (51 g m^{-2}) than in CONTROL (26 g m^{-2}; $p < 0.01$; MANURE: 32 g m^{-2}; N2P2K2Mg: 43 g m^{-2}). Treatment differences did not occur in the intermediate and deep layer (data not shown).

3.2. Below ground carbon partitioning to root biomass and rhizodeposition

In DOK and ZOFE, respectively, rhizodeposition C in the entire profile accounted for 63 and 57% of total BGC inputs for maize and 54 and 58% for wheat. The proportions differed between treatments (Tables 2 and 4) for maize in DOK (BIOORG2 > CONFYM2; $p < 0.05$), maize in ZOFE (MANURE > N2P1K1; $p < 0.05$), and wheat in ZOFE (CONTROL and MANURE > N2P1K1; $p < 0.05$ and 0.01, respectively). However, they were not related to fertilization intensity.

The proportions of rhizodeposition C of total BGC inputs increased with depth except for wheat in ZOFE and were lower in the top than in the intermediate and deep layer ($p < 0.001$ each; Tables 2 and 5). For maize in DOK, they were also lower in the intermediate than deep layer ($p < 0.05$; Tables 2 and 5). The proportions differed between treatments in the top layer only and the differences reflected those in the entire profile (Table 2).

3.3. Above ground carbon

Above ground C increased consistently with fertilization intensity (Fig. 1). In DOK, it was higher in CONFYM2 than in BIOORG1 ($p < 0.001$) and BIOORG2 ($p < 0.01$) for both maize and wheat. In ZOFE, it was higher in N1P1K1 and N2P2K2Mg than in CONTROL ($p < 0.01$ each; MANURE intermediate) for maize and higher in N1P1K1 and N2P2K2Mg than in CONTROL and MANURE ($p < 0.001$ each) for wheat. Treatment differences in product and straw C reflected those in above ground C for the most part (Fig. 1, Table 4).

3.4. Whole-plant carbon allocation to below and above ground pools

Maize and wheat, respectively, allocated on average 26 and 18% of whole-plant C below ground in DOK and 18 and 24% in ZOFE. In DOK, the proportion of BGC inputs was higher in BIOORG1 and BIOORG2 than in CONFYM2 ($p < 0.01$ each) for maize and higher in BIOORG1 than in CONFYM2 ($p < 0.01$; BIOORG2 intermediate) for wheat. In ZOFE, the proportion was higher in CONTROL than in N2P1K1 ($p < 0.05$) and N2P2K2Mg ($p < 0.01$; MANURE intermediate) for maize and higher in CONTROL and MANURE than in N2P1K1 and N2P2K2Mg ($p < 0.001$ each) for wheat (Tables 3 and 4).

Allocation coefficients (i.e. proportions of whole-plant C) for root biomass C tended to decrease with increasing fertilization intensity for maize and wheat in DOK (not significant) and wheat in ZOFE (significant), while maize in ZOFE had the lowest coefficient in MANURE (Tables 3 and 4). Allocation coefficients for rhizodeposition C decreased with increasing fertilization intensity and showed the same treatment differences as the proportions of total BGC inputs of whole-plant C (Tables 3 and 4). Reciprocal to allocation coefficients for BGC, those for above ground C increased with increasing fertilization intensity except for product C of wheat in DOK, which was similar between treatments, and straw C of maize in ZOFE, which was highest in MANURE (Tables 3 and 4).

4. Discussion

4.1. Net below ground carbon inputs and partitioning to root biomass and rhizodeposition

Net BGC inputs at harvest on two field sites were 220 and 93 g C m^{-2} for maize and 134 and 110 g C m^{-2} for wheat with densities of 10 maize and 400 wheat plants m^{-2}. These amounts were within the range of earlier findings for mature maize and wheat: 100 g C m^{-2} in the field (Balesdent and Balabane, 1992) and 125–400 g C m^{-2} in the greenhouse (Davenport and Thomas, 1988; Qian et al., 1997) for maize and 35–200 g C m^{-2} in the field (Gregory and Atwell, 1991; Keith et al., 1986; Martens et al., 2009; Swinnen, 1994) and 90–240 g C m^{-2} in the greenhouse (Martin and Merckx, 1992; Sauerbeck and Johnen, 1977; Sun et al., 2018) for wheat. The strong variation in BGC inputs may be due to differences in crop root system size (Gregory, 2006) and environmental and genotypic characteristics affecting the amounts of C deposited in the rhizosphere (Nguyen, 2003), but also due to variation in plant densities (e.g. for this experiment and the cited studies: maize: 8.3–15.2 m^{-2}; wheat: 110–400 m^{-2}).

