Acta Universitatis Agriculturae Sueciae

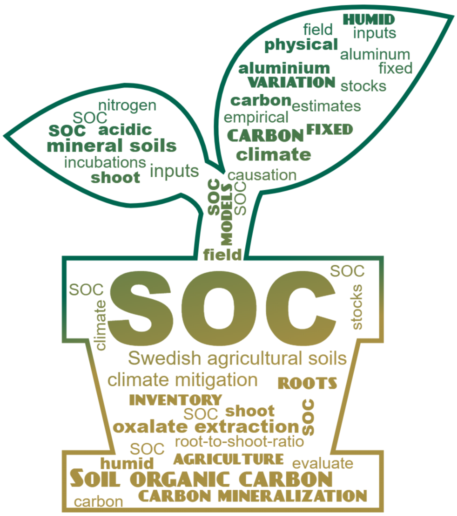
Doctoral Thesis No. 2026:18

Faculty of Natural Resources and Agricultural Sciences

The role of oxalate-extractable aluminum and root inputs in carbon storage in Swedish agricultural soils.

'Beyond the average'

Miyanda Chilipamushi



The role of oxalate-extractable aluminum and root inputs in carbon storage in Swedish agricultural soils.

'Beyond the average'

Miyanda Chilipamushi
Faculty of Natural Resources and Agricultural Sciences
Department of Soil and Environment
Uppsala

SLU

SWEDISH UNIVERSITY
OF AGRICULTURAL
SCIENCES

DOCTORAL THESIS

Uppsala 2026

Acta Universitatis Agriculturae Sueciae
2026:18

Cover: Word cloud generated using WordCloud.app (© 2026 WordCloud.app)
(Miyanda Chilipamushi, 2026)
ISSN 1652-6880
ISBN (print version) 978-91-8124-215-7
ISBN (electronic version) 978-91-8124-235-5
https://doi.org/10.54612/a.6namn9oq6a

Swedish University of Agricultural Sciences, Department of Soil and Environment, Uppsala, Sweden
 Print: SLU Grafisk service, Uppsala 2026

The role of oxalate-extractable aluminum and root inputs in carbon storage in Swedish agricultural soils

Abstract

Soil organic carbon (SOC) supports multiple ecosystem services, yet SOC pool estimates remain too uncertain for reliable policy and climate-mitigation measures. Many SOC models inadequately represent soil properties and carbon inputs, often relying on clay content for storage predictions and fixed root-to-shoot ratios for root-derived inputs, neglecting within-field variability. This thesis empirically evaluates these two sources of uncertainty (i.e. soil properties and carbon inputs) and their implications for SOC storage in Swedish agricultural mineral soils in three studies (**Papers I–III**). In **Paper I**, roots (0–40 cm depth) and shoots were sampled during the milking/early dough stage in a 50 × 50 cm square at 11 locations within a field in southwestern Sweden over two years. The field was cultivated with spring barley (*Hordeum vulgare L.*) both years. Root-to-shoot ratios varied (quartile coefficients of variation = 7–18 %), suggesting that the use of fixed ratios may introduce uncertainty in modelled root-derived carbon inputs within a field. Acidic mineral topsoils (n=100; 0–20 cm) from the Swedish soil and crop monitoring program (SMP) were analyzed for physical and geochemical characteristics (**Paper II**). Dispersion and oxalate extractions (in darkness) were used to determine silt-sized aggregation and reactive mineral phases, respectively. A random forest model using these data and SMP soil physical and management variables, and climate variables, identified oxalate-extractable aluminum (Al_{ox}) as a stronger predictor than clay content for SOC content. Partial dependence plots suggested a potential for SOC accrual in soils with higher Al_{ox}. Long-term (ca. 500 days) laboratory incubations of sieved soil samples (n=35; 3–10 cm) from the field used in **Paper I,** analyzed via partial least squares regression**,** did not support a protective effect of Al_{ox} on SOC content (**Paper III).** At quasi-steady-state, specific respiration rates declined with increasing SOC, total nitrogen (TN), and C:N ratios, suggesting SOC protection and possible effect of C:N ratios and TN in regulating SOC mineralization (**Paper III)**. These results urge models to transcend clay content and fixed ratios, incorporating variable inputs and mineral phases for better SOC estimates in Swedish contexts.

Keywords: Soil organic carbon; Root-to-shoot ratio; Oxalate extractable aluminum; Soil monitoring; Long-term incubation; Humid climate.

Oxalat-extraherbart aluminium och rötters roll för kolinlagring i svensk jordbruksmark

Sammanfattning

Organiskt kol i marken (SOC) är viktigt för flera ekosystemtjänster. Trots det är uppskattningar av SOC-förråd i marken ännu för osäkra för att ge ett tillförlitligt underlag för policy och klimatåtgärder. Många SOC-modeller beskriver markegenskaper och koltillförsel bristfälligt eftersom de i hög grad förlitar sig på lerhalt för att förutsäga lagring och på fasta rot-skott-kvoter för rottillförsel av kol, samtidigt som inomfältsvariation ignoreras. I denna avhandling utvärderas empiriskt dessa två osäkerhetskällor (dvs. markegenskaper och koltillförsel) och deras betydelse för SOC-lagring i svensk jordbruksmark genom tre studier. Rötter (0–40 cm djup) och skott provtogs under mjölkmognad/tidig degmognad i en 50 × 50 cm ruta vid 11 positioner inom ett fält i sydvästra Sverige under två år. Under båda åren odlades vårkorn (*Hordeum vulgare L.*). Rot-skott-kvoten varierade (kvartilvariationskoefficient = 7–18%), vilket indikerar att användning av fasta kvoter kan introducera osäkerhet i modellerade kolbalanser. Sur mineralmatjord (n = 100; 0–20 cm) från den svenska mark- och grödoinventeringen analyserades med avseende på fysikaliska och geokemiska egenskaper. Dispergering och oxalatextraktion i mörker användes för att bestämma aggregering i siltfraktionen respektive reaktiva mineralfaser. En random-forest-modell där mark-, bruknings- och klimatvariabler ingick identifierade oxalatextraherbart aluminium (Al_{ox}) som en starkare prediktor än lerhalt för SOC-halt, vilket antyder potential för ytterligare SOC-inlagring i jordar med högre Al_{ox}. Långtidsinkubationer i laboratoriemiljö (ca 500 dagar) med siktade jordprover (n = 35; 3–10 cm djup) från samma fält, analyserade med partial least squares-regression, gav däremot inget stöd för en skyddande effekt av SOC från Al_{ox}. Vid kvasi-steady state minskade den specifika respirationshastigheten med ökande halter av markens organiska kol (SOC), totalt kväve (TN) och C:N-kvoter, vilket tyder på ett skydd av SOC samt en möjlig inverkan av C:N-kvoten och TN på regleringen av SOC-mineralisering. Sammantaget visar resultaten att SOC-modeller behöver utvecklas till att utöver lerhalt och fasta rot-skott-kvoter även inkludera variabla koltillflöden och mineralfaser för att bättre kunna parameteriseras under svenska förhållanden.

Nyckelord: Jordens organiska kol; rot-skott-förhållande; oxalat-extraktionsbart aluminium; markövervakning; långtidinkubation; fuktigt klimat.

Preface

Whether or not the term kappa was always intended, its resonance in Swedish—as “coat”—feels fitting in this context. In that spirit, this kappa gathers and wraps the work undertaken over the past four (plus) years, while acknowledging the seams and openings that remain. Those openings are, to me, windows for future inquiry and places where new ideas may be stitched in. Questions will meet the reader throughout this kappa, and my hope is that they are approached with the same curiosity that has guided my work through these years. Like any coat, it both covers and invites adjustments, yet is always shaped by the body it covers.

I would like to preface this kappa by noting that my research explores soil organic carbon (SOC) in the context of mineral agricultural soils in Sweden. Since the industrial revolution, much of the land that once served as natural carbon sinks, such as forests and peatlands, has been converted for human use, particularly for agriculture, and has since undergone significant degradation (i.e. decrease in carbon stocks). Consequently, this thesis focuses on agricultural mineral soils, which both support local food production and offer considerable potential to store carbon in soil organic matter (SOM), thereby contributing to climate stability and the maintenance of ‘healthy’ soils essential for food production. SOC is central to this work because it underpins many of the ecosystem services that soils provide: Its storage can help reduce soil degradation and mitigate climate change impacts, but the size of the SOC pool is often uncertain. Hence, the guiding question of this thesis within a three-paper framework (**Paper I-III**) is: What are the factors influencing SOC storage in Swedish agricultural land?

SOC is primarily plant-derived, with roots serving as the main source. Once introduced into the soil, SOC interacts with a range of biotic and abiotic components, including minerals. My focus is on root biomass distribution and SOC interactions with reactive mineral phases of aluminum, which are believed to play key roles in long-term carbon stabilization. Although biological interactions also shape these processes, they are discussed here to contextualize the long-term carbon stabilization by reactive mineral phases. Other pathways of SOC stabilization, while relevant, are addressed in the appended papers but not elaborated in this kappa to avoid redundancy. I offer insights that may help frame new questions and bridge past and future understandings of current paradigms.

Dedication

In loving memory of my father, Davison. M. Chilipamushi (19th April 1959 to 28th June 2025) and my nephew, Levi James King (13th January 2025 to 3rd October 2025). May your memories remain immortalized.

Miyanda
/miˈandə/
noun
roots

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. Chilipamushi, M., von Brömssen, C., Colombi, T., Kätterer, T., & Larsbo, M. (2026). Within-field variation in root-to-shoot ratios and root traits in spring barley: Implications for estimating carbon inputs. Soil and Tillage Research, 260,107103. https://doi.org/10.1016/j.still.2026.107103.

II. Chilipamushi, M., von Brömssen, C., Colombi, T., Kätterer, T., & Larsbo, M. (2026). Oxalate-extractable aluminium is a key predictor of organic carbon content in Swedish agricultural topsoils. Geoderma Regional, e01038. https://doi.org/10.1016/j.geodrs.2025.e01038.

III. Chilipamushi, M., von Brömssen, C., Colombi, T., Kätterer, T., & Larsbo, M. Results from long-term incubations of agricultural topsoil did not indicate soil organic matter protection by reactive metal phases (manuscript).

The contribution of Miyanda Chilipamushi (MC) and each collaborator to the papers included in this thesis are described using the following abbreviations: Claudia von Brömssen (CvB), Tino Colombi (TC), Thomas Kätterer (TK), and Mats Larsbo (ML). The contributions are as follows:

I. MC: writing – original draft, writing – review and editing, visualization, validation, software, methodology, investigation, formal analysis, data curation. CvB: writing – review and editing, validation, supervision, methodology. TC: writing – review and editing, validation, supervision, methodology, conceptualization. TK: writing – review and editing, validation, supervision. ML: writing – review and editing, writing – original draft, validation, supervision, methodology, funding acquisition, conceptualization.

II. MC: writing – original draft, writing – review and editing, visualization, validation, methodology, investigation, formal analysis, data curation. CvB: writing – review and editing, validation, supervision, software, methodology, formal analysis, conceptualization. TC: writing – review and editing, visualization, validation, supervision, conceptualization. TK: writing – review and editing, validation, supervision, investigation, conceptualization. ML: writing – review and editing, visualization, validation, supervision, resources, investigation, funding acquisition, formal analysis, conceptualization.

III. MC: writing – original draft, writing – review and editing, visualization, validation, methodology, investigation, formal analysis, data curation. CvB: writing – review and editing, validation, supervision, software, methodology, formal analysis, conceptualization. TC: writing – review and editing, visualization, validation, supervision, conceptualization. TK: writing – review and editing, validation, supervision, investigation, conceptualization. ML: writing – review and editing, visualization, validation, supervision, resources, investigation, funding acquisition, formal analysis, conceptualization.

List of tables

List of figures

Abbreviations

Al_{ox}	Oxalate-extractable aluminum
BBCH	Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie
Ca_{ex}	Exchangeable calcium
CO_2	Carbon dioxide
C:N	Carbon-to-nitrogen ratio
DMAI	De Martonne aridity index
Fe_{ox}	Oxalate-extractable iron
GHG	Greenhouse gases
Gt CO_2-eq	Gigatonnes (1 billion metric tonnes) of carbon dioxide equivalent
ICP-SFMS	Inductively coupled plasma sector field mass spectrometry
ICBM	Introductory carbon balance model
KOH	Potassium hydroxide
K_{SOC}	Specific respiration rate at quasi-steady state
LV	Latent variable
MAP	Mean annual precipitation
MAT	Mean annual temperature
Mg_{ex}	Exchangeable magnesium
MSE	Mean squared error
NEON	National ecological observatory network
NPP	Net primary productivity
PDP	Partial dependence plot
Pg C	Petagram (1 billion metric tons) of carbon
pH(KCl)	Soil pH in potassium chloride
PLSR	Partial least squares regression
P_{ox}	Oxalate-extractable phosphorus
PTHBV	Precipitation–temperature hydrological agency water model

QCV	Quartile coefficient of variation
RFM	Random forest model
RMP	Reactive mineral phases
RothC	Rothamsted carbon model
SDG	Sustainable development goals
SLU	Swedish University of Agricultural Sciences
SMHI	Swedish meteorological and hydrological institute
SMP	Swedish national soil and crop monitoring programme
SOC	Soil organic carbon
SOM	Soil organic matter
SRO	Short-range order phases
SRR	Specific respiration rate
TN	Total nitrogen content

Nomenclature

Location	A georeferenced sampling point within a Site (see below), defined by coordinates and, where applicable, a field identifier, and represented in this study by a pooled composite sample.
Manuring	Application of animal manure to fields at the Site, categorized by the animal source, where available.
Operation	The primary production type at the Site, classified as crop-only, livestock-only, mixed crop–livestock, or none.
Practice	The management standard applied at the Site, classified as conventional or organic (self-reported or certified).
Reactive mineral phases	Al and Fe oxides, hydroxides and oxyhydroxides (often referred to as ‘oxides’), including short-range ordered (poorly crystalline) forms such as allophane and (partly) imogolite, as well as Al in organic complexes, interlayers and exchangeable forms. The oxides have small particle sizes, large specific surface areas and therefore high chemical reactivity (Rennert, 2019); this definition is here extended to the reactive phases of Mg and Ca which refer to a group of divalent base cations from geological or anthropogenic sources.
Rotation	The planned sequence of land use at the Site or field (e.g. annual crops only; annual crops with multi-year ley; almost exclusively ley).
Site	A single farm treated as one study unit, containing one or more sampling Locations (see above) and where applicable, represented in this study by a pooled composite sample.
Soil organic carbon (SOC)	Carbon in soil derived from organic matter (e.g. plant and animal residues), existing along a continuum from relatively fresh material to highly transformed forms produced by physical and oxidative transformation (Rowley, 2020).
SOC protection	A reduction in the mineralization rate of SOC relative to similar, unprotected organic materials, rather than a

	permanent or complete prevention of organic carbon mineralization (Baldock & Skjemstad, 2000).
SOC storage	'The size of the SOC pool (i.e., SOC stock or SOC content)' (Don et al., 2023).
Topsoil	The uppermost mineral soil layer, operationally defined in this thesis as the 0–20 cm depth interval, unless stated otherwise.

AI declaration

During the preparation of this thesis, I used Perplexity to assist in improving the readability and language of the manuscript. I subsequently reviewed and edited all content as necessary and take full responsibility for the final version of this publication.

