

Roots are key to increasing the mean residence time of organic carbon entering temperate agricultural soils

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Abstract

The ratio of soil organic carbon stock (SOC) to annual carbon input gives an estimate of the mean residence time of organic carbon that enters the soil (MRT_{OC}). It indicates how efficiently biomass can be transformed into SOC, which is of particular relevance for mitigating climate change by means of SOC storage. There have been few comprehensive studies of MRT_{OC} and their drivers, and these have mainly been restricted to the global scale, on which climatic drivers dominate. This study used the unique combination of regional-scale cropland and grassland topsoil (0–30 cm) SOC stock data and average site-specific OC input data derived from the German Agricultural Soil Inventory to elucidate the main drivers of MRT_{OC} . Explanatory variables related to OC input composition and other soil-forming factors were used to explain the variability in MRT_{OC} by means of a machine-learning approach. On average, OC entering German agricultural topsoils had an MRT of 21.5 ± 11.6 years, with grasslands (29.0 ± 11.2 years, $n = 465$) having significantly higher MRT_{OC} than croplands (19.4 ± 10.7 , $n = 1635$). This was explained by the higher proportion of root-derived OC inputs in grassland soils, which was the most important variable for explaining MRT_{OC} variability at a regional scale. Soil properties such as clay content, soil group, C:N ratio and groundwater level were also important, indicating that MRT_{OC} is driven by a combination of site properties and OC input composition. However, the great importance of root-derived OC inputs indicated that MRT_{OC} can be actively managed, with maximization of root biomass input to the soil being a straightforward means to extend the time that assimilated C remains in the soil and consequently also increase SOC stocks.

KEYWORDS

carbon, carbon sequestration, clay content, root input, soil carbon, soil organic matter, turnover

1 | INTRODUCTION

Increasing soil organic carbon (SOC) stocks is viewed globally as a promising measure to mitigate climate change (Minasny et al., 2017;

Paustian et al., 2016). Storing additional SOC in soils can best be achieved by increasing SOC inputs (Kätterer et al., 2011). However, not all soils (Amelung et al., 2020) and organic carbon (OC) input types (Lemke et al., 2010) might be equally suitable for building up

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SOC. Understanding the efficiency with which OC inputs to soils are transformed into SOC is of utmost importance to inform climate change mitigation strategies involving SOC sequestration.

The mean residence time of OC entering the soil (MRT_{OC}), as derived from the ratio of total SOC stock to average annual C input or efflux, can be used as an indicator of biogeochemical stabilization of OC in soils (Chen et al., 2013; Luo et al., 2019). The concept has been criticized as an oversimplification due to the assumptions that SOC (a) is in steady state, (b) is built up by exactly the amount and type of input that is currently entering the soil and (c) is considered to consist of only one kinetic pool (Sierra et al., 2017). Indeed, it is well known that persistence of OC in the soil can range from hours to millennia (Schmidt et al., 2011; Trumbore, 2000). However, the word 'mean', instead of the frequently used terms 'residence time' or 'turnover time' (Bloom et al., 2016), implies that it does not equal the time that every individual C atom that enters the soil needs to pass through. Instead it gives an indication of the relative efficiency of SOC sequestration in specific situations, for example, in a specific soil in certain climatic conditions that is managed in a specific way. Thus, it might be helpful to identify the management practices and soil properties to focus on to stabilize assimilated OC in soils most efficiently. This study further argues that this ratio should not be called MRT of SOC, since a large proportion of OC entering the soil, for example, as root exudates or crop residues, is rapidly oxidized and released as CO_2 before even entering the pool that is usually defined and measured as SOC, that is, OC in the fine soil fraction (<2 mm) (Luo et al., submitted). It is therefore proposed that the term MRT be used for OC entering the soil (MRT_{OC}) in this context to avoid the confusion highlighted by Sierra et al. (2017).

Globally, MRT_{OC} is found to be mainly driven by climatic variables such as temperature and precipitation, with topsoil MRT_{OC} ranging from <1 year in the tropics (high biomass production and OC inputs, low SOC stocks) to >60 years in the Arctic (low biomass production and OC inputs, high SOC stocks) (Chen et al., 2013). Soil properties and abiotic conditions, such as pH, texture, mineralogy and hydrology, also play a major role in SOC stabilization, accessibility and thus turnover in the soil (Doetterl et al., 2015; Dungait et al., 2012). Barré et al. (2016) used a network of long-term bare fallow experiments to show that centennially persistent SOC has a distinct energetic signature, which could potentially be related to depletion of hydrogen or interactions with the mineral matrix, while no uniform chemical composition of the most stable SOC across experiments was detected. In accordance, Schmidt et al. (2011) summarized recent advances in soil organic matter research and also stated that its persistence is predominantly controlled by environmental and biological drivers while the molecular composition and recalcitrance of the organic matter are less important in the long term.

Nonetheless, MRT_{OC} has also been found to be strongly compound specific, with Gleixner et al. (1999) finding OC turnover times in various pyrolysis products ranging from 9 to 202 years. Furthermore, agricultural long-term experiments revealed that the type and quality of organic matter input play a major role in their

transformation into more stable SOC pools, which is usually expressed as 'humification' (particularly in the modelling community) or the retention coefficient (Kätterer et al., 2011). Those coefficients can range from 0 to 1, with 1 indicating that 100% of the OC added to the soil is retained as SOC. In reality, retention coefficients of OC inputs have been found to range between <0.1 and, in extreme cases, >0.6 (Kätterer et al., 2011; Maillard & Angers, 2014; Poeplau, Kätterer, et al., 2015), indicating that the type and quality of OC input do play a significant role in its turnover and stabilization in the soil. However, there may be many mechanisms behind these differences and their individual importance is not fully understood. For example, in recent decades, a wealth of studies have reported a higher degree of stabilization for root-derived OC than for shoot-derived OC, with several of the mechanisms involved being discussed (Kätterer et al., 2011; Rasse et al., 2005; Sokol & Bradford, 2019). It is therefore evident that the MRT_{OC} in a specific soil can to some extent be managed, for example, by crop type or cultivar selection as well as via external OC inputs.

In temperate soils, grasslands store roughly 30% more SOC than cropland soils (Poeplau et al., 2011). This SOC stock difference between croplands and perennial systems is often explained by alterations in net primary production (NPP) and its appropriation (Haberl et al., 2007), and thus total OC input differences (Hu et al., 2019; Post & Kwon, 2000). However, in central Europe, grassland NPP is similarly appropriated as cropland NPP, resulting in similar total OC inputs. Based on the results of the farmer survey within the German Agricultural Soil Inventory, Jacobs et al. (2020) estimated a country-wide average annual OC input of $3.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ for both croplands and permanent grasslands. For the same sites, Poeplau et al. (2020) found SOC stock differences of 27 Mg ha^{-1} (44%) to a depth of 30 cm. This difference in SOC stocks cannot be explained by the quantity of OC inputs and implies that the MRT_{OC} in grassland soils is considerably higher than the MRT_{OC} in cropland soils. This is in line with the estimates of Carvalhais et al. (2014) who also found land-use type-specific ecosystem OC turnover times in a global analysis. However, the reasons for the difference in MRT_{OC} under cropland and grassland are unclear.

Estimates on MRT_{OC} on scales exceeding single plots are fairly rare due to the limited availability and high uncertainty of OC input data. A specific strength of the German Agricultural Soil Inventory, which was conducted for the first time between 2011 and 2018, is that at least 10 years of management information was collected for each of the 3104 sampling points (Jacobs et al., 2020). Combined with regional C allocation coefficients, these data could be used to derive site-specific average OC inputs. The main aim of this study was to derive MRT_{OC} values for each site by combining OC inputs with measured SOC stocks. The study further evaluated how MRT_{OC} is influenced by land use, management and site properties to elucidate the extent and ways in which agricultural management can influence the efficiency of assimilated OC stabilization in soil. It was hypothesized that grassland soils have a higher MRT_{OC} than cropland soils, and that this is strongly driven by the higher proportion of root-derived OC input in grasslands.

2 | MATERIALS AND METHODS

2.1 | Datasets

This study was based on data from the German Agricultural Soil Inventory. In a grid $8 \times 8 \text{ km}^2$, agricultural soils were sampled to a depth of 100 cm to comprehensively evaluate SOC stocks as well as more or less related soil parameters and site properties for the first time. In total, 3104 soils were sampled, with 2234 being located on croplands, 820 on permanent grasslands and 50 on sites with permanent crops (vineyards and orchards). Permanent grasslands are defined as sites under grassland use for at least five successive years (Jacobs et al., 2018), referred to below as grasslands.

In the present study, only 2100 sites were considered after excluding (a) organic soils (as defined by Jacobs et al. (2018)), (b) sites with missing or unreliable management information (including vineyards and orchards), (c) sites with a C:N ratio >13 and thus a high share of relictic, recalcitrant SOC often originating from former heathland cover (Springob & Kirchmann, 2010) and (d) extremely shallow soils with profile depths <30 cm. Sites with more than 50% of all site years reported as fallow were also excluded since (a) OC input estimates are highly uncertain for fallows, and (b) it is likely that SOC stocks of these soils classified as cropland were not in steady state. For the latter reason, we finally also did not consider sites that had a land-use change in 20 years before the sampling event. Land-use history of each individual sampling point was retrieved from the farmers' questionnaire as well as aerial photographs and historical maps (not published). Among the 1635 croplands, 141 sites (8.6%) had at least 1 year of temporary grassland (ley), referred to below as cropland with ley. In the analysis, 465 grasslands were included.

At each site, a profile pit was dug and soils were sampled in fixed depth increments of 0–10, 10–30, 30–50, 50–70 and 70–100 cm for soil physical and chemical analyses. In addition, the soil profiles were pedologically described according to German soil description guidelines (Ad-Hoc-Ag Boden, 2005). This pedological description also included the geomorphology of the immediate surrounding area. The core soil dataset with blurred coordinates can be downloaded from https://www.openagrar.de/receive/openagrar_mods_00054877. In addition, at least 10 years of management data (since 2001) were collected via a questionnaire sent to the farmers. Crop rotations, yields, fertilizer inputs and a whole range of other parameters were requested. A complete list of parameters evaluated in the German Agricultural Soil Inventory has been published by Jacobs et al. (2018). The management data are not publicly available.

