Soil organic carbon fractions in response to soil, environmental and agronomic factors under cover cropping systems: A global meta-analysis

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Abstract

Cover crops may improve soil health and increase soil carbon sequestration, thus contributing to both the adaptation to and mitigation of climate change. Despite these potential benefits, there currently lacks a global synthesis of the impacts of cover crops on soil organic carbon (SOC) fractions. We conducted a global meta-analysis of 93 peer-reviewed studies to quantify the effect of cover crops on changes in SOC fractions and the influence of environmental and management factors. Compared to bare soil management, cover crops increased SOC by 12% and increased seven SOC fractions, including microbial biomass carbon (MBC) by 33%, dissolved organic carbon (DOC) by 18%, particulate organic carbon (POC) by 15%, light-fraction organic carbon (LFOC) by 14%, permanganate oxidizable carbon (POXC) by 13%, short-term mineralizable carbon (SMC) by 10%, and mineral-associated organic carbon (MAOC) by 7%. The effect size of SOC was positively correlated with the effect sizes of MBC, POC, LFOC, and MAOC, but negatively correlated with the effect size of DOC. Soil taxonomic order and experimental duration were key factors affecting the beneficial effect of cover crops on the SOC fractions. Greater increases in SOC fractions due to cover crops were found in Entisols and Ultisols in comparison with other soil orders. The effect size of MAOC increased with experimental duration. Our study suggests that cover crops can significantly increase various SOC fractions, which likely serves as a building block for SOC sequestration and improvement of many aspects of soil health.

Keywords: Green manure, meta-analysis, SOC sequestration, microbial biomass carbon, mineral-associated organic carbon

1. Introduction

Cover crops are generally grown at times when soil would otherwise be bare, typically in the period after a crop is harvested and the next crop is planted (Lal, 2015). They may be cultivated into the soil prior to sowing the subsequent crop or terminated with herbicide. In some situations, they may be grazed by animals during their period of growth, but generally, they have no direct economic benefit to the farmer (Ruis and Blanco-Canqui, 2017); instead, they are grown for environmental reasons or to contribute to the gradual improvement of soil conditions, with the expectation that this will benefit future crops (Blanco-Canqui et al., 2020). Another use of cover crops is their growth at locations where soil would otherwise be bare, such as the area between rows of perennial plants in orchards or vineyards (Repullo-Ruibérriz de Torres et al., 2021). Cover crops have the potential to confer numerous benefits to the soil, including enhancing soil nutrients, promoting soil organic carbon (SOC) sequestration, and improving soil health. However, the degree to which these benefits materialize may vary depending on the specific agronomic situation and location.

Studies have shown that cover crops enhance soil physicochemical properties, leading to improved soil health (Blanco-Canqui and Ruis, 2020; Stewart et al., 2018). These include the following: a) Increasing nitrogen inputs to agricultural systems if legumes are included in the mixture of plants, with the aim that biologically fixed nitrogen will be released to the subsequent crop (Abdalla et al., 2019). b) Improving soil physical properties through the input of organic matter from cover crop roots and foliage (Blanco-Canqui and Ruis, 2020). Impacts also include improved aggregate stability and the formation of pores through the production of polysaccharides by the decomposition of organic inputs by soil microbes (Garcia-Franco et al., 2015). c) Improved soil biological properties, including earthworm and microbial activity (Lal, 2015). d) Increased SOC stocks and contribution to climate change mitigation through carbon sequestration (Seitz et al., 2022). The positive effect of cover crops on inhibiting SOC loss by erosion and promoting SOC content has been reported by numerous studies and meta-analyses (Bai et al., 2019; Ball et al., 2020; Garcia-Franco et al., 2015; Das et al., 2022; Poeplau and Don, 2015). However, examining total SOC alone may not wholly account for the effects of cover crop on SOC sequestration, especially in the early years after cover crop introduction (Fulton-Smith and Cotrufo, 2019). SOC fractions, determined through physical, chemical, and biological fractionation, are considered to be transitory or early responders to management practices (Von Lützow et al., 2007; Sequeira et al., 2011; Thomas et al., 2016). Therefore, information on SOC fractions may provide a more comprehensive understating of the potential benefits of cover crops on SOC (Plaza-Bonilla et al., 2014).

Based on differences related to their formation, persistence, and function, SOC is classified into different fractions such as particulate organic carbon (POC), light-fraction organic carbon (LFOC), mineral-associated organic carbon (MAOC), dissolved organic carbon (DOC), microbial biomass carbon (MBC), short-term mineralizable carbon (SMC), and permanganate oxidizable carbon (POXC) (Bongiorno et al., 2019; Li et al., 2021; Plaza-Bonilla et al., 2014; Singh et al., 2020). Combining changes in SOC fractions with the SOC formation concepts can aid in understand the process of SOC sequestration (Li et al., 2021). Recent concepts of SOC formation support that SOC formation is a continuous process whereby soil fauna and microbes gradually transform large plant residues into small molecules that bind to mineral surfaces or enter the soil aggregates and become stabilized (Cotrufo and Lavallee, 2022; Lehmann and Kleber, 2015; Liang et al., 2017). While delineating clear stages for these processes can be difficult, exploring the different SOC fractions can reveal the mechanisms of SOC formation (Li et al., 2021). According to SOC formation concepts and previous studies (Cotrufo and Lavallee, 2022; Lehmann and Kleber, 2015; Liang et al., 2017; Li et al., 2021), the above SOC fractions can be broadly classified into different groups, including plant-associated (POC and LFOC), water/salt-soluble (DOC), microbial-associated (MBC, SMC and POXC), and mineral-associated (MAOC) fractions. Understanding changes in SOC fractions can uncover the mechanisms of SOC formation under cover crops. There is a need to further investigate the response of SOC fractions with different origins, formation mechanisms and functions to cover crops and the environmental factors influencing them.

The effect of cover crops on SOC fractions depends on several factors, such as climatic, edaphic, management conditions, and cover crop types (Wiesmeier et al., 2019). First, climate has a direct effect on plant growth and the soil microbial activity (Cavicchioli et al., 2019), so cover crops may have a more favourable effect on SOC in warmer and wetter areas (Bai et al., 2019). Second, changes in SOC fractions as affected by cover crops may be modified by soil order and properties (Stockmann et al., 2015). For instance, soils with a lower initial SOC content may have a higher potential for SOC sequestration (Zhao et al., 2018). In contrast, in high-productivity soils, cover crops did not affect SOC but increased POC and SMC (Cates et al., 2019). Furthermore, the impact of cover crops on SOC fractions can vary depending on the soil depth. For example, introduction of winter cover crops in cropping systems can increase SOC in the topsoil layer (0-30 cm) but decrease it in deeper soil layers (30-200 cm) (Tautges et al. 2019). Additionally, the type of cover crop may significantly influence SOC fractions. Legume cover crops have generally been reported to have a greater potential to increase SOC fractions than non-legume cover crops (Ladoni et al., 2016; Veloso et al., 2019), but this remains debatable (Ball et al., 2020). Studies have found that non-legume cover crops more significantly contribute to SOC fractions such as DOC (Kauer et al., 2019) and MBC (Muhammad et al., 2021) than legume cover crops. However, the complex mechanisms and interactions among cover crop types and environmental factors constrain our understanding of how SOC fractions respond to cover crops. There is a need to explore the origins and causes of heterogeneity within the various SOC fractions under cover crops.

This study focuses on the changes in SOC fractions under cover crops and their relative contribution to SOC changes. We report results from a global meta-analysis of cover crops on SOC fractions. The results are categorized according to soil order, climate and agronomic factors, including the duration of the experiment, cover crop types, and tillage intensity. The hypothesis of our study was that cover crops would increase SOC fractions, particularly microbial-associated fractions, with the magnitude of the effect size modulated by environmental and agronomic factors. We aim to a) quantify the extent to which SOC fractions respond to cover crops at the global scale and b) clarify SOC responses to cover crops by examining the change of SOC fractions.

2. Materials and methods

2.1. Literature search and database generation

Data were collected from peer-reviewed publications between June 1980 and December 2021 using five databases: Web of Science, Springer, Elsevier's Scopus, Wiley, and China National Knowledge Infrastructure. Search terms included "cover crop" or "green manure" or "catch crop" and "soil organic carbon" or "soil organic matter" or "soil carbon fraction" or "soil carbon component". After duplicates were deleted and the titles and abstracts reviewed, 395 articles were selected (Fig. S1). We then compiled data from 93 peer-reviewed publications that met the following criteria: i) the targeted studies included at least one comparison across treatments, that is, cover crops (treatment group) and bare soil managed without cover crops (control group), ii) reported experimental durations and cover crop types, iii) reported at least one SOC fraction, and provided enough information for us to classify the fractions into distinct categories based on their composition and functionality, iv) only field studies were included, and v) the mean value and sample size could be extracted.

In this study, we collected data for seven SOC fractions. The POC and LFOC are primarily derived from plant residues, whereas MAOC is mainly of microbes origin (Lavallee et al., 2020; Sokol et al., 2019). DOC is produced by soil microorganisms consuming soluble organic matter produced by root secretions and plant material leachate (Cotrufo and Lavallee, 2022; Wu et al., 2021). Microbial-associated SOC fractions (MBC, POXC, and SMC) are commonly used to describe microbial carbon use efficiency (CUE; Liptzin et al., 2022; Wang et al., 2021). To ensure the comparability and validity of the data, we manually validated the classification of each SOC fraction according to the measurement method. The MBC was determined by the Chloroform fumigation method. The POC (> 0.053 mm) and MAOC (< 0.053 mm) were distinguished by size fractionation following dispersion with 5.0 g L^{-1} sodium hexametaphosphate solution, while LFOC was separated by density fractionation and dispersed using 1.8 g cm^{-3} solution of Sodium iodide. The POXC and SMC were determined by permanganate oxidation and incubation method, respectively. Notably, our data comprises both water-extracted and salt-extracted methods of DOC, with the majority being water-extracted. This is because these are the two most common and widely used methods in the literature.