Rhizodeposition C is more often reported as proportion of total BGC inputs or rhizodeposition-to-root ratio (Nguyen, 2003; Pausch and Kuzyakov, 2018) than as absolute amount. Here, we present proportions since their distribution is bounded and less skewed than that of ratios, facilitating a more straight-forward statistical analysis and an easier interpretation of the results (Poorter and Sack, 2012). The proportions of 63 and 57% for maize on our two field sites at harvest are higher than the proportion of 30% found by Balesdent and Balabane

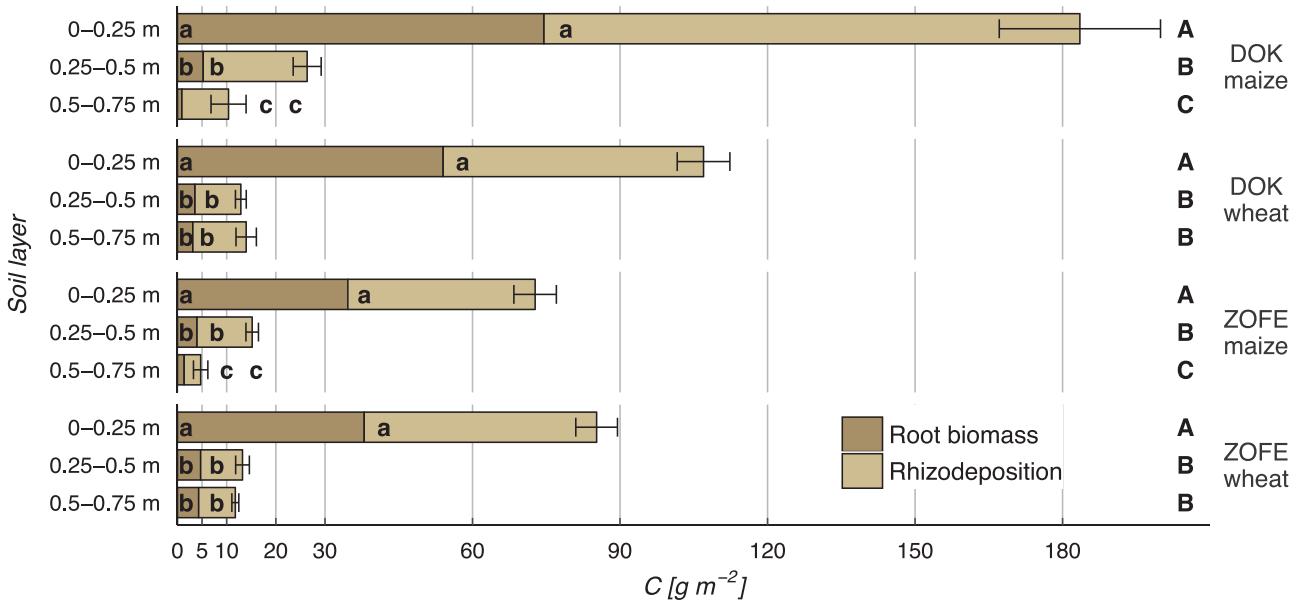

Fig. 2. BGC inputs to soil in the top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) layer, respectively, of field-grown maize and wheat at harvest in the two long-term field trials DOK and ZOFE. Error bars: SEs of total below ground C (4 field replications). Different letters (lower case: root biomass and rhizodeposition C; upper case: total below ground C inputs) denote significant ($p < 0.05$) differences in least squares means of log-transformed C pools between layers within crops and sites.

