

RESEARCH ARTICLE

No detectable upper limit of mineral-associated organic carbon in temperate agricultural soils

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Abstract

Soil organic carbon (SOC) sequestration is a promising climate change mitigation option. In this context, the formation of the relatively long-lived mineral-associated organic carbon (MAOC) is key. To date, soils are considered to be limited in their ability to accumulate MAOC, mainly by the amount of clay and silt particles present. Using the comprehensive German Agricultural Soil Inventory, we selected 189 samples with a wide range of SOC (5–118 g kg⁻¹) and clay contents (30–770 g kg⁻¹) to test whether there is a detectable upper limit of MAOC content. We found that the proportion of MAOC was surprisingly stable for soils under cropland and grassland use across the whole range of bulk SOC contents. Soil texture influenced the slope of the relationship between bulk SOC and MAOC, but no upper limit was observed in any texture class. Also, C content in the fine fraction (g C kg⁻¹ fraction) was negatively correlated to fine fraction content (g kg⁻¹ bulk soil). Both findings challenge the notion that MAOC accumulation is limited by soil fine fraction content per se.

KEYWORDS

carbon saturation, carbon sequestration, national soil monitoring, organic matter fractionation

1 | INTRODUCTION

Since the beginning of agriculture some 12,000 years ago, anthropogenic activities have caused a loss of around 116 Pg organic carbon (OC) from the top 2 m of soil (Sanderman et al., 2017). However, this loss is potentially reversible to some extent if sustainable OC sequestration practices are implemented and up-scaled (Jobbágy & Jackson, 2000). If managed accordingly, soils may take up between 0.79 and 1.54 G Gt C year⁻¹ from the atmosphere (Fuss et al., 2018). To better understand soil organic carbon (SOC) dynamics, SOC is conceptually divided into fractions of contrasting properties, functions and residence times (von Lützw et al., 2007). In recent years, the concept of having two specific, operationally defined fractions becomes more and more accepted: those two are particulate organic

carbon (POC) and mineral-associated organic carbon (MAOC), which are often separated by size (Lavalée et al., 2020). POC is formed by fragmentation and translocation of structural litter residues and thus resembles the young and rather labile part of SOC, with turnover times of years to decades. In contrast, MAOC is formed either by direct sorption of plant-derived dissolved OC to mineral surfaces (*ex vivo*) or microbially mediated transformation and necromass association with minerals (*in vivo*; Liang et al., 2017). MAOC was found to contain less chemically complex compounds (e.g. polysaccharides, proteins, lipids) as compared to POC (e.g. lignin, cellulose, hemicellulose), have a longer turnover time (from decades to centuries), and lower C:N ratios (Lavalée et al., 2020). It is thus particularly the MAOC fraction, that is SOC stored in the fine fraction of the soil (clay and silt-sized particles), that should be targeted for long-term

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SOC sequestration in the context of climate change mitigation. This does not imply that POC storage is ineffective, considering its importance for soil structure and as a nutrient and energy source.

However, it is claimed that the capacity of a soil to stabilise additional C as MAOC is limited by the amount of fine fraction and its mineral surfaces (Cotrufo et al., 2019; Hassink, 1997). It is a common perception that the fine fraction 'saturates' at a certain point, which would restrict measures fostering C-sequestration to so-called 'undersaturated' soils (Georgiou et al., 2022). The theory originated from observations that the amount of C and N associated with fine silt and clay particles was positively correlated with the amount of such particles in uncultivated and grassland soils (Hassink, 1997). Based on this, numerous studies have estimated the 'saturation deficit' and subsequently the SOC sequestration potential of soils, leading to the conclusion that mineral surface area must be one of the most limiting factors in SOC stabilisation (Angers et al., 2011; Georgiou et al., 2022). The original saturation limit of mineral soils, as suggested by Hassink (1997), has been changed by several authors who have detected 'oversaturated' soils (Feng, Plante, et al., 2014; Feng, Xu, et al., 2014; Fornara et al., 2020; Wenzel et al., 2022) that is soils with more MAOC than the theoretical upper limit would allow. This indicates that the upper limit of MAOC storage as derived from upper quantiles (Feng, Plante, et al., 2014; Feng, Xu, et al., 2014) of the correlation of MAOC and fine fraction mass is strongly context specific, that is dependent on factors such as mineralogy, sampling depth or land use types (Beare et al., 2014; Georgiou et al., 2022). It might also raise the question of whether an upper limit set by mineral surface area for SOC stabilisation actually exists at all, which has however not been investigated systematically. Furthermore, recent studies have suggested that OC accrual in MAOC is decoupled from the availability of 'free' mineral surfaces and that it might even preferentially pile up on surfaces already loaded with OC (Schweizer et al., 2021; Vogel et al., 2014). In that sense, evaluating and explaining the content of C in the fine fraction (g C kg^{-1} fine fraction) rather than the content of MAOC (g MAOC kg^{-1} bulk soil) might be key to a better understanding of MAOC formation and its potential constraints.