1. Introduction

Soil organic carbon (SOC) in soils has been at the heart of research and even public interest in the recent past. SOC constitutes the largest terrestrial reservoir of organic carbon (C) (Stockmann et al., 2013). SOC is the principal component of soil organic matter (SOM), typically making up about 50% of SOM (Banwart et al., 2019; Pribyl, 2010), and plays a crucial role in determining the soil's capacity to perform key functions (Bonfante et al., 2020) and broader ecosystem functioning (Meurer et al., 2024). Consequently, SOC is commonly monitored to assess whether management practices effectively sequester C—that is, increase the C content of pools other than the atmosphere (Watson et al., 2000)—as part of efforts to mitigate climate change (Harbo et al., 2023; Poeplau et al., 2015) and to guide policy development (Reinsch et al., 2025). Even small relative changes in SOC stocks, determined as a product of the mass fraction (i.e. the SOC concentration) and soil mass soil per area, can significantly influence atmospheric carbon dioxide (CO_2) concentrations (Poeplau, 2021).

Agriculture currently occupies approximately 44% of the habitable land surface (Ritchie & Roser, 2019) and is a source of C to the atmosphere. This appropriation of land for agriculture has emitted approximately 133 Pg C over the past 12,000 years from the top 200 cm of soil, with losses rising much faster during the last 200 years (Sanderman et al., 2017; Stockmann et al., 2013). Within the European Union, agriculture accounts for 10% of total greenhouse gas (GHG) emissions; on a national level, in Sweden, for instance, it accounts for 14% of national emissions (Ibrahim & Johansson, 2021; Kuylenstierna et al., 2021). In 2023, GHG emissions from the Swedish agricultural sector were on the order of 6–7 million tonnes of CO_2 -eq (ca. 1.7×10^{-6} Pg C) (NID SE, 2025). One partial consequence: 13% globally and ca. 60–70% of European soils are considered degraded (Kay et al., 2022), with climate change further accelerating this trend (Veerman et al., 2020).

On the global stage, efforts to achieve C neutrality are anchored by the United Nations Sustainable Development Goals (SDG) complemented by the Paris Agreement (Sachs et al., 2019). In 2015, the United Nations established SDG, which include "climate action" and "life on land," aimed to combat climate change. The SDGs have been translated into national and global commitments to achieve net-zero GHG emissions and C neutrality by focusing on protecting and restoring natural C sinks, particularly forests, land, and soil (Mishra et al., 2024). According to Articles 4 and 12 of the United Nations Framework Convention on Climate Change under the Paris agreement, parties are required to annually submit national inventories of anthropogenic emissions by sources and removals by sinks of all GHG emissions (NID SE, 2025). This is done to monitor global progress, and ensure accountability for climate action (Friedlingstein et al., 2024; Hermwille et al., 2017).

However, global estimates of SOC stocks remain uncertain. For instance, within the upper 100 cm C contents have been estimated to 1,395 Pg (Post et al., 1982), 1,462–1,548 Pg (Batjes, 1996), 1,600 Pg plus 360 Pg in peatlands (Jacobson et al., 2000), 2,011 Pg (Watson et al., 2000), 2,500 Pg (Lal, 2004), and up to 3,250 Pg (Field et al., 2007).

1.1 What are the sources of uncertainty for SOC storage in agricultural land?

“*Plurality should not be posited without necessity.*”
William of Ockham

Soil organic carbon stocks are commonly estimated through models that rely on the principle of parsimony. For instance, soil C models such as ICBM (Andrén & Kätterer, 1997; Menichetti et al., 2024) or RothC (Coleman & Jenkinson, 1996; Poeplau, 2016) often use simplifying assumptions to determine C allocation, and subsequently for estimating SOC stocks (Menichetti et al., 2024; Poeplau, 2016). Moreover, soil properties are often insufficiently represented in models such as the ICBM (Andrén & Kätterer, 1997) or are simplified by relying primarily on clay content as an input parameter that determines and affects SOC storage by partitioning decomposition products (Coleman & Jenkinson, 1996). This means a higher clay content leads to a larger share of SOC being stabilized in the soil and less being mineralized and released as CO_2, which directly influences the accuracy of SOC stock predictions. The following sections elaborate on these two key input parameters—carbon inputs and soil properties, with particular emphasis on clay content—as possible sources of uncertainty that motivate the focus of this thesis.

1.1.1 Carbon inputs

One of the possible sources of uncertainty, when modelling SOC stocks, is the estimation of C inputs into the soil (Keel et al., 2017; Menichetti et al., 2024; Pausch & Kuzyakov, 2018). Root-derived C (i.e. root biomass and rhizodeposits) tend to form more stable SOC compared to input from above-ground plant residues (Gasser et al., 2022; Kätterer et al., 2011; Rasse et al., 2005). Roots therefore constitute major sources of SOM and influence SOC storage in agricultural systems (Kätterer et al., 2012; Paustian et al., 2016).

However, collecting and quantifying root biomass requires a considerable effort, which means that there is a limited availability of root data (Böhm, 1979; Cabal et al., 2021; Lux & Rost, 2012). This means that field specific data on root C inputs are often unavailable. Instead, estimates on how much C plant roots add to the soil are often derived from above-ground biomass or yield data using fixed "rules-of-thumb" based average root-to-shoot ratios (Jacobs et al., 2020). These fixed root-to-shoot ratios are averages derived from different kinds of studies, for example regional datasets (Bolinder et al., 2007).

The problem with this approach is that the root-to-shoot ratio varies considerably. Previous studies have focused on variation that occurs both between different crops (Bolinder et al., 1997; Bolinder et al., 2007; Mattila & Häkkinen, 2025) and within different crops (Heinemann et al., 2023; Mattila & Häkkinen, 2025), as well as between farming systems (Hirte et al., 2021) or differences due to fertilization regimes (Poeplau, 2016). Different weather conditions between years in perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) swards (Vinther, 2006) and between different barley cultivars and plant growth stages (Xu & Juma, 1992) have been suggested as reasons for variations in root-to-shoot ratios. In pot experiments under controlled greenhouse conditions, studies have focused on genetic differences expressed in different cultivars of a crop (Mathew et al., 2019), along with soil texture effects observed in barley (*Hordeum vulgare* L.) (Poeplau & Kätterer, 2017), ryegrass (*Lolium perenne* L.), and alfalfa *(Medicago sativa)* (Junchao et al., 2023).

Using average root-to-shoot ratios and ignoring within-field heterogeneity may therefore introduce uncertainty when estimating carbon inputs and SOC stocks. Due to spatial variation, field-average values may not be appropriate for soil C modelling. For instance, Poeplau (2016) demonstrated that applying a single fixed root-to-shoot ratio across all temperate grasslands in RothC could lead to incorrect estimates of belowground carbon inputs and SOC accumulation potential. These findings suggest that neglecting within-field variation, which remains unquantified in agricultural land, may introduce uncertainty in estimating carbon inputs and SOC stocks. This provides the first motivation (**M1**) for this thesis.

Until now, the magnitude of within-field variations in root-to-shoot ratios have not been quantified, since the focus has primarily been on soil and crop management effects. This means that variations in root-to-shoot ratio at the field scale under identical management practices and climate are unknown. In their European-scale study, Heinemann et al. (2023) suggested that variation in soil properties was an underlying reason for unexplained variations in root-to-shoot ratios in winter wheat. Investigating this field-scale variation would help to separate the individual effects of soil properties from those of management and climate influences, which are confounded in regional studies.

Thereafter, these carbon inputs encounter a heterogeneous and dynamic soil matrix, making their fate difficult to predict. This introduces the second source of uncertainty investigated in this thesis.

1.1.2 Soil properties

It remains unclear which and how soil properties affect SOC storage, as the scientific understanding of how SOM is stabilized—thereby limiting atmospheric losses through SOC mineralization (i.e., SOC protection)—is still inconsistent (Lehmann & Kleber, 2015). SOM associated with the mineral phase has been suggested to be particularly well protected, and roughly two-thirds of SOM occurs as mineral-associated organic matter (Sokol et al., 2022). In this context, clay content is commonly used as a predictor of SOC storage (Hassink & Whitmore, 1997; Martin et al., 2011; Poeplau et al., 2020) and as an input model parameter which directly influences the accuracy of SOC stock predictions. The following section will detail uncertainties related to the use of clay content as a predictor of SOC content and as an input parameter that determines and affects SOC storage.

Clay content as a predictor of SOC storage.

Clay content is often used as predictor for SOC storage at a regional scale, especially in agricultural soils (Feng et al., 2013; Martin et al., 2011; Poeplau et al., 2020; Prout et al., 2021; Six et al., 2002). It has often been suggested that finer particles (< 20 μm) such as clay, which exhibit a larger specific surface area, have a higher capacity to bind SOM or form stable aggregates (Hassink & Whitmore, 1997; Oades et al., 1989; Rabot et al., 2018). These mechanisms provide the scientific basis for soil C models to utilize clay content as a primary parameter for determining SOC storage in RothC for instance.

The notion that clay content is a good predictor of SOC storage gave rise to estimates of SOC storage capacity encapsulated in the '*carbon saturation concept'* (Hassink, 1997), which describes the capacity of a mineral soil to store carbon, i.e. its '*mineralogical capacity'*. The concept of SOC saturation is based on the finite capacity of soil to protect SOC, suggested by Hassink (1997) and re-iterated by Dexter *et al.*, (2008), among others (Beare *et al.*, 2014; Barré *et al.*, 2017). Soil is considered C-saturated when the amount of protected C is at its maximum, and additional inputs can no longer increase this pool (Castellano et al., 2015).

When the soil is not saturated, an increase in C inputs can increase the store of protected C. The difference between saturation and the current SOC storage is referred to as the *saturation deficit* (Castellano et al., 2015). In simple terms, soil with no protected SOC has a saturation deficit of 100%. In contrast, a C-saturated soil has zero saturation deficit (Castellano et al., 2015). From a different perspective, the term '*ecosystem capacity'* was introduced in the literature to argue that SOC accrual is primarily limited by the net primary productivity (NPP)—the actual amount of carbon input available from plants, modulated by site-specific factors, including soil texture, mineralogy, and climate (Poeplau et al., 2024). In this respect, Swedish agricultural soils may have the potential to accrue more carbon, since changes are positively related to the proportion of grass leys and the use of animal manure in dairy farms (Henryson et al., 2022; Poeplau, Bolinder, et al., 2015). Moreover, plotting SOM against clay content revealed a lower boundary that gradually rises with increasing clay content (Eriksson et al., 2000).

More recently, other geochemical factors have been suggested to be the best predictors of the spatial variation in SOC storage in agricultural soils

(Doetterl et al., 2015; Fukumasu et al., 2021; Georgiou et al., 2022; Hall & Thompson, 2021; Salonen et al., 2024; von Fromm et al., 2021; von Fromm et al., 2024; Weiglein et al., 2022). For instance, it has been shown that oxalate-extractable aluminum (Al_{ox}) and iron (Fe_{ox}), representing reactive mineral phases (RMP) (Rennert, 2019), are good predictors of SOC storage in acidic to neutral soils (Kleber et al., 2015; Rasmussen et al., 2018).

Studies have shown that Al_{ox} is a good predictor of SOC content in New Zealand and the US (Beare et al., 2014; Hall & Thompson, 2021). For instance, Hall and Thompson (2021) showed that Al_{ox} was the best predictor for SOC content in the National Ecological Observatory Network (NEON). The NEON database covers soils from continental northern America, Puerto Rico, Alaska, and Hawaii with diverse vegetation cover (Hall & Thompson, 2021; NEON, 2020; Yu et al., 2021). Furthermore, a strong positive correlation has been observed between Al_{ox} and SOC storage for soils sampled at 35 locations within a single field in southwestern Sweden (Fukumasu et al., 2021).

Although Al_{ox} and Fe_{ox} have been identified as strong predictors of SOC storage in acidic mineral soils under humid conditions, exchangeable cations such as calcium (Ca_{ex}) and magnesium (Mg_{ex}) have also been shown to be robust predictors of SOC storage. Mg_{ex}, often considered together with Ca_{ex}, represents a group of divalent base cations (Hall & Thompson, 2021; Lavallee et al., 2025; Yu et al., 2021), whose concentrations tend to increase with SOC in soils with acidic to neutral pH (King et al., 2023; Yu et al., 2021). For example, Ca_{ex} has been shown to be a strong predictor of SOC content at various spatial scales. At national and continental scales, Ca_{ex} predicts SOC content effectively under water-limited conditions characterized by alkaline pH, such as in North America (Rasmussen et al., 2018). Similar relationships have been observed in Sub-Saharan Africa (von Fromm et al., 2021) and in Japanese lowland soils under less acidic conditions (Ichinose et al., 2025).

However, there are also instances, where elevated Ca_{ex} concentrations are correlated with SOC content due to geological or anthropogenic factors. In Sweden and Switzerland, for example, Ca_{ex} enrichment has been attributed to carbonate-bearing parent materials and liming practices in agriculture (Ladenberger et al., 2013; Rowley, 2020). In Sweden, although carbonate-bearing lithologies are relatively rare, they occur in several cultivated areas and, together with anthropogenic calcium inputs from liming (Clason &

Granström, 1992; Ladenberger et al., 2013), which could be important for SOC storage.

These recent findings suggest that RMP are better predictors of SOC content than clay content in acidic agricultural mineral soils, providing the second motivation (**M2**) for this thesis.

It is unknown to which the extent observed relationships between RMP and SOC storage are universal and whether they are generally applicable for Swedish mineral agricultural soils. This should be investigated, as this knowledge is necessary for accurate model estimates of potential C storage at the reginal scale (Andrén & Kätterer, 1997; Bolinder et al., 2018).

However, it remains unclear whether the above-mentioned relationships between RMP and SOC reflect correlation or causation, as the underlying mechanisms are not fully understood. The following section introduces the third source of uncertainty addressed in this thesis.

Clay content as an input parameter for SOC mineralization.

Some SOC models still represent soil properties in a simplified or incomplete manner when simulating SOC mineralization using first-order kinetics (Andrén & Kätterer, 1997) and clay content to partition carbon between CO_2 emissions and soil retention (Coleman & Jenkinson, 1996). Since SOC content is often better predicted by RMP than by clay content, prevailing frameworks suggest RMP-mediated protection as a constraint on SOC mineralization—and thus a determinant of SOC storage—alongside environmental conditions (Conant et al., 2011; Cotrufo & Lavallee, 2022; Cotrufo et al., 2019; Creamer et al., 2011; Dungait et al., 2012; Fukumasu et al., 2021; Kleber et al., 2021). Mechanisms of SOC protection have been suggested in conceptual frameworks (Kleber et al., 2021) and empirically using sorption experiments that quantify carbon removal from solution (Bruneel & Spohn, 2025; Chen et al., 2020), as well as implicitly in correlations between RMP and SOC storage as discussed above.

In a comprehensive review, Kleber et al. (2021) suggested that the main mechanisms of RMP–organic interactions are: (1) Adsorption**.** Organic molecules accumulate on mineral surfaces through various bonding types, including ligand exchange (forming strong inner-sphere complexes), cation bridging, and weaker outer-sphere interactions such as van der Waals forces.

This process is often conceptualized as a zonal or multilayer architecture, where the initial monolayer binds directly to mineral surfaces and subsequent layers form through organo–organo interactions. (2) Co-precipitation. This mechanism involves the formation of insoluble organo–mineral complexes and is considered particularly important in acidic soils where RMP of Al and Fe form flocs that occlude SOC (Jamoteau et al., 2023).