Cumulative SOC stocks were calculated using bulk density of the fine soil, rock fragment fraction and carbon contents of each individual depth increment. These are presented in detail by Poeplau et al. (2020).

Yield and fertilizer input data were used to estimate average annual OC inputs and their composition for each sampling point. In the original questionnaire, the following input types were distinguished: aboveground litter, stubbles, roots and root exudates of main and cover crops, as well as various types of organic fertilizers including

animal excretions on pastures. The methodology to estimate OC inputs is presented in detail by Jacobs et al. (2020). In brief, two different approaches were used to estimate plant-derived OC inputs. For croplands, regionalized crop-specific allocation coefficients were used. The concept of yield-based allocation coefficients is the most often used approach to estimate OC inputs (Bolinder et al., 2007). For each crop type, reported yields are used to estimate aboveground crop residues, stubbles, roots and rhizodeposition. The latter was estimated by the latest available literature average for annual crops (31% of root biomass) (Pausch & Kuzyakov, 2018). In grasslands, yields were often not reported so these gaps had to be filled with NUTS3 statistics of the respective year that were scaled by reported management (e.g. number of cuts, fertilization and livestock units). We further assumed that an additional 30% of the harvested grass was harvest losses and regrowth after the last cut (Christensen et al., 2009), of which 50% was turned over each year (Poeplau, 2016). Root-derived OC inputs were fixed to $2.22 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ which was developed from root biomass measurements in seven long-term grassland experiments throughout Germany and the Netherlands (Poeplau et al., 2018) combined with estimates on annual root turnover (50%) (Gill & Jackson, 2000) as well as rhizodeposition (31% of annual root growth) (Pausch & Kuzyakov, 2018). Root-derived OC inputs in grasslands were fixed because root biomass has been found to be rather unresponsive to aboveground management intensity (Poeplau et al., 2018; Sochorová et al., 2016; Taghizadeh-Toosi et al., 2016), which is of particular importance for the diversely managed German grasslands. A fixed root:shoot ratio for all grasslands would thus strongly overestimate root-derived OC inputs in intensively managed and underestimate those in less intensively managed grasslands. Of course, this is an assumption, which also strongly influences total OC inputs and thus MRT_{OC} in grasslands. We therefore also used the traditional approach to calculate root-derived OC inputs to grasslands, that is, by using a fixed root:shoot ratio (Bolinder et al., 2007). For given reasons, we however did not consider this a realistic approach for grasslands and thus reported the results of this additional test only in the supplement. Since only topsoils (0–30 cm) were assessed in the present study, the belowground OC input was adjusted by a factor of 0.7 for croplands and 0.8 for grasslands, which are typical proportions of root biomass to a soil depth of 30 cm (Fan et al., 2016; Jackson et al., 1996). To establish the impact of OC input composition on MRT_{OC} , the various OC input types were aggregated into the following components: root-derived OC inputs (root biomass and rhizodeposition of main crops and cover crops), shoot-derived OC inputs (all aboveground residues including stubbles and aboveground biomass of green manure cover crops), animal-manure-derived OC inputs and other organic fertilizer-derived OC inputs (e.g. compost, sewage sludge and other organic fertilizers).

2.2 | Calculation of the mean residence time of organic carbon entering the soil

Among other methods such as the use of stable and radioactive C isotopes (Sanderman et al., 2003), MRT can be calculated by the

ratio of total pool size to either influx or efflux, assuming approximate steady state of a given pool (Carvalho et al., 2014). Here, the unique availability of site-specific SOC stocks [Mg ha^{-1}] and corresponding average OC inputs [$\text{Mg ha}^{-1} \text{ yr}^{-1}$] on a regional (national) scale were used, and MRT_{OC} [yrs] calculated for each individual sampling point as follows:

$$\text{MRT}_{\text{OC}} = \frac{\text{SOC stock}}{\text{Annual OC input}}$$

The ratio thus indicates how many years a certain OC input needs to be applied until as much OC as is currently stored in the soil has been added. If the pool of OC in the soil is assumed to be in approximate steady state, by definition OC entering the soil can remain no longer than the MRT_{OC} calculated here on average, otherwise it would accumulate in the soil and increase SOC. For a global assessment of MRT_{OC} , Chen et al. (2013) used SOC stocks and heterotrophic respiration from global databases. However, they mention both heterotrophic respiration estimates and different soil sampling methods to derive SOC stocks as major uncertainties in their study. These uncertainties were cancelled out in the present study by using SOC stock data that were determined equally for all sampling points, as well as input data derived from first-hand, site-specific management data. The analysis was restricted to topsoils (0–30 cm) since one of the critical assumptions of this MRT_{OC} approach is that SOC is autochthonous, that is, it has been entirely built up in situ by the estimated carbon inputs. This is not always correct for topsoils, but is even more problematic for subsoils, which often contain allochthonous, translocated, relictic or geogenic OC (Kalks et al., 2020; Schneider et al., 2020). As mentioned above, SOC in soils with a C:N ratio >13 , which have been classified as 'black sands' (Poeplau et al., 2020; Vos et al., 2018), were excluded since they constitute an extreme example of relictic SOC. The derived MRT_{OC} in these soils would not necessarily correspond to the stability of recent OC inputs or specific pedogenic properties that stabilize SOC.

2.3 | Statistics

Data analysis was performed using R v4.0.2 (R Core Team, 2020) in Rstudio v1.3.959 (RStudio Team, 2020). A machine-learning algorithm was applied to examine the extent to which OC input composition (proportion of roots, shoots, manure and other of total OC input) along with other variables related to land use, soil properties, geology, geomorphology and climate could explain the variability in observed values of MRT_{OC} . Variables were excluded that are directly related to one of the parameters of MRT_{OC} , that is, SOC stock, SOC and total N content, bulk density and all absolute OC input variables. We also reduced the number of continuous variables in case of high collinearity, that is, with a Spearman rank correlation coefficient exceeding 0.8. Total inorganic carbon (TIC) and elevation were removed due to their high collinearity with pH and temperature and for the grassland model also manure-derived OC input proportion

(highly correlated to root-derived OC input proportion) (Figure S1). The finally considered variables are displayed and explained in the supplement (Table S1). Models were built three times: for all sites ($n = 2100$), for croplands only ($n = 1635$) and for grasslands only ($n = 465$). For machine learning, random forest models were used (Breiman, 2001). These models consist of an ensemble of decision trees that reflect associations between the target variable (here MRT) and predictor variables (here OC inputs and other soil forming factors). Every tree is built using a variable subset of observations and predictor variables, which attributes random forest models high robustness against outliers and high predictive power even in the presence of large numbers of potential predictor variables (see Table S1) (Hastie et al., 2009). In the present study, specifically, the cforest implementation of random forest (package party) and bagging ensemble algorithms were used (Hothorn et al., 2006; Strobl et al., 2007, 2008) owing to the underlying strength of this algorithm in deriving variable importance from a mix of continuous and categorical predictors (Hapfelmeier et al., 2014). The hyperparameter *mtry* was chosen based on the square root of the number of predictor variables (Hastie et al., 2009), and the number of trees was set to 100. Reported R^2 values reflect the mean results from random five-fold cross-validations. Individual predictors were ranked according to their permutation importance. Collinearity was considered unproblematic since none of the continuous predictor pairs showed Spearman rank coefficients $|r_s| > 0.8$. Finally, the `pdp::partial()` function was used to illustrate partial dependence plots of the five most influential predictors (Molnar, 2020).

Differences in MRT_{OC} between land-use types (croplands and grasslands) and subtypes (croplands with and without ley) were assessed using analysis of variance (ANOVA). Contents of dithionite and oxalate-extractable aluminium (Al) and iron (Fe) were only measured for a minor share of all soils ($n = 307$), and were thus not included in the random forest models. Their effect on MRT_{OC} was assessed using linear regression. The significance level was $p < 0.05$. Numbers in the text are presented as mean \pm standard deviation.

3 | RESULTS

3.1 | Average organic carbon stocks, inputs and mean residence times in German agricultural soils

On average, the topsoils of the sites selected for this study stored $63.1 \pm 25.1 \text{ Mg C ha}^{-1}$, with $56.1 \pm 19.1 \text{ Mg C}$ in croplands and $87.4 \pm 28.3 \text{ Mg C}$ in grasslands (Table 1). In contrast, average carbon inputs were estimated to be equal in grassland ($3.3 \pm 1.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and cropland soils ($3.3 \pm 1.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Consequently, the resulting grassland MRT_{OC} was estimated to be 9.6 years longer on average in grassland than in cropland soils, which accounted for a relative difference of 49%. The average MRT_{OC} of all investigated topsoils was 21.5 ± 11.6 years. In accordance with the difference between croplands and grasslands, croplands with ley in the rotation had intermediate SOC stocks and MRT_{OC} (Figure 1), while OC

TABLE 1 Mean soil organic carbon (SOC) stocks and OC input [Mg ha^{-1}] as well as average mean residence time (MRT) of OC entering the soil [yrs] in 0–30 cm, with standard deviation (SD) for the different land-use types and subtypes and all soils combined. The number of observations (n) in each stratum is also given

Land use	n	SOC stocks		Annual OC input		MRT _{OC}	
		Mean	SD	Mean	SD	Mean	SD
All croplands	1635	56.1	19.1	3.2	1.1	19.4	10.7
Croplands without ley	1494	55.7	19.3	3.3	1.1	19.0	10.6
Croplands with ley	141	60.5	17.5	2.8	0.9	23.8	10.2
Grasslands	465	87.4	28.3	3.3	1.3	29.0	11.9
All soils	2100	63.1	25.1	3.3	1.1	21.5	11.6

inputs were lowest in these soils. The differences between land-use types and subtypes in SOC stocks and MRT_{OC} were highly significant ($p < 0.001$). The same was true for the two cropland categories (croplands with or without ley), as well as for both cropland categories tested against grassland. Total OC inputs were significantly lowest in croplands with ley only.