Another, and much more direct approach to test the saturation concept or detect a potential MAOC saturation limit of a soil is to add different rates of OC and investigate the increase in MAOC as a function of C inputs (Abramoff et al., 2021; Feng, Plante, et al., 2014; Feng, Xu, et al., 2014; Six et al., 2002; Stewart et al., 2008). This approach has the disadvantages that (i) such experiments require high amounts of organic amendments until saturation might be reached and (ii) MAOC formation is a slow and steady process so that such experiments need to be run for many years. However, the concept that soils might have a certain universal capacity to store carbon as MAOC and any excess carbon will be stored as POC (Carter, 2002) can also be tested across various soils, by investigating the MAOC–SOC relationship. A recent study (Cotrufo et al., 2019) on European forest and grassland soils from the Land Use/Land Cover Area Frame Survey (LUCAS) database predicted that soils cannot generally store more than 45 g C kg^{-1} bulk soils as MAOC (fraction $< 53 \mu\text{m}$) and that

above a total SOC content of 50 g kg^{-1} only the relatively labile POC can accumulate further (original data plotted in Figure S1). This suggested upper limit contradicts findings of other authors, who found MAOC values of up to $100 \text{ g MAOC kg}^{-1}$ bulk soil (Beare et al., 2014; Georgiou et al., 2022). The distinct upper limit shown by Cotrufo et al. (2019) might be attributed to the scarcity of soils with SOC contents higher than 50 g kg^{-1} in their specific dataset, which led to a strong prediction bias of the machine learning model. It is highly unlikely that the same inflection point would occur for all soils, regardless of soil texture, mineralogy and potentially other soil properties.

Here, we used a comprehensive national soil archive to determine (i) whether an upper limit of MAOC storage in temperate agricultural soils can be detected or not and (ii) which factors explain the OC content in the fine fraction. To do so, a systematic random sample ($n=189$) with a wide range of SOC ($5\text{--}118 \text{ g kg}^{-1}$) and clay content ($30\text{--}770 \text{ g kg}^{-1}$) was taken from a total of 3104 topsoil samples from the German Agricultural Soil Inventory. In contrast to the natural distribution of SOC in soils, an equal number of samples was selected in each SOC content class in 10 g kg^{-1} intervals, ensuring an unbiased evaluation of the existence of a potential upper limit of MAOC in temperate agricultural soils.