Aggregation has also been proposed as an important mechanism for SOC protection. In Andisols, it was suggested that SRO minerals and Al–organo complexes promote aggregation in soils with low pH and high C content (Matus et al., 2014). Also, microaggregates in surface horizons of Andisols were characterized by high concentrations of SOM and SRO minerals, particularly allophane and imogolite (Asano & Wagai, 2014). Microaggregates may endure significant mechanical, physicochemical, and water-slaking stressors, and thereby persist in soils (Totsche et al., 2018). The RMP enhance the association of OM bound by cementing and gluing agents (Rowley et al., 2018; Schlüter et al., 2022; Totsche et al., 2018). This leads to the third motivation (**M3**) for this thesis.

> *Empirical evidence is lacking that demonstrates if RMP constrain SOC mineralization in agricultural soils. It is possible to investigate the role of RMP in mineralization of the protected SOC pool in long-term incubations under controlled conditions; such multi-month to multi-year studies have been carried out far less frequently than shorter-term incubations (Bond-Lamberty et al., 2024; Liu et al., 2006; Zhang et al., 2025). The initial phase of long-term laboratory incubation experiments is characterized by a rapid decline in SOC mineralization rates, which then transition to a much slower, more constant phase, eventually reaching a quasi-steady state (Birge et al., 2015; Gasser et al., 2022; Joergensen et al., 1990; Lomander et al., 1998; Tian et al., 2016). This state can be used to access how RMP may constrain SOC mineralization in agricultural soils.*

Soil organic carbon is the largest terrestrial organic carbon pool. Yet global SOC stock estimates remain uncertain because process-based models rely on simplified representations of carbon inputs and soil properties. This thesis therefore addresses three sources of uncertainty that may affect SOC storage predictions in Swedish agricultural soils: (**M1**) spatially variable carbon inputs (especially root-derived inputs) within a field, (**M2**) the relative importance of clay content versus RMP in controlling SOC storage, and (**M3**) whether RMP constrain SOC mineralization and thereby influence SOC storage. These questions are examined in a three-paper framework (**Papers I–III**) using an empirical approach based on field data and a statistically representative subsample of Swedish agricultural soils spanning major humidity gradients and contrasting soil properties.

2. Aims and objectives

The overarching aim was to evaluate the sources of uncertainty that influence estimates of the storage of SOC in Swedish agricultural soils using an empirical approach. Figure 1 summarizes the conceptual framework of the included studies; these are referred to as Papers **I–III**, each having one specific objective below.

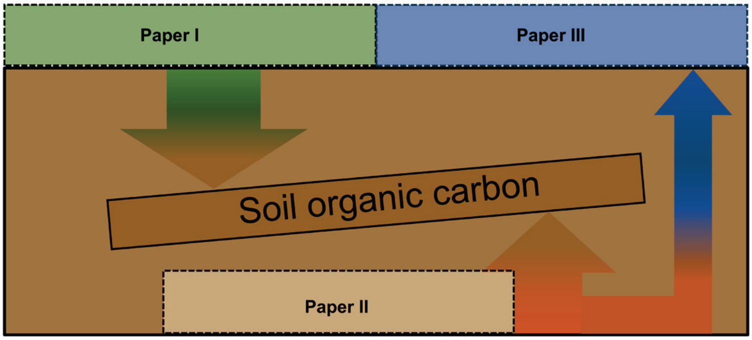


Figure 1 Conceptual framework of the thesis showing how **Papers I–III** operationalize the stated aims and objectives. Arrows indicate carbon flux between the soil and the atmosphere in the context of this thesis.

The specific objectives based on the motivations **M1-M3** were:

- **O1** To quantify within-field variation in the root-to-shoot ratio in spring barley and test whether soil properties explain this variation (**M1**, **Paper I**).
- **O2** To identify the strongest predictors of SOC content across a humidity gradient in Swedish agricultural soils, with particular focus on oxalate-extractable aluminum (Al_{ox}) and iron (Fe_{ox}) (**M2**, **Paper II**).
- **O3** To test whether the predictors identified as the most important in **Paper II** can explain variability in SOC mineralization rates, and thus the protection of SOC in agricultural soils, using long-term incubation experiments (**M3**, **Paper III**).

3. Methods and materials

3.1 Site description

The Swedish national soil and crop monitoring programme (SMP; accessible at https://miljodata.slu.se/mvm/aker) was used to access an inventory of agricultural topsoil samples in **Paper II**. In addition, a previously characterized field in southwestern Sweden served as the study site in **Paper I** and in **Paper III.** A total of 101 agricultural sites in Sweden, across a climatic (temperature and precipitation) gradient, were included in this study (Fig. 2). Samples for **Papers I** and **III** were collected at the same agricultural site (Bjertorp), whereas **Paper II** drew on sites distributed across the entire country, thereby encompassing the geographical context of Bjertorp. Sites (n=100) used in **Paper II**, were selected from the Swedish national soil inventory (Inventory III from 2011–2017), which is part of the SMP managed by the Swedish University of Agricultural Sciences (SLU) shown in Fig. 2A.

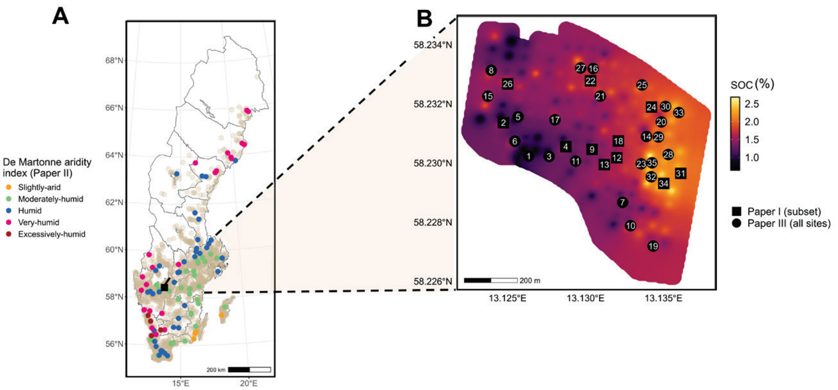


Figure 2 Map of Sweden and the Bjertorp agricultural field. (A) Locations of fields included in **Paper II** from the national soil inventory within Swedish national soil and crop monitoring programme, based on archived topsoil samples from Inventory III (2011–2017); colors show the geographical location of each site according to De Martonne aridity index, and sites shaded in tan in the background are all the sites sampled in 2011–2017 in Inventory III of the SMP. (B) Sampling locations in the Bjertorp field used in **Papers I** and **III**; **Paper III** includes all 35 points (represented by circles and squares), whereas **Paper I** includes only the locations indicated by squares.

Across the 100 sites in **Paper II**, 43% of the farms were arable (crop-only), 31% livestock-only, 24% mixed crop–livestock, and 2% reported no specific activity. Crop rotations were classified as annual crops only (34%), annual crops with several years of ley (31%), and almost exclusively ley (27%). Manure was applied at 46% of the sites, while 54% reported no manure application. Conventional farming practices dominated (86%), with the remaining 14% of sites practicing organic farming.

To delineate climatic regions in **Paper II**, the De Martonne aridity index (DMAI) was used as a humidity–aridity measure, where low scores denote arid conditions and high scores denote humid conditions (De Martonne, 1925), as shown in Fig. 2A. Temperature and precipitation for each field were obtained from gridded interpolated datasets provided by the Swedish meteorological and hydrological institute (SMHI) and averaged over 1961–2017 to determine the DMAI. According to the DMAI, climatic conditions across the selected sites in **Paper II** range from slightly arid (30 ≤ DMAI ≤ 35) to excessively humid (60 ≤ DMAI ≤ 187) (Fig. 2A). Of the sites, 4% were classified as slightly arid (30 ≤ DMAI ≤ 35), 31% as moderately humid (35 < DMAI ≤ 40), 39% as humid (40 < DMAI ≤ 50), 22% as very humid (50 < DMAI ≤ 60), and 4% as excessively humid (60 < DMAI ≤ 187). Sites in northern and central Sweden are characterized as humid. For the sites in northern Sweden, conditions span from very humid to humid, while the central regions range from moderately humid to humid. Southern Sweden is characterized by a mixture of humid and slightly arid conditions: from slightly arid to excessively humid.

Samples in **Papers I** and **III** were collected from a 47.9 ha conventionally managed field in Bjertorp in south-western Sweden (58°14′00″N, 13°08′00″E; Fig. 2B). The site is humid (40 < DMAI ≤ 50) according to the DMAI classification using temperature and precipitation averaged over 1961–2024 from SMHI. The site was selected because extensive physical and chemical soil analyses have previously been conducted on samples from this field (Fukumasu et al., 2021; Lindahl et al., 2008), and because its clay content (8–42%) and SOC content (1.1–2.7%) show large within-field variability (Fig.2; Table 1).

Table 1 Mean, standard deviation (S.D.), minimum and maximum values of basic soil properties (n = 35) measured on samples taken at Bjertorp in August 2017 and elevation at respective soil sampling locations (Fukumasu et al., 2021).

Variable	Abbreviation	Units	Mean	SD	Minimum	Maximum
Elevation	Elevation	m (above sea level)	92.61	2.73	87.37	95.41
Clay content	Clay	%	27.15	9.14	8.40	42.20
Silt content	Silt	%	47.04	11.97	19.5	61.30
Sand content	Sand	%	25.81	20.35	4.70	72.00
Oxalate extractable aluminum	Al_{ox}	g kg^{-1}	1.61	0.25	1.08	2.13
Oxalate extractable iron	Fe_{ox}	g kg^{-1}	5.64	1.91	2.53	8.81
Soil organic carbon content	SOC	g kg^{-1}	17.04	4.48	11.24	27.18

3.2 Sampling

Samples for **Papers I** and **III** were collected from the Bjertorp field over three different years. For **Paper III**, soils (3–13 cm depth) were sampled at all 35 locations within this site, as previously stratified by Fukumasu et al. (2021) based on the SOC–clay relationship (Fig. 2B; Table 1). In **Paper I**, a subset of 11 locations was selected from the 35 locations using systematic sampling at a fixed interval based on SOC content, ensuring representativeness in clay content and SOC content from the 35 locations in **Paper III**. At each of these 11 locations, shoot and root biomass of two-rowed spring barley (*Hordeum vulgare* L.; cultivars Laureate in 2023 and Lexy in 2024) were sampled in two consecutive years (2023–2024) using 50 cm × 50 cm quadrats. Roots were collected to 40 cm depth in two increments (0–20 cm and 20–40 cm), sampled both within and between crop rows.

For **Paper III**, soil sampling was conducted after wheat (*Triticum aestivum*) harvest between 30 August and 1 September 2021. For **Paper I**, spring barley sampling took place on 25–26 July 2023 and 29–30 July 2024 during early to mid-reproductive growth stages (BBCH 71–83). Weather conditions differed between the two years: April 2023, the sowing month, had the lowest precipitation of the growing season (18.1 mm); April 2024 received about six times more precipitation than April 2023. Between April and June, cumulative precipitation was smaller in 2023 (97.1 mm) than in 2024 (254 mm), whereas mean temperatures were similar at about 12 °C.

Sites for **Paper II** were selected to represent the geographic extent of Swedish agricultural soils. The analysis used the most recent complete sampling campaign (Inventory III, 2011–2017) from the SMP available at the time of data synthesis. From Inventory III, mineral (SOC $\leq$ 70 g kg^{-1}) and acidic (pH $<$ 7) soils were selected , given evidence that RMP contribute to SOC stabilization under acidic conditions (Rasmussen et al., 2018). The sampling strategy for the 100 sites used in **Paper II** is illustrated in Fig. 3. Briefly, a subset of mineral, acidic soils was stratified into four groups representing all combinations of low and high pH and SOC, and 100 sites were then randomly selected, with 25 sites drawn from each group. From each site composite samples of pre-existing air-dried topsoil (0–20 cm) were used.

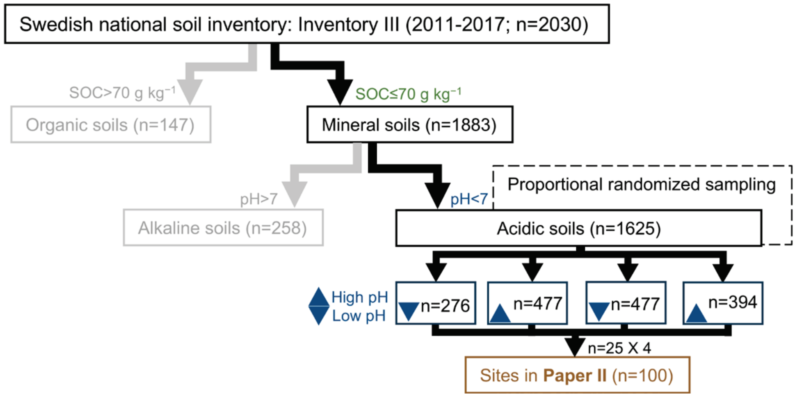


Figure 3 Selection of the 100 sites included in **Paper II** from the Swedish national soil inventory, based on archived topsoil samples from Inventory III (2011–2017). A subset of mineral soils with soil organic carbon (SOC) ≤ 70 g kg^{-1} and pH < 7 was stratified into four groups: two groups at lower pH (≈5.0–6.0) and two groups at higher pH (≈6.1–6.9), all with overlapping SOC ranges. These groups do not represent strict "high" versus "low" thresholds, but rather partially overlapping intervals used for stratified random sampling. From each group, 25 sites were selected by proportional random sampling, yielding 100 sites in total. Triangles indicate group membership: blue symbols high versus low pH (upward-pointing triangles represent "high", downward-pointing "low").

3.3 Core analyses

All three papers include SOC content and soil physical properties (clay and silt contents) analyzed using standard laboratory methods for SOC and soil texture. Unless stated otherwise, data were obtained from pre-existing sources: Inventory III of SMP and Fukumasu et al. (2021). In **Paper II**, oxalate-extractable aluminum (Al_{ox}), iron (Fe_{ox}), and phosphorus (P_{ox}) and silt-sized aggregation were analyzed using samples from Inventory III (n = 100), as detailed in the subsections below. Silt-sized aggregation is described as difference in the volume of fine particles released upon destroying the aggregate structure after mechanical dispersion and dispersed by SOM removal (Fukumasu et al., 2021). In this study, the aggregates were destroyed by shaking soil samples overnight on a reciprocating shaker set to 210 strokes per minute, following the method described by Svensson et al. (2022). The difference is the

Bjertorp samples were collected in the field and analyzed according to the methods specified for **Papers I** and **III** (see Table 2). The specific respiration rate (SRR) analyzed in **Paper III** for the Bjertorp samples (n=35) is described below in Table 2. The root-to-shoot-ratio was determined for a subset of locations (n=11) from the root and shoot biomass across two consecutive years for **Paper I**. Climatic variables for **Papers I** and **II** were obtained from the SMHI, and farm management data for **Paper II** were taken from the SMP. Table 2 summarizes the variables, methods, sampling depths, data sources, and references used across datasets and papers.