We collected the data through manual extraction from tables and texts in published literature or indirect extraction from figures using the Engauge Digitizer 12.1 software

(Free Software Foundation, Inc., Boston, USA), followed by manual verification. These criteria were followed when extracting data: i) for the same study, data for various experimental durations, cover crop types, and soil layers were recorded independently, and ii) when the test was constantly sampled over a short period (less than a year), the data from the last sampling were recorded. The final dataset included 1113 pairs of data for SOC and SOC fractions, with 340 for SOC, 138 for DOC, 141 for MBC, 120 for MAOC, 255 for POC, 44 for LFOC, 47 for POXC, and 28 for SMC. The geographical distribution of the studies is shown in Fig. 1.

The standard deviation (SD) or standard error (SE) was recorded together with the mean value, which was used to calculate the effect size. The SD value was assigned as 1/10th of the corresponding mean value in certain cases where no SD or SE was provided (Han et al., 2020; Shakoor et al., 2021). The SD value was calculated by the following Eq. (1) when SE and sample size (*n*) was reported:

$$SD = SE \times \sqrt{n} \qquad (1)$$

For each observation, the following climatic, edaphic, and management information was collected in the database: mean annual temperature (MAT) (cold, MAT ≤ 10 °C; warm, MAT >10 °C), mean annual precipitation (MAP) (arid/semiarid, MAP ≤ 450 mm; semi-humid, MAP between 450 mm and 600 mm; humid, MAP > 600 mm) (Wang et al., 2019), land use type (arable, orchard, vegetable, and other), soil order (USDA soil taxonomic orders: Ultisols, Anthrosols, Oxisols, etc.), soil layer (< 30 cm, and 30–120 cm), cover crop types (legume cover crops, non-legume cover crops and a mix of legume cover crops and non-legume cover crops), experimental duration (< 5, 5–10, 10–20 and > 20 years), tillage intensity (conventional, i.e., common agricultural practices used by farmers; conservation, i.e., reduced tillage, and no-till), utilization methods of cover crop (incorporation and surface mulching). Each factor was considered to be a moderator, and a subgroup analysis was performed to determine the mean effect size and sources of heterogeneity across subgroups (Kim et al., 2020).

2.2. Data analysis

Meta-analysis was conducted in OpenMEE software (Inc., Boston, USA; Wallace et al., 2017). The effect sizes of the SOC fractions in response to cover crops were determined using the ln-response ratio (*lnRR*), which is commonly employed in ecology (McDaniel et al., 2014). For each observation, the *lnRR* was calculated using Eq. (2):

$$lnRR = ln\left(\frac{X_t}{X_c}\right) \tag{2}$$

where X_t and X_c represent the mean values of the cover crops and bare soil managed without cover crops, respectively. The *lnRR* and 95% bootstrap confidence interval (CI) were calculated using OpenMEE software (Deng et al., 2021). A restricted maximum likelihood (REML) random effects model was calculated with 999 iterations to determine the *lnRR* for the effects of cover crops on each SOC fraction. Significant responses ($p < 0.05$) were determined if the bootstrap CI did not overlap with zero (Koricheva et al., 2013).

The variance (v) of each individual *lnRR* is then estimated as Eq. (3):

$$v = \frac{s_t^2}{n_t x_t^2} + \frac{s_c^2}{n_t x_c^2} \quad (3)$$

where s_t and s_c represent the SD of treatment and control groups, respectively; n_t and n_c were the sample sizes for the treatment and control groups, respectively. For each research study, the weighting factor (ω) was measured as the inverse of the pooled variance ($1 / v$). Then, the weighted $lnRR$ were calculated by using Eq. (4):

$$\overline{lnRR} = \frac{\sum(lnRRi \times \omega i)}{\sum \omega i} \quad (4)$$

where ωi and $lnRRi$ were the weight and effect size from the ith comparison, respectively. If the CI of the weighted $lnRR$ does not cross zero, the difference between treatment and control is significant. A positive value shows that cover crops significantly increase the SOC fraction, whereas a negative value suggests the reverse. The total between-study heterogeneity (τ^2) was used to describe the percent variation, with high or moderate heterogeneity indicated by τ^2 values ≥ 75% or 50%.

For the convenience of description, Eq. (5) was used to convert weighted $lnRR$ into effect size:

$$Effect\ size(\%) = (e^{lnRR} - 1) \times 100\% \quad (5)$$

2.3. Publication bias test

Publication bias may occur when statistically significant results are more likely to be published than statistically insignificant results (Borenstein et al., 2009). To ensure the most robust and credible results, we evaluated publication bias using the following approach. Only data that passed the bias tests were included in the calculation of the effect size. First, we used OpenMEE software to conduct sensitivity analysis and fail-safe numbers. We excluded one pair of data at a time to check the impact of each pair's exclusion on the overall results. We removed any data that significantly altered the meta-analysis results until further elimination of data no longer impacted the results of the standard meta-analysis. Next, the fail-safe number, which usually indicates the magnitude of publication bias in a meta-analysis, was tested. A fail-safe value greater than 5 n + 10 (where n is the number of studies included in the meta-analysis summary) suggests a small publication bias (Rosenberg, 2005). Finally, funnel plots and normal distribution plots were plotted in OpenMEE and SPSS software (version 25.0, SPSS Inc., Chicago, USA). All of the aforementioned tests indicated that the results of the meta-analysis were reliable (for details, see Table S1 and Figs. S2 and S3).

2.4. Statistical analysis

To investigate the effect of different groups in each factor on the effect sizes of SOC fractions, we conducted a subgroup analysis using OpenMEE. Statistical significance was considered when $p < 0.05$ for each group in the factor. Then, we used the Permuted Meta-regression in OpenMEE. Specifically, we used the factor as a covariate and *lnRR* as the dependent variable in the meta-regression using the REML mixed-effects model with 999 iterations. The total heterogeneity (Q_t) was divided into total heterogeneity among covariate levels explained by the model (Q_m) and residual error not explained by the models (Q_E) (Albert et al., 2021). The relationship is significant if $p < 0.05$. A significant Q_m means that differences exist among the effect size of factor levels. Additionally, the relative variance contribution rate (RC) for each factor, which describes the response of each factor to the SOC fractions, was calculated by dividing the Q_m of each factor by the sum of the Q_m of all factors (Deng et al., 2021).

To better illustrate the relationship between SOC and SOC fractions, a linear regression of the effect sizes of SOC and SOC fractions was performed and polar plot was produced based on the R^2 values using paired SOC and SOC fractions data from each study. The linearity of the effect sizes of SOC and SOC fractions in relation to MAP, MAT, and experimental duration was used to assess variation in SOC fractions in response to cover crops. We used the package maps and ggplot2 in R (version 3.5.3; R Foundation for Statistical Computing, Vienna, Austria) to generate the site spatial distribution.

3. Results

3.1. Overall effects of cover crops on soil organic carbon fractions

Cover crops had a significantly positive impact on the effect sizes of SOC fractions. Averaged across all data, cover crops increased total SOC by 12%, and increases were observed for DOC (18%), MBC (33%), MAOC (7%), POC (15%), LFOC (14%), POXC (13%), and SMC (10%), compared to control bare soil management (Fig. 2a). A linear regression was conducted to investigate the relationship between SOC and the SOC fractions (Fig. 2b). Regression analysis revealed that the effect sizes of MBC (R^2

= 0.186, $p < 0.001$), MAOC ($R^2 = 0.666$, $p < 0.001$), POC ($R^2 = 0.208$, $p < 0.001$) and LFOC ($R^2 = 0.401$, $p < 0.001$) exhibited significant positive correlations with the effect size of SOC (Fig. 2b). The effect size of DOC was inversely associated with the effect size of SOC ($R^2 = 0.041$, $p < 0.05$).

3.2. Effects of cover crops on soil organic carbon fractions with various environmental and edaphic conditions

The cover crops led to greater effect sizes on SOC fractions in warmer and wetter areas (MAT > 10 °C, MAP > 600 mm; Fig. 3). In warmer areas (MAT > 10 °C), cover crops lead to effect sizes of SOC, DOC and POC that were 1.45, 5.03, and 1.64 times that, respectively, of those observed in colder areas (MAT ≦ 10 °C) ($p < 0.05$). The responses of SOC, DOC and MBC to cover crops were significantly influenced by different MAPs ($p < 0.05$), but the observed pattern was inconsistent (Fig. 3a–c). Regression analysis showed a significant increase in the effect sizes of SOC, MAOC and LFOC with increasing MAP (Fig. S4). Conversely, there were limited linear correlations between MAT and the effect sizes of SOC fractions.

Furthermore, cover crops had a significant impact on SOC, MBC, and LFOC across various land use types (Fig. 3). The positive effects of cover crops on SOC fractions were most pronounced in orchards than in other land use types. Specifically, the effect sizes of SOC, MBC, and LFOC were 1.77, 1.29, and 5.98 times that in orchards than in arable land, respectively.