2 | MATERIALS AND METHODS

2.1 | Selection of soil samples

Soil samples, sieved to 2 mm, were selected from the archive of the first German Agricultural Soil Inventory where soil sampling was performed in a fixed grid of $8 \times 8 \text{ km}$ grid covering the whole agricultural area of Germany. Agricultural soils comprise croplands, permanent grasslands (defined as sites with more than five consecutive years of grassland use) and permanent crops (vineyards and orchards). Out of a total of 3104 topsoil samples (0–10 cm), 189 soils were selected with a wide range of SOC ($5\text{--}118 \text{ g kg}^{-1}$) and clay content (3%–77%) by applying a systematic random approach. After excluding soils with a C:N ratio > 13 as a clear sign of heath or peatland history or similar reasons for large amounts of recalcitrant plant material (including plaggens soils; Poeplau et al., 2020; Springob & Kirchmann, 2010; Vos et al., 2018), an equal number of samples were collected in each SOC content class in 10 g kg^{-1} intervals (Figure 1). Up to a SOC content of 80 g kg^{-1} , 20 samples were selected per content class ($n=160$). Within each SOC content class, the clay content distribution of the randomly selected 20 samples was visually inspected and compared with the clay content distribution of all samples within that content class. This was done to ensure a selection of samples that represent the full range of clay content within each SOC content class. Random selection per SOC content class was repeated up to three times. Above 80 g kg^{-1} of SOC, only 29 samples were available, which were all included without further selection. Ultimately, 71 cropland and 118 grasslands soils were selected. The SOC content range in croplands was comparatively lower, ranging from 5 to 79 g kg^{-1} , in contrast to grasslands which exhibited a broader range ($28\text{--}118 \text{ g kg}^{-1}$).

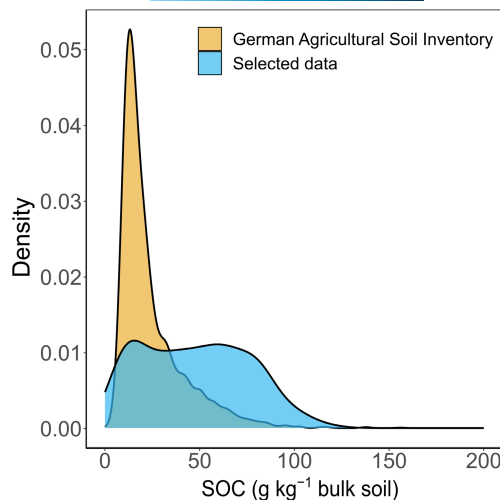


FIGURE 1 Distribution of soil organic carbon (SOC) contents at 0–10 cm depth of all samples in the German Agricultural Soil Inventory (BZW-LW) and the selected samples.

2.2 | SOC fractionation and analysis

Physical fractionation was conducted to derive MAOC and POC using a 50 μm sieve. In brief, 10 g of soil was immersed in 150 mL of distilled water and ultrasonic dispersion (100 J/mL) was performed according to Just et al. (2021), followed by wet sieving. For wet sieving, a dispersed soil sample was placed on top of the sieve and then a continuous flush of deionised water was applied. The coarse fraction was collected as the fraction that remained on the sieve ($>50 \mu\text{m}$) and was oven-dried at 60°C. However, the fraction that passed through the sieve ($<50 \mu\text{m}$) was treated with 0.8 g $\text{CaCl}_2 \text{L}^{-1}$ to obtain the maximum fine fraction ($<50 \mu\text{m}$) from the soil–water solution, followed by centrifugation for 15 min at 3800 g and drying at 60°C. The fractionated soil samples were then milled to obtain an homogeneous sample for analysis. SOC and total nitrogen (N) were analysed by dry combustion using an elemental analyser (LECO TRUMAC and RC612). POC refers to SOC in the coarse fraction, while MAOC refers to SOC in the fine fraction. Average C recovery was 95%. When recovery was less than 85% or more than 100%, the bulk soil sample was reanalysed. Thus, a few samples changed the SOC content class from which they had initially been selected.

2.3 | Further soil properties

Soil pH was determined using a soil-to-water ratio of 1:5 (5 g of soil with 25 g of water). The pH value was measured using a pH meter (ProLab 4000, SI Analytics) in combination with a pH combination electrode (Blue Line 28 pH, SI Analytics). Soil texture was determined based on sieving and sedimentation of suspended fine particles classifying clay $<2 \text{ mm}$, silt 2–63 μm and sand $>63 \mu\text{m}$ but $<2000 \mu\text{m}$. To determine pedogenic metal oxides (Fe, Al, Mn) in the fine fraction ($<50 \mu\text{m}$), 1 g of dried and sieved soil sample was shaken with 50 mL of 0.2 M ammonium oxalate solution for 4 h under

protection against UV radiation. The mixture was then centrifuged for 10–15 min. Therefore, the easily soluble, poorly crystalline oxides and hydroxide compounds of iron and aluminium were dissolved by complexation and brought into solution. Fe and Al oxides were then determined via inductively coupled plasma optical emission spectroscopy (iCap7000, Thermo Scientific) in this extract. At the same time, the plant-available proportions of phosphorus and sulphur were also mobilised and analysed in the same extract (Batjes, 2012; Utermann et al., 2000).