Table 2 Summary of soil-, biological, physical, climatic, and management variables used in **Papers I–III** with analytical methods, sampling depths, data sources, and references

Variable	Units	Method	Sampling depth	Data/soil sampling source	Reference
Soil organic carbon					
Soil Organic Carbon content	g kg^{-1} soil	Dry combustion (elementary analysis); ISO 10694:1995	0–20 cm	Inventory III (n=100)	Paper II
			3–13 cm	Bjertorp (post-incubation; n=35)	Paper III
			3–13 cm	Fukumasu et al., 2021 (pre-incubation; n =35 and subset; n=11)	Paper I & III
Biological variables					
Root-to-shoot ratio	-	Visual identification	0–40 cm	Bjertorp (n=11)	Paper I
Specific respiration rate	µg CO_2-C g^{-1} SOC h^{-1}	Incubation with chamber alkali trap respirometry	3–13 cm	Bjertorp (n=35)	Paper III
Soil physical variables					
Soil texture (Clay and silt content)	%	Pipette method after organic matter oxidation; ISO 17892-4:2016	0–20 cm	Inventory III (n=100)	Paper II
			3–13 cm	Fukumasu et al., 2021 (n=35)	Paper I & III
Silt-sized soil aggregation	-	Laser diffraction (Partica LA-950 V2, Horiba); ISO 13320:2020	0–20 cm	Inventory III (n=100)	Paper II
Soil chemical variables					

Exchangeable magnesium (Mg_{ex}), manganese (Mn_{ex}), calcium (Ca_{ex}), and potassium (K_{ex})	g kg^{-1} soil	Element concentrations analyzed using the 200.8 method by Inductively Coupled Plasma Optical Emission Spectroscopy (ICP SFMS)	0–20 cm	Inventory III (n=100)	Paper II
Oxalate-extractable Aluminum (Al_{ox}), Iron (Fe_{ox}) and Phosphorus (P_{ox})	g kg^{-1} soil	Acid extraction followed by element concentration analyzed by ICP SFMS; SLU marklabb, 09.06.2021	0–20 cm	Inventory III (n=100)	Paper II
			3–13 cm	Fukumasu et al., 2021 (n=35)	Paper III
Soil pH	-	Sodium chloride; SS-ISO 10390:2007	3–13 cm	Bjertorp (n=35)	Paper III
		Water; SS-ISO 10390	0–20 cm	Inventory III (n=100)	Paper II
		Climatic variables			
Mean annual temperature (MAT)	°C	Gridded data: Precipitation temperature hydrological agency water model (PTHBV)		SMHI (1961–2017)	Paper II
				SMHI (2023 and 2022)	Paper I
Mean annual precipitation (MAP)	mm	Gridded data; Precipitation temperature hydrological agency water model (PTHBV)		SMHI (1961–2017)	Paper II
				SMHI (2023 and 2022)	Paper I

De Martonne aridity index (DMAI)	-	$\frac{MAP}{MAT + 10}$		SMHI	Paper II
		Management variables			
Practice	-	Farmer interviews for current crop, farm type, crop rotation, and manure application		SMP (n=100)	Paper II
Operation	-			SMP (n=100)	Paper II
Rotation	-			SMP (n=100)	Paper II
Manuring	-			SMP (n=100)	Paper II

3.3.1 Oxalate extraction

Since routine measurements of RMP and phosphorus are not available in the SMP, targeted oxalate-extraction analyses were conducted to expand the pre-existing SMP dataset (**Paper II**). Oxalate-extractable aluminum (Al_{ox}), iron (Fe_{ox}), and phosphorus (P_{ox}) were determined on the samples from Inventory III using acid ammonium oxalate extraction (a mixture of ammonium oxalate and oxalic acid, pH ≈ 3, performed in the dark to prevent photochemical reactions (Deb, 1950; Rennert, 2019)) followed by inductively coupled plasma sector field mass spectrometry (ICP-SFMS). For **Paper III**, pre-existing Al_{ox} and Fe_{ox} data from Fukumasu et al. (2021) were used.

Acid ammonium oxalate in the dark is a widely used extraction method that selectively dissolves reactive mineral Al and Fe phases and P (Dahlgren & Ugolini, 1991; Ichinose et al., 2025; McKeague, 1967; McKeague & Day, 1966). The Al extracted with oxalate (Al_{ox}) in the dark is considered to represent hydroxy-interlayer Al, poorly crystalline Al oxides, allophane (which may be underestimated if present in large amounts; Rennert, 2019), imogolite and other poorly crystalline aluminosilicates (Hall & Thompson, 2021; Matus et al., 2008), as well as Al in Al–SOM complexes (McKeague & Day, 1966). The Fe extracted with oxalate (Fe_{ox}) in the dark is interpreted as a group of Fe-bearing phases, including poorly crystalline Fe oxides and Fe–SOM complexes, and may also include a portion of Fe in more crystalline minerals (Rennert, 2019). In this thesis, Al and Fe oxides, hydroxides, and oxide–hydroxides are collectively referred to as oxides.

3.3.2 Root-to-shoot ratio

The root-to-shoot ratio in **Paper I** was calculated from oven-dry masses of root and shoot biomass and determined in the sequence illustrated in Fig. 4. Briefly, shoots were harvested in 50 cm × 50 cm quadrats using an electric clipper at 1 cm stubble height each year.

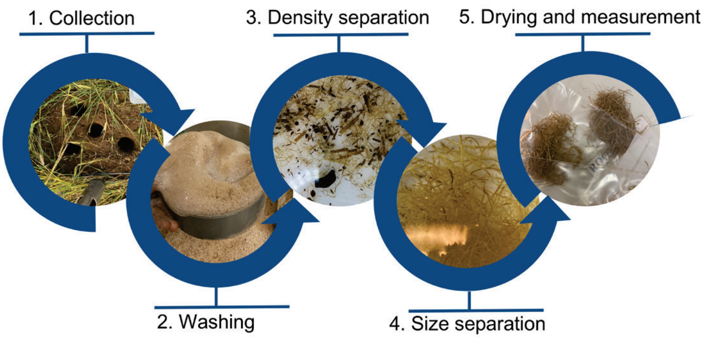


Figure 4 Workflow for root sample processing: (1) field collection within 50 cm × 50 cm quadrats with coring to 40 cm depth in 20 cm increments; (2) washing to free roots from soil using unscented liquid detergent; (3) density separation by flotation/settling to separate soil particles from plant material; (4) size/color separation under a 127 mm magnifying lamp (570-lumen LED) using tweezers to isolate roots from non-root material; and (5) drying at 60 °C for 48 h to constant mass, followed by biomass determination.

The shoot biomass, SB (g m^{-2}), was determined by:

$$SB = \frac{M}{A_Q} \quad \text{...(i)}$$

where M (g) is the dry weight of the shoots, and A_Q (m^2) is the quadrat area.

Within the same quadrats, four root cores were taken with a 7-cm-diameter auger to 40 cm depth in two increments (0–20 and 20–40 cm), both within and between crop rows. Samples were stored at −20 °C until processing. Roots were separated and quantified as described in Fig. 4; this involved washing to remove soil, density separation, size/color separation, drying at 60 °C for 48 h, and weighing.

Total root biomass was calculated from the sum of the samples collected between and within the rows in the quadrant following the procedures of Frasier et al. (2016) adapted by Hirte et al. (2021) as follows:

$$RB_{within} = \frac{M_{within}}{\pi * \left(\frac{d}{2}\right)^2} * \frac{d}{s} \quad \text{(ii)}$$

$$RB_{between} = \frac{M_{between}}{\pi * \left(\frac{d}{2}\right)^2} * \frac{s-d}{s} \quad \text{(iii)}$$

where RB_{within} (g m^{-2}) and $RB_{between}$ (g m^{-2}) denote root biomass within and between rows respectively, M_{within} (g) and $M_{between}$ (g) denote the dry weight of roots extracted from the soil cores taken within and between rows respectively, d (m) is the inner diameter of the auger, and s (m) is the distance between rows. Root biomass (0–40 cm) and shoot biomass data were then used to calculate root-to-shoot ratios.

3.3.3 Incubation experiment

The incubation experiment used to determine the SRR and K_{SOC} in **Paper III** is described briefly here and illustrated in Fig. 5. The experiment ran for a total of 579 days using 40 g of air-dried and sieved topsoil (<2 mm) collected from the field in Bjertorp (n=35), with three replicates. The air-dried sieved soil samples were placed in perforated containers in 65-mL polypropylene containers (Haney & Haney, 2010). Samples were rewetted to 65% of water holding capacity and re-moistened when approximately 5% water loss was observed. A filter paper was placed at the bottom of the containers to prevent soil loss during incubation, since we added water from below (Haney & Haney, 2010).

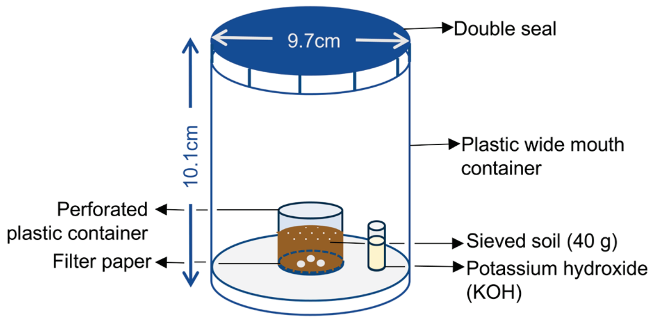


Figure 5 Soil respiration incubation setup: 40-g soil replicates (n=3) in polypropylene beakers with filter paper, incubated in 0.65-L airtight chambers with 15 ml 0.05 M potassium hydroxide (KOH) traps at 22 °C, at 65% water holding capacity, measured over 579 days from daily to monthly intervals

3.4 Statistical analysis

Across **Papers I–III**, non-parametric methods, multivariate, linear or machine-learning models were applied as appropriate to data type and assumptions. A summary and rationale of each method and model used in each paper is given in Table 3. I used Spearman rank correlation matrices for exploratory analyses in all studies. In **Paper I**, the small sample size made normality difficult to verify, so inference relied on non-parametric procedures, including the Wilcoxon signed rank test for group comparisons using a significance threshold of $p < 0.05$. Additionally, the quartile coefficient of variation (QCV) was used to characterize variability (Bonett, 2006; Botta-Dukát, 2023). The QCV was calculated from the first and third quartiles as:

$$QCV = \frac{Q3-Q1}{Q3+Q1} \quad \text{(iv)}$$

where Q1 is the population 25th percentile and Q3 is the population 75th percentile.

In **Paper II**, a random forest model (RFM) was used to identify informative predictor variables using SOC content as the response variable. From the RFM, the variable importance was quantified based on the increase in mean squared error (MSE) observed when each variable was excluded from the model. Furthermore, the Boruta algorithm was used to select the relevant variables with respect to the response variable. Additionally, partial dependence plots (PDP) were generated to illustrate the marginal effect of each predictor on the response variable, while holding other predictors constant.

In **Paper III**, the response variable K_{SOC} was quantified as the mean specific respiration rate, calculated from estimated marginal means (n=4) over the incubation period between days 296 and 426 using a linear mixed model. Partial least squares regression (PLSR), as detailed in Table 3, was used to explain variation in the response variable. Loadings on latent variables (LV) indicated the contribution of each explanatory variable, which facilitated mechanistic interpretation.

Table 3 Description of all the statistical methods used, the rationale, response variables and packages used in **Paper I–III.**

Method/model	Rationale	Response variable	R-package
Spearman's rank correlation	Used to examine pairwise relationships among non-normal variables.	-	Base
	Paper I		
Quartile coefficient of variation	Used to examine magnitude of variation.	-	Base
Wilcoxon signed rank test	Used to examine pairwise relationships among non-normal variables.	Root-to-shoot ratio	Base
	Paper II		
Random forest model (RFM)	Predict the response and determine the variable importance.	Soil organic carbon content	"RandomForest" (Friedman, 2001; Liaw & Wiener, 2002)
Partial dependency plots (PDP)	Show the marginal effect of each predictor on the response while the remaining predictors were held constant.	Soil organic carbon predictions	"PDP" (Greenwell, 2017)
	Paper III		
Partial least squares regression (PLSR) model	To explain variation in the response, aiming to better understand potential mechanisms underlying SOM protection.	Specific respiration rate at quasi-steady state (K_{SOC})	"pls" package (Mevik & Wehrens, 2007)
Linear mixed models (LMM)	Fit a mixed linear model to determine the estimated marginal means at quasi-steady state used in the PLSR as the response variable.	Specific respiration rate (SRR)	"lme4" package (Bates et al., 2015) "emmeans" R package (Lenth & Lenth, 2018)

Data processing and analyses were carried out using R version 4.4.1 (R Core Team, 2025). Unless stated otherwise, descriptive statistics were generated with the "psych" package (Revelle & Revelle, 2015), and all figures and geographical illustrations were created using the "ggplot2" package (Wickham, 2016), “ggspatial” (Dunnington, 2023), and “ggtern” (Hamilton & Ferry, 2018).

4. Results and discussion

4.1 Within-field variation in root-to-shoot ratios and root traits: Implications for estimating carbon inputs (Paper I)

The following section addresses **O1**, which was to quantify within-field variation in the root-to-shoot ratio of spring barley, assess whether soil properties explain this variation, and discuss the implications for estimating below-ground carbon inputs, as presented in **Paper I**.

4.1.1 What is the magnitude of variation in the root-to-shoot ratio of barley within a single field with the same management?

Figure 6A shows that within-field variability in the root-to-shoot ratio was about 18% in 2023 and 7% in 2024. In 2023, shoot biomass ranged from 600 to 1,100 g m^{-2} (QCV = 10%), while total root biomass ranged from 65 to 153 g m^{-2} (QCV = 9%). In 2024, shoot biomass ranged from 737 to 1,445 g m^{-2} (QCV = 10%), and total root biomass ranged from 114 to 226 g m^{-2} (QCV = 25%). Consequently, root-to-shoot ratios across both years spanned 0.08–0.20. Year-to-year comparisons revealed inconsistent spatial patterns (Fig. 6B), with location-level changes ranging from decreases of up to 54% to increases exceeding 100% (Fig. 6C).

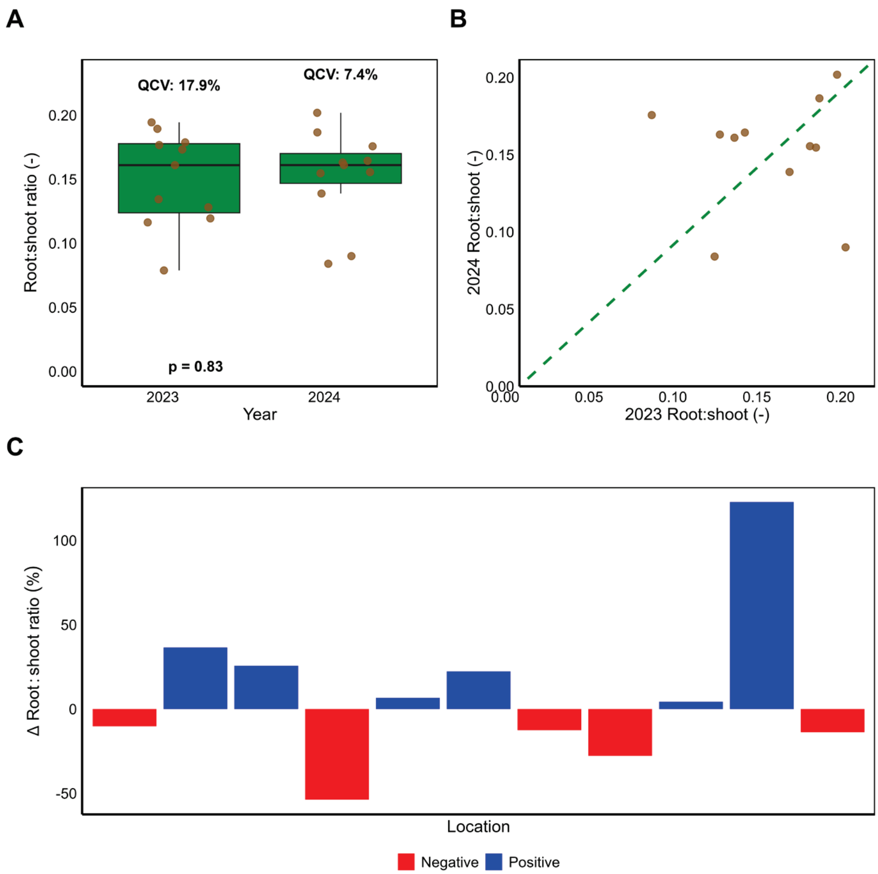


Figure 6 Distribution of: (A) root-to-shoot ratios by year (each point represents the ratio at one location) and (B) year-to-year differences in root-to-shoot ratio (each point shows the ratio at the same location in 2023 and 2024). (C) Relative change in root-to-shoot ratio at each sampling location between 2023 and 2024, with sampling conducted at the early to mid-reproductive stage (milking to early-dough; BBCH 71–83) in Bjertorp. The quartile coefficient of variation (QCV) describes relative variability, and p-values are from Wilcoxon signed-rank tests.