The impact of cover crops on the effect sizes of SOC fractions differed significantly with respect to soil order, while exhibiting comparatively lower sensitivity to soil layer in comparison to other factors (Fig. 4). Cover crops increased SOC fractions more in the Entisols and Ultisols than in the other soil orders. For instance, Entisols had a larger effect size with respect to SOC (23%; Fig. 4a), DOC (35%; Fig. 4b), MBC (46%; Fig. 4c), and LFOC (52%; Fig. 4f). Cover crops also significantly increased the effect sizes of MBC, POC, and MAOC in Alfisols and Mollisols ($p < 0.05$, Fig. 4c to e). Oxisols showed a negative effect on the effect size of LFOC (−14%; Fig. 4f). Additionally, Oxisols showed a weak negative effect on the effect sizes of DOC (Fig. 4b), and MBC (Fig. 4c), although this effect was not significant. The soil layer had a significant effect only on the effect sizes of SOC and LFOC ($p < 0.05$, Figs. 4a and 4f).

3.3. Effects of cover crops on SOC fractions with respect to various agronomic factors

Among the different cover crop types, legume cover crops showed a greater increase in the effect sizes of SOC fractions, especially MBC (37%) and LFOC (29%), compared to other cover crop types ($p < 0.01$, Figs. 5c and 5f). The experimental duration was found to significantly impact the effect sizes of DOC and MAOC ($p < 0.05$, Fig. 5). The effect size of MAOC showed a significantly positive response across all experimental durations, with the greatest effect occurring in the long-term (10–20 years; Fig. 5d). Only in the short-term (<5 years and 5–10 years) did cover crop duration have a positive effect on the effect size of DOC (Fig. 5b). Regression analysis showed that experimental duration was positively associated with the effect size of SOC ($R^2 = 0.043$, $p < 0.05$; Fig. S5a) and the effect size of MAOC ($R^2 = 0.119$, $p < 0.001$; Fig. S5d), but negatively associated with the effect size of DOC ($R^2 = 0.056$, $p < 0.05$; Fig. S5b).

Furthermore, tillage intensity had a minor influence on the response of SOC fractions to cover crops (Fig. 5). Conservation tillage exhibited a greater effect size of LFOC in comparison to conventional tillage ($p < 0.001$; Fig. 5f). In addition, the incorporation of cover crops significantly increased the effect sizes of DOC (Fig. 5b), MBC (Fig. 5c), and POC (Fig. 5e), compared to mulched soil surface.

3.4. Relative variance contribution rate of factors to SOC fractions

The impact of cover crops on various SOC fractions was assessed in relation to several factors in this study. Soil order and experimental duration were the two most important factors that controlled the effect of cover crops on SOC fractions (Fig. 6; Table S2). The effect size of cover crops with respect to SOC, MBC, POC, LFOC, SMC, and POXC was significantly influenced by soil order. The experimental duration had the largest influence on the effect sizes of DOC and MAOC, followed by soil order. Land use type was observed to significantly affect the responses of SOC, MBC, MAOC, and LFOC to cover crops. The cover crop utilization method significantly impacted the effect sizes of SOC, DOC, MBC, MAOC, and POC. The responses of MBC and LFOC to cover crops were also significantly affected by cover crop types. In contrast, soil layer and tillage intensity had little influence on the effect sizes of SOC fractions under cover crops.

4. Discussion

4.1 Cover crops increase soil organic carbon sequestration by building its fractions

When broadly considering the evidence that cover crops positively effect SOC fractions, we propose a mechanism whereby in the short term, cover crops drive increases in DOC content by increasing translocation of carbon to soil from aboveground residue and root exudates. In the short term, the microbial biomass responds by consuming the additional DOC, but as the MBC fraction increases it draws down the DOC as CUE improves with the growing microbial biomass (Cotrufo et al., 2013). This may be why the effect size of SOC and DOC were weakly negatively correlated in this meta-analysis (Fig. 2b). As the MBC fraction increases in size, it increases the production of microbial by-products, such as amino sugars, amino acids, and polysaccharides, that may become stabilized in MAOC (DOC-microbial path) and this explains why there is an apparent lag between cover crop implementation and MAOC accumulation since it takes longer time horizons to build MAOC (Cotrufo and Lavallee, 2022; Liang et al., 2017). With increased plant residues entering the soil, the plant-associated SOC fractions derived from incompletely decomposed plant residues or other labile organic matter also increases (physical transfer path), as they are mainly transferred through fragmentation (Lavallee et al., 2020; Sequeira et al., 2011).

Microorganisms play an important role in both the DOC-microbial path and the physical transfer path of plant-associated fractions (Cotrufo and Lavallee, 2022; Liang et al., 2017).

Previous studies showed microorganisms accelerated changes in SOC dynamic by facilitating organic matter turnover (Kim et al., 2020; Frasier et al., 2016; Muhammad et al., 2021). In this study, microbial-associated fractions, especially MBC, showed the greatest increase, up to 2–3 times more than other fractions, indicating that MBC is the most sensitive fraction to cover crops. This is due to microbial biomass playing a central role in SOC decomposition and formation processes (Bhattacharyya et al., 2012). Furthermore, the increase in microbial-associated SOC fractions under cover crops implies an increase in microbial CUE (Li et al., 2021; Liang et al., 2017). Since cover crops, especially legumes, supply litter with relatively low carbon to nitrogen ratio and significantly increase DOC, soil carbon and nitrogen availability become more synchronized with microbial demand (Frasier et al., 2016; Cotrufo et al., 2013).

This study found that cover crops increase MAOC, which can be attributed to the increase in DOC and microbial-associated SOC fractions (Cotrufo and Lavallee, 2022; Lavallee et al., 2020). Microorganisms transform DOC, which subsequently binds to mineral surfaces, leading to the formation of MAOC (DOC-microbial path) (Kleber et al., 2015; Liang et al., 2017). The MAOC is usually attached to clay and silt surfaces or encapsulated by small aggregates (Lavallee et al., 2020; Sokol et al., 2019), forming a resistant structure with a long turnover time that makes it less sensitive to shorter-term environmental changes (Conant et al., 2011). This is particularly important for SOC sequestration, and is why the strongest positive correlation was between the effect sizes of SOC and MAOC (Fig. 2b). However, the slow rate that MAOC changes and the fact that 89% of the experiments in our database were shorter than 10 years, resulted in the smallest response of MAOC to cover crops among the seven SOC fractions. Longer-term studies are necessary to adequately assess this, especially for the accumulation of MAOC and the transformations that build this SOC fraction. In summary, SOC formation and sequestration are complex, and the interconversion of SOC fractions may collectively contribute to the increase in SOC (e.g. DOC to MBC to MAOC).

4.2. Soil organic carbon fractions in response to environmental factors under cover cropping system

4.2.1. Soil order regulates the response of soil organic carbon fractions to cover crops

The formation and loss of SOC fractions are controlled by environmental and management factors (Von Lützow et al., 2007). Soil orders were found to be the most important factor affecting the impact of cover crops on SOC fractions (Fig. 6). First, we observed a smaller increase in effect size of SOC caused by cover crops in Alfisols and Mollisols, which are mainly found in highly productive agricultural areas in the Americas and China (Kim et al., 2020). This result supports the previous finding that planting cover crops in productive soils may have limited effect on the enhancement of total SOC (Cates et al., 2019; Kauer et al., 2019; Kim et al., 2020). Notably, we found that cover crops significantly increased the effect sizes of MBC, POC, and MAOC in Alfisols and Mollisols (Fig. 4). Thus, these SOC fractions should be the focus of future studies exploring the effect of cover crops on SOC in highly productive soils. Second, we showed that the effect sizes of SOC fractions were greater in less productive soil orders (e.g. Entisols and Ultisols; Fig. 4). In this study, orchards were the main land use type for these two orders, comprising 73% of our database. Orchards are typically located on slopes with fragile soil structure and low SOC content, which makes them highly suitable for SOC sequestration (García-Díaz et al., 2018; Zhao et al., 2018). This could explain the large increase in the effect size of SOC fractions observed in Entisols, Ultisols, and orchards (Figs. 3 and 4). Moreover, cover crops significantly reduced the effect size of LFOC in Oxisols (Fig. 4f). Oxisols are usually developed in tropical or subtropical lowlands, and their characteristics are accompanied by strong weathering and leaching (Wang et al., 2019). In such soil conditions, LFOC, mainly derived from plant residues, may be easily lost. Conversely, soils with higher oxide content may reduce DOC leaching from the soil solution (Gmach et al., 2020). By reducing LFOC with cover crops in Oxisols, it could have reduced the soluble carbon for the DOC pool and limited carbon availability to microbes, explaining the weak negative (not significant) or lack of, effect of cover crops on DOC and MBC in the Oxisols.