2.4 | Carbon input data

Data on average annual C inputs, including total C inputs, organic fertiliser inputs, as well as aboveground and belowground C inputs, were derived from Jacobs et al. (2020), in which the farmers' questionnaire of the German Agricultural Soil Inventory and a crop-specific C allocation coefficient framework were used to estimate C inputs.

2.5 | Statistical analyses

All data visualisation as well as data analysis was performed using R version 4.1.1 (R Core Team, 2020). Linear regressions were fitted to describe the relationships between total SOC and MAOC. Generalised linear models were used to explain the variation in SOC content of the fine fraction ($<50 \mu\text{m}$). Due to the large number of potential explanatory variables, multi-model inference was applied for a priori model selection based on the Akaike information criterion using the MuMIn package (Barton & Barton, 2015).

3 | RESULTS AND DISCUSSION

3.1 | Linear relationship between SOC and MAOC

For both cropland and grassland soils, linear relationships between MAOC and SOC were observed up to the highest investigated SOC content of 118 g kg^{-1} (Figure 2). Particularly for croplands, a very close positive relationship was observed across the whole range of SOC and clay contents ($y=0.86x$, $R^2=.99$). This indicates that irrespective of soil properties and total SOC content, intensively managed temperate cropland soils store about 86% of their total SOC as MAOC and 14% as POC. This is well in line with the 83% observed for a wide range of cropland, grassland and forest soils in a recent meta-analysis (Matus, 2021). Grassland soils had a higher scatter and thus more variability in the fraction of MAOC and POC. They had also a slightly lower slope than cropland soils with 72% of SOC being stored as MAOC and 18% as POC ($y=0.72x$, $R^2=.77$). As indicated by the size of the bubbles (Figure 2), the scatter in the grassland data was partly related to fine fraction content, with the lowest MAOC/SOC ratios observed for coarse-textured grassland soils (Figure 2). To test

for potential texture-specific inflection points, the MAOC/SOC ratio was further investigated in the fine fraction content classes <300 , $300\text{--}600$ and $>600\text{g kg}^{-1}$ (Figure 3), which revealed linear relationships in all cases. Indeed, the proportion of MAOC increased with fine fraction content, indicating that a relatively higher proportion of SOC is stored as POC in coarser-textured soils. The mechanisms behind these relationships are not entirely clear, but might be related to texture-driven differences in POC turnover time, or a lower efficiency of converting POC to MAOC in more coarse-textured soils (Poeplau et al., 2015). Certainly, it cannot be explained by saturation of the fine fraction: the three soils with the highest SOC and MAOC contents had an average fine fraction SOC content of 172g kg^{-1} in the low fine fraction class, of 136 in the medium fine fraction class and of 89 in the high fine fraction class, indicating a much higher C loading in the fine fraction of the coarser-textured soils.

In fact, in contrast to Cotrufo et al. (2019), no inflection point and thus no upper limit of MAOC storage was detected in the present dataset (Figures 2 and 3). The simplest explanation for the very clear inflection point in the previous study (Cotrufo et al., 2019) might be