(1992) in the field but similar to the 55% found by Davenport and Thomas (1988) in the greenhouse. Studies, in which measurements were taken until earlier stages of the reproductive phase, reveal an average of 23% (median 22%; Liang et al., 2002; Martens, 1990; Qian et al., 1997), but might not be representative for the end of the growing season (see below). The proportions of 54 and 58% for wheat on our two field sites are close to the average of 52% (median 60%) for wheat at harvest maturity in the field or greenhouse (Gregory and Atwell, 1991; Keith et al., 1986; Martens, 1990; Martens et al., 2009; Martin and Merckx, 1992; Sauerbeck and Johnen, 1977; Sun et al., 2018; Swinnen, 1994). As BGC inputs of field-grown maize have rarely been studied to the end of the growing season, it is difficult to assess differences in proportional rhizodeposition C between crops at harvest. Studies with younger plants suggest lower C partitioning to rhizodeposition in maize than wheat (Martens, 1990; Merckx et al., 1986; Van Veen et al., 1989), possibly due to less active exudation (Hétier et al., 1986).

The proportions determined in the present study are much larger than the currently widely adopted 40% (reported as rhizodeposition-to-root ratio of 0.65) assumed by Bolinder et al. (2007) for field-grown cereals at harvest. This previous number relies on data from tracer studies mainly conducted on juvenile small-grain cereals under controlled conditions using single-pulse labelling (Kuzyakov and Domanski, 2000; Kuzyakov and Schneckenberger, 2004). From our point of view, several aspects of this approach deserve attention. First, the type of study, i.e. field or greenhouse, might affect total amounts of BGC inputs and proportional rhizodeposition C. While field-grown plants experience a multitude of environmental stress factors that entail a shift in C partitioning below ground (Amos and Walters, 2006; Baetz and Martinoia, 2014; Bais et al., 2006; Bengough and McKenzie, 1997; Boeuf-Tremblay et al., 1995; Holland et al., 1996), those factors usually play only a minor role in controlled experiments. Higher photosynthetically active radiation also results in higher rhizodeposition C in the field than greenhouse (Zagal, 1994).

Table 2
Average proportions of rhizodeposition C of BGC inputs (± SEs of 4 field replications) in the entire (0–0.75 m) profile and top (0–0.25 m), intermediate (0.25–0.5 m), and deep (0.5–0.75 m) layer, respectively, of field-grown maize and wheat at harvest in different treatments of the long-term field trials DOK and ZOFE. Proportions are multiplied with 100 for readability. Different letters denote significant ($p < 0.05$) differences in least squares means of proportions between treatments within layers, crops, and sites (lower case) and between layers within crops and sites (upper case).

	Rhizodeposition C as proportion of BGC inputs [%]							
	maize				wheat			
Treatment (intensity)	0–0.75 m	0–0.25 m	0.25–0.5 m	0.5–0.75 m	0–0.75 m	0–0.25 m	0.25–0.5 m	0.5–0.75 m
— DOK —								
BIOORG1 (0.4)	63 ± 2 **ab**	60 ± 3 **ab**	75 ± 2	88 ± 3	57 ± 2	52 ± 1	74 ± 2	78 ± 4
BIOORG2 (0.8)	68 ± 2 **a**	65 ± 2 **a**	84 ± 3	85 ± 4	56 ± 1	49 ± 2	79 ± 1	79 ± 2
CONFYM2 (1.2)	59 ± 2 **b**	51 ± 6 **b**	80 ± 3	90 ± 3	50 ± 3	46 ± 3	62 ± 8	68 ± 4
average		59 ± 3 **C**	80 ± 2 **B**	89 ± 2 **A**		49 ± 1 **B**	72 ± 3 **A**	75 ± 2 **A**
— ZOFE —								
CONTROL (0)	57 ± 3 **ab**	54 ± 3 **ab**	73 ± 4	71 ± 8	61 ± 1 **a**	60 ± 2 **a**	63 ± 8	64 ± 4
MANURE (0.5)	65 ± 5 **a**	60 ± 6 **a**	79 ±	56 ± 12	65 ± 2 **a**	63 ± 2 **a**	69 ± 5	67 ± 3
N2P1K1 (0.7)	51 ± 3 **b**	46 ± 4 **b**	68 ± 5	62 ± 9	49 ± 3 **b**	47 ± 4 **b**	53 ± 2	57 ± 4
N2P2K2Mg (1.1)	56 ± 4 **ab**	50 ± 4 **ab**	71 ± 6	76 ± 7	56 ± 1 **ab**	54 ± 1 **ab**	62 ± 3	64 ± 3
average		53 ± 2 **B**	73 ± 2 **A**	66 ± 5 **A**		56 ± 2	62 ± 3	63 ± 2

Table 3
Average C allocation coefficients (± SEs of 4 field replications) for crop product, straw, root biomass, and rhizodeposition of field-grown maize and wheat at harvest in different treatments of the long-term field trials DOK and ZOFE. Coefficients are multiplied with 100 for readability. Different letters denote significant ($p < 0.05$) differences in least squares means of coefficients (lower case) and total BGC inputs (upper case) between treatments within crops and sites.