3.2 | Variables explaining mean residence time of organic carbon entering German agricultural soils

The explanatory variables used in the random forest models explained 49%, 41% and 48% of the observed variability in MRT_{OC} for all soils, croplands and grasslands, respectively (Figure 2). In all models, the most important variable was the relative proportion of root-derived OC input to total OC input, which was positively correlated with MRT_{OC} (Figure 3, Figure 4). The regression lines in Figure 4 for croplands and grasslands were almost identical,

indicating that the response of MRT_{OC} to the root input proportion was very similar in both land-use types. Figure 4 also indicates that the root-derived OC input proportion was higher in grassland soils (on average $62 \pm 17\%$) than cropland soils (on average $41 \pm 13\%$), which is a likely reason for the significant difference between these land-use types. This is further reinforced by the fact that land use was only the fifth most meaningful explanatory variable—the major difference between both systems was better accounted for by the composition of OC inputs. In accordance with the strong positive correlation of MRT_{OC} and the proportion of root-derived OC inputs, the relative proportions of shoot-derived and manure-derived OC inputs were also among the 10 most important predictors of MRT_{OC}, while their effect was negative (Figure 3). In croplands, a strong negative correlation was found between the proportions of root-derived and shoot-derived OC inputs ($R^2 = 0.37$, $p < 0.001$). Absolute root and manure-derived OC inputs also had a weak, yet significantly positive correlation with SOC stocks, while shoot-derived OC input was negatively correlated with SOC stocks (Table S2).

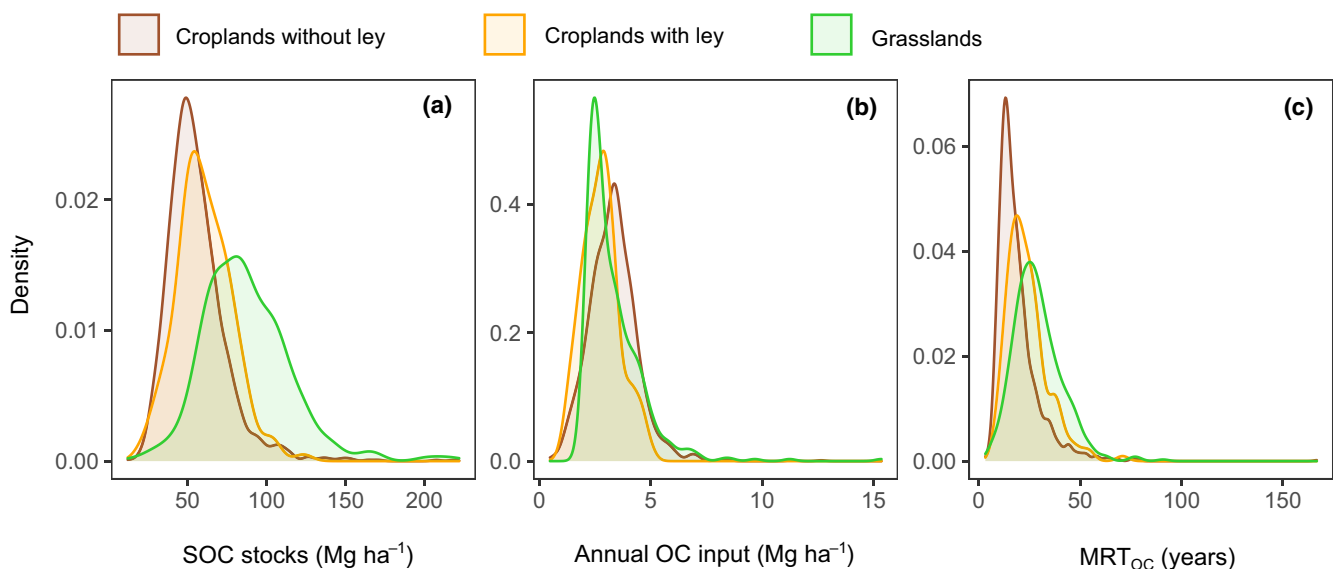


FIGURE 1 Density plots for (a) soil organic carbon (SOC) stocks, (b) total organic carbon (OC) input to the soil, and (c) mean residence time of OC that enters the soil in the topsoil (0–30 cm) for croplands with and without ley (temporary grassland) in the rotation and permanent grasslands

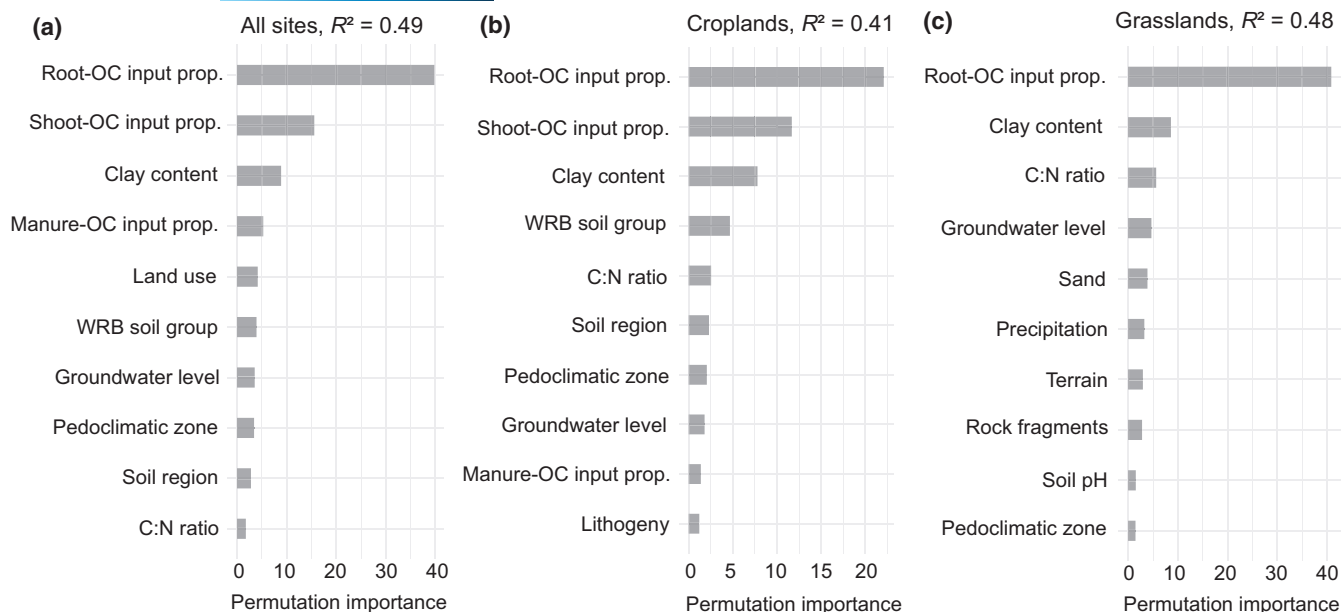


FIGURE 2 Variable importance plots of the 10 most important explanatory variables used in the random forest models explaining the mean residence time of organic carbon entering the soil. The higher the importance of an explanatory variable, the larger the mean decrease in accuracy of the random forest model when permuting (=deleting the information of) this variable. R^2 values represent the mean result from fivefold cross-validation in which the data were randomly split in five mutually exclusive subsets of approximately equal size. Each subset served once as the test set while independent models were trained on the remaining four subsets, respectively. The explanatory variables, factor levels and data sources are explained in the supplement (Table S1)

When using a fixed root:shoot ratio in grasslands, the results did not change dramatically: while the overall explanatory power of the models was strongly reduced, root-derived OC input remained the most important driver (Figure S2). Furthermore, the average proportion of root-derived OC inputs in grasslands was equal in both approaches (0.62), indicating that the comparison with croplands is valid despite a major methodological difference.

Apart from the composition of OC inputs, the most important explanatory variables for MRT_{OC} were clay content and soil group, with an exponential increase in MRT_{OC} with increasing clay content up to a clay content of approximately 350 g kg^{-1} for croplands and all sites together (Figure 3). The highest MRT_{OC} was found in Vertisols (not shown due to small number of observations), Gleysols and also Chernozems (Figure 3). Vertisols ($n = 16$) had an average clay content of $523 \pm 160 \text{ g kg}^{-1}$ and a MRT_{OC} of 36.4 ± 12.0 years, which is in line with the considerable importance of clay content. Despite the exclusion of soils with a C:N ratio >13 , the C:N ratio remained an important explanatory variable. Groundwater level was also important in all models (Figure 2), with the highest MRT_{OC} values observed when the average annual groundwater level was about 1 m or less (Figure 3). This is in line with the very high MRT_{OC} in Gleysols that are characterized by a high groundwater level. Furthermore, the extractable pedogenic oxides were all positively correlated with MRT_{OC} , with the highest R^2 observed for Al_{ox} (Table 2). In contrast, climate variables were not important in explaining the variability of MRT_{OC} at the scale of Germany, with 'pedoclimatic zones' being the only indirectly climate-related variable among the 10 most important variables in the model for all sites and model for croplands only.