The observed variation (Fig. 6A) in this study suggests that within-field variability exists even under uniform management of the same crop. Larger variation in root-to-shoot ratios has also been reported in the literature for cereals and other crops across different climates and management regimes, both at regional scales and in plot experiments. For instance, a Finnish study (values derived from raw data) found QCVs of 40% in 2021 and 54% in 2023 across multiple farms and spring crops when considering roots down to 40 cm depth (Mattila & Häkkinen, 2025). Similarly, Canadian field and plot studies reported root-to-shoot ratios for small grain crops ranging from 0.1 in western Canada to 0.6 in the east (Bolinder et al., 1997; Xu & Juma, 1992). In eastern Canada, barley (cultivars: Leger, Chapais, and Codac) showed average ratios of 0.4–0.6 in plot experiments to 30 cm depth, under a mean annual temperature of approximately 5.2 °C and precipitation around 987 mm—values comparable to long-term conditions at Bjertorp (6.8 °C and 706 mm between 1961–2024) (Bolinder et al., 1997). In western Canada, ratios ranged from about 0.08 to 0.1 during the heading-to-ripening period for barley cultivars: Abee, Bonanza, Harrington, and Samson, under drier conditions with an average precipitation of 452 mm (Xu & Juma, 1992).

Studies in northern Switzerland (root-to-shoot ratios 0.07–0.22) and Finland (0.04–3.18 for annual crops) further emphasize the variation between different management practices, crops, soil texture, and local pedoclimatic factors shaping root-to-shoot allocation (Hirte et al., 2021; Mattila & Häkkinen, 2025). Collectively, these findings demonstrate that variability in root-to-shoot ratios occurs not only across regions and management systems but also within individual fields under uniform management for the same crop. This underscores the importance of local-scale patterns in belowground carbon allocation and motivates the questions examined in the following subsection.

4.1.2 What drives within-field variation in root-to-shoot ratios under uniform management?

In addition to the inconsistency in the year-to-year comparisons and location-level changes (see section 4.1.1; Fig. 6B-C), the root-to-shoot ratio showed no significant correlation with either clay content or elevation in either year (Fig. 7).

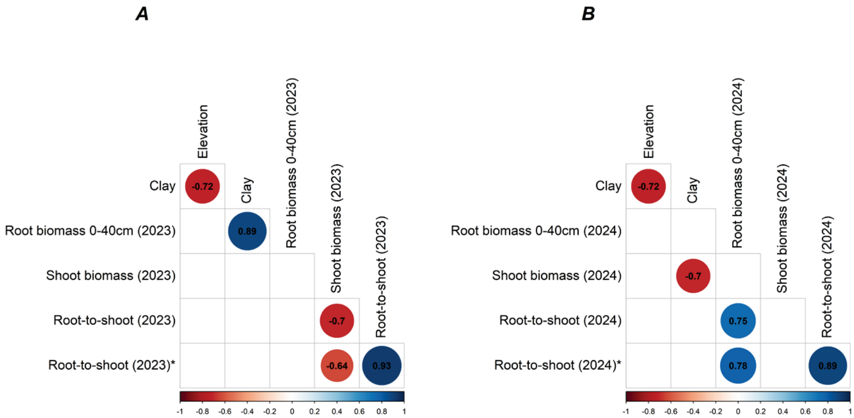


Figure 7 Spearman rank correlation coefficients (rho) between soil and site parameters measured in 2017 at 0–20 cm (Fukumasu et al., 2021) and four response metrics: root-to-shoot ratio at 0–20 cm in: (A) 2023 and in (B) 2024, and the ratio computed using total root biomass (0–40 cm; Root-to-shoot*). Only statistically significant correlations are displayed.

In response to the question posed in this subsection's title, the short answer is that the source of the observed variation remains unclear, as the root-to-shoot ratios were inconsistent between years and (Fig. 6B) showed no significant correlation with either clay content or elevation in both years (Fig. 7). Although no significant correlation with clay content was found for the ratio itself, a strong positive relationship was observed between clay content and root biomass in 2023 (Fig. 7A), while clay content was negatively correlated with shoot biomass in 2024 (Fig. 7B). These contrasting relationships coincided with different precipitation patterns during the early growing season, with 2023 being drier than 2024.

It is therefore reasonable to hypothesize that year-specific factors, such as the interaction between site-specific soil properties and inter-annual weather variability, may explain the differences observed. The absence of correlation in root-to-shoot ratios between years (Fig. 6B) further supports the idea that environmental conditions and soil factors may interact differently from one year to the next, influencing belowground and aboveground biomass allocation.

Climate conditions and their interaction with local soil properties may influence plant allocation patterns (Thornley, 1972). Clay soils typically exhibit higher water-holding capacity (Jacobsen, 1989; Palta & Turner, 2019), better nutrient accessibility (Mathew et al., 2020; Poorter & Nagel, 2000) but poorer drainage than sandy soils (Palta & Turner, 2019), all of which can affect root-to-shoot ratios. In our study, the clay content ranged from 8% to 42%, while cumulative precipitation between sowing and harvest differed between the two sampled years.

For instance, drier years have been associated with reduced topsoil root biomass but increased rooting depth in Nordic cereals under field conditions (Hu et al., 2018; Mattila & Häkkinen, 2025). Alternatively, under climatic conditions comparable to southern Sweden (mean daily temperature 12.5 °C), with irrigation every 3 days initially and daily toward the end of the experiment, Poeplau and Kätterer (2017) found that root-to-shoot ratios in spring barley (cultivar: Tipple) decreased significantly with increasing clay content (8%, 18%, and 30%), demonstrating the isolated effect of soil texture with constant irrigation. However, root-to-shoot ratios in our study showed no significant correlation with either clay content or elevation in either year.

Another plausible explanation for the observed differences involves crop cultivars (cultivars: Lexy and Laureate). For instance, a field study of 10 winter wheat cultivars grown at 11 sites across Europe found substantial variation in root-to-shoot ratios, driven by both cultivar genetics and site conditions (Heinemann et al., 2025). Similarly, a western Canadian study reported variation among four barley cultivars (cultivars: Abee, Bonanza, Harrington, and Samson) during the heading-to-ripening period (Xu & Juma, 1992). Since different barley cultivars were used in 2023 and 2024, they may have interacted differently with environmental conditions. These findings underscore the multifactorial nature of belowground carbon allocation and raise questions addressed in the following subsection.

4.1.3 What is the implication of the variation in the root-to-shoot ratio on soil organic carbon storage?

The regional-scale storage of SOC is typically estimated using soil carbon models such as RothC (Coleman & Jenkinson, 2014) or ICBM (Bolinder et al., 2019). These models require a set of input parameters, among them estimates of belowground carbon inputs derived from root biomass. Even though root-derived carbon inputs are of greater importance for carbon balances than above ground plant residues (Kätterer et al., 2011; Rasse et al., 2005), SOC input through roots are not properly accounted for, since estimating root carbon inputs are labor-intensive, and are thus calculated using yield-based allometric relationships such as the root-to-shoot ratio. Commonly, these carbon inputs are estimated to have a fixed root-to-shoot ratio, often based on site-specific (Poeplau, 2016) or regionally averaged data (Bolinder et al., 2007).

The assumption of a static root-to-shoot ratio neglects spatial-related variability. Several studies have shown that this ratio varies with management practices and environmental conditions, including soil properties and inherent crop differences discussed in section 4.1.2. Although the specific drivers of variation were not identified in our study, our results show that even under uniform management, the root-to-shoot ratio can vary within a single field. Consequently, using a static root-to-shoot ratio to determine carbon inputs in carbon models could oversimplify belowground carbon dynamics. These findings underscore the need to incorporate field-scale variability into SOC modelling frameworks to improve the accuracy of carbon input and storage estimates.

Once carbon input enters the soil, it encounters heterogeneous soil conditions that make its fate unpredictable. The following section identifies the strongest predictors of SOC content.

4.2 Oxalate-extractable aluminum is a key predictor of organic carbon content in Swedish agricultural topsoils (Paper II)

The following section addresses **O2** which is to identify the strongest predictors of SOC content across a humidity gradient in Swedish agricultural soils addressed in **Paper II** and briefly discusses the implications on the potential of SOC storage in Swedish agricultural topsoils.

4.2.1 Which is the strongest predictor for SOC content in Swedish agricultural topsoil?

Soil organic carbon content in the soils selected from Inventory III ranged from 10 to 70 g kg^{-1}. Oxalate-extractable aluminum (Al_{ox}) concentrations varied between 0.4 and 4.3 g kg^{-1} while oxalate-extractable iron (Fe_{ox}) ranged from 1.2 to 13 g kg^{-1}. The soils' clay contents ranged from

1.4% to 52%, and silt contents from 9.6% to 95%. Silt-sized aggregation was between 0% and 38 %. Oxalate-extractable phosphorus (P_{ox}) values were between 0.2 and 1.1 g kg^{-1} and exchangeable manganese (Mn_{ex}) between 0.1 and 2 g kg^{-1}. Exchangeable calcium (Ca_{ex}) concentrations ranged from 0.2 to 6 g kg^{-1}, and exchangeable magnesium (Mg_{ex}) from 0.0 to 0.7 g kg^{-1}.

The random forest model (RFM) identified Al_{ox} as the most important predictor, with its removal causing an approximate 21% increase in MSE (Fig. 8). Several other variables selected by the Boruta algorithm—including DMAI, Mn_{ex}, P_{ox}, silt, MAP, MAT, and Ca_{ex}—each increased MSE by 5–9% when omitted, underscoring their predictive importance (Fig. 8). In contrast, neither clay content nor Fe_{ox} were selected as important predictors in the model. However, the RFM tended to over-estimate SOC content below 20 g kg^{-1} and under-estimate SOC content above 40 g kg^{-1}.

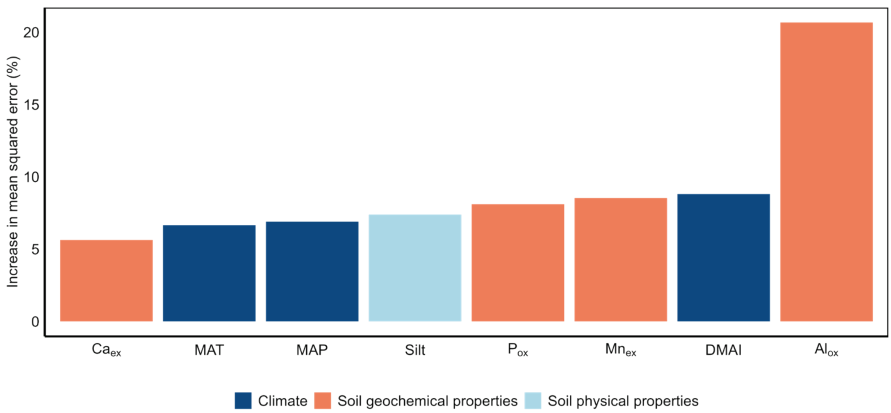


Figure 8 Variable importance, expressed as the increase in mean squared error (MSE) after removal of each predictor from the random forest model with soil organic carbon (SOC) content as the response. Variables are grouped by category: climate, soil geochemical properties, and soil physical properties. Abbreviations: Al_{ox}, oxalate-extractable aluminum; DMAI, De Martonne aridity index; P_{ox}, oxalate-extractable phosphorus; Mn_{ex}, exchangeable manganese; Ca_{ex}, exchangeable calcium; Mg_{ex}, exchangeable magnesium; Silt, silt-sized soil particles (2–63 µm).

Oxalate-extractable aluminum has previously been identified as important predictor of SOC content across different scales and climatic conditions. Large-scale syntheses, such as those from the North American national ecological observatory network, highlight Al_{ox}'s importance (Hall & Thompson, 2021; Rasmussen et al., 2018; Yu, Weintraub, et al., 2021), as do studies across Sub-Saharan Africa (von Fromm et al., 2021). At regional scales, strong Al_{ox}–SOC relationships have been reported in Austria (Wenzel et al., 2024), Canada (Beauchemin et al., 2003), Japan (Ichinose et al., 2025), Chile (Matus et al., 2006), and in Nordic countries including Finland (Salonen et al., 2024), Norway (Grønsten & Børresen, 2009), and Denmark (Paradelo et al., 2016). At local scales, similar patterns occur in Swedish agricultural fields, in central and southern Sweden (Blombäck et al., 2021), eight cultivated Swedish soils (Börling et al., 2001), and specifically at Bjertorp in **Paper I** (Fukumasu et al., 2021). Our findings thus confirm results from previous studies conducted with smaller datasets or more limited geographical coverage in humid continental climates.

Both Al_{ox} and Fe_{ox} are widely recognized as predictors of SOC content in acidic soils under humid conditions, largely due to the chemical and hydrological status of such soil systems that promote high rates of mineral weathering (Rasmussen et al., 2018). However, several studies indicate that Al_{ox} often emerges as a stronger predictor than Fe_{ox} under these conditions. For instance, across North America, Al_{ox} showed stronger SOC relationships than Fe_{ox} (Rasmussen et al., 2018; Yu et al., 2021). In Finnish soils, Al_{ox} was a significant predictor across low-clay soils (<30%), matching 75% of the samples with clay content less than 30% in our study, while Fe_{ox} was significant only for high-clay soils (>30%) (Salonen et al., 2024). In the humid, acidic soils of Lower Austria, Al_{ox} was the sole significant predictor (Wenzel et al., 2024). Notably, a field study at Bjertorp found a negative correlation between Fe_{ox} and SOC (Fukumasu et al., 2021).

For our dataset Fe_{ox} was not an important predictor of SOC contents (Fig. 8). It is possible that the combination of frequent precipitation events combined with relatively low MAT that limit evapotranspiration in the boreal north (Metzger et al., 2012), low-lying agricultural areas in southern and eastern Sweden, coastal zones around the Gulf of Bothnia and the Baltic Sea, and the heavy glacial to postglacial clays of the Central Scandinavian clay belt derived from till deposits (Ladenberger et al., 2013) could create fluctuating redox conditions which may limit the effect of Fe_{ox} in SOC storage (Chen et al., 2020).

4.2.2 What is the implication for soil organic carbon storage in Swedish agricultural topsoil?

The partial dependence plots (PDP) show that predicted SOC content from the RFM increased with Al_{ox} at concentrations larger than 2 g kg^{-1} and reached a plateau at 4 g kg^{-1} (Fig. 9A). Similarly, SOC content predictions increased with DMAI for values larger than about 40 and then plateaued at higher values (Fig. 9B). For DMAI, values were rather constant under very humid ($50 \leq$ DMAI ≤ 60) and excessively humid ($60 \leq$ DMAI ≤ 187) conditions and slightly arid ($30 \leq$ DMAI ≤ 35) and moderately humid ($35 <$ DMAI ≤ 40) conditions.