	C allocation coefficient (proportion of whole-plant C) [%]									
	maize					wheat				
	above ground		below ground			above ground		below ground		
Treatment (intensity)	product	straw	root biomass	rhizodeposition	BGC inputs	product	straw	root biomass	rhizodeposition	BGC inputs
— DOK —										
BIOORG1 (0.4)	71.1 ± 3.3 **b**	0	10.7 ± 1.6	17.6 ± 1.8 **a**	**A**	25.9 ± 0.7	52.4 ± 1.0 **c**	9.3 ± 0.6	12.4 ± 0.8 **a**	**A**
BIOORG2 (0.8)	70.0 ± 1.1 **b**	0	9.4 ± 0.9	20.4 ± 0.8 **a**	**A**	24.7 ± 0.8	57.8 ± 0.7 **b**	7.8 ± 0.8	9.7 ± 0.5 **ab**	**AB**
CONFYM2 (1.2)	80.7 ± 1.3 **a**	0	8.0 ± 0.8	11.3 ± 0.9 **b**	**B**	25.3 ± 0.6	61.4 ± 1.9 **a**	6.5 ± 0.4	6.8 ± 1.1 **b**	**B**
— ZOFE —										
CONTROL (0)	54.0 ± 4.0 **b**	21.6 ± 2.1 **a**	10.3 ± 0.7 **a**	14.0 ± 1.9 **a**	**A**	25.6 ± 2.9 **b**	38.5 ± 0.8 **b**	13.9 ± 1.6 **a**	21.9 ± 1.2 **a**	**A**
MANURE (0.5)	64.5 ± 1.8 **a**	17.9 ± 0.3 **b**	6.0 ± 0.6 **b**	11.6 ± 1.9 **ab**	**AB**	29.3 ± 1.7 **ab**	38.5 ± 0.6 **b**	11.5 ± 1.2 **ab**	20.7 ± 0.6 **a**	**A**
N2P1K1 (0.7)	64.3 ± 2.6 **a**	20.4 ± 1.0 **ab**	7.5 ± 1.0 **ab**	7.8 ± 1.1 **b**	**B**	38.0 ± 1.4 **a**	46.3 ± 0.6 **a**	8.0 ± 0.7 **bc**	7.8 ± 1.0 **b**	**B**
N2P2K2Mg (1.1)	65.8 ± 2.1 **a**	20.2 ± 0.4 **ab**	6.3 ± 1.3 **ab**	7.6 ± 0.7 **b**	**B**	37.5 ± 0.8 **a**	49.1 ± 0.4 **a**	5.9 ± 0.4 **c**	7.5 ± 0.4 **b**	**B**

Second, the great majority of reference values, especially for maize (Pausch et al., 2013), has been collected for plants in the vegetative phase (Kuzyakov and Domanski, 2000; Kuzyakov and Schneckenberger, 2004). While BGC allocation to both root biomass and rhizodeposition declines with plant age (Nguyen, 2003), an increasing proportion of root biomass decays with time after flowering (Gregory, 2006). Although functionally different from rhizodeposition, this root biomass C adds to the rhizodeposition pool (Pausch and Kuzyakov, 2018) and needs to be accounted for in net balances of whole-plant C. The long time period between flowering and harvest maturity of almost three months for grain maize as compared to six weeks for winter wheat in temperate climate (Holzkämper et al., 2013; Semenov et al., 2014) suggests that the shift in BGC inputs from root biomass to rhizodeposition might be more relevant for maize than wheat. This is supported by the greater root biomass reduction between flowering and harvest for maize than wheat observed in other studies (Gregory et al., 1978; Liu et al., 2011; Mengel and Barber, 1974; Peng et al., 2012). Consequently, the post-anthesis shift in BGC inputs differs between crops and growing regions and underlines the urgent need for studies covering the entire growing season, especially for crops with a long reproductive phase.