4 | DISCUSSION

4.1 | Mean residence time of organic carbon entering German agricultural soils

Despite major deviations in methodology and data sources, the average MRT_{OC} in German agricultural topsoils of 21.9 ± 11.9 years was similar to values reported by other authors. Chen et al. (2013) used global datasets of SOC and soil heterotrophic respiration to estimate MRT of topsoil SOC and found a global average of 22 years. For the temperate and boreal climate zones of the northern hemisphere (45°N – 75°N), they estimated an average MRT_{OC} of 35 years. They recently confirmed these findings using 1400 soil samples from across the globe, with MRT_{OC} ranging from 0.5 to 57 years (Chen et al., 2020). Sanderman et al. (2003) used a global eddy covariance network to estimate MRT_{OC} and, similar to Chen et al. (2013), found a strong negative correlation with mean annual temperature (MAT) at the global scale. For a MAT of 10°C , which equals the average temperature for Germany, Sanderman et al. (2003) found a MRT of about 48 years for SOC in 0–100 cm depth. Interestingly, Sanderman et al. (2003) also compared the MRT_{OC} estimates derived from eddy covariance measurement with four other common methods, namely laboratory incubations, flux chamber measurements, radiocarbon uptake and changes in stable isotope (^{13}C) natural abundance after C3 to C4 vegetation change. Only the latter method, that is, estimating MRT_{OC} from changes in $\delta^{13}\text{C}$, yielded significantly higher values (>100 years), which is in line with other studies (Balesdent et al., 1990; Rasse et al., 2006; Schneider et al., 2020). It would appear

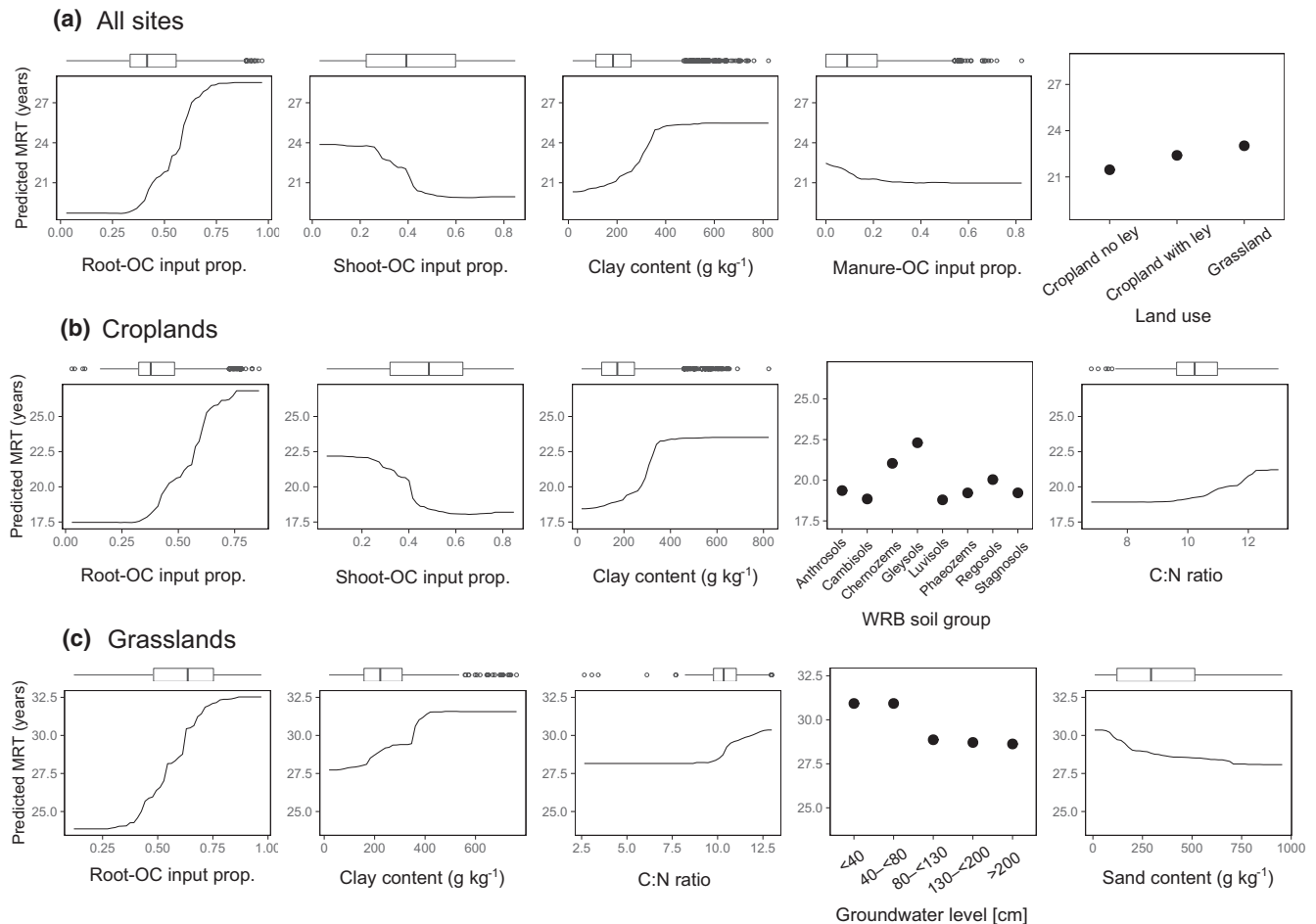


FIGURE 3 Partial dependence plots of the five most important explanatory variables in each of the random forest models. This illustrates the dependence of MRT on influential explanatory variables after averaging out the effects of other explanatory variables included in the model. Only the most abundant soil groups (eight out of 11) are displayed

that turnover times calculated by the stable isotope method refer to the pool that is ultimately measured as SOC, that is, OC measured in the bulk mineral soil <2 mm. In contrast, those calculated from SOC stocks and total inputs or total heterotrophic respiration also include the most labile constituents of OC that decompose quickly and only make a small contribution to the SOC pool as measured in intervals of at least 1 year and in the <2 mm fraction of the soil. The retention coefficient, that is, the fraction of mid- and long-term stabilized OC input of plant residues and common organic fertilizers, ranges between <0.1 and ~0.3 (Berti et al., 2016; Kätterer et al., 2011; Poeplau, Kätterer, et al., 2015; Rasse et al., 2006), with common average retention coefficients of 0.1–0.2 (Barber, 1979; Rasse et al., 2006) in temperate agricultural soils. This implies that about 80–90% of the OC entering the soil is mineralized within 1 year on average; thus, for example, in the C3–C4 vegetation change, only a small part of the OC input contributes to the C4 signal of the bulk SOC. Including or excluding this very fast cycling fraction from the estimate has a strong effect on MRT, as recently also elaborated by Luo et al., submitted. When only accounting for the proportion of retained OC (10–20% of the actual total input), the estimated MRT of SOC in croplands would have been 108–216 years in this study,

which is well in line with studies using the ^{13}C approach with C3–C4 vegetation changes (Sanderman et al., 2003; Schneider et al., 2020). The MRT_{OC} values presented here should thus be interpreted as the MRT of OC entering the soil, not OC that has been retained in the soil and is measured as SOC.

4.2 | The importance of site properties

Drivers of SOC stocks in German agricultural soils have previously been presented and discussed (Poeplau et al., 2020; Vos et al., 2019). The SOC stocks are strongly influenced by clay content, groundwater level and soil group (Poeplau et al., 2020), which is in line with the drivers for MRT_{OC} identified in the present study (Figure 2). Clay, groundwater and soil group are reflections of pedological and hydrological site conditions as well as land-use history. In addition, the C:N ratio was found to be the most important predictor of SOC stocks in Germany (Poeplau et al., 2020). Soils with a C:N ratio >13 are a phenomenon of northwest Germany and also neighbouring countries, and are typically characterized by a sandy texture and a high proportion of particulate organic matter, undecomposed plant

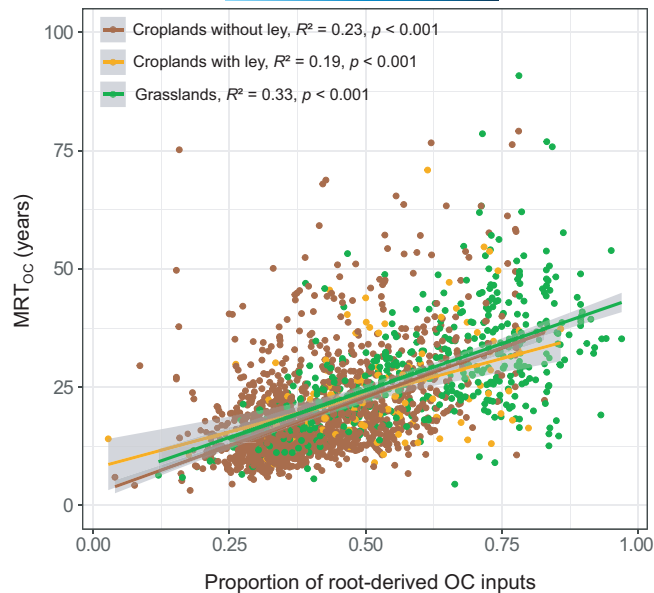


FIGURE 4 Mean residence time of organic carbon entering the soil (MRT_{OC}) in topsoils (0–30 cm) of croplands (with and without ley) and grasslands as a function of the proportion of root-derived C input, with regression lines and their 95% confidence intervals

TABLE 2 Summary table of the linear regression models with oxalate and dithionite extractable aluminium (Al_{ox} , Al_{di}) and iron (Fe_{ox} , Fe_{di}) [$g\ kg^{-1}$] explaining the mean residence time of organic carbon entering the soil (MRT_{OC}) [yrs]

Parameter	Intercept	Slope	R ²	p
Al_{ox}	17.94	3.79	0.075	<0.001
Fe_{ox}	21.41	0.38	0.040	0.004
Al_{di}	17.22	2.94	0.051	0.002
Fe_{di}	19.31	0.03	0.028	0.016

material, of high stability (Sleutel et al., 2008; Springob & Kirchmann, 2002). These soils, often podzols, are referred to as ‘black sands’ and often have a peat or heathland history. The MRT of all sites with a C:N ratio >13 (463 out of 2657 sites) was 34 ± 20 years, which was 55% higher than that of soils with a C:N ratio <13. Due to their high share of relictic, refractory SOC, those soils were excluded from the overall analysis. However, when applying the approach proposed by Springob and Kirchmann (2010) to determine and factor out relictic, refractory SOC (C:N ratio of ~35), the average MRT_{OC} of non-relictic SOC in these soils decreased to 16.0 ± 14.8 years. This relatively low MRT_{OC} fits well with the fact that sandy soils were found to have lower SOC stocks and MRT_{OC} than finer textured soils. Furthermore, the retention coefficient of straw in Swedish agricultural soils increases with increasing clay content (Poeplau et al., 2015). The positive effect of clay content on SOC stocks and MRT_{OC} can be explained by the stabilizing effects of microaggregates and mineral surfaces (Keiluweit et al., 2017; Sollins et al., 1996). In soils with a high groundwater level, SOC stabilization is mainly triggered by oxygen limitation (Tiemeyer et al., 2016). These stabilizing effects were

reflected in the fact that Vertisols (high clay content) and Gleysols (groundwater influenced) were among the soil groups with the highest topsoil MRT_{OC} (Figure 3). Extractable Al and Fe contents were also positively correlated with MRT_{OC} , although data on pedogenic oxides were not included in the random forest models due to the relatively small number of observations. Al and Fe oxides and hydroxides, even when their absolute content is small, are acknowledged to form organo-metal complexes that protect organic matter from enzymatic breakdown in a wide range of soils, even in circumneutral pH and with relatively low contents of Al and Fe (Doetterl et al., 2015; Kleber et al., 2015; Porras et al., 2017).