4.2.2. Climatic conditions regulate the response of SOC fractions to cover crops

Temperature and precipitation have been identified as prominent predictors of SOC change on a global scale (Wiesmeier et al., 2019). According to a recent meta-analysis, warmer sites exhibited a negative effect on POC (Rocci et al., 2021). To the contrary, our results indicated that cover crops caused significantly greater increases in the effect size of POC in warmer sites than in colder sites (Fig. 3e). This may be attributed to increased carbon inputs that exceeded carbon decay rates, as suggested by Yuan et al. (2021). In addition, this study indicated that cover crops had a larger effect on the SOC, DOC, and MBC in sites with higher MAP (Fig. 3). The possible impact of a wetter environment on the SOC fractions may be explained in two principal ways: a) wetter sites generally have higher net primary carbon input rates than arid sites, implying that well-grown cover crops will promote carbon input and increase microbial carbon use (Bai et al., 2019; Crowther et al., 2019); b) the high-precipitation environment accelerates the formation of clay minerals and oxides, which favors DOC accumulation (Singh et al., 2020; Jeewani et al., 2021). Interestingly, the results of this study also revealed a positive effect of cover crops on SOC in arid sites (MAP < 450 mm; Fig. 3a). This could be related to the distribution of arid areas in this study, which were mainly located in orchards in Brazil, Spain, and Australia (accounting for 62% of the SOC database). The low carbon sequestration potential of orchards resulted in a significant enhancement of SOC (García-Díaz et al., 2018). On the other hand, irrigation compensates for the use of water by cover crops (19% of SOC database).

Rationalizing the balance between water use and cover crop growth remains a continuing challenge when cover crops are grown in arid sites (Blanco-Canqui et al., 2021).

4.3. Soil organic carbon fractions in response to agronomic factors under cover cropping systems

4.3.1. Experimental duration regulates the response soil organic carbon to cover crops

The experimental duration was identified as the second most important factor, after soil order, that affected the response of SOC fractions to cover crops (Figs. 5 and 6). The results showed that the response of SOC fractions to cover crops varied depending on the short-term or long-term duration of the experiment, which was likely related to the turnover and persistence of different SOC fractions (Plaza-Bonilla et al., 2014). The effect sizes of DOC and MAOC were observed to be sensitive to the experimental duration (Fig. S5). A positive correlation was found between experiment duration and the effect size of MAOC (Fig. S5), indicating that SOC stability increased with increasing experiment duration. Specifically, cover crops accumulated more MAOC in the long-term duration (> 10 years) than the short-term duration (< 10 years) (Fig. 5d). Observing large changes in slow-cycling MAOC may require a longer duration, as some studies have suggested (Kleber et al., 2015; Lavallee et al., 2020). Furthermore, a decreasing trend in the effect size of DOC was observed as the experimental duration (Fig. 6b). However, caution is advised when drawing conclusions based on this observation, because of the small amount of data collected over a period longer than 10 years accounted for only 20% of the database. Notably, cover crops had a significant impact on the effect sizes of POC and MBC, regardless of the experiment duration (Fig. 5c and e). It is a characteristic of POC that it does not become saturated (Castellano et al., 2015). The constant input of organic matter from cover crops may lead to a continuous supply of POC (Lavallee et al., 2020). Similarly, the high turnover and metabolism of microorganisms under cover crops result in significant MBC growth (Kim et al., 2020), which contributes to MAOC formation (Cotrufo and Lavallee, 2022; Kleber et al., 2015).

4.3.2. Cover crop types influence the response of soil organic carbon fractions

In addition to the experimental duration, cover crop types have different effects on the SOC fractions due to differences in carbon to nitrogen ratio, biomass, and root activity (Santos et al., 2011). The types of cover crops used in this study included legumes, non-legumes, or a mix of legume and non-legume. However, the results showed that most SOC fractions were not significantly affected by the different cover crop types (Fig. 5c and f). A possible explanation for this is that global data averages might not have changed significantly due to differences in climate and soils across studies (Ruis and Blanco-Canqui, 2017). Interestingly, legume cover crops resulted in 37% and 29% increases in the effect sizes of MBC and LFOC, respectively, which were 0.42 and 5.47 times higher than those of the non-legume cover crops ($p < 0.05$; Fig. 5c and f). Furthermore, the effect sizes of SOC, DOC, and POXC were also highest under legume cover crops, but the differences were not significant (Fig. 5). These findings suggest that legume cover crops more effective than other cover crop types in enhancing some SOC fractions. Legume cover crops residues have a lower carbon to nitrogen ratio because they can fix atmospheric nitrogen via root nodules (Dabney et al., 2001). Therefore, they are more susceptible to microbial assimilation and the activation of microbial functional activity, species, and abundance, thus facilitating SOC turnover (Castellano et al., 2015; Karl et al., 2016). This study suggests that legume cover crops may be a preferable alternative for increasing SOC fractions.

4.3.3. Cover crop management practices influence soil organic carbon fractions

The impact of cover crops management practices, such as tillage intensity and utilization methods, can influence their effect on SOC fractions (Figs. 5 and 6). Conservation tillage resulted in a significantly larger effect on LFOC ($p < 0.001$) and other SOC fractions (e.g., MBC, MAOC, POC, POXC; $p > 0.05$) compared to conventional tillage (Fig. 5). This indicates that combining cover crops with conservation tillage tend to promote SOC accumulation (Veloso et al., 2019). The slower decomposition rate of cover crops residue under conservation tillage may explain this finding, as it allows for easier detection of changes in SOC fractions (Blanco-Canqui et al., 2015). In addition, the results showed that cover crops incorporation significantly increased the effect sizes of DOC (Fig. 5b), MBC (Fig. 5c) and POC (Fig. 5e) more than mulching. These effects are related to the cycling and turnover among SOC fractions. With incorporation, POC increases because of the physically fragmentation of plant residues, resulting in greater surface area in direct contact with the soil. This, allow for greater enzymatic and microbial accessibility, thus leading to the easy release of biodegradable organic matter and an increase in DOC (Kauer et al., 2019). Targeted investigations of the direct effects of cover crop management methods on SOC fractions are necessary to elucidate specific mechanisms of changes in SOC.

4.4. Limitations and implications

We discussed three limitations to our meta-analysis that highlight gaps in research on SOC fractions in response to cover crops. First, in the present study, case studies of the effects of cover crops on SOC fractions were unevenly distributed, with three primary focal areas in the USA, China, and Europe. In contrast, other regions have been less thoroughly investigated. The majority of the studies were conducted in subtropical and temperate regions, limiting the results offered in this study at a worldwide scale most to those climate types. Second, since most of the samples studied were topsoil (< 30 cm), our study was unable to determine the effects of cover crops on SOC at deeper soil layers. Studies indicate that there is a substantial potential for SOC sequestration in deeper soil layers (Tautges et al., 2019). However, the changes in SOC fractions in soil layers below 30 cm have been less studied, and there are even fewer studies related to cover crops. More attention needs to be paid to the effects of cover crops on SOC dynamics in soil layers below 30 cm. Furthermore, although the link between POC and MAOC remains unresolved (Cotrufo and Lavallee, 2022), it is generally accepted that POC is dominated by plant-derived compounds and MAOC by microbial-derived compounds (Grandy and Neff, 2008). There is a clear need for more studies to trace the plant or microbial origin of POC and MAOC to improve mechanistic knowledge of how these two principal SOC fractions form and transform under cover crops.

5. Conclusion

This study reveals the influence of cover crops on SOC fractions. Our findings demonstrate that cover crops caused an accumulation of POC and LFOC, probably by increasing crop residue levels. This increase was also associated with an increase in DOC and microbial-associated SOC fractions, which likely contributed to the formation of MAOC. The effect size of MAOC was strongly correlated with the effect size of SOC, indicating its significant influence on SOC changes. The increase in SOC fractions with different sources and functions, under cover crops, collectively contributed to the sequestration of SOC. In addition, soil order and experiment duration were critical factors regulating changes in SOC fractions. The effect of soil order on SOC fractions varied depending on fertility level and physicochemical properties. The effect size of MAOC increased with the duration of the experiment. More research on the response of SOC fractions to cover crops, especially over long-term (> 10 years) durations, is needed to better understand how cover crops affect accumulation and transformation of SOC fractions as building blocks for SOC sequestration.

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References

Abdalla, M., Hastings, A., Cheng, K., Yue, Q., Chadwick, D., Espenberg, M., Truu, J., Rees, R.M., Smith, P., 2019. A critical review of the impacts of cover crops on nitrogen leaching, net greenhouse gas balance and crop productivity. Glob. Chang. Biol. 25, 2530–2543. https://doi.org/10.1111/gcb.14644

Albert, H.A., Li, X., Jeyakumar, P., Wei, L., Huang, L., Huang, Q., Kamran, M., Shaheen, S.M., Hou, D., Rinklebe, J., Liu, Z., Wang, H., 2021. Influence of biochar and soil properties on soil and plant tissue concentrations of Cd and Pb: A meta-analysis. Sci. Total Environ. 755, 142582. https://doi.org/10.1016/j.scitotenv.2020.142582

Bai, X., Huang, Y., Ren, W., Coyne, M., Jacinthe, P., Tao, B., Hui, D., Yang, J., Matocha, C., 2019. Responses of soil carbon sequestration to climate-smart agriculture practices: A meta-analysis. Glob. Chang. Biol. 25, 2591–2606. https://doi.org/10.1111/gcb.14658

Ball, K.R., Baldock, J.A., Penfold, C., Power, S.A., Woodin, S.J., Smith, P., Pendall, E., 2020. Soil organic carbon and nitrogen pools are increased by mixed grass and legume cover crops in vineyard agroecosystems: Detecting short-term management effects using infrared spectroscopy. Geoderma 379, 114619. https://doi.org/10.1016/j.geoderma.2020.114619

Bhattacharyya, P., Roy, K.S., Neogi, S., Adhya, T.K., Rao, K.S., Manna, M.C., 2012. Effects of rice straw and nitrogen fertilization on greenhouse gas emissions and carbon storage in tropical flooded soil planted with rice. Soil Tillage Res. 124, 119–130. https://doi.org/10.1016/j.still.2012.05.015