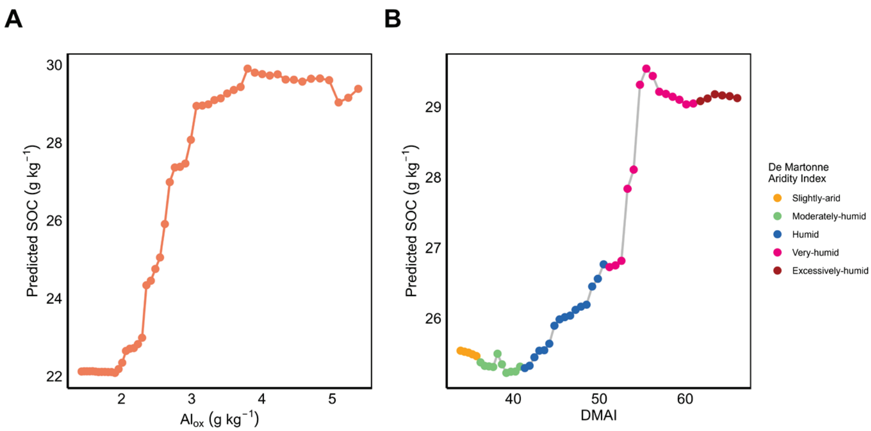


Figure 9 Partial dependence plots (PDP) for: (A) oxalate-extractable aluminium (Al_{ox}) and (B) De Martonne aridity index (DMAI) with the highest relative importance, as identified by the Boruta algorithm, in the random forest model (RFM) for soil organic carbon (SOC) content.

Given that Al_{ox} rather than clay content emerged as the strongest predictor of SOC content, the data (**Paper II**) and data from previous studies could suggest reframing the carbon saturation concept (Hassink, 1997) to explain the possible implications for SOC storage. This concept describes the mineralogical capacity of a soil to store carbon, which has traditionally been linked to clay content. The concept was later extended to "ecosystem capacity", influenced also by management and climate as drivers for net primary productivity (NPP) modulated by soil properties (Poeplau et al., 2024).

The partial dependence plots (Fig. 9) indicate that predicted SOC content increases with Al_{ox} concentration up to a point, after which it approaches a plateau. A similar pattern is observed along the climatic gradient, where predicted SOC content accumulation approaches a plateau under very humid ($50 \leq DMAI \leq 60$) to excessively humid ($60 \leq DMAI \leq 187$) conditions. This suggests that short growing seasons or low NPP may limit organic matter inputs under these conditions. The observed plateau may therefore indicate that SOC content accumulation is limited by carbon inputs, preventing the system from reaching its full mineralogical capacity for carbon storage (Yu et al., 2021). Hence, the plateau-like responses to both Al_{ox} and DMAI (Fig. 9A–B) could reflect NPP limitations.

Positive SOC content trends have been observed, largely attributed to management shifts such as increased ley cultivation, which enhances belowground carbon inputs (Henryson et al., 2022; Poeplau, Bolinder, et al., 2015). Further gains may be possible by increasing SOM inputs in soil with higher Al_{ox} contents or lower Al_{ox} content in very humid and excessively humid conditions. Alternatively, this may reflect progressive Al_{ox} weathering along the humidity gradient.

It remains unclear whether these patterns reflect correlation or causation. The following section investigates one aspect of the causal significance of the Al_{ox}-SOC relationship.

4.3 Results from long-term incubations of arable topsoil did not indicate soil organic carbon protection by reactive metal phases (Paper III)

The following section addresses **O3** by testing whether the key predictor identified in **Paper II**, oxalate-extractable aluminum (Al_{ox}), can explain variability in SOC mineralization rates, and thus indicate SOC protection in agricultural soils. This was examined using long-term incubation experiments in **Paper III**.

4.3.1 Is oxalate-extractable aluminum an indicator of soil organic carbon protection in long-term incubated agricultural topsoil?

The mean estimated marginal means from the linear mixed model representing the respiration rate at quasi-steady state (incubation days 296–426; n = 4), K_{SOC}, ranged from 3.1 to 17.9 µg CO_2-C g SOC^{-1} h^{-1}. SOC content ranged from 10.2 to 25.1 g kg^{-1}, and total nitrogen (TN) from 1.0 to 2.1 g kg^{-1}, corresponding to C:N ratios between 9.6 and 13.0 at the end of the incubation. Table 4 presents the partial least squares regression (PLSR) model relating K_{SOC} to soil physical properties (silt, clay), chemical properties (pH, Fe_{ox}, Al_{ox}), SOC and TN contents, their C:N ratios, RMP-to-SOC ratios (Fe_{ox}:SOC, Al_{ox}:SOC), and the clay-to-SOC ratio. These ratios were assumed to be proxies for possible SOC protection.

The PLSR model retained one latent variable (LV), which explained approximately 27% of the variation in K_{SOC} and about 56% of the variation in the predictors (Table 4). The negative loading (−0.4) on this LV that shows that higher SOC contents were associated with lower K_{SOC}, which indicates SOC protection. However, the proxies for mineral-associated SOC protection (Al_{ox}:SOC, Fe_{ox}:SOC and clay:SOC) all had positive loadings on the same LV (0.3–0.4; Table 4), indicating that higher values of these ratios were related to higher K_{SOC}, which does not support a protective effect of Al_{ox}, Fe_{ox} and clay content. In contrast, TN content and the C:N ratio had negative loadings on this LV (approximately −0.3 to −0.4), indicating that higher TN contents and higher C:N ratios were associated with lower K_{SOC}.

Table 4 Variable loadings for the included latent variable in the partial least squares regression (PLSR) model.

Variable name	Variable description	Fraction/Unit	Variable contributions to the latent variable
SOC	Total organic carbon content	g kg^{-1}	−0.38
TN	Total nitrogen content	g kg^{-1}	−0.32
C:N	Carbon-to-nitrogen ratio	-	−0.36
pH.KCl	pH measured in potassium chloride	-	0.19
Silt	Silt content	%	0.16
Clay	Clay content	%	0.27
Al_{ox}	Oxalate extracted aluminium	g kg^{-1}	−0.19
Fe_{ox}	Oxalate extracted iron	g kg^{-1}	0.34
Clay:SOC	Clay to SOC ratio	-	0.38
Al_{ox}:SOC	Oxalate extracted aluminium to SOC ratio	-	0.35
Fe_{ox}:SOC	Oxalate extracted iron to SOC ratio	-	0.40
Variance explained by the latent variable (%)			
Explanatory variables			55.5
Response (K_{SOC})	Specific respiration rate at quasi-steady state	µg CO_2-C g SOC^{-1} h^{-1}	27.4

In this study, there was no evidence that Al_{ox} protected SOC, as Al_{ox}:SOC had a positive loading on the LV that explained variation in K_{SOC} (Table 4). This contrasts with the commonly proposed role of Al in SOC protection in conceptual frameworks (Kleber et al., 2021) and empirical studies of SOC adsorption (Bruneel & Spohn, 2025) and with the positive relationships between Al_{ox} and SOC content observed at different scales (see Section 4.2). It is possible that the mechanisms expressed during long-term laboratory incubations are not fully expressed under field conditions, where repeated wetting–drying cycles, continuous root inputs, transport processes, soil structure and longer contact times with RMP may alter SOC dynamics.

Another possible explanation is the misinterpretation of 'mineral' protection when using oxalate extraction in the dark, which is non-selective with respect to Al species (Rennert et al., 2026). For instance, in temperate agricultural soils, the actual content of separate poorly crystalline Al oxides within Al_{ox} was found to be very low, whereas a substantial, and in some cases dominant, proportion of Al_{ox} may represent Al in organic association (Rennert et al., 2026). In such cases, Al_{ox} primarily reflects organic Al co-precipitates, rather than Al in distinct mineral phases that provide additional protection. If, in contrast, a larger share of Al_{ox} in these soils reflects a protective effect through adsorption, the process may be influenced by several concurrent kinetic mechanisms, such as diffusion, exchange reactions, and competition (Bruneel & Spohn, 2025; Kleber et al., 2021). Consequently, adsorption cannot be regarded as a static, irreversible event and potential protection mechanisms may be obscured under the tested conditions.

4.3.2 What are the implications for soil organic carbon storage in agricultural topsoil?

To address this question, a summary of the results in section 4.3.1 (Table 4) show that the PLSR model retained one latent variable (LV) that explained approximately 27 % of the variation in K_{SOC} and about 56 % of the variation in the predictors. Although the RMP (Al_{ox} and Fe_{ox}) and clay content did not seem to govern SOC protection, the negative loading of SOC content (−0.4; Table 4) on the LV explaining the variation in K_{SOC} indicates SOC protection. In addition, both TN content and the C:N ratio exhibited negative loadings on the same LV (approximately −0.3 to −0.4), indicating that higher TN contents and higher C:N ratios were associated with lower K_{SOC} values.

These findings lend themselves to the following hypotheses: (1) Unmeasured explanatory variables. Additional variables not included in the PLSR model may help explain the variability in K_{SOC} and thus SOC storage. (2) Stoichiometric control by the C:N ratio. The C:N ratio may exert stoichiometric control over microbial processing. SOM with lower C:N ratios may be decomposed more efficiently by microbes than SOM with higher ratios, which could explain the negative loading of the C:N ratio on the LV explaining the variation in K_{SOC} (Lehmann & Kleber, 2015). Resulting microbial necromass could therefore represent an important source of stabilized SOM through its interaction with RMP, consistent with the microbial efficiency–matrix stabilization framework (Cotrufo et al., 2013). (3) Nitrogen mining hypothesis. In soils with low TN content, microorganisms may respire more carbon to obtain the energy required for nitrogen acquisition, resulting in higher K_{SOC} values (Spohn et al., 2016).

These findings point to underlying complexities in SOC storage that are not immediately obvious, but that may have important implications for SOC storage and protection in agricultural topsoil.

5. Conclusions and future outlook

5.1 Conclusions

"All models are wrong, some are useful."
-George E. P. Box.

Enhancing soil organic carbon stocks in agricultural mineral soils offers an opportunity to support local food production while helping to mitigate climate change and enhance associated ecosystem services. However, estimating the carbon storage of a soil using models is subject to considerable uncertainty in model structure and parameterization. Therefore, the overarching goal of this thesis was to look beyond the commonly used predictors of topsoil SOC content and standard assumptions on inputs, to suggest ways to potentially help improve model processes and parameterization and in a long-term perspective, reduce uncertainty in SOC stock estimates, stated in objectives **O1**, **O2** and **O3** and addressed in **Papers I–III.**

Using an empirical approach and statistical modelling in **Papers I–III**, three main findings emerged summarized in Fig. 10. First, within-field variability in root-to-shoot ratios was observed under uniform climate and soil and crop management (**Paper I**), which could introduce uncertainty when estimating carbon inputs and SOC stocks. Second, oxalate-extractable aluminum (Al_{ox}) emerged as a key predictor of SOC content, suggesting that RMP may be important for SOC stocks and indicate a potential for additional SOC storage in Swedish arable soils with high Al_{ox} contents (**Paper II**). Third, results from long-term incubations did not, however, support a protective effect of Al_{ox} for SOC, as the specific respiration rate at quasi-steady state under near-optimal microbial conditions increased with increasing Al_{ox}:SOC ratios (**Paper III**). Results from this experiment suggest a possible role of TN content and the C:N ratio in regulating SOC storage (**Paper III**).

Taken together, these findings highlight the need to look beyond the average commonly used predictors of SOC content in the topsoil and the potential for accrual, such as clay content and assumptions for carbon inputs based on fixed root-to-shoot ratios. However, several questions remain unresolved in the context of this thesis, which are outlined in the next section.

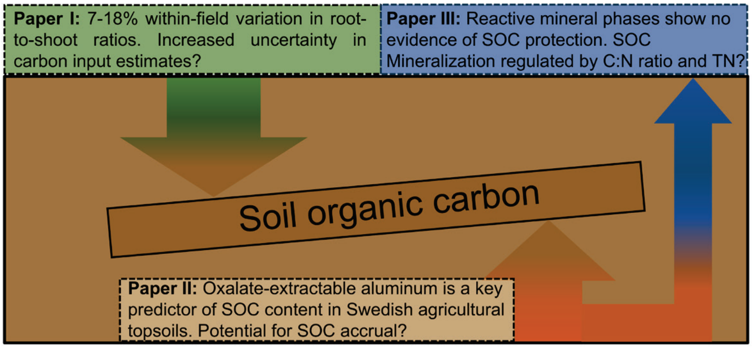


Figure 10 Conceptual framework of the thesis illustrating the conclusions drawn from **Papers I–III** in relation to the stated aims and objectives. Arrows indicate carbon fluxes between the soil and the atmosphere within the context of this study. SOC refers to soil organic carbon; TN denotes total nitrogen content; and C:N represents the carbon-to-nitrogen ratio.

5.1.1 Limitations

Sampling

Experimental constraints, which limited the study to two sampling years (**Paper I**) leave the sources of spatial variation in root-to-shoot ratios, discussed in Section 4.1, unresolved. Additionally, it was not clear whether the root biomass here is related to the SOC content. Future studies could address this by expanding sampling to include parameters like bulk density and crop nutrient availability, clarifying their influence on root-to-shoot ratios and if it correlated to the SOC content, possibly for a longer time frame. However, these efforts are labor-intensive, necessitating careful planning of personnel and resources for detailed campaigns, or out-of-the-box thinking to reduce the workload.

Furthermore, it is difficult to compare studies since root sampling methodologies varied considerably between studies. For example, Heinemann et al. (2025) and Xu and Juma (1992) collected only two cores per plot (one between the rows and one within the rows) using 6 cm and 8 cm diameter augers, respectively. In contrast, Mattila and Häkkinen (2025) stated that each observation comprised three cores taken from fixed GPS-locations in each field using a 7 cm diameter auger. Standardized sampling methodologies for root measurements would therefore be desirable in **Paper I**.

Dataset

Even though Al_{ox} was the strongest single predictor of SOC content in **Paper II**, the RFM tended to overestimate low SOC content and estimate high SOC content. Also, only 11% of samples had SOC < 20 g kg^{-1} and 26% had SOC > 40 g kg^{-1}. These biases likely meant that the model was optimized for the 20–40 g kg^{-1} range. Increasing the number of samples in the low and high SOC ranges would probably improve model performance across the full SOC gradient in Swedish agricultural soils in the context of this thesis.

Methods

The oxalate extraction method in **Papers II** and **III** does not provide information on distinct Al phases. Rennert et al. (2026) highlights its limitations as a non-selective, heterogeneous measure of Al species, obscuring contributions from distinct Al phases to the Al_{ox}. For instance, complementary techniques, such as X-ray diffraction, could resolve individual Al phases (e.g., poorly crystalline Al hydroxides), providing a fuller understanding of their role in SOC protection.

Additional variables

In the incubation set-up for **Paper III**, since TN—along with C:N ratios—may have had implications for SOC protection, parallel long-term incubations with labelled C and N would isolate the influence of TN on SOC protection more clearly (with and without SOM addition to also disentangle the effects related to the kinetics of SOM addition and microbial C mineralization). Additionally, uncharacterized microbial biomass composition or other RMP in the incubations likely contributed to the unexplained variability. The PLSR's first latent variable captured ~50% of the response variation but only ~27% of predictor variation (specific respiration rate under near-optimal conditions), pointing to missing factors. Future analyses of microbial-community composition and carbon-use efficiency or other RMP could clarify their role in SOC mineralization patterns found in **Paper III**.