Climate variables did not play an important role in explaining the variability in MRT_{OC} in German agricultural soils. This is in contrast to global studies on MRT (Chen et al., 2013, 2020; Sanderman et al., 2003), in which temperature and precipitation were the dominant drivers. We explain this by the fact that within Germany, climate variability is relatively small as compared to the global scale. Nevertheless, the estimated average values of MRT_{OC} are certainly greatly controlled by the prevailing temperate climate conditions. Chen et al. (2020) highlight soil total nitrogen and bulk density as major explanatory variables for MRT_{OC} . The authors explain the positive effect of total nitrogen on MRT_{OC} in their study with the nitrogen status of the soil and fertilization effects on microbial activity and enzyme kinetics. However, it is more likely that the total nitrogen stock of a soil reflects the total organic matter level, and thus also total SOC stock (Cleveland & Liptzin, 2007). The use of soil total nitrogen as an explanatory variable for MRT_{OC} , which has SOC stock as the numerator, should thus be avoided. The same applies to variable bulk density, which is also highly correlated with SOC stocks and thus also MRT_{OC} (Schneider & Don, 2019). Therefore, these two variables of total nitrogen and bulk density, which are not independent of the target variable, were not considered.

4.3 | The importance of land use and carbon input composition

For SOC stocks, previous works on German agricultural soils have not detected any influence of management or OC input quantity or quality on the regional variability of SOC stocks (Poeplau et al., 2020; Vos et al., 2019). Only land-use type, that is, cropland vs. grassland, has been found to be important in topsoil SOC stocks, with grasslands having on average about 44% higher topsoil SOC stocks than croplands. The present study provided evidence that the type of OC input is of utmost importance to MRT_{OC} and thus also to SOC stabilization at a regional scale. Among all the variables considered, the relative proportion of root-derived OC had the highest explanatory power in all models, that is, in cropland soils, grassland soils and all soils combined (Figure 2). The particularly high stabilization of belowground OC inputs has been highlighted by many studies, with retention coefficients often being at least twice as high as those of shoots (Berti et al., 2016; Kätterer et al., 2011; Rasse et al., 2005). There may be various reasons for this. In a literature review, Rasse

et al. (2005) identify several mechanisms that might potentially be responsible for the efficient stabilization of root-derived carbon in soil: (a) chemical recalcitrance: roots have been shown to have higher lignin, tannin, cutin and suberin contents than shoots, all of which are among the most recalcitrant plant molecular structures (Bull et al., 2000; Dignac et al., 2005), and root-derived OC might thus be transformed at a slower rate than shoot-derived OC; (b) interactions with the soil mineral matrix: roots grow and release charged compounds as well as aggregate binding agents in direct proximity to the mineral matrix, which can foster OC stabilization in several ways, such as sorption and stable aggregate formation (Jones, 1998; Oades, 1978), and the very fine root hairs might even grow into aggregates, where they become inaccessible for decomposers (Rasse et al., 2005); (c) the microbial pathway: root exudates have long been thought to be labile substrates that do not contribute to the stable SOC pool or might even negatively affect SOC via rhizosphere priming (Kuzaykov, 2002). However, recent insights suggest that the formation of microbial biomass is very efficient in the rhizosphere, due to the high availability of labile substrates, and that such efficient microbial growth can significantly contribute to the formation of stable SOC (Kallenbach et al., 2016; Sokol & Bradford, 2019). Following the logic of the latter mechanism, living roots in particular are highly relevant for stable SOC formation, which has recently been proven by Sokol et al. (2019). In this sense, permanent plant cover, such as in grasslands or perennial crops, might be especially beneficial for the microbial pathway and thus stable SOC formation. Apart from this direct pathway of the 'microbial carbon pump' (Liang et al., 2017), some organisms, such as arbuscular mycorrhizal fungi, that benefit from permanent root exudation can also indirectly increase MRT_{OC} via aggregate stabilization (Rillig et al., 2002). All the above-mentioned mechanisms are a likely explanation for the observed importance of the proportion of root-derived OC for MRT_{OC} to various extents. Consequently, the clear difference between cropland and grassland in the proportion and amount of root-derived C input could be the major driver of differences in MRT_{OC} and SOC stocks between these land-use types. The impact of the relative root proportion on MRT_{OC} , as indicated by the regression lines in Figure 4, is basically the same for croplands and grasslands. The two regression lines have an almost identical slope with almost no offset between them, emphasizing that no other land-use-specific parameter (e.g. frequency/extent of soil disturbance) should be of similar importance to MRT_{OC} as the proportion of root-derived C. This is a crucial finding, for example for informing SOC models, which to date only have a limited ability to accurately predict SOC dynamics after land-use change (Gottschalk et al., 2010; Nyawira et al., 2016).

4.4 | Implications for agricultural management

The fact that the proportion of roots was the most important driver of MRT_{OC} indicates that the average time that each assimilated C atom will be stored in the soil can largely be managed. The composition of OC input into the soil, which is dependent on farmers'

decisions, strongly affects the efficiency of climate mitigation by SOC sequestration. Straw and aboveground residue incorporation can also increase SOC stocks (Lemke et al., 2010) and is thus often a recommended management practice for climate-smart agriculture (Minasny et al., 2017). However, when considering the low efficiency of aboveground residues (Berti et al., 2016), the climate mitigation potential of such a measure is doubtful. The results of the present study emphasize that increasing the amount of root biomass and root-derived OC inputs is an effective and straightforward management option to increase SOC stocks and MRT_{OC} . Large-scale land-use change from cropland to grassland is not a realistic option and may result in indirect land-use changes as a leakage effect. However, an increase in root-derived OC inputs can also be achieved in croplands by (a) increasing the proportion of leys in the rotation (Loaiza Puerta et al., 2018), (b) optimizing the proportion of species with large root biomass (including cover crops), (c) breeding with a focus on greater root biomass (Friedli et al., 2019; Kell, 2011) and (d) adjusting crop rotations to maximize root biomass production. Trade-offs with yields and potentially other functions of agricultural production systems need to be considered, but are not discussed further here. Maximizing the production of root biomass in arable rotations requires in-depth, crop-specific knowledge on expected average root-derived OC inputs. However, Figure 5 shows the annual crops that input the highest root OC to the soil according to the available data used in this study. As expected, the root-derived OC input of root and tuber crops, such as potato and beet but also asparagus, radish and onion, was negligible (Figure 5). Small grain cereals and maize had similar, intermediately high root-derived OC inputs of around $1.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, which was considerably lower than the estimated annual root C input of grasslands ($2.22 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, Figure 5a). However, rapeseed was the annual crop with the highest root-derived OC inputs, with on average only slightly lower inputs than perennial grasses. The specific root length of rapeseed has also been found to be about twice that of a typical winter wheat root system (Barraclough, 1989). The proportion of root-derived OC inputs, however, tended to be highest for maize because most maize in Germany is grown for silage, with most of the aboveground biomass being harvested, which reduces the aboveground OC input but increases the relative proportion of root OC input (Figure 5b). Thus, farmers largely determine OC input, MRT_{OC} and finally SOC stocks through their selection of crop types. In addition to crop type, crop breeds can also be optimized towards more roots, which is a largely ignored field of research and development. Higher root proportions may ultimately not only serve to maintain and build up SOC in agricultural soils but also to stabilize crop yields under increasingly difficult conditions with global warming (Friedli et al., 2019).

4.5 | Limitations related to dataset and approach

It should be noted that the presented, crop-specific estimates of root-derived OC inputs (Figure 5) are a combination of literature allocation coefficients and yield/management data reported by farmers.