Blanco-Canqui, H., Ruis, S.J., Holman, J.D., Creech, C.F., Obour, A.K., Humberto Blanco-Canqui, C., 2021. Can cover crops improve soil ecosystem services in water-limited environments? A review. Soil Sci. Soc. Am. J. https://doi.org/10.1002/SAJ2.20335

Blanco-Canqui, H., Shaver, T.M., Lindquist, J.L., Shapiro, C.A., Elmore, R.W., Francis, C.A., Hergert, G.W., 2015. Cover Crops and Ecosystem Services: Insights from Studies in Temperate Soils. Agron. J. 107, 2449–2474. https://doi.org/10.2134/agronj15.0086

Blanco-Canqui, H., Ruis, S.J., 2020. Cover crop impacts on soil physical properties: A review. Soil Sci. Soc. Am. J. 84, 1527–1576. https://doi.org/10.1002/saj2.20129

Bongiorno, G., Bünemann, E.K., Oguejiofor, C.U., Meier, J., Gort, G., Comans, R., Mäder, P., Brussaard, L., de Goede, R., 2019. Sensitivity of labile carbon fractions to tillage and organic matter management and their potential as comprehensive soil quality indicators across pedoclimatic conditions in Europe. Ecol. Indic. 99, 38–50. https://doi.org/10.1016/j.ecolind.2018.12.008

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2009. Introduction to Meta-analysis. John Wiley and Sons, Chichester. https://doi.org/10.1002/ 9780470743386.index

Castellano, M.J., Mueller, K.E., Olk, D.C., Sawyer, J.E., Six, J., 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. Glob. Chang. Biol. 21, 3200–3209. https://doi.org/10.1111/GCB.12982

Cates, A.M., Ruark, M.D., Grandy, A.S., Jackson, R.D., 2019. Small soil C cycle responses to three years of cover crops in maize cropping systems. Agric. Ecosyst. Environ. 286, 106649. https://doi.org/10.1016/j.agee.2019.106649

Cavicchioli, R., Ripple, W.J., Timmis, K.N., Azam, F., Bakken, L.R., Baylis, M., Behrenfeld, M.J., Boetius, A., Boyd, P.W., Classen, A.T., Crowther, T.W., Danovaro, R., Foreman, C.M., Huisman, J., Hutchins, D.A., Jansson, J.K., Karl, D.M., Koskella, B., Mark Welch, D.B., Martiny, J.B.H., Moran, M.A., Orphan, V.J., Reay, D.S., Remais, J. V., Rich, V.I., Singh, B.K., Stein, L.Y., Stewart, F.J., Sullivan, M.B., van Oppen, M.J.H., Weaver, S.C., Webb, E.A., Webster, N.S., 2019. Scientists' warning to humanity: microorganisms and climate change. Nat. Rev. Microbiol. 2019 179 17, 569–586. https://doi.org/10.1038/s41579-019-0222-5

Conant, R.T., Ryan, M.G., Ågren, G.I., Birge, H.E., Davidson, E.A., Eliasson, P.E., Evans, S.E., Frey, S.D., Giardina, C.P., Hopkins, F.M., Hyvönen, R., Kirschbaum, M.U.F., Lavallee, J.M., Leifeld, J., Parton, W.J., Megan Steinweg, J., Wallenstein, M.D., Martin Wetterstedt, J.Å., Bradford, M.A., 2011. Temperature and soil organic matter decomposition rates – synthesis of current knowledge and a way forward. Glob. Chang. Biol. 17, 3392–3404. https://doi.org/10.1111/J.1365-2486.2011.02496.X

Cotrufo, M.F., Lavallee, J.M., 2022. Soil organic matter formation, persistence, and functioning: A synthesis of current understanding to inform its conservation and regeneration. Adv. Agron. 172, 1–66. https://doi.org/10.1016/BS.AGRON.2021.11.002

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob. Chang. Biol. 19, 988–995. https://doi.org/10.1111/gcb.12113

Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. Science (80-.). https://doi.org/10.1126/science.aav0550

Dabney, S.M., Delgado, J.A., Reeves, D.W., 2001. Using winter cover crops to improve soil and water quality. Commun. Soil Sci. Plant Anal. 32, 1221–1250. https://doi.org/10.1081/CSS-100104110

Das, S., Chatterjee, S., Rajbanshi, J., 2022. Responses of soil organic carbon to conservation practices including climate-smart agriculture in tropical and subtropical regions: A meta-analysis. Sci. Total Environ. 805, 150428. https://doi.org/10.1016/j.scitotenv.2021.150428

Deng, L., Peng, C., Kim, D.-G., Li, J., Liu, Y., Hai, X., Liu, Q., Huang, C., Shangguan, Z., Kuzyakov, Y., 2021. Drought effects on soil carbon and nitrogen dynamics in global natural ecosystems. Earth-Science Rev. 214, 103501. https://doi.org/10.1016/j.earscirev.2020.103501

Frasier, I., Noellemeyer, E., Figuerola, E., Erijman, L., Permingeat, H., Quiroga, A., 2016. High quality residues from cover crops favor changes in microbial community and enhance C and N sequestration. Glob. Ecol. Conserv. 6, 242–256. https://doi.org/10.1016/j.gecco.2016.03.009

Fulton-Smith, S., Cotrufo, M.F., 2019. Pathways of soil organic matter formation from above and belowground inputs in a Sorghum bicolor bioenergy crop. GCB Bioenergy 11, 971–987. https://doi.org/10.1111/GCBB.12598

García-Díaz, A., Marqués, M.J., Sastre, B., Bienes, R., 2018. Labile and stable soil organic carbon and physical improvements using groundcovers in vineyards from central Spain. Sci. Total Environ. 621, 387–397. https://doi.org/10.1016/j.scitotenv.2017.11.240

Garcia-Franco, N., Albaladejo, J., Almagro, M., Martínez-Mena, M., 2015. Beneficial effects of reduced tillage and green manure on soil aggregation and stabilization of organic carbon in a Mediterranean agroecosystem. Soil Tillage Res. 153, 66–75. https://doi.org/10.1016/j.still.2015.05.010

Gmach, M.R., Cherubin, M.R., Kaiser, K., Cerri, C.E.P., 2020. Processes that influence dissolved organic matter in the soil: a review. Sci. Agric. 77. https://doi.org/10.1590/1678-992x-2018-0164

Han, Y., Feng, J., Han, M., Zhu, B., 2020. Responses of arbuscular mycorrhizal fungi to nitrogen addition: A meta-analysis. Glob. Chang. Biol. 26, 7229–7241. https://doi.org/10.1111/gcb.15369

Jeewani, P.H., Van Zwieten, L., Zhu, Z., Ge, T., Guggenberger, G., Luo, Y., Xu, J., 2021. Abiotic and biotic regulation on carbon mineralization and stabilization in paddy soils along iron oxide gradients. Soil Biol. Biochem. 160, 108312. https://doi.org/10.1016/j.soilbio.2021.108312

Karl, A.D., Merwin, I.A., Brown, M.G., Hervieux, R.A., Vanden Heuvel, J.E., 2016. Under-vine management impacts soil properties and leachate composition in a New York State Vineyard. HortScience 51, 941–949. https://doi.org/10.21273/hortsci.51.7.941

Kauer, K., Astover, A., Viiralt, R., Raave, H., Kätterer, T., 2019. Evolution of soil organic carbon in a carbonaceous glacial till as an effect of crop and fertility management over 50 years in a field experiment. Agric. Ecosyst. Environ. 283, 106562. https://doi.org/10.1016/j.agee.2019.06.001

Kim, N., Zabaloy, M.C., Guan, K., Villamil, M.B., 2020. Do cover crops benefit soil microbiome? A meta-analysis of current research. Soil Biol. Biochem. 142, 107701. https://doi.org/10.1016/j.soilbio.2019.107701

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., Nico, P.S., 2015. Mineral-Organic Associations: Formation, Properties, and Relevance in Soil Environments. Adv. Agron. 130, 1–140. https://doi.org/10.1016/BS.AGRON.2014.10.005

Koricheva, J., Gurevitch, J., Mengersen, K.L., 2013. Handbook of Meta-Analysis in Ecology and Evolution. Princeton University Press, Princeton, USA.