Third, the method of plant C tracking is crucial for estimating rhizodeposition C. The use of natural abundance ^{13}C or continuous labelling would facilitate precise quantifications of plant C budgets (Kuzyakov and Domanski, 2000), but multiple-pulse labelling has been found to provide close estimates as well (Warembourg and Estelrich, 2000). By contrast, single-pulse labelling underestimates C allocation to below ground pools, possibly due to short chase periods, after which C partitioning might not yet be completed (Nguyen, 2003). For the reasons discussed above we argue that proportional rhizodeposition C of single-pulse labelled juvenile plants under controlled conditions is lower than that of field-grown crops at harvest and might not provide a sufficient approximation for net C balances at the end of the growing season.

4.2. Fertilization intensity and below ground carbon inputs

Although root biomass C of wheat in ZOFE (discussed in Hirte et al., 2018) and rhizodeposition C of maize in DOK differed between treatments, total BGC inputs were not affected by treatment. This is in line with earlier findings for wheat, although the same study showed lower BGC inputs in integrated compared to conventional farming for barley (Swinnen, 1994). Studies using single-pulse labelling can give an indication of fertilization effects on BGC inputs of maize and wheat several days after labelling: In high- compared to low-intensity treatments, total BGC inputs were found to be similar (An et al., 2015; Chowdhury et al., 2014; Liljeroth et al., 1994) or higher (Qiao et al., 2017). Rhizodeposition C generally tended to increase with fertilization (Chowdhury et al., 2014; Liljeroth et al., 1994; Qiao et al., 2017; Swinnen, 1994; but see An et al., 2015). This was not evident in our study, which might again be related to the late time of sampling and possible interactions between treatment effects on C accrual and loss by decomposition.

Partitioning of BGC inputs to root biomass and rhizodeposition was

Table 4
Analysis of variance for treatment and crop effects on below (0–0.75 m) and above ground C pools, proportion of rhizodeposition C of total BGC inputs, and proportions of below and above ground C pools of whole-plant C (allocation coefficient). Levels of significance (*, **, ***: $p < 0.001, 0.01, 0.05$, respectively; ns: not significant) refer to data presented in Fig. 1 and Tables 2 and 3.

	Below ground C				Above ground C			Proportion of whole-plant C				
	Fig. 1			Table 2	Fig. 1			Table 3				
	total	root biomass	rhizodeposition	rhizodeposition / total	total	product	straw	product	straw	root biomass	rhizodeposition	BGC inputs
— DOK —												
Treatment	ns	ns	ns	*	***	***	**	*	**	ns	**	**
Crop	***	*	***	***	ns	***	***	***	***	ns	***	***
Treatment x crop	ns	ns	*	ns	ns	**	**	**	**	ns	*	ns
— ZOFE —												
Treatment	ns	*	ns	**	***	***	***	***	***	**	***	***
Crop	**	*	*	ns	ns	***	***	**	***	**	***	***
Treatment x crop	ns	ns	ns	ns	**	ns	***	ns	***	*	***	***

Table 5
Analysis of variance for treatment, crop, and depth effects on below ground C pools and proportion of rhizodeposition C of total BGC inputs in the top, intermediate, and deep layers. Levels of significance (*, **, ***: $p < 0.001$, 0.01, 0.05, respectively; ns: not significant) refer to data presented in Fig. 2 and Table 2. Total below ground, root biomass, and rhizodeposition C were log-transformed for analysis.

	Below ground C			
	Fig. 2			Table 2
	total	root biomass	rhizodeposition	rhizodeposition / total
— DOK —				
Treatment	ns	ns	ns	*
Crop	*	ns	**	***
Layer	***	***	***	***
Treatment x crop	ns	ns	ns	ns
Treatment x layer	ns	ns	ns	ns
Crop x layer	***	***	***	ns
Treatment x crop x layer	ns	ns	ns	*
— ZOFE —				
Treatment	ns	ns	ns	*
Crop	***	***	**	ns
Layer	***	***	***	***
Treatment x crop	ns	ns	ns	ns
Treatment x layer	ns	*	ns	ns
Crop x layer	***	***	***	*
Treatment x crop x layer	ns	*	ns	ns