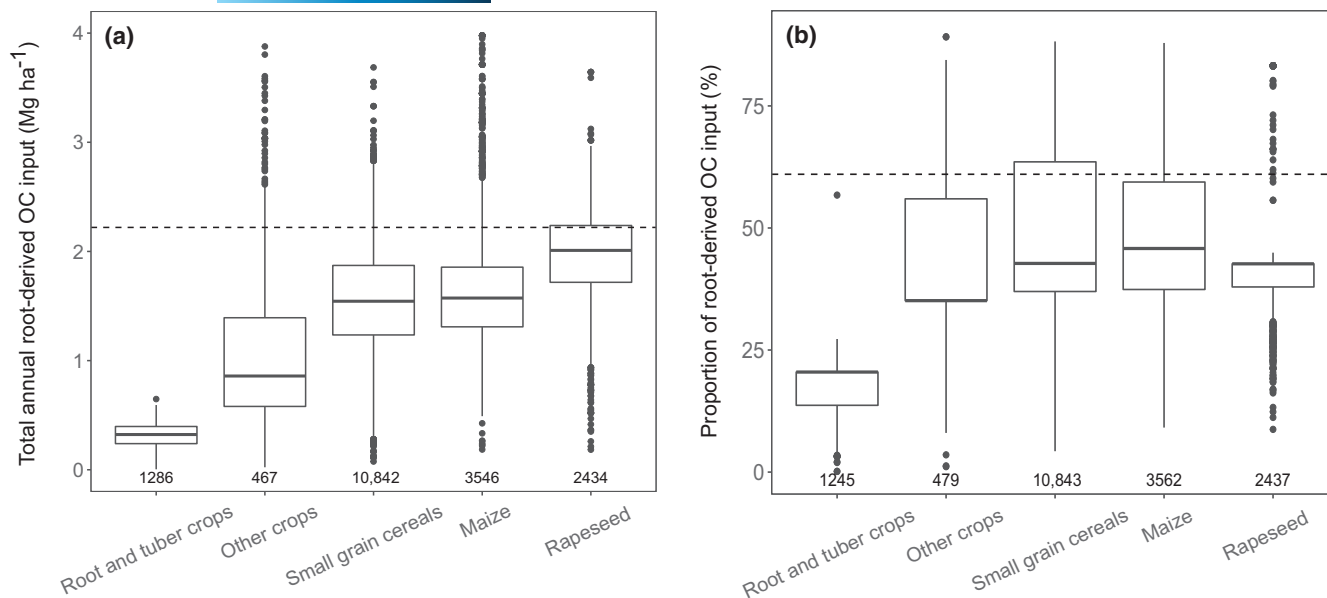


FIGURE 5 (a) Estimated root-derived organic carbon (OC) inputs and (b) relative proportion of root-derived OC inputs for annual crop-type classes derived from management data reported by farmers participating in the German Agricultural Soil Inventory and allocation coefficients, as described by Jacobs et al. (2020). Dashed lines depict average values for grasslands and the number of observations (site years) is given below the boxes. The small category 'Other crops' comprises mostly grain legumes (47%), fodder legumes (25%) and sunflower (10%) but also vegetables such as broccoli, cabbage, cauliflower, celery, cucumber, kale, pumpkin, salad and spinach, as well as clover, flax, hemp, herbs, strawberry and tobacco (18%)

They should be interpreted accordingly, that is, bearing in mind the following limitations: (a) It is a German dataset representing best estimates for German arable crops, which means that it also reflects the productivity pattern of German agricultural soils, and the aggregated crop types presented were not grown under equal pedoclimatic conditions. (b) Although it might be the best available dataset for root-derived OC inputs in Germany, the dataset is highly diverse with regard to data sources: yield data were reported by several thousand individual farmers, thus a heterogeneous data quality can be expected. Furthermore, depending on the crop, allocation coefficients are based on a few observations only and are thus uncertain. More work on crop-specific root allocation is needed, since even coefficients derived from meta-analyses are partly based on only a few observations (Bolinder et al., 2007) that might rapidly become out-dated due to breeding advances. (c) The assumption that plants have fixed allocation coefficients, that is, stable root:shoot ratios, has recently been questioned (Hirte et al., 2018; Taghizadeh-Toosi et al., 2016). Potential differences in plant C allocation due to cultivar (Kell, 2012) or soil properties (phenotypic plasticity) (Schneider & Don, 2019) are not represented here. However, (a) the allocation coefficient approach is the most comprehensive, since data for basically all crops are available and (b) the authors of the abovementioned studies found variable root:shoot ratios primarily in response to varying fertilization regimes in agronomic field trials. For annual crops in central European intensive agricultural systems, and thus also in the present dataset, it can be assumed that near optimum conditions with respect to nutrient availability are usually given. Therefore, estimating root-derived OC inputs in croplands by using

fixed, crop-specific root:shoot ratios derived from the literature was considered most reliable. For permanent grasslands, the intensity gradient with respect to fertilization, grazing and cutting frequency is much larger across Germany; therefore, a fixed root-derived OC input was considered to be more robust and more realistic than a yield-dependent estimate, which has been suggested in earlier studies (Poeplau, 2016; Sochorová et al., 2016; Taghizadeh-Toosi et al., 2020). Nevertheless, the most important driver of MRT_{OC} was an estimated parameter with considerable uncertainty. However, the fact that MRT_{OC} in croplands and grasslands responded in a similar way and without any offset in the proportion of root-derived OC inputs (Figure 4) might indicate that a combination of both methods was valid in this case. Furthermore, the additional model runs with fixed root:shoot ratios in grasslands revealed that the importance of root-derived OC inputs and also the average difference between croplands and grasslands was robust and not driven by the chosen method combination.

The approach to estimate MRT_{OC} by dividing present stocks by present inputs is based on the assumption that current measured topsoil SOC stocks were entirely built up by OC inputs that are of similar quality to those found currently. This was not exactly the case for many sites. As discussed, the black sands of northern Germany constitute an extreme example of relictic SOC with a distinct quality, and were therefore excluded from this analysis. Other soils, such as Chernozems, can also have high proportions of centennially stable SOC that are different in OC quality and might have entered the soil under contrasting environmental conditions (Franko & Merbach, 2017), potentially also as charred organic matter (Ponomarenko &

Anderson, 2001). Furthermore, other OC inputs such as allochthonous OC, for example in colluvial soils, may be of a different quality to the current OC input (Schneider et al., 2020). The MRT_{OC} estimated in this study is thus unlikely to reflect exactly the average time that the entering C will remain in the soil. Nevertheless, even in those cases, the applied ratio adds valuable information about the overall stability of SOC: a high MRT_{OC} at sites with high SOC stocks indicates that the latter are not driven by extraordinary high OC inputs, but by a high stability of either the material that is currently (in the present land-use regime) entering the soil or the material that has been stabilized in the soil for a long time.

4.6 | Concluding remarks

This study is the first to quantify the mean residence time of organic carbon entering agricultural soil and its drivers on a regional scale in the temperate climate zone. The combination of two closely associated datasets, that is, topsoil SOC stocks of German agricultural soils and corresponding first-hand OC input data, was used to quantify this indicator of OC retention efficiency and SOC stability. The study highlighted that the MRT of OC entering the soil is driven by both management and abiotic soil properties. Out of all the considered variables, the proportion of root-derived OC input was found to be the most important driver, which also explained the difference in MRT and total SOC stocks between cropland and grassland soils. It can be concluded that the time that assimilated OC remains in the soil to effectively reduce atmospheric CO_2 can be managed and optimized in a straightforward way by maximizing root-derived OC input.

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DATA AVAILABILITY STATEMENT:

The data on SOC stocks and soil variables of the German Agricultural Soil Inventory are openly available in openagrar.de, <https://doi.org/10.3220/DATA20200203151139>. Carbon input data cannot be shared.

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REFERENCES

- Amelung, W., Bossio, D., de Vries, W., Kögel-Knabner, I., Lehmann, J., Amundson, R., Bol, R., Collins, C., Lal, R., Leifeld, J., Minasny, B., Pan, G., Paustian, K., Rumpel, C., Sanderman, J., van Groenigen, J. W., Mooney, S., van Wesemael, B., Wander, M., & Chabbi, A. (2020). Towards a global-scale soil climate mitigation strategy. *Nature Communications*, 11, 5427. <https://doi.org/10.1038/s41467-020-18887-7>.
- Balesdent, J., Mariotti, A., & Biosgontier, D. (1990). Effect of tillage on soil organic carbon mineralization estimated from ^{13}C abundance in maize fields. *Journal of Soil Science*, 41, 587–596. <https://doi.org/10.1111/j.1365-2389.1990.tb00228.x>.
- Barber, S. A. (1979). Corn residue management and soil organic matter1. *Agronomy Journal*, 71, 625–627.
- Barraclough, P. B. (1989). Root growth, macro-nutrient uptake dynamics and soil fertility requirements of a high-yielding winter oilseed rape crop. *Plant and Soil*, 119, 59–70. <https://doi.org/10.1007/BF02370269>.
- Barré, P., Planté, A. F., Cécillon, L., Lutfalla, S., Baudin, F., Bernard, S., Christensen, B. T., Eglin, T., Fernandez, J. M., Houot, S., Kätterer, T., Le Guillou, C., Macdonald, A., van Oort, F., & Chenu, C. (2016). The energetic and chemical signatures of persistent soil organic matter. *Biogeochemistry*, 130, 1–12. <https://doi.org/10.1007/s10533-016-0246-0>.
- Berti, A., Morari, F., Dal Ferro, N., Simonetti, G., & Polese, R. (2016). Organic input quality is more important than its quantity: C turnover coefficients in different cropping systems. *European Journal of Agronomy*, 77, 138–145. <https://doi.org/10.1016/j.eja.2016.03.005>.
- Bloom, A. A., Exbrayat, J.-F., Van Der Velde, I. R., Feng, L., & Williams, M. (2016). The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times. *Proceedings of the National Academy of Sciences*, 113, 1285–1290. <https://doi.org/10.1073/pnas.1515160113>.
- Boden, A.-H.-A. (2005). *Bodenkundliche Kartieranleitung*. E.Schweizerbart'sche Verlagsbuchhandlung.
- Bolinder, M., Janzen, H., Gregorich, E., Angers, D., & Vandenbygaart, A. (2007). An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Agriculture, Ecosystems & Environment*, 118, 29–42. <https://doi.org/10.1016/j.agee.2006.05.013>.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.
- Bull, I. D., Nott, C. J., Van Bergen, P. F., Poulton, P. R., & Evershed, R. P. (2000). Organic geochemical studies of soils from the Rothamsted classical experiments – VI. The occurrence and source of organic acids in an experimental grassland soil. *Soil Biology and Biochemistry*, 32, 1367–1376. [https://doi.org/10.1016/S0038-0717\(00\)00054-7](https://doi.org/10.1016/S0038-0717(00)00054-7).
- Carvalho, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M., Thurner, M., Weber, U., Ahrens, B., Beer, C., Cescatti, A., Randerson, J. T., & Reichstein, M. (2014). Global covariation of carbon turnover times with climate in terrestrial ecosystems. *Nature*, 514, 213–217. <https://doi.org/10.1038/nature13731>.
- Chen, S., Huang, Y., Zou, J., & Shi, Y. (2013). Mean residence time of global topsoil organic carbon depends on temperature, precipitation and soil nitrogen. *Global and Planetary Change*, 100, 99–108. <https://doi.org/10.1016/j.gloplacha.2012.10.006>.
- Chen, S., Zou, J., Hu, Z., & Lu, Y. (2020). Temporal and spatial variations in the mean residence time of soil organic carbon and their relationship with climatic, soil and vegetation drivers. *Global and Planetary Change*, 195, 103359. <https://doi.org/10.1016/j.gloplacha.2020.103359>.
- Christensen, B. T., Rasmussen, J., Eriksen, J., & Hansen, E. M. (2009). Soil carbon storage and yields of spring barley following grass leys of different age. *European Journal of Agronomy*, 31, 29–35. <https://doi.org/10.1016/j.eja.2009.02.004>.
- Cleveland, C. C., & Liptzin, D. (2007). C: N: P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry*, 85, 235–252. <https://doi.org/10.1007/s10533-007-9132-0>.
- Dignac, M.-F., Bahri, H., Rumpel, C., Rasse, D. P., Bardoux, G., Balesdent, J., Girardin, C., Chenu, C., & Mariotti, A. (2005). Carbon-13 natural abundance as a tool to study the dynamics of lignin monomers in soil:

- an appraisal at the Closeaux experimental field (France). *Geoderma*, 128, 3–17. <https://doi.org/10.1016/j.geoderma.2004.12.022>.
- Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., & Boeckx, P. (2015). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, 8, 780–783. <https://doi.org/10.1038/ngeo2516>.
- Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012). Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*, 18, 1781–1796. <https://doi.org/10.1111/j.1365-2486.2012.02665.x>.
- Fan, J., McConkey, B., Wang, H., & Janzen, H. (2016). Root distribution by depth for temperate agricultural crops. *Field Crops Research*, 189, 68–74. <https://doi.org/10.1016/j.fcr.2016.02.013>.
- Franko, U., & Merbach, I. (2017). Modelling soil organic matter dynamics on a bare fallow Chernozem soil in Central Germany. *Geoderma*, 303, 93–98. <https://doi.org/10.1016/j.geoderma.2017.05.013>.
- Friedli, C. N., Abiven, S., Fossati, D., & Hund, A. (2019). Modern wheat semi-dwarfs root deep on demand: response of rooting depth to drought in a set of Swiss era wheats covering 100 years of breeding. *Euphytica*, 215, 85. <https://doi.org/10.1007/s10681-019-2404-7>.
- Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *The New Phytologist*, 147, 13–31. <https://doi.org/10.1046/j.1469-8137.2000.00681.x>.
- Gleixner, G., Bol, R., & Balesdent, J. (1999). Molecular insight into soil carbon turnover. *Rapid Communications in Mass Spectrometry*, 13, 1278–1283. [https://doi.org/10.1002/\(SICI\)1097-0231\(19990715\)13:13<1278:AID-RCM649>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1097-0231(19990715)13:13<1278:AID-RCM649>3.0.CO;2-N).
- Gottschalk, P., Bellarby, J., Chenu, C., Foereid, B., Smith, P., Wattenbach, M., Zingore, S., & Smith, J. O. (2010). Simulation of soil organic carbon response at forest cultivation sequences using ¹³C measurements. *Organic Geochemistry*, 41, 41–54. <https://doi.org/10.1016/j.orggeochem.2009.04.017>.
- Haberl, H., Erb, K. H., Krausmann, F., Gaube, V., Bondeau, A., Plutzer, C., Gingrich, S., Lucht, W., & Fischer-Kowalski, M. (2007). Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. *Proceedings of the National Academy of Sciences*, 104, 12942–12947. <https://doi.org/10.1073/pnas.0704243104>.
- Häpfelmeier, A., Hothorn, T., Ulm, K., & Strobl, C. (2014). A new variable importance measure for random forests with missing data. *Statistics and Computing*, 24, 21–34. <https://doi.org/10.1007/s11222-012-9349-1>.
- Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning: Data mining, inference, and prediction*. Springer Science & Business Media.
- Hirte, J., Leifeld, J., Abiven, S., Oberholzer, H.-R., & Mayer, J. (2018). 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. *Agriculture, Ecosystems & Environment*, 265, 556–566. <https://doi.org/10.1016/j.agee.2018.07.010>.
- Hothorn, T., Hornik, K., & Zeileis, A. (2006). Unbiased recursive partitioning: A conditional inference framework. *Journal of Computational Graphical Statistics*, 15, 651–674. <https://doi.org/10.1198/106186006X133933>.
- Hu, T., Taghizadeh-Toosi, A., Olesen, J. E., Jensen, M. L., Sørensen, P., & Christensen, B. T. (2019). Converting temperate long-term arable land into semi-natural grassland: decadal-scale changes in topsoil C, N, ¹³C and ¹⁵N contents. *European Journal of Soil Science*, 70, 350–360.
- Jackson, R., Canadell, J., Ehleringer, J., Mooney, H., Sala, O., & Schulze, E. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411. <https://doi.org/10.1007/BF00333714>.
- Jacobs, A., Flessa, H., Don, A. et al (2018). Landwirtschaftlich genutzte Böden in Deutschland: Ergebnisse der Bodenzustandserhebung. Thünen Report.
- Jacobs, A., Poeplau, C., Weiser, C., Fahrion-Nitschke, A., & Don, A. (2020). Exports and inputs of organic carbon on agricultural soils in Germany. *Nutrient Cycling in Agroecosystems*, 118(3), 249–271. <https://doi.org/10.1007/s10705-020-10087-5>.
- Jones, D. L. (1998). Organic acids in the rhizosphere—a critical review. *Plant and Soil*, 205, 25–44.
- Kalks, F., Noren, G., Mueller, C., Helfrich, M., Rethemeyer, J., & Don, A. (2020). Geogenic organic carbon in terrestrial sediments and its contribution to total soil carbon. *SOIL Discuss.*, 2020, 1–26.
- Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications*, 7, 13630. <https://doi.org/10.1038/ncomms13630>.
- Kätterer, T., Bolinder, M. A., Andrén, O., Kirchmann, H., & Menichetti, L. (2011). Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agriculture, Ecosystems & Environment*, 141, 184–192. <https://doi.org/10.1016/j.agee.2011.02.029>.
- Keiluweit, M., Wanzek, T., Kleber, M., Nico, P., & Fendorf, S. (2017). Anaerobic microsites have an unaccounted role in soil carbon stabilization. *Nature Communications*, 8, 1771. <https://doi.org/10.1038/s41467-017-01406-6>.
- Kell, D. B. (2011). Breeding crop plants with deep roots: Their role in sustainable carbon, nutrient and water sequestration. *Annals of Botany*, 108, 407–418. <https://doi.org/10.1093/aob/mcr175>.
- Kell, D. B. (2012). Large-scale sequestration of atmospheric carbon via plant roots in natural and agricultural ecosystems: why and how. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 1589–1597. <https://doi.org/10.1098/rstb.2011.0244>.
- Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., & Nico, P. S. (2015). Chapter one - mineral-organic associations: Formation, properties, and relevance in soil environments. In D. L. Sparks (Ed.), *Advances in agronomy*. Academic Press.
- Kuzyakov, Y. (2002). Factors affecting rhizosphere priming effects. *Journal of Plant Nutrition and Soil Science*, 165, 382–396.
- Lemke, R., Vandenbygaart, A., Campbell, C., Lafond, G., & Grant, B. (2010). Crop residue removal and fertilizer N: Effects on soil organic carbon in a long-term crop rotation experiment on a Udic Boroll. *Agriculture, Ecosystems & Environment*, 135, 42–51. <https://doi.org/10.1016/j.agee.2009.08.010>.
- Liang, C., Schimel, J. P., & Jastrow, J. D. (2017). The importance of anabolism in microbial control over soil carbon storage. *Nature Microbiology*, 2, 17105. <https://doi.org/10.1038/nmicrobiol.2017.105>.
- Loaiza Puerta, V., Pujol Pereira, E. I., Wittwer, R., Van Der Heijden, M., & Six, J. (2018). Improvement of soil structure through organic crop management, conservation tillage and grass-clover ley. *Soil and Tillage Research*, 180, 1–9. <https://doi.org/10.1016/j.still.2018.02.007>.
- Luo, Z., Wang, G., & Wang, E. (2019). Global subsoil organic carbon turnover times dominantly controlled by soil properties rather than climate. *Nature Communications*, 10, 3688. <https://doi.org/10.1038/s41467-019-11597-9>.
- Luo, Z., Wang, G., Xiao, L., Mao, X., Guo, X., Cowie, A., Zhang, S., Wang, M., Chen, S., Ganlin, Z., & Shi, Z. (submitted) Most root-derived carbon inputs do not contribute to the global bulk soil carbon pool. *Research Square*. <https://doi.org/10.21203/rs.3.rs-65178/v1>
- Maillard, É., & Angers, D. A. (2014). Animal manure application and soil organic carbon stocks: A meta-analysis. *Global Change Biology*, 20, 666–679. <https://doi.org/10.1111/gcb.12438>.
- Minasny, B., Malone, B. P., McBratney, A. B., Angers, D. A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.-S., Cheng, K., Das, B. S., Field, D. J., Gimona, A., Hedley, C. B., Hong, S. Y., Mandal, B., Marchant, B. P., Martin, M., McConkey, B. G., Mulder, V. L., ... Winowiecki, L. (2017). Soil carbon 4 per mille. *Geoderma*, 292, 59–86. <https://doi.org/10.1016/j.geoderma.2017.01.002>.