Ladoni, M., Basir, A., Robertson, P.G., Kravchenko, A.N., 2016. Scaling-up: Cover crops differentially influence soil carbon in agricultural fields with diverse topography. Agric. Ecosyst. Environ. 225, 93–103. https://doi.org/10.1016/j.agee.2016.03.021

Lal, R., 2015. Soil carbon sequestration and aggregation by cover cropping. J. Soil Water Conserv. 70, 329–339. https://doi.org/10.2489/jswc.70.6.329

Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Chang. Biol. 26, 261–273. https://doi.org/10.1111/gcb.14859

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature. https://doi.org/10.1038/nature16069

Li, Y., Li, Z., Cui, S., Liang, G., Zhang, Q., 2021. Microbial-derived carbon components are critical for enhancing soil organic carbon in no-tillage croplands: A global perspective. Soil Tillage Res. 205, 104737. https://doi.org/10.1016/j.still.2020.104758

Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. 2, 1–6. https://doi.org/10.1038/nmicrobiol.2017.105

Liptzin, D., Norris, C.E., Cappellazzi, S.B., Bean, G. Mac, Cope, M., Greub, K.L.H., Rieke, E.L., Tracy, P.W., Aberle, E., Ashworth, A., Bañuelos Tavarez, O., Bary, A.I., Baumhardt, R.L., Borbón Gracia, A., Brainard, D.C., Brennan, J.R., Briones Reyes, D., Bruhjell, D., Carlyle, C.N., Crawford, J.J.W., Creech, C.F., Culman, S.W., Deen, B., Dell, C.J., Derner, J.D., Ducey, T.F., Duiker, S.W., Dyck, M.F., Ellert, B.H., Entz, M.H., Espinosa Solorio, A., Fonte, S.J., Fonteyne, S., Fortuna, A.-M., Foster, J.L., Fultz, L.M., Gamble, A. V., Geddes, C.M., Griffin-LaHue, D., Grove, J.H., Hamilton, S.K., Hao, X., Hayden, Z.D., Honsdorf, N., Howe, J.A., Ippolito, J.A., Johnson, G.A., Kautz, M.A., Kitchen, N.R., Kumar, S., Kurtz, K.S.M., Larney, F.J., Lewis, K.L., Liebman, M., Lopez Ramirez, A., Machado, S., Maharjan, B., Martinez Gamiño, M.A., May, W.E., McClaran, M.P., McDaniel, M.D., Millar, N., Mitchell, J.P., Moore, A.D., Moore, P.A., Mora Gutiérrez, M., Nelson, K.A., Omondi, E.C., Osborne, S.L., Osorio Alcalá, L., Owens, P., Pena-Yewtukhiw, E.M., Poffenbarger, H.J., Ponce Lira, B., Reeve, J.R., Reinbott, T.M., Reiter, M.S., Ritchey, E.L., Roozeboom, K.L., Rui, Y., Sadeghpour, A., Sainju, U.M., Sanford, G.R., Schillinger, W.F., Schindelbeck, R.R., Schipanski, M.E., Schlegel, A.J., Scow, K.M., Sherrod, L.A., Shober, A.L., Sidhu, S.S., Solís Moya, E., St Luce, M., Strock, J.S., Suyker, A.E., Sykes, V.R., Tao, H., Trujillo Campos, A., Van Eerd, L.L., van Es, H., Verhulst, N., Vyn, T.J., Wang, Y., Watts, D.B., Wright, D.L., Zhang, T., Morgan, C.L.S., Honeycutt, C.W., 2022. An evaluation of carbon indicators of soil health in long-term agricultural experiments. Soil Biol. Biochem. 172, 108708. https://doi.org/10.1016/J.SOILBIO.2022.108708

McDaniel, M.D., Tiemann, L.K., Grandy, A.S., 2014. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. Ecol. Appl. 24, 560–570. https://doi.org/10.1890/13-0616.1

Muhammad, I., Wang, J., Sainju, U.M., Zhang, S., Zhao, F., Khan, A., 2021. Cover cropping enhances soil microbial biomass and affects microbial community structure: A meta-analysis. Geoderma 381, 114696. https://doi.org/10.1016/j.geoderma.2020.114696

Plaza-Bonilla, D., Álvaro-Fuentes, J., Cantero-Martínez, C., 2014. Identifying soil organic carbon fractions sensitive to agricultural management practices. Soil Tillage Res. 139, 19–22. https://doi.org/10.1016/j.still.2014.01.006

Poeplau, C., Don, A., 2015. Carbon sequestration in agricultural soils via cultivation of cover crops - A meta-analysis. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2014.10.024

Repullo-Ruibérriz de Torres, M.A., Carbonell-Bojollo, R.M., Moreno-García, M., Ordóñez-Fernández, R., Rodríquez-Lizana, A., 2021. Soil organic matter and nutrient improvement through cover crops in a Mediterranean olive orchard. Soil Tillage Res. 210, 104977. https://doi.org/10.1016/j.still.2021.104977

Rocci, K.S., Lavallee, J.M., Stewart, C.E., Cotrufo, M.F., 2021. Soil organic carbon response to global environmental change depends on its distribution between mineral-associated and particulate organic matter: A meta-analysis. Sci. Total Environ. 793, 148569. https://doi.org/10.1016/j.scitotenv.2021.148569

Rosenberg, M.S., 2005. The gile-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. Evolution (N. Y). 59, 464–468. https://doi.org/10.1111/J.0014-3820.2005.TB01004.X

Ruis, S.J., Blanco-Canqui, H., 2017. Cover Crops Could Offset Crop Residue Removal Effects on Soil Carbon and Other Properties: A Review. Agron. J. 109, 1785–1805. https://doi.org/10.2134/agronj2016.12.0735

Santos, N.Z. dos, Dieckow, J., Bayer, C., Molin, R., Favaretto, N., Pauletti, V., Piva, J.T., 2011. Forages, cover crops and related shoot and root additions in no-till rotations to C sequestration in a subtropical Ferralsol. Soil Tillage Res. 111, 208–218. https://doi.org/10.1016/j.still.2010.10.006

Shakoor, A., Shakoor, S., Rehman, A., Ashraf, F., Abdullah, M., Shahzad, S.M., Farooq, T.H., Ashraf, M., Manzoor, M.A., Altaf, M.M., Altaf, M.A., 2021. Effect of animal manure, crop type, climate zone, and soil attributes on greenhouse gas emissions from agricultural soils—A global meta-analysis. J. Clean. Prod. https://doi.org/10.1016/j.jclepro.2020.124019

Seitz, D., Fischer, L.M., Dechow, R., Wiesmeier, M., Don, A., 2022. The potential of cover crops to increase soil organic carbon storage in German croplands. Plant Soil. https://doi.org/10.1007/s11104-022-05438-w

Sequeira, C.H., Alley, M.M., Jones, B.P., 2011. Evaluation of potentially labile soil organic carbon and nitrogen fractionation procedures. Soil Biol. Biochem. 43, 438–444. https://doi.org/10.1016/j.soilbio.2010.11.014

Singh, Surendra, Nouri, A., Singh, Shikha, Anapalli, S., Lee, J., Arelli, P., Jagadamma, S., 2020. Soil organic carbon and aggregation in response to thirty-nine years of tillage management in the southeastern US. Soil Tillage Res. 197, 104523. https://doi.org/10.1016/j.still.2019.104523

Sokol, N.W., Sanderman, J., Bradford, M.A., 2019. Pathways of mineral-associated soil organic matter formation: Integrating the role of plant carbon source, chemistry, and point of entry. Glob. Chang. Biol. 25, 12–24. https://doi.org/10.1111/gcb.14482

Stewart, R.D., Jian, J., Gyawali, A.J., Thomason, W.E., Badgley, B.D., Reiter, M.S., Strickland, M.S., 2018. What We Talk about When We Talk about Soil Health. Agric. Environ. Lett. 3, 180033. https://doi.org/10.2134/AEL2018.06.0033

Stockmann, U., Padarian, J., McBratney, A., Minasny, B., de Brogniez, D., Montanarella, L., Hong, S.Y., Rawlins, B.G., Field, D.J., 2015. Global soil organic carbon assessment. Glob. Food Sec. 6, 9–16. https://doi.org/10.1016/J.GFS.2015.07.001

Tautges, N.E., Chiartas, J.L., Gaudin, A.C.M., O'Geen, A.T., Herrera, I., Scow, K.M., 2019. Deep soil inventories reveal that impacts of cover crops and compost on soil carbon sequestration differ in surface and subsurface soils. Glob. Chang. Biol. 25, 3753–3766. https://doi.org/10.1111/gcb.14762

Thomas, B.W., Whalen, J.K., Sharifi, M., Chantigny, M., Zebarth, B.J., 2016. Labile organic matter fractions as early-season nitrogen supply indicators in manure-amended soils. J. Plant Nutr. Soil Sci. 179, 94–103. https://doi.org/10.1002/JPLN.201400532

Veloso, M.G., Cecagno, D., Bayer, C., 2019. Legume cover crops under no-tillage favor organomineral association in microaggregates and soil C accumulation. Soil Tillage Res. 190, 139–146. https://doi.org/10.1016/j.still.2019.03.003

Von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39, 2183–2207. https://doi.org/10.1016/j.soilbio.2007.03.007

Wallace, B.C., Lajeunesse, M.J., Dietz, G., Dahabreh, I.J., Trikalinos, T.A., Schmid, C.H., Gurevitch, J., 2017. OpenMEE: Intuitive, open-source software for meta-analysis in ecology and evolutionary biology. Methods Ecol. Evol. 8, 941–947. https://doi.org/10.1111/2041-210X.12708

Wang, J., Zhang, S., Sainju, U.M., Ghimire, R., Zhao, F., 2021. A meta-analysis on cover crop impact on soil water storage, succeeding crop yield, and water-use efficiency. Agric. Water Manag. 256, 107085. https://doi.org/10.1016/J.AGWAT.2021.107085

Wang, X., Liu, B., Ma, J., Zhang, Y., Hu, T., Zhang, H., Feng, Y., Pan, H., Xu, Z., Liu, G., Lin, X., Zhu, J., Bei, Q., Xie, Z., 2019. Soil aluminum oxides determine biological nitrogen fixation and diazotrophic communities across major types of paddy soils in China. Soil Biol. Biochem. 131, 81–89. https://doi.org/10.1016/j.soilbio.2018.12.028

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Ließ, M., Garcia-Franco, N., Wollschläger, U., Vogel, H.J., Kögel-Knabner, I., 2019. Soil organic carbon storage as a key function of soils - A review of drivers and indicators at various scales. Geoderma 333, 149–162. https://doi.org/10.1016/j.geoderma.2018.07.026