strongly affected by treatment but was neither positively nor negatively related to fertilization intensity. The highest proportions of rhizodeposition C occurred in medium-intensity treatments, which were solely organically fertilized. Organic fertilizers might have stimulated root exudation or attenuated microbial utilization of root-derived C or both. Exudate-mediated mineralization of N-rich organic compounds can increase N availability in N-limited soils (Dijkstra et al., 2013; Huo et al., 2017). Nitrogen was found to be the most limiting nutrient under sole organic fertilization in DOK (Mayer et al., 2015) and ZOFE (Oberholzer et al., 2014). Increasing root exudation may therefore be a strategy of crop plants to mobilize organically bound N (Dijkstra et al., 2013), thereby inflating the rhizodeposition pool. Further, longer residence times of root-derived C under organic as compared to mineral fertilization in the medium- (months) and long- (years) term have previously been related to preferential microbial utilization of manure over root residues in organically fertilized treatments (Kong and Six, 2010; Zhang et al., 2015). Within the time period of several weeks until harvest, this may have been more relevant for rhizodeposition than root biomass in our study.

4.3. Below ground carbon partitioning to root biomass and rhizodeposition in different soil layers

The proportion of rhizodeposition C of total BGC inputs was strongly affected by soil depth and increased from, on average, 55% in the topsoil to 65–80% below 0.25 m depth. The magnitude of increase varied between sites and crops; while the effect was only a trend between top- and subsoil for wheat in ZOFE, it was also prominent between the two subsoil layers for maize in DOK. This may be attributed to the differences in vertical distribution patterns of absolute amounts of root biomass and rhizodeposition C between crops and sites (discussed for root biomass in Hirte et al., 2018).

The increase of proportional rhizodeposition C from top- to subsoil may have different reasons. First, higher mechanical impedance of the denser subsoil than ploughed topsoil (Hirte et al., 2018) might have increased mucilage and exudate production and sloughing off of root cap cells to facilitate root growth (Bengough and McKenzie, 1997; Boeuf-Tremblay et al., 1995). Second, at the time of sampling, root-derived C was supposedly younger in the sub- than topsoil as the vast majority of rhizodeposits are released at or near the tip of actively growing roots (Jones et al., 2009), which appear much later in the season in deep than surface soil (Borg and Grimes, 1986; Thorup-Kristensen et al., 2009). Hence, the subsoil was characterized by more fresh root-derived C and less time for decomposition compared to the topsoil at harvest. Third, vertical translocation of recent photoassimilates as dissolved organic matter may have also played a role (Flessa et al., 2000; Müller et al., 2016) and might have been more relevant for maize than wheat due to differences in soil water balances towards the end of the growing seasons (Hirte et al., 2018). Fourth, our purely size-based definition of rhizodeposition comprised not only actual rhizodeposits but also root biomass ≤ 0.5 mm. The share of those finest roots in total root biomass presumably increased with soil depth, as was the case for fine (≤ 2 and > 0.5 mm) root biomass (Hirte et al., 2018), indicating that the proportion of rhizodeposition C was more affected by this shift in deep than surface soil.

The increase in C partitioning to rhizodeposition with soil depth has implications for total BGC input estimations based on root biomass C and proportions (e.g. Pausch et al., 2013). When proportions derived from topsoil data are applied to the entire soil profile, BGC inputs to subsoils would be systematically underestimated. As a consequence, BGC inputs to subsoils might be higher than has been assumed (e.g. Rumpel et al., 2012). When vertical distributions of soil organic C and root biomass C are linked, a discrepancy in relative amounts between top- and subsoils becomes evident (Dietzel et al., 2017; Gleixner, 2013). Besides different stabilization rates and leaching of dissolved organic C (Gleixner, 2013; Ota et al., 2013), the increase in proportional rhizodeposition C with depth could provide an additional explanation for this discrepancy.

4.4. Fertilization effects on whole-plant carbon allocation below and above ground

Decreasing fertilization intensity led to an increase in C allocation below ground as a consequence of photoassimilate partitioning to those plant organs that experience the most severe resource limitation (Poorter et al., 2012). As water was not limiting in our study (Hirte et al., 2018), higher BGC inputs relative to above ground C in low-intensity (bio-organic in DOK; zero and manure-fertilized in ZOFE) than high-intensity (conventional in DOK; mineral-fertilized in ZOFE) treatments were most likely induced by nutrient shortage. Nitrogen was the most limiting nutrient under zero and sole organic fertilization due to insufficient amounts of directly plant-available N (Hirte et al., 2018) and was presumably the main factor for differences in whole-plant C allocation (see Nguyen, 2003; Pausch and Kuzyakov, 2018). By contrast, half compared to full long-term supply of mineral P and K did not entail significant changes in C allocation in our study.