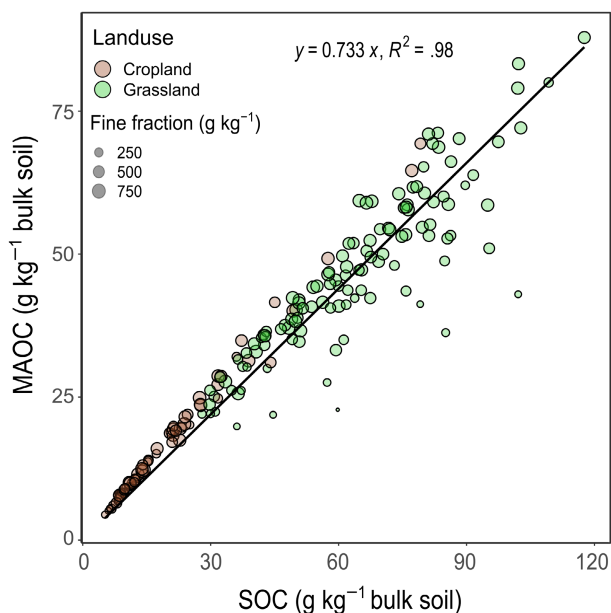


FIGURE 2 Relationship between soil organic carbon (SOC) and mineral-associated organic carbon (MAOC) for cropland ($n=71$) and grassland ($n=118$) soils. The size of the bubbles is directly proportional to the fine fraction content of the soils.

that the authors did not select a sample set that allowed a prediction of soils with more than 45g kg^{-1} MAOC. None of the soils in the sample set that was fractionated and analysed contained more than 47g kg^{-1} MAOC (Cotrufo et al., 2019). Additionally, (supervised) machine-learning models are generally optimised in a way that the values within the central tendency of the target distribution greatly impact their performance (Ribeiro & Moniz, 2020). Thus, extreme values are normally underrepresented in their predictions. In other words, the natural distribution of SOC on a national to global scale is strongly right skewed, with high SOC contents being rather rare exemptions. A random sample selection may thus not be suitable for answering the question if MAOC formation generally has an upper limit. Our dataset included soils of extremely high SOC contents. Such high amounts of MAOC will certainly not be achievable under every condition, especially not under average agricultural management regimes. For example, many of the soils with high SOC contents studied here were Gleysols with high groundwater level and the vast majority of the soils with more than 60g C kg^{-1} were used as permanent grasslands. However, the clear linear relationship as well as the fact that the average MAOC proportion was very similar to the one found in the global meta-analysis of Matus (2021) raises the question if and by which factors soils should be limited to accrual even higher than observed MAOC contents. Apart from one exception, the C:N ratio of the observed MAOC fractions was well constrained across all soils (Figure 5) and in the typical value range for MAOC (10.5 ± 1.2 ; Hassink, 1994). We can thus exclude the possibility of artefacts, for example, contaminations of MAOC with large amounts of fine POC, charcoal particles or similar.

3.2 | What drives the content of OC in the fine fraction?

The amount of fine particles, and with that the total mineral surface area, has been central to the theory of MAOC saturation (Hassink, 1997). Indeed, in the present study too, the content of fine fraction was significantly correlated with total MAOC content in croplands and grasslands (Figure 4a,b). However, fine fraction content explained only 21% (cropland; $y=0.02x+4.9$, $R^2=.21$) and 19% (grassland; $y=0.03x+26$, $R^2=.19$) of the variability in MAOC across the 189 sites. The positive correlation is expected, because MAOC is calculated by the amount of fine fraction and the C content of the

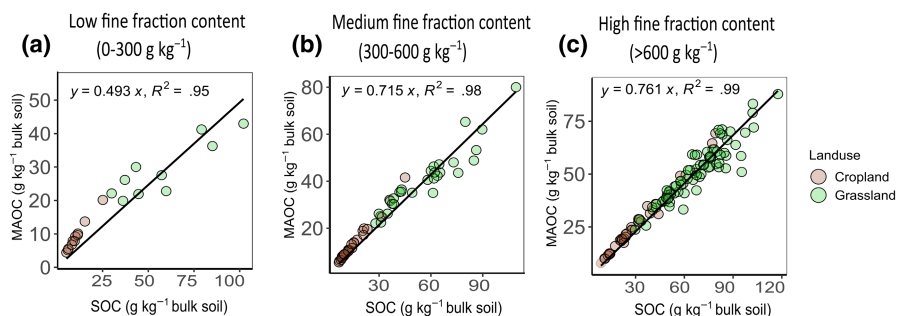


FIGURE 3 Relationship between soil organic carbon (SOC) and mineral-associated organic carbon (MAOC) ($<50\mu\text{m}$) for cropland and grassland soils grouped by fine fraction content; $<300\text{g kg}^{-1}$ ($n=21$; a) $300\text{--}600\text{g kg}^{-1}$ ($n=58$; b) $>600\text{g kg}^{-1}$ ($n=110$; c).