- Molnar, C. (2020) *Interpretable machine learning- A Guide for Making Black Box Models Explainable*. <https://christophm.github.io/interpretable-ml-book/>.
- Nyawira, S. S., Nabel, J. E. M. S., Don, A., Brovkin, V., & Pongratz, J. (2016). Soil carbon response to land-use change: evaluation of a global vegetation model using observational meta-analyses. *Biogeosciences*, 13, 5661–5675. <https://doi.org/10.5194/bg-13-5661-2016>.
- Oades, J. M. (1978). Mucilages at the root surface. *European Journal of Soil Science*, 29, 1–16. <https://doi.org/10.1111/j.1365-2389.1978.tb02025.x>.
- Pausch, J., & Kuzyakov, Y. (2018). Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology*, 24, 1–12. <https://doi.org/10.1111/gcb.13850>.
- Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-smart soils. *Nature*, 532, 49–57. <https://doi.org/10.1038/nature17174>.
- Poeplau, C. (2016). Estimating root: Shoot ratio and soil carbon inputs in temperate grasslands with the RothC model. *Plant and Soil*, 407, 293–305. <https://doi.org/10.1007/s11104-016-3017-8>.
- Poeplau, C., Bolinder, M. A., Eriksson, J., Lundblad, M., & Kätterer, T. (2015). Positive trends in organic carbon storage in Swedish agricultural soils due to unexpected socio-economic drivers. *Biogeosciences Discuss.*, 12, 3991–4019.
- Poeplau, C., Don, A., Vesterdal, L., Leifeld, J., Van Wesemael, B., Schumacher, J., & Gensior, A. (2011). Temporal dynamics of soil organic carbon after land-use change in the temperate zone - carbon response functions as a model approach. *Global Change Biology*, 17, 2415–2427. <https://doi.org/10.1111/j.1365-2486.2011.02408.x>.
- Poeplau, C., Jacobs, A., Don, A. et al (2020). Stocks of organic carbon in German agricultural soils—Key results of the first comprehensive inventory. *Journal of Plant Nutrition and Soil Science*, 183, 665–681.
- Poeplau, C., Kätterer, T., Bolinder, M. A., Börjesson, G., Berti, A., & Lugato, E. (2015). Low stabilization of aboveground crop residue carbon in sandy soils of Swedish long-term experiments. *Geoderma*, 237–238, 246–255. <https://doi.org/10.1016/j.geoderma.2014.09.010>.
- Poeplau, C., Zopf, D., Greiner, B., Geerts, R., Korvaar, H., Thumm, U., Don, A., Heidkamp, A., & Flessa, H. (2018). Why does mineral fertilization increase soil carbon stocks in temperate grasslands? *Agriculture, Ecosystems & Environment*, 265, 144–155. <https://doi.org/10.1016/j.agee.2018.06.003>.
- Ponomarenko, E. V., & Anderson, D. W. (2001). Importance of Charred Organic Matter in Black Chernozem Soils of Saskatchewan. *Canadian Journal of Soil Science*, 81, 285–297.
- Porras, R. C., Hicks Pries, C. E., Mcfarlane, K. J., Hanson, P. J., & Torn, M. S. (2017). Association with pedogenic iron and aluminum: Effects on soil organic carbon storage and stability in four temperate forest soils. *Biogeochemistry*, 133, 333–345. <https://doi.org/10.1007/s10533-017-0337-6>.
- Post, W. M., & Kwon, K. C. (2000). Soil carbon sequestration and land-use change: Processes and potential. *Global Change Biology*, 6, 317–327. <https://doi.org/10.1046/j.1365-2486.2000.00308.x>.
- R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rasse, D. P., Mulder, J., Moni, C., & Chenu, C. (2006). Carbon turnover kinetics with depth in a french loamy soil. *Soil Science Society of America Journal*, 70, 2097–2105. <https://doi.org/10.2136/sssaj2006.0056>.
- Rasse, D. P., Rumpel, C., & Dignac, M. F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269, 341–356. <https://doi.org/10.1007/s11104-004-0907-y>.
- Rillig, M. C., Wright, S. F., & Eviner, V. T. (2002). The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: Comparing effects of five plant species. *Plant and Soil*, 238, 325–333.
- Rstudio Team (2020). *RStudio: Integrated Development Environment for R*. <http://www.rstudio.com/>
- Sanderman, J., Amundson, R. G., & Baldocchi, D. D. (2003). Application of eddy covariance measurements to the temperature dependence of soil organic matter mean residence time. *Global Biogeochemical Cycles*, 17(2), n/a–n/a. <https://doi.org/10.1029/2001GB001833>.
- Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, 478, 49–56. <https://doi.org/10.1038/nature10386>.
- Schneider, F., Amelung, W., & Don, A. (2020). Origin of carbon in agricultural soil profiles deduced from depth gradients of C: N ratios, carbon fractions, $\delta^{13}C$ and $\delta^{15}N$ values. *Plant and Soil*. <https://doi.org/10.1007/s11104-020-04769-w>.
- Schneider, F., & Don, A. (2019). Root-restricting layers in German agricultural soils. Part I: Extent and cause. *Plant and Soil*, 442, 433–451. <https://doi.org/10.1007/s11104-019-04185-9>.
- Sierra, C. A., Müller, M., Metzler, H., Manzoni, S., & Trumbore, S. E. (2017). The muddle of ages, turnover, transit, and residence times in the carbon cycle. *Global Change Biology*, 23, 1763–1773. <https://doi.org/10.1111/gcb.13556>.
- Sleutel, S., Leinweber, P., Begum, S. A., Kader, M. A., Van Oostveldt, P., & De Neve, S. J. B. (2008). Composition of organic matter in sandy relict and cultivated heathlands as examined by pyrolysis-field ionization MS. *Biogeochemistry*, 89, 253–271. <https://doi.org/10.1007/s10533-008-9217-4>.
- Sochorová, L., Jansa, J., Verbruggen, E., Hejcman, M., Schellberg, J., Kiers, E. T., & Johnson, N. C. (2016). Long-term agricultural management maximizing hay production can significantly reduce belowground C storage. *Agriculture, Ecosystems & Environment*, 220, 104–114. <https://doi.org/10.1016/j.agee.2015.12.026>.
- Sokol, N. W., & Bradford, M. A. (2019). Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nature Geoscience*, 12, 46–53. <https://doi.org/10.1038/s41561-018-0258-6>.
- Sokol, N. W., Kuebbing, S. E., Karlsen-Ayala, E., & Bradford, M. A. (2019). Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. *New Phytologist*, 221, 233–246. <https://doi.org/10.1111/nph.15361>.
- Sollins, P., Homann, P., & Caldwell, B. A. (1996). Stabilization and destabilization of soil organic matter: Mechanisms and controls. *Geoderma*, 74, 65–105. [https://doi.org/10.1016/S0016-7061\(96\)00036-5](https://doi.org/10.1016/S0016-7061(96)00036-5).
- Springob, G., & Kirchmann, H. (2002). C-rich sandy Ap horizons of specific historical land-use contain large fractions of refractory organic matter. *Soil Biology and Biochemistry*, 34, 1571–1581. [https://doi.org/10.1016/S0038-0717\(02\)00127-X](https://doi.org/10.1016/S0038-0717(02)00127-X).
- Springob, G., & Kirchmann, H. (2010). Ratios of carbon to nitrogen quantify non-texture-stabilized organic carbon in sandy soils. *Journal of Plant Nutrition and Soil Science*, 173, 16–18. <https://doi.org/10.1002/jpln.200900289>.
- Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., & Zeileis, A. (2008). Conditional variable importance for random forests. *BMC Bioinformatics*, 9, 307. <https://doi.org/10.1186/1471-2105-9-307>.
- Strobl, C., Boulesteix, A.-L., Zeileis, A., & Hothorn, T. (2007). Bias in random forest variable importance measures: Illustrations, sources and a solution. *BMC Bioinformatics*, 8, 25. <https://doi.org/10.1186/1471-2105-8-25>.
- Taghizadeh-Toosi, A., Christensen, B. T., Glendining, M., & Olesen, J. E. (2016). Consolidating soil carbon turnover models by improved estimates of belowground carbon input. *Scientific Reports*, 6, 32568. <https://doi.org/10.1038/srep32568>.
- Taghizadeh-Toosi, A., Cong, W.-F., Eriksen, J., Mayer, J., Olesen, J. E., Keel, S. G., Glendining, M., Kätterer, T., & Christensen, B. T. (2020). Visiting dark sides of model simulation of carbon stocks in European temperate agricultural soils: Allometric function and model initialization. *Plant and Soil*, 450, 255–272. <https://doi.org/10.1007/s11104-020-04500-9>.

- Tiemeyer, B., Albiac Borraz, E., Augustin, J., Bechtold, M., Beetz, S., Beyer, C., Drösler, M., Ebli, M., Eickenscheidt, T., Fiedler, S., Förster, C., Freibauer, A., Giebels, M., Glatzel, S., Heinichen, J., Hoffmann, M., Höper, H., Jurasinski, G., Leiber-Sauheitl, K., ... Zeitz, J. (2016). High emissions of greenhouse gases from grasslands on peat and other organic soils. *Global Change Biology*, 22, 4134–4149. <https://doi.org/10.1111/gcb.13303>.
- Trumbore, S. (2000). Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecological Applications*, 10, 399–411.
- Vos, C., Don, A., Hobbey, E. U., Prietz, R., Heidkamp, A., & Freibauer, A. (2019). Factors controlling the variation in organic carbon stocks in agricultural soils of Germany. *European Journal of Soil Science*, 70, 550–564. <https://doi.org/10.1111/ejss.12787>.
- Vos, C., Jaconi, A., Jacobs, A., & Don, A. (2018). Hot regions of labile and stable soil organic carbon in Germany-Spatial variability and driving factors. *SOIL*, 4, 153–167. <https://doi.org/10.5194/soil-4-153-2018>.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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