The negative relation between fertilization intensity and C allocation at harvest was more pronounced for rhizodeposition than root biomass. This is contradictory to Nguyen (2003), who found a highly significant effect of N supply on whole-plant C allocation to root biomass but not to rhizodeposition irrespective of labelling type (28 mainly grassland experiments). Studies with cereals under controlled conditions even suggest a positive relation between fertilization intensity and C allocation to rhizodeposition (Chowdhury et al., 2014; Qiao et al., 2017), which was also found for field-grown barley but not wheat (no difference) at harvest (Swinnen, 1994). The different findings of fertilization effects on whole-plant C allocation to rhizodeposition might be related to differences between studies in decomposition dynamics and time of sampling (see above).

4.5. Deep soil carbon inputs

Besides crop breeding, agricultural management has been proposed

as a viable option to increase C inputs to deep soil and sequester C in the long term (Kell, 2012; Lynch and Wojciechowski, 2015). As an important aspect of agricultural management, increasing fertilization is expected to increase C inputs to soil in nutrient-deficient systems (Paustian et al., 2016). Our results clearly show that, while total BGC inputs to deep soil might be generally higher than previously assumed, long-term fertilization has little to no effect on BGC inputs below the ploughing layer. This finding supports previous studies of root biomass C inputs to deep soil (Hirte et al., 2018; Russell et al., 2009). Moreover, similar root biomass C inputs under a large N fertilization gradient was found to explain the lack of fertilization effects on soil C sequestration in the long-term (Russell et al., 2009). By contrast, crop choice seems to have a substantial impact on root biomass C inputs (Hirte et al., 2018; Mathew et al., 2017; Russell et al., 2009). The same can be inferred from this study for total BGC inputs, which followed different distribution patterns for maize and wheat within the soil profile on both sites. The higher proportion of deep C inputs of total BGC inputs may result in up to 2.5-times higher C inputs of wheat compared to maize to soil below 0.5 m, suggesting a great potential for C sequestration in deep soil.

4.6. Below ground carbon inputs and soil carbon modelling

Broadly summarized, maize and wheat allocated 10% more whole-plant C below ground under sole organic than adequate mineral N fertilization. This has major consequences for yield-based estimations of BGC inputs in organic and conventional farming. For example, when C allocation coefficients of silage maize and winter wheat in conventional farming (CONFYM2) are applied to maize and wheat in organic farming (BIOORG2) based on product C (shoot biomass of silage maize and grain yield of wheat), annual inputs would be underestimated by 115 and 30 g C m^{-2}, respectively. Consequently, simulations of soil C dynamics, which strongly rely on C input data, may also be severely affected. This has been shown for DOK, where five different allometric functions yielded differences in estimated crop C inputs of up to 200 g C m^{-2} yr^{-1} and, consequently, simulated changes of soil organic C over a 28-year period of -6 to +1.5 Mg C ha^{-1} (Keel et al., 2017b). This underlines that input data do not only affect the magnitude but can even influence the direction of model outcomes.

Based on our findings from different farming systems and fertilization treatments covering a large gradient of long-term fertilization intensity on two sites, we conclude that BGC inputs of maize and wheat to soil are independent of net primary productivity and yield-independent values provide closer estimates for BGC inputs than yield-based functions. This outcome is of great importance for the Swiss greenhouse gas inventory. Up to date, C stocks in agricultural mineral soils have been assumed to be in equilibrium for Switzerland's National Inventory Report (tier 1; Federal Office for the Environment FOEN, 2017), but the use of a soil C model that captures the annual variability in soil C dynamics is planned for the future (tier 3; Keel et al., 2017b). Following an evaluation of different methods to estimate crop C inputs to soil including allometric functions and the findings of the present study, yield-independent values for BGC inputs are advocated for cereals in soil C simulations for forthcoming inventories (S. Keel; personal communication).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.07.010.

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