Wu, M., Li, P., Li, G., Petropoulos, E., Feng, Y., Li, Z., 2021. The chemodiversity of paddy soil dissolved organic matter is shaped and homogenized by bacterial communities that are orchestrated by geographic distance and fertilizations. Soil Biol. Biochem. 161, 108374. https://doi.org/10.1016/J.SOILBIO.2021.108374

Yuan, X., Chen, Y., Qin, W., Xu, T., Mao, Y., Wang, Q., Chen, K., Zhu, B., 2021. Plant and microbial regulations of soil carbon dynamics under warming in two alpine swamp meadow ecosystems on the Tibetan Plateau. Sci. Total Environ. 790, 148072. https://doi.org/10.1016/J.SCITOTENV.2021.148072

Zhao, Y., Wang, M., Hu, S., Zhang, X., Ouyang, Z., Zhang, G., Huang, B., Zhao, S., Wu, J., Xie, D., Zhu, B., Yu, D., Pan, X., Xu, S., Shi, X., 2018. Economics- and policy-driven organic carbon input enhancement dominates soil organic carbon accumulation in Chinese croplands. Proc. Natl. Acad. Sci. 115, 4045–4050. https://doi.org/10.1073/pnas.1700292114

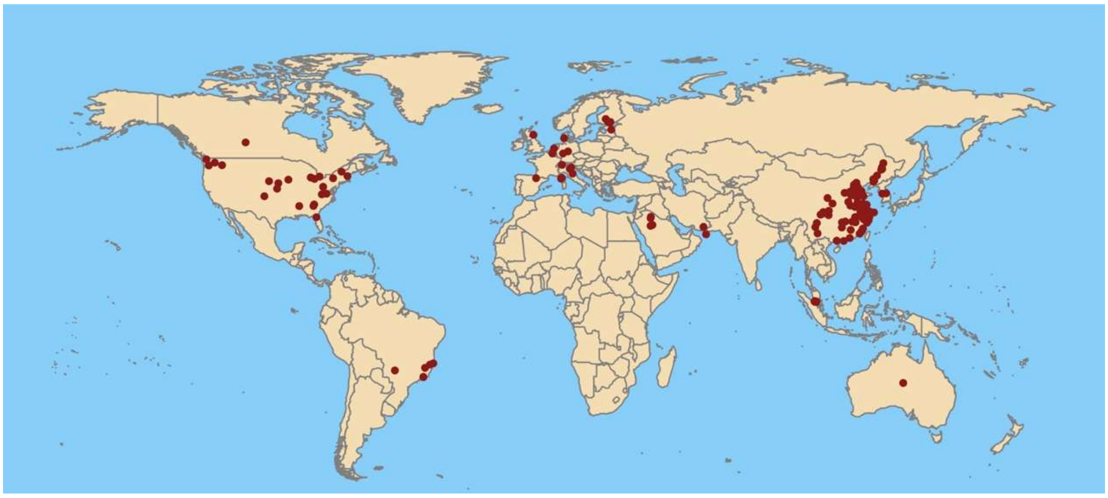

Fig. 1. Global distribution of data points included in the present study. Ninety-three data points with geographical coordinates are shown on the map.

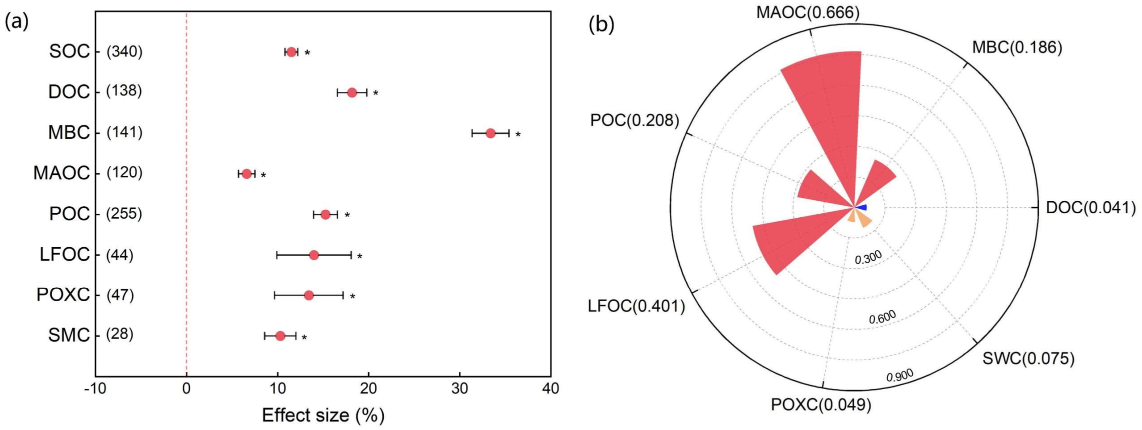

Fig. 2. Impact of cover crops on SOC fractions and linear relationship between the effect sizes of SOC and SOC fractions. (a) The red dot and black line segments in the graph represent the mean and 95% confidence interval, respectively, with confidence intervals excluding 0 indicating a significant response. The dashed lines represent effect size = 0. Asterisks represent $p < 0.05$. The number in parentheses represents the number of included studies. (b) The numbers in parentheses are the R^2 values. The R^2 values of 0.300, 0.600, and 0.900 are represented by the concentric circles. The red and blue colours represent a significant positive or negative linear correlation between the effect sizes of SOC and SOC fractions, respectively, and the orange colour indicates no significant linear relationship between the effect sizes of SOC and SOC fractions. Abbreviations: SOC, soil organic carbon; POC, particulate organic carbon; LFOC, light-fraction organic carbon; MAOC, mineral-associated organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; POXC, permanganate oxidizable carbon; SMC, short-term mineralizable carbon.

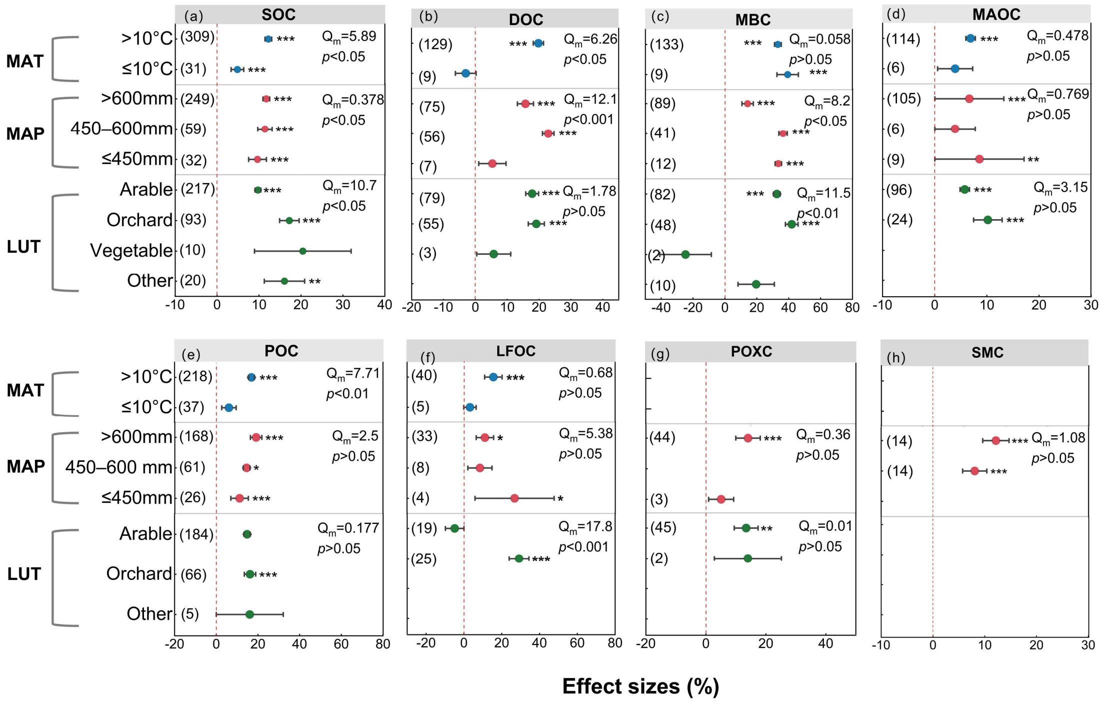

Fig. 3. Influence of different environmental factors on the effect sizes of SOC fractions. Asterisks indicate a significant response of SOC fractions to cover crops (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). The dashed lines represent effect size = 0. Q_m represents total heterogeneity among covariate levels explained by the meta-regression model; $p < 0.05$ indicates that there are differences in effect size among factor levels; $p > 0.05$ indicates there are no significant differences in effect size among factor levels. The number in parentheses represents the number of included studies. Abbreviations: SOC, soil organic carbon; POC, particulate organic carbon; LFOC, light-fraction organic carbon; MAOC, mineral-associated organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; POXC, permanganate oxidizable carbon; SMC, short-term mineralizable carbon; MAT, mean annual temperature; MAP, mean annual precipitation; LUT, land use type.