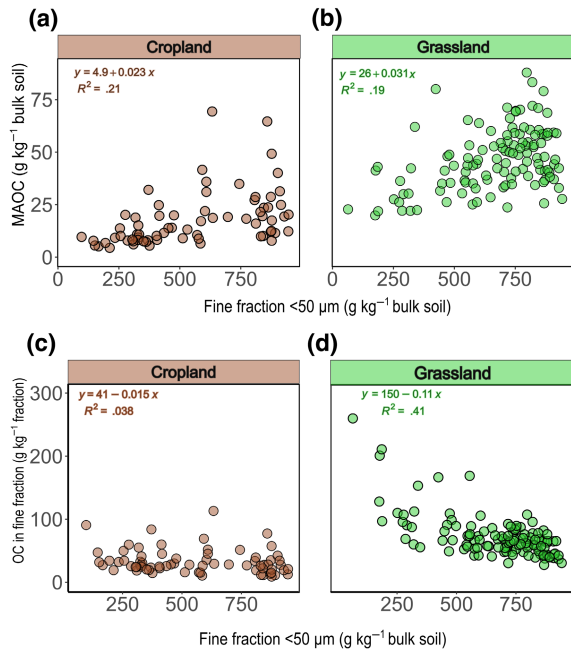


FIGURE 4 Relationship between mineral-associated organic carbon (MAOC) and fine fraction content (a, b) and between organic carbon (OC) in the fine fraction and the fine fraction content (c, d).

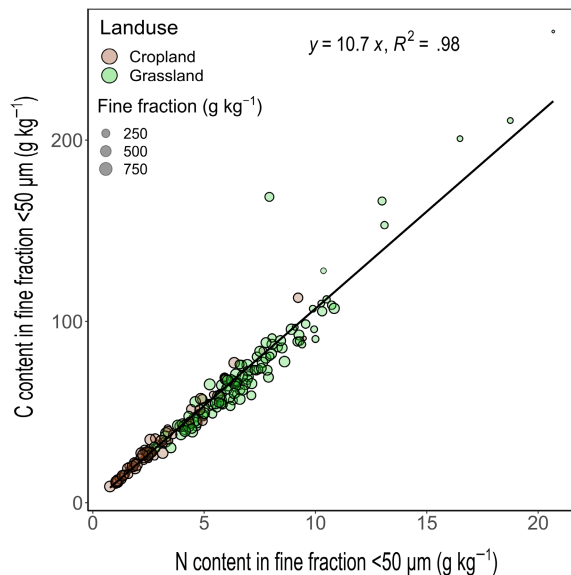


FIGURE 5 Fine fraction organic carbon (C) and total nitrogen (N) contents of the selected samples. The size of the bubbles is directly proportional to the fine fraction content of the soils.

fine fraction. As observed in this and previous studies, the content of fine fraction can vary from close to zero to close to 100% (Beare et al., 2014), which is not the case for the carbon content in the fine fraction, which ranged from 9 to 260 g kg⁻¹ in this study (Figure 5). Thus, even when a soil is strongly C depleted, it can have a relatively high MAOC content just because it is fine textured. Furthermore, Figure 4 indicates that the upper limit of this relationship, which is

often assumed to be the saturation limit, was not well constrained by our observations, especially for the grassland soils. Also soils with low fine fraction contents could have relatively high MAOC contents (Figure 4b), which can also be seen in the datasets of previous studies (Beare et al., 2014). Fitting an upper linear interval to such observations might thus not lead to the ultimate upper limit of MAOC storage, although it can be helpful to understand interactive effects of fine fraction content and other factors, such as mineralogy or land use, on the observed MAOC contents of soils (Georgiou et al., 2022).