5.2 Future outlook

5.2.1 Beyond clay content?

This thesis, along with other recent studies (Fukumasu et al., 2021; Georgiou et al., 2022; Hall & Thompson, 2021; von Fromm et al., 2021; von Fromm et al., 2024; Weiglein et al., 2022), suggests that clay content may not be the most important predictor of the potential of soil to stabilize SOC. However, evidence from different environments suggests that clay content is an important factor in predicting SOC content under specific conditions. At a regional scale, clay content also remains one of the key explanatory variables of SOC content, particularly in agricultural soils with near-neutral pH (Martin et al., 2011; Poeplau et al., 2020). In sandy soil, clay content was also shown to increase with C derived from straw (Poeplau, Kätterer, et al., 2015).

This thesis supports the view that Al_{ox}, rather than clay content, is a stronger predictor of SOC content in acidic mineral soils, but additional work on the role of clay across soil types not represented in this dataset is warranted. Such work could refine our understanding of how soil properties control SOC storage, beyond what can be inferred from Al_{ox} alone.

5.2.2 Beyond fixed root-to-shoot ratios?

The root-to-shoot ratio is a practical tool for estimating root carbon inputs to soil, particularly for large-scale carbon accounting at national levels (Mokany et al., 2006). However, as shown by the within-field heterogeneity observed in **Paper I**, such fixed ratio-based approaches from field averages can introduce uncertainty in carbon input estimates and, consequently, in inferred SOC stocks. Future work could therefore focus on advancing direct measurement approaches, such as minirhizotron techniques (Huo & Cheng, 2019), and related image-based methods, and on integrating these with remote sensing and machine-learning models to enable high-throughput, non-destructive monitoring of root dynamics and SOC inputs across fields and landscapes (Dlamini et al., 2025; Neumann et al., 2020), reducing reliance on fixed ratios to come closer to reality.

In addition, moving beyond fixed root-to-shoot ratios towards approaches that explicitly consider root-system architecture and growth—that is, the spatial configuration and development of root systems in soil—would allow improved process representation and parameterization of below-ground components in soil–crop and SOC models (Raza et al., 2025). A stronger integration of root-architectural traits, included in the context of **Paper I**, could support the use of soil–crop simulation models to explore SOC dynamics and other ecosystem processes under varying environmental and management conditions.

References

Andrén, O., & Kätterer, T. (1997). ICBM: The introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications*, 7(4), 1226–1236. https://doi.org/10.1890/1051-0761(1997)007[1226:ITICBM]2.0.CO;2

Asano, M., & Wagai, R. (2014). Evidence of aggregate hierarchy at micro- to submicron scales in an allophanic Andisol. *Geoderma*, 216, 62–74. https://doi.org/10.1016/j.geoderma.2013.10.009

Baldock, J., & Skjemstad, J. (2000). Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry*, 31(7–8), 697–710. https://doi.org/10.1016/S0146-6380(00)00049-8[3]

Banwart, S. A., Nikolaidis, N. P., Zhu, Y.-G., Peacock, C. L., & Sparks, D. L. (2019). Soil functions: Connecting earth's critical zone. *Annual Review of Earth and Planetary Sciences*, 47, 333–359. https://doi.org/10.1146/annurev-earth-063016-020749

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Batjes, N. H. (1996). Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science*, 47(2), 151–163. https://doi.org/10.1111/j.1365-2389.1996.tb01386.x

Beare, M. H., McNeill, S. J., Curtin, D., Parfitt, R. L., Jones, H. S., Dodd, M. B., & Sharp, J. (2014). Estimating the organic carbon stabilisation capacity and saturation deficit of soils: A New Zealand case study. *Biogeochemistry*, 120(1–3), 71–87. https://doi.org/10.1007/s10533-014-9982-1

Beauchemin, S., Simard, R. R., Bolinder, M. A., Nolin, M. C., & Cluis, D. (2003). Prediction of phosphorus concentration in tile-drainage water from the Montreal Lowlands soils. *Canadian Journal of Soil Science*, 83(1), 73–87. https://doi.org/10.4141/S01-058

Birge, H. E., Conant, R. T., Follett, R. F., Haddix, M. L., Morris, S. J., Snapp, S. S., Wallenstein, M. D., & Paul, E. A. (2015). Soil respiration is not limited by reductions in microbial biomass during long-term soil incubations. *Soil Biology and Biochemistry*, 81, 304–310. https://doi.org/10.1016/j.soilbio.2014.11.028

Blombäck, K., Bolster, C. H., Lindsjö, A., Hesse, K., Linefur, H., & Parvage, M. M. (2021). Comparing measures for determination of phosphorus saturation as a method to estimate dissolved P in soil solution. *Geoderma*, 383, 114708. https://doi.org/10.1016/j.geoderma.2020.114708

Böhm, W. (1979). *Methods of studying root systems*. Ecological Studies, 33. Springer. https://doi.org/10.1007/978-3-642-67282-8

Bolinder, M. A., Angers, D. A., & Dubuc, J. P. (1997). Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. *Agriculture, Ecosystems & Environment*, 63(1), 61–66. https://doi.org/10.1016/S0167-8809(96)01121-8[3]

Bolinder, M. A., Janzen, H. H., Gregorich, E. G., Angers, D. A., & VandenBygaart, A. J. (2007). An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. *Agriculture, Ecosystems & Environment*, 118(1–4), 29–42. https://doi.org/10.1016/j.agee.2006.05.013

Bond-Lamberty, B., Ballantyne, A., Berryman, E., Fluet-Chouinard, E., Jian, J., Morris, K. A., Rey, A., & Vargas, R. (2024). Twenty years of progress, challenges, and opportunities in measuring and understanding soil respiration. *Journal of Geophysical Research: Biogeosciences*, 129(2), e2023JG007637. https://doi.org/10.1029/2023JG007637

Bonett, D. G. (2006). Confidence interval for a coefficient of quartile variation. *Computational Statistics & Data Analysis*, 50(11), 2953–2957. https://doi.org/10.1016/j.csda.2005.05.007

Bonfante, A., Basile, A., & Bouma, J. (2020). Targeting the soil quality and soil health concepts when aiming for the United Nations Sustainable Development Goals and the EU Green Deal. *Soil*, 6(2), 453–466. https://doi.org/10.5194/soil-6-453-2020

Botta-Dukát, Z. (2023). Quartile coefficient of variation is more robust than CV for traits calculated as a ratio. *Scientific Reports*, 13, 4671. https://doi.org/10.1038/s41598-023-31676-4

Bruneel, Y., & Spohn, M. (2025). Organic matter, and particularly phosphorylated organic matter, coprecipitates very strongly with aluminium. *European Journal of Soil Science*, 76(6), e70221. https://doi.org/10.1111/ejss.70221

Börling, K., Otabbong, E., & Barberis, E. (2001). Phosphorus sorption in relation to soil properties in some cultivated Swedish soils. *Nutrient Cycling in Agroecosystems*, 59(1), 39–46. https://doi.org/10.1023/A:1017512100506

Cabal, C., De Deurwaerder, H. P., & Matesanz, S. (2021). Field methods to study the spatial root density distribution of individual plants. *Plant and Soil*, 462(1–2), 25–43. https://doi.org/10.1007/s11104-021-04891-2

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. *Global Change Biology*, 21(9), 3200–3213. https://doi.org/10.1111/gcb.12982

Chen, C., Hall, S. J., Coward, E. K., & Thompson, A. (2020). Iron-mediated organic matter decomposition in humid soils can counteract protection. *Nature Communications*, 11, 2255. https://doi.org/10.1038/s41467-020-16071-5

Clason, Å., & Granström, B. (1992). Agriculture. In *National Atlas of Sweden*. Publisher not specified. (ISBN: 9170248877)

Coleman, K., & Jenkinson, D. S. (1996). RothC-26.3 – A model for the turnover of carbon in soil. In D. S. Powlson, P. Smith, & J. U. Smith (Eds.), *Evaluation of soil organic matter models* (pp. 237–246). Springer. https://doi.org/10.1007/978-3-642-61094-3_17

Coleman, K., & Jenkinson, D. S. (2014). *RothC – A model for the turnover of carbon in soil: Model description and users guide (Windows version) (updated June 2014)*. Rothamsted Research. http://www.rothamsted.ac.uk/sites/default/files/RothC_guide_0.pdf

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. (2011). Temperature and soil organic matter decomposition rates: Synthesis of current knowledge and a way forward. *Global Change Biology*, 17(11), 3392–3404. https://doi.org/10.1111/j.1365-2486.2011.02496.x

Cotrufo, M. F., Ranalli, M. G., Haddix, M. L., Six, J., & Lugato, E. (2019). Soil carbon storage informed by particulate and mineral-associated organic matter. *Nature Geoscience*, 12, 989–994. https://doi.org/10.1038/s41561-019-0484-6

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. *Global Change Biology*, 19(4), 988–995. https://doi.org/10.1111/gcb.12113

Creamer, C. A., Filley, T. R., Boutton, T. W., Oleynik, S., & Kantola, I. B. (2011). Controls on soil carbon accumulation during woody plant encroachment. *Soil Biology and Biochemistry*, 43(8), 1678–1687. https://doi.org/10.1016/j.soilbio.2011.04.013

Dahlgren, R. A., & Ugolini, F. C. (1991). Distribution and characterization of short-range-order minerals in Spodosols from the Washington Cascades. *Geoderma*, 48(3–4), 391–413. https://doi.org/10.1016/0016-7061(91)90052-6[3]

Deb, B. (1950). The estimation of free iron oxides in soils and clays and their removal. Journal of Soil Science, 1 (2). 212-220. 10.1111/j.1365-2389.1950.tb00733.x

Dexter, A. R., Richard, G., Arrouays, D., Czyż, E. A., Jolivet, C., & Duval, O. (2008). Complexed organic matter controls soil physical properties. *Geoderma*, 144(3–4), 620–627. https://doi.org/10.1016/j.geoderma.2008.01.022

Dlamini, C. M., Odindi, J., Matongera, T. N., & Mutanga, O. (2025). Exploring the utility of remote sensing technology in vegetation below-ground biomass

(BGB) estimation. *Frontiers in Remote Sensing*, 6, 1668676. https://doi.org/10.3389/frsen.2025.1668676
Doetterl, S., Stevens, A., Six, J., Merckx, R, Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., & Zagal Venegas, E. (2015). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, 8(10), 780–783. https://doi.org/10.1038/ngeo2516
Don, A., Seidel, F., Leifelfeld, J., Kätterer, T., Martin, M., Pellerin, S., Emde, D., Seitz, D., & Chenu, C. (2023). Carbon sequestration in soils and climate change mitigation—Definitions and pitfalls. *Global Change Biology*, 29, 5753–5766. https://doi.org/10.1111/gcb.16983
Dungait, J. A. J., Hopkins, D. W., Gregory, A. S., & Whitmore, A. P. (2012). Soil organic matter turnover is governed by accessibility not recalcitrance. *Global Change Biology*, 18(6), 1781–1796. https://doi.org/10.1111/j.1365-2486.2012.02665.x
Eriksson, J., Stenberg, B., Andersson, A., & Andersson, R. (2000). *Tillståndet i svensk åkermark och spannmålsgröda – jordartens betydelse för markegenskaperna, samband markfaktorer och elementhalter i kärna* [Survey of Swedish arable soils and cereal crops]. Stockholm (Sweden): Swedish Environmental Protection Agency, Report 5062.
Feng, W., Plante, A. F., & Six, J. (2013). Improving estimates of maximal organic carbon stabilization by fine soil particles. *Biogeochemistry*, 112(1–3), 81–93. https://doi.org/10.1007/s10533-012-9710-7
Field, C. B., Sarmiento, J. L., & Hales, B. (2007). The carbon cycle of North America in a global context. In *The first state of the carbon cycle report (SOCCR): The North American carbon budget and implications for the global carbon cycle* (pp. 21–28). U.S. Climate Change Science Program. https://www.globalcarbonproject.org/global/pdf/SOCCR.2007.Final.pdf
Friedlingstein, P., O'Sullivan, M., Jones, M. W., Andrew, R. M., Hauck, J., Landschützer, P., Le Quéré, C., Li, H., Luijkx, I. T., & Olsen, A. (2024). Global carbon budget 2024. *Earth System Science Data Discussions*. https://doi.org/10.5194/essd-17-965-2025
Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *Annals of Statistics*, 29(5), 1189–1232. https://doi.org/10.1214/aos/1013203451
Fukumasu, J., Poeplau, C., Coucheney, E., Jarvis, N., Klöffel, T., Koestel, J., Kätterer, T., Svensson, D. N., Wetterlind, J., & Larsbo, M. (2021). Oxalate-extractable aluminum alongside carbon inputs may be a major determinant for organic carbon content in agricultural topsoils. *Geoderma*, 402, 115345. https://doi.org/10.1016/j.geoderma.2021.115345
Gasser, A. A., Diel, J., Nielsen, K., Mewes, P., Engels, C., & Franko, U. (2022). A model ensemble approach to determine the humus building efficiency of

organic amendments in incubation experiments. *Soil Use and Management*, 38(1), 179–190. https://doi.org/10.1111/sum.12750

Georgiou, K., Jackson, R. B., Vindušková, O., Abramoff, R. Z., Ahlström, A., Feng, W., Harden, J. W., Pellegrini, A. F., Polley, H. W., & Soong, J. L. (2022). Global stocks and capacity of mineral-associated soil organic carbon. *Nature Communications*, 13, 3797. https://doi.org/10.1038/s41467-022-31540-9

Grønsten, H., & Børresen, T. (2009). Comparison of two methods for assessment of aggregate stability of agricultural soils in southeast Norway. *Acta Agriculturae Scandinavica Section B – Soil and Plant Science*, 59(6), 567–575. https://doi.org/10.1080/09064710802106829

Greenwell, B. M. (2017). pdp: An R package for constructing partial dependence plots. *The R Journal*, 9(1), 421–436. https://doi.org/10.32614/RJ-2017-016

Hall, S. J., & Thompson, A. (2021). What do relationships between extractable metals and soil organic carbon concentrations mean? *Soil Science Society of America Journal*, 85(4), 1005–1024. https://doi.org/10.1002/saj2.20235

Hamilton, N. E., & Ferry, M. (2018). ggtern: Ternary diagrams using ggplot2. *Journal of Statistical Software*, 87(3), 1–17. https://doi.org/10.18637/jss.v087.c03

Haney, R. L., & Haney, E. B. (2010). Simple and rapid laboratory method for rewetting dry soil for incubations. *Communications in Soil Science and Plant Analysis*, 41(12), 1493–1501. https://doi.org/10.1080/00103624.2010.482171

Harbo, L. S., Olesen, J. E., Lemming, C., Christensen, B. T., & Elsgaard, L. (2023). Limitations of farm management data in analyses of decadal changes in SOC stocks in the Danish soil-monitoring network. *European Journal of Soil Science*, 74(3), e13379. https://doi.org/10.1111/ejss.13379

Hassink, J. (1997). The capacity of soils to preserve organic C and N by their association with clay and silt particles. *Plant and Soil*, 191(1), 77–87. https://doi.org/10.1023/A:1004213929699

Hassink, J., & Whitmore, A. P. (1997). A model of the physical protection of organic matter in soils. *Soil Science Society of America Journal*, 61(1), 131–139. https://doi.org/10.2136/sssaj1997.03615995006100010020x

Heinemann, H., Durand-Maniclas, F., Seidel, F., Ciulla, F., Bárcena, T. G., Camenzind, M., Corrado, S., Csűrös, Z., Czakó, Z., & Eylenbosch, D. (2025). Optimising root and grain yield through variety selection in winter wheat across a European climate gradient. *European Journal of Soil Science*, 76(2), e70077. https://doi.org/10.1111/ejss.70077