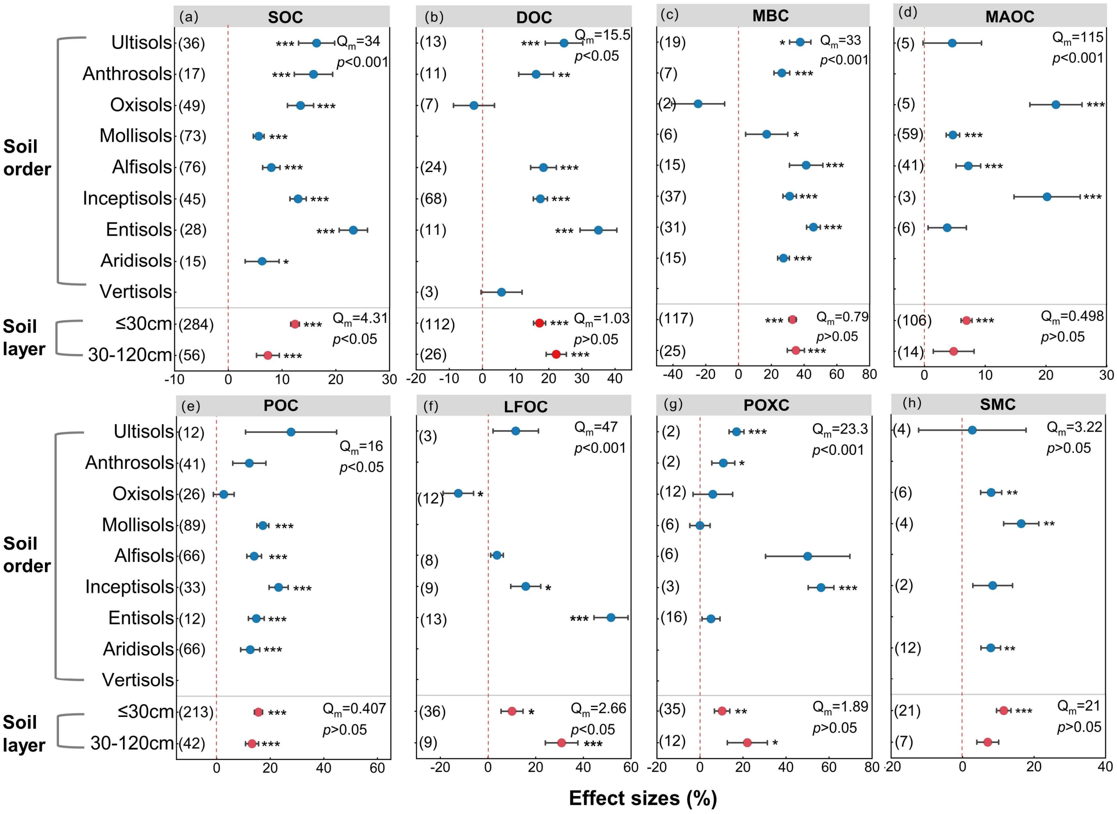

Fig. 4. Influence of different edaphic factors (soil order and layer) on the effect sizes of SOC fractions under cover crops. Asterisks indicate a significant response of SOC fractions to cover crops (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). The dashed lines represent effect size = 0. Q_m represents total heterogeneity among covariate levels explained by the meta-regression model; $p < 0.05$ indicates that there are differences in effect size among factor levels; $p > 0.05$ indicates there are no significant differences in effect size among factor levels. The number in parentheses represents the number of included studies. Abbreviations: SOC, soil organic carbon; POC, particulate organic carbon; LFOC, light-fraction organic carbon; MAOC, mineral-associated organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; POXC, permanganate oxidizable carbon; SMC, short-term mineralizable carbon.

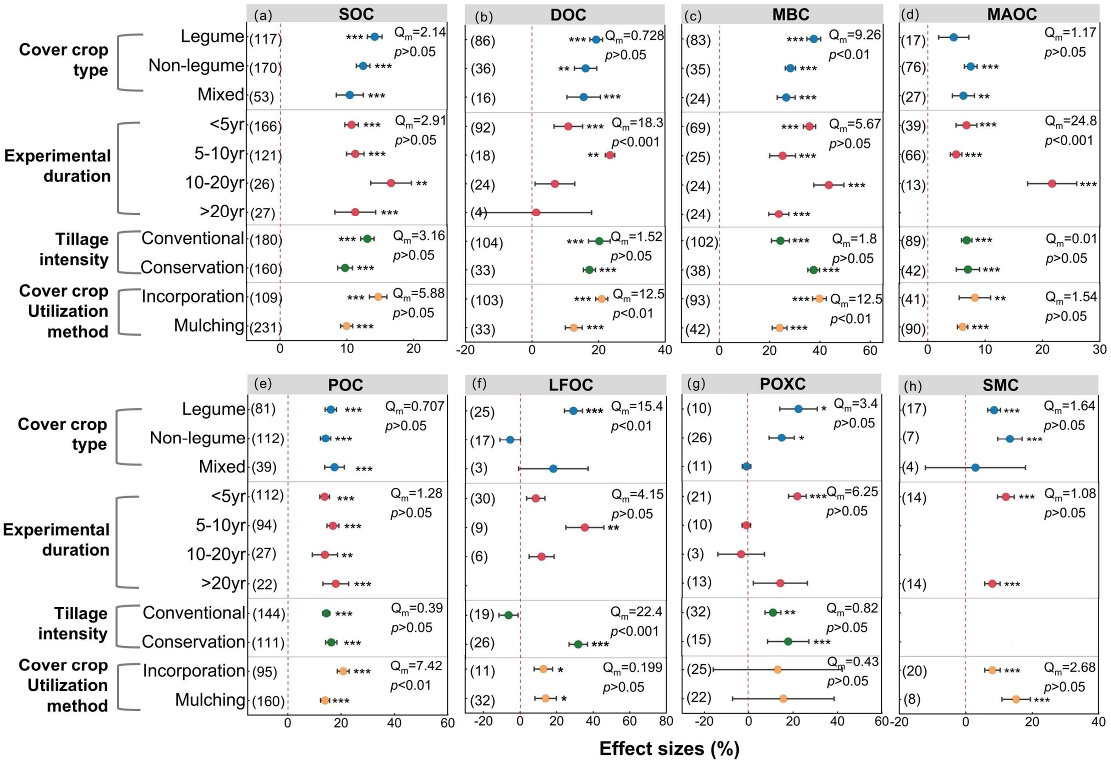

Fig. 5. Influence of different agronomic factors on the effect sizes of SOC fractions under cover crops. Asterisks indicate a significant response of SOC fractions to cover crops (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). The dashed lines represent effect size = 0. Q_m represents total heterogeneity among covariate levels explained by the meta-regression model; $p < 0.05$ indicates that there are differences in effect size among factor levels; $p > 0.05$ indicates there are no significant differences in effect size among factor levels. The number in parentheses represents the number of included studies. Abbreviations: SOC, soil organic carbon; POC, particulate organic carbon; LFOC, light-fraction organic carbon; MAOC, mineral-associated organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; POXC, permanganate oxidizable carbon.

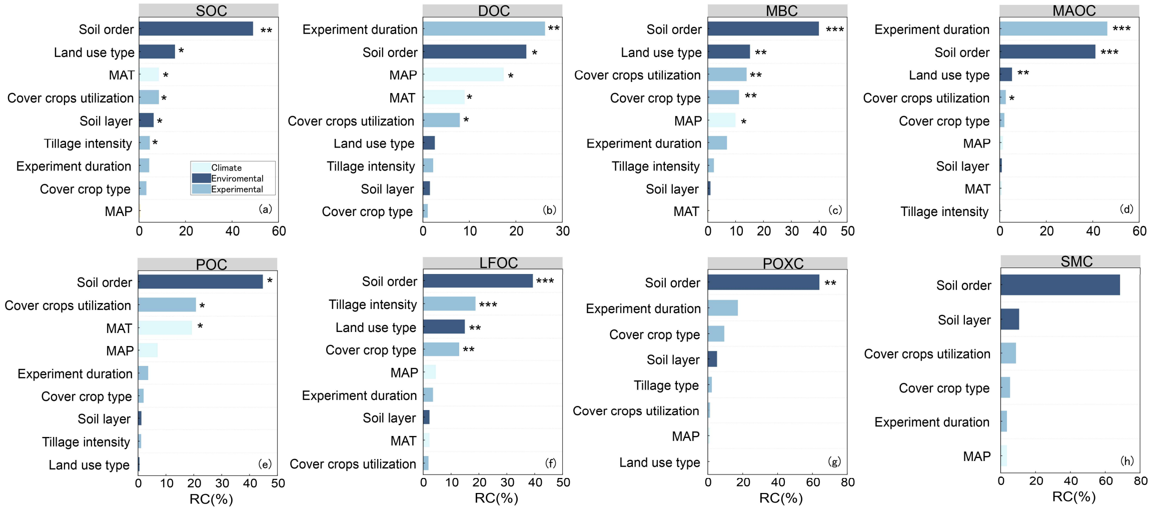

Fig. 6. Relative variance contribute (RC) of environment and agronomic factors to SOC fractions under cover crops. The higher the RC, the greater the influence of this factor on the effect sizes of the SOC fractions under cover crops. Asterisks indicate a significant difference in SOC fractions in response to cover crops (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Abbreviations: SOC, soil organic carbon; POC, particulate organic carbon; LFOC, light-fraction organic carbon; MAOC, mineral-associated organic carbon; DOC, dissolved organic carbon; MBC, microbial biomass carbon; POXC, permanganate oxidizable carbon; SMC, short-term mineralizable carbon; MAT, mean annual temperature; MAP, mean annual precipitation.