However, what is often overlooked in studies investigating the MAOC storage capacity is the OC content of the fine fraction (<50 μm), which might help to understand the actual physicochemical capacity of the clay and silt particles to bind and stabilise C. In this study, the OC content in the fine fraction was highly variable, ranging from 9 to 260 g kg⁻¹ fine fraction (Figure 5). The silt and clay fraction can thus become highly enriched in OC. Agricultural management alone cannot fully explain such variation. Instead, this C content is influenced by mineralogy, hydrology, pedogenesis, land-use history and potentially other factors (Rasmussen et al., 2018; Schneider et al., 2021). Therefore, multiple regression models were applied to elucidate the most important factors influencing the content of OC in the fine fraction. The models could explain up to 67% of the variability, with important explanatory variables being the annual carbon inputs to the soil via crop residues, root litter and organic amendments as well as pedogenic oxides, groundwater level, amount of fine fraction, soil pH (ranges from 4–8) and C:N ratio (8–12.8; Table S1).

Interestingly, the fine fraction content was negatively correlated with the C content in the fine fraction in both models (Table 1). This was particularly true for grassland soils, as depicted in Figure 4d, and indicates a certain concentration, or piling up of OC in the fine fraction when the binding sites are limited. For a limited range of soils with similar SOC but variable clay contents, Schweizer et al. (2021) found a similar negative relationship between clay content and C stock as well as its proportion in the fraction <6.3 μm in temperate cropland soils. NanoSims imaging revealed that MAOC was associated with a similar extent of surface across the whole clay gradient, pointing towards organic matter piling up on a relatively low surface area (Schweizer et al., 2021). This implies that MAOC can form and grow even when mineral surfaces are limited, which is in contrast to the saturation concept, predicting that no additional MAOC can form once all mineral surfaces are covered. Metaphorically spoken, MAOC in soils might either resemble a mega city with a lot of skyscrapers on a small island (high OC content piling up in the fine fraction of a coarse-textured soils), or, when space is not limiting, many small distant settlements with an overall low population density (low OC content in the fine fraction of a fine-textured soil). Another NanoSims study actually confirms this settlement analogy, since it showed that MAOC was not homogeneously distributed across the available mineral surfaces but was found in organo-mineral clusters. Interestingly, newly added carbon was mainly recovered at those clusters (Vogel et al., 2014). This, together with the fact that the proportion of SOC stored as MAOC was found to be surprisingly stable across the whole range of investigated soils, challenges the assumption that every soil

TABLE 1 Best models for explaining soil organic carbon (SOC; g kg^{-1} bulk soil) in the fine fraction ($<50\ \mu\text{m}$) with multiple explanatory variables, including total inorganic carbon (TIC; g kg^{-1}), carbon inputs, which includes C_{fert} (average annual carbon inputs from organic fertilisers in Mg Cha^{-1}), C_{roots} (average belowground organic carbon inputs in Mg Cha^{-1} (Jacobs et al., 2020)), C_{total} (average annual total organic carbon inputs including roots, shoots and manure in Mg Cha^{-1}), C:N ratio (organic carbon-to-total nitrogen ratio of the soil), total fine fraction content (g kg^{-1}), GWL (mean depth to groundwater table (levels according to AD-HOC-AG Boden (2005))), soil pH, pedogenic oxides Al, Fe (g kg^{-1}), Mn (mg kg^{-1}) and sulphur (mg kg^{-1}). Model equations with degrees of freedom (df) and adjusted R -squared (R^2) values are displayed. Pedogenic oxides, phosphorus and sulphur could only be determined in 130 out of the 189 samples due to sample availability, thus models including these data were run for a smaller sample set, resulting in two different models.

Models	Equation	df	R^2
SOC in fine fraction (g C kg^{-1} fraction; without pedogenic oxides and sulphur)	$-85.94 + 20.62 \times C_{\text{fert}} + 9.38 \times \text{C:N ratio} + 49.96 \times C_{\text{roots}} - 13.07 \times C_{\text{total}} - 5.64 \times \text{fine fraction} - 7.23 \times \text{GWL} + 9.04 \times \text{pH} + 0.38 \times \text{TIC}$	158	.61
SOC in fine fraction (g C kg^{-1} fraction; with pedogenic oxides and sulphur)	$-118.67 + 12.98 \times C_{\text{fert}} + 4.17 \times \text{C:N ratio} + 37.44 \times C_{\text{roots}} - 7.30 \times C_{\text{total}} + 0.03 \times \text{C:S} + 5.40 \times \text{Fe} - 5.5 \times \text{fine fraction} - 25.92 \times \text{Mn} + 12.79 \times \text{pH} + 0.43 \times \text{TIC}$	102	.67

has, determined by the amount of silt and clay particles, a certain maximum capacity to store MAOC (Georgiou et al., 2022). At least for temperate agricultural soils, in which high activity clays prevail, and at least for SOC contents of up to $118\ \text{g C kg}^{-1}$, the 'saturation deficit' might not be a helpful concept to judge upon the ability to further build up the MAOC pool of a specific soil.

For instance, if megacities with skyscrapers can be built on small islands, why should they not be able to last on larger land surfaces? In the end, it might be primarily a question of material to build up such skyscrapers, thus biomass to build up MAOC. If more than $100\ \text{g C kg}^{-1}$ of carbon in the fine fraction is possible in rather coarse-textured soils, why should it not be possible to enrich the silt and clay fraction of fine-textured soils in a similar way? At the same time, the question comes up why such an enrichment is rarely observable in nature. A clayey soil with a hypothetical fine fraction OC content of $100\ \text{g C kg}^{-1}$ fine fraction, 80% of fine fraction, an average MAOC proportion of 79% (as found in this study) and a hypothetical bulk density of $1.3\ \text{g cm}^{-3}$, would lead to a SOC stock of $394\ \text{Mg ha}^{-1}$ and a MAOC stock of $312\ \text{Mg ha}^{-1}$ in 0–30 cm. This is a multiple of SOC of what is usually observed in topsoil across the globe, so along the lines of the saturation concept all mineral soils in the world are 'undersaturated' (Georgiou et al., 2022). However, our data indicate that mineral surfaces are not the major limitations of SOC stabilisation. Certainly, an important limitation for MAOC formation is the availability of biomass carbon (Janzen et al., 2022). Substrate quality, which can affect microbial carbon use efficiency and priming of native SOC, might also play an important role for the rate of MAOC formation (Guenet et al., 2018; Ridgeway et al., 2022). On the other hand, it might also be that the degree of stabilisation of the composite fraction, that is commonly isolated as MAOC, is not as homogeneous throughout this fraction as conceptualised (Ridgeway et al., 2022). For example, if MAOC is piling up in organo-mineral clusters, there might be gradients in decomposability within each pile (Kleber et al., 2007; Schweizer, 2022) with organo-organism interactions being less stable than direct organo-mineral interactions. Such gradients, or growth conditions of organo-mineral

clusters might again strongly depend on abiotic soil properties, such as mineralogy, pH or oxygen supply. The findings of our study call for further mechanistic investigations to better understand the potential constraints of MAOC formation. One important unsolved question evolving from our study is, whether the C content in the fine fraction limits further MAOC formation or not. Yet, we conclude that the surprisingly constant proportion of MAOC in a large variety of soils and up to very high bulk SOC contents questions if the saturation concept can help to estimate the SOC sequestration potential of soils.

AUTHOR CONTRIBUTIONS

Christopher Poeplau and Axel Don designed the study, Christopher Poeplau selected the samples, Neha Begill carried out the fractionation work and data analysis, Neha Begill and Christopher Poeplau wrote the manuscript, which was reviewed and edited by Axel Don.

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CONFLICT OF INTEREST STATEMENT

The authors declare to have no competing interests.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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