Heinemann, H., Hirte, J., Seidel, F., & Don, A. (2023). Increasing root biomass derived carbon input to agricultural soils by genotype selection – A review. *Plant and Soil*, 490(1–2), 19–30. https://doi.org/10.1007/s11104-022-05632-5

Henryson, K., Meurer, K. H. E., Bolinder, M. A., Kätterer, T., & Tidåker, P. (2022). Higher carbon sequestration on Swedish dairy farms compared with other farm types as revealed by national soil inventories. *Carbon Management*, 13(1), 266–278. https://doi.org/10.1080/17583004.2022.2078634

Hermwille, L., Obergassel, W., Ott, H. E., & Beuermann, C. (2017). UNFCCC before and after Paris – What's necessary for an effective climate regime? *Climate Policy*, 17(2), 150–170. https://doi.org/10.1080/14693062.2015.1115231

Hirte, J., Walder, F., Hess, J., Büchi, L., Colombi, T., van der Heijden, M. G. A., & Mayer, J. (2021). Enhanced root carbon allocation through organic farming is restricted to topsoils. *Science of the Total Environment*, 755, 143551. https://doi.org/10.1016/j.scitotenv.2020.143551

Hu, T., Sørensen, P., Wahlström, E. M., Chirinda, N., Sharif, B., Li, X., & Olesen, J. E. (2018). Root biomass in cereals, catch crops and weeds can be reliably estimated without considering aboveground biomass. *Agriculture, Ecosystems & Environment*, 251, 141–148. https://doi.org/10.1016/j.agee.2017.09.025

Huo, C., & Cheng, W. (2019). Improved root turnover assessment using field scanning rhizotrons with branch order analysis. *Ecosphere*, 10(8), e02793. https://doi.org/10.1002/ecs2.2793

Ibrahim, M. A., & Johansson, M. (2021). Attitudes to climate change adaptation in agriculture – A case study of Öland, Sweden. *Journal of Rural Studies*, 86, 1–15. https://doi.org/10.1016/j.jrurstud.2021.05.017

Ichinose, Y., Matsui, K., Fukumasu, J., Matsuura, S., Takata, Y., & Wagai, R. (2025). How do reactive aluminum and iron phases control soil organic carbon and phosphate adsorption capacity in agricultural topsoils across Japan? *Soil Science and Plant Nutrition*, 71(1), 38–52. https://doi.org/10.1080/00380768.2024.2370725

Jacobs, A., Poeplau, C., Weiser, C., Fahrion-Nitschke, A., & Don, A. (2020). Exports and inputs of organic carbon on agricultural soils in Germany. *Nutrient Cycling in Agroecosystems*, 118(3), 249–271. https://doi.org/10.1007/s10705-020-10089-7

Jacobsen, O. H. (1989). Unsaturated hydraulic conductivity for some Danish soils. *Tidsskrift for Planteavls specialserie S*, 2030. https://dcapub.au.dk/pub/S_beretning_2030_1989.pdf

Jacobson, M. C., Charlson, R. J., Rodhe, H., & Orians, G. H. (2000). *Earth system science: From biogeochemical cycles to global changes* (Vol. 72). Academic Press.

Jamoteau, F., Cam, N., Levard, C., Doelsch, E., Gassier, G., Duvivier, A., Boulineau, A., Saint-Antonin, F., & Basile-Doelsch, I. (2023). Structure and chemical composition of soil C-rich Al–Si–Fe coprecipitates at nanometer

scale. *Environmental Science & Technology*, 57(49), 20615–20626. https://doi.org/10.1021/acs.est.3c04268
Joergensen, R. G., Brookes, P. C., & Jenkinson, D. S. (1990). Survival of the soil microbial biomass at elevated temperatures. *Soil Biology and Biochemistry*, 22(8), 1129–1136. https://doi.org/10.1016/0038-0717(90)90039-6[3]
Junchao, J., Chaodong, L., & Zhangyue, C. (2023). Soil texture rather than water potential determines the root:shoot ratio in ryegrass and alfalfa. *Journal of Soil Science and Plant Nutrition*, 23(1), 1297–1305. https://doi.org/10.1007/s42729-022-01159-9
Kätterer, T., Bolinder, M. A., Berglund, K., & Kirchmann, H. (2012). Strategies for carbon sequestration in agricultural soils in northern Europe. *Acta Agriculturae Scandinavica, Section A – Animal Science*, 62(4), 181–198. https://doi.org/10.1080/09064702.2013.779316
Kätterer, T., Bolinder, M. A., Andrén, O., Kirchmann, H., & Menichetti, L. (2011). Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. *Agriculture, Ecosystems & Environment*, 141(1–2), 184–192. https://doi.org/10.1016/j.agee.2011.02.029
Kay, M., Bunning, S., Burke, J., Boerger, V., Bojic, D., Bosc, P.-M., Clark, M., Dale, D., England, M., & Hoogeveen, J. (2022). *The state of the world's land and water resources for food and agriculture 2021: Systems at breaking point*. FAO & Routledge. https://doi.org/10.4324/9781003162540
Keel, S. G., Leifeld, J., Mayer, J., Taghizadeh-Toosi, A., & Olesen, J. E. (2017). Large uncertainty in soil carbon modelling related to method of calculation of plant carbon input in agricultural systems. *European Journal of Soil Science*, 68(6), 953–963. https://doi.org/10.1111/ejss.12483
King, A. E., Amsili, J. P., Córdova, S. C., Culman, S., Fonte, S. J., Kotcon, J., Liebig, M., Masters, M. D., McVay, K., & Olk, D. C. (2023). A soil matrix capacity index to predict mineral-associated but not particulate organic carbon across a range of climate and soil pH. *Biogeochemistry*, 165(1), 1–14. https://doi.org/10.1007/s10533-023-01039-4
Kleber, M., Bourg, I. C., Coward, E. K., Hansel, C. M., Myneni, S. C. B., & Nunan, N. (2021). Dynamic interactions at the mineral–organic matter interface. *Nature Reviews Earth & Environment*, 2, 402–421. https://doi.org/10.1038/s43017-021-00162-y
Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., & Nico, P. S. (2015). Mineral–organic associations: Formation, properties, and relevance in soil environments. *Advances in Agronomy*, 130, 1–140. https://doi.org/10.1016/bs.agron.2014.10.005
Kuylenstierna, J., Hermansson, C., Bäckstrand, K., Eckerberg, K., Kåberger, T., Rummukainen, M., Söderholm, P., & Sörlin, S. (2021). *2021 report of the*

Swedish Climate Policy Council. Klimatpolitiska rådet. https://www.klimatpolitiskaradet.se
Ladenberger, A., Andersson, M., Reimann, C., Tarvainen, T., Filzmoser, P., Uhlbäck, J., Morris, G., & Sadeghi, M. (2013). *Geochemical mapping of agricultural soils and grazing land (GEMAS) in Norway, Finland and Sweden – Regional report*. Geological Survey of Sweden. (No DOI.)
Lal, R. (2004). Soil carbon sequestration to mitigate climate change. *Geoderma*, 123(1–2), 1–22. https://doi.org/10.1016/j.geoderma.2004.01.032
Lavallee, J. M., Haddix, M. L., Swan, A., Hoover, J. D., & Cotrufo, M. F. (2025). Using aridity as an overarching factor to advance understanding of soil organic carbon storage at the continental scale. *Biogeochemistry*, 168(5), 1–25. https://doi.org/10.1007/s10533-025-01273-0
Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, 528(7580), 60–68. https://doi.org/10.1038/nature16069
Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, 69(1), 1–33. https://doi.org/10.18637/jss.v069.i01
Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News*, 2(3), 18–22.
Lindahl, A. M., Söderström, M., & Jarvis, N. (2008). Influence of input uncertainty on prediction of within-field pesticide leaching risks. *Journal of Contaminant Hydrology*, 98(3–4), 106–114. https://doi.org/10.1016/j.jconhyd.2008.02.010
Liu, H. S., Li, L. H., Han, X. G., Huang, J. H., Sun, J. X., & Wang, H. Y. (2006). Respiratory substrate availability plays a crucial role in the response of soil respiration to environmental factors. *Applied Soil Ecology*, 32(3), 284–292. https://doi.org/10.1016/j.apsoil.2005.07.006
Lomander, A., Kätterer, T., & Andrén, O. (1998). Carbon dioxide evolution from top- and subsoil as affected by moisture and constant and fluctuating temperature. *Soil Biology and Biochemistry*, 30(14), 2017–2022. https://doi.org/10.1016/S0038-0717(98)00072-9[3]
Lux, A., & Rost, T. L. (2012). Plant root research: The past, the present and the future. *Annals of Botany*, 110(2), 201–204. https://doi.org/10.1093/aob/mcs136
Martin, M. P., Wattenbach, M., Smith, P., Meersmans, J., Jolivet, C., Boulonne, L., & Arrouays, D. (2011). Spatial distribution of soil organic carbon stocks in France. *Biogeosciences*, 8(5), 1053–1065. https://doi.org/10.5194/bg-8-1053-2011
Mathew, I., Shimelis, H., Mutema, M., Clulow, A., Zengeni, R., Mbava, N., & Chaplot, V. (2019). Selection of wheat genotypes for biomass allocation to improve drought tolerance and carbon sequestration into soils. *Journal of Agronomy and Crop Science*, 205(4), 385–400. https://doi.org/10.1111/jac.12331

Mathew, I., Shimelis, H., Mutema, M., Minasny, B., & Chaplot, V. (2020). Crops for increasing soil organic carbon stocks – A global meta-analysis. *Geoderma*, 367, 114230. https://doi.org/10.1016/j.geoderma.2020.114230

Mattila, T. J., & Häkkinen, L. (2025). Exploring the effects of soil structure, nutrients, and farm management on crop root biomass and depth distribution. *Field Crops Research*, 327, 109909. https://doi.org/10.1016/j.fcr.2024.109909

Matus, F., Amigo, X., & Kristiansen, S. M. (2006). Aluminium stabilization controls organic carbon levels in Chilean volcanic soils. *Geoderma*, 132(1–2), 158–168. https://doi.org/10.1016/j.geoderma.2005.04.023

Matus, F., Garrido, E., Sepúlveda, N., Cárcamo, I., Panichini, M., & Zagal, E. (2008). Relationship between extractable Al and organic C in volcanic soils of Chile. *Geoderma*, 148(2), 180–188. https://doi.org/10.1016/j.geoderma.2008.09.008

Matus, F., Rumpel, C., Neculman, R., Panichini, M., & Mora, M. L. (2014). Soil carbon storage and stabilisation in andic soils: A review. *Catena*, 120, 102–110. https://doi.org/10.1016/j.catena.2014.04.008

McKeague, J. A. (1967). An evaluation of 0.1 M pyrophosphate and pyrophosphate-dithionite in comparison with oxalate as extractants of the accumulation products in podzols and some other soils. *Canadian Journal of Soil Science*, 47(2), 95–99. https://doi.org/10.4141/cjss67-017

McKeague, J. A., & Day, J. H. (1966). Dithionite- and oxalate-extractable Fe and Al as aids in differentiating various classes of soils. *Canadian Journal of Soil Science*, 46(1), 13–22. https://doi.org/10.4141/cjss66-003

Menichetti, L., Kätterer, T., & Bolinder, M. A. (2024). Bayesian calibration of the ICBM/3 soil organic carbon model constrained by data from long-term experiments and uncertainties of C inputs. *Carbon Management*, 15(1), 2304749. https://doi.org/10.1080/17583004.2024.2304749

Metzger, M. J., Shkaruba, A., Jongman, R. H. G., & Bunce, R. G. H. (2012). *Descriptions of the European environmental zones and strata*. Alterra Report 2281. https://edepot.wur.nl/197197

Meurer, K. H. E., Hendriks, C. M., Faber, J. H., Kuikman, P. J., van Egmond, F., Garland, G., Putku, E., Barancikova, G., Makovníková, J., & Chenu, C. (2024). How does national SOC monitoring on agricultural soils align with the EU strategies? *European Journal of Soil Science*, 75(2), e13477. https://doi.org/10.1111/ejss.13477

Mevik, B.-H., & Wehrens, R. (2007). The pls package: Principal component and partial least squares regression in R. *Journal of Statistical Software*, 18(2), 1–23. https://doi.org/10.18637/jss.v018.i02

Mishra, M., Desul, S., Santos, C. A. G., Mishra, S. K., Kamal, A. H. M., Goswami, S., Kalumba, A. M., Biswal, R., da Silva, R. M., & Dos Santos, C. A. C.

(2024). A bibliometric analysis of sustainable development goals (SDGs). *Environment, Development and Sustainability*, 26(5), 11101–11143. https://doi.org/10.1007/s10668-023-03029-2

Mokany, K., Raison, R. J., & Prokushkin, A. S. (2006). Critical analysis of root:shoot ratios in terrestrial biomes. *Global Change Biology*, 12(1), 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x

National Ecological Observatory Network. (2020). *Soil physical and chemical properties, distributed initial characterization (DP1.10086.001)*. NEON. https://doi.org/10.48443/9Z63-YF15

National Inventory Document Sweden (NID SE). (2025). *UNFCCC National Inventory Document*. United Nations Framework Convention on Climate Change. https://unfccc.int/sites/default/files/resource/NID%20SE%20submission%202025.pdf

Neumann, M., Godbold, D. L., Hirano, Y., & Finér, L. (2020). Improving models of fine root carbon stocks and fluxes in European forests. *Journal of Ecology*, 108(2), 496–514. https://doi.org/10.1111/1365-2745.13271

Oades, J. M., Gillman, G. P., Uehara, G., Hue, N., Van Noordwijk, M., Robertson, G. P., & Wada, K. (1989). Interactions of soil organic matter and variable-charge clays. In *Dynamics of soil organic matter in tropical ecosystems* (pp. 69–96). University of Hawaii Press.

Palta, J. A., & Turner, N. C. (2019). Crop root system traits cannot be seen as a silver bullet delivering drought resistance. *Plant and Soil*, 439(1–2), 31–43. https://doi.org/10.1007/s11104-019-03934-4

Paradelo, M., Hermansen, C., Knadel, M., Moldrup, P., Greve, M. H., & de Jonge, L. W. (2016). Field-scale predictions of soil contaminant sorption using visible–near infrared spectroscopy. *Journal of Near Infrared Spectroscopy*, 24(3), 281–291. https://doi.org/10.1255/jnirs.1217

Pausch, J., & Kuzyakov, Y. (2018). Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology*, 24(1), 1–12. https://doi.org/10.1111/gcb.13850

Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-smart soils. *Nature*, 532(7597), 49–57. https://doi.org/10.1038/nature17174

Poeplau, C. (2016). Estimating root:shoot ratio and soil carbon inputs in temperate grasslands with the RothC model. *Plant and Soil*, 407(1–2), 293–305. https://doi.org/10.1007/s11104-016-3037-5

Poeplau, C. (2021). *Soil organic carbon in the 'Anthropocene' – Human pressure on an important natural resource via agricultural management and climate change*. Habilitationsschrift, University of Hildesheim. https://hilpub.uni-hildesheim.de/handle/ubhi/15575

Poeplau, C., Bolinder, M. A., Eriksson, J., Lundblad, M., & Kätterer, T. (2015). Positive trends in organic carbon storage in Swedish agricultural soils due to unexpected socio-economic drivers. *Biogeosciences*, 12(11), 3241–3251. https://doi.org/10.5194/bg-12-3241-2015

Poeplau, C., Dechow, R., Begill, N., & Don, A. (2024). Net primary production rather than saturation of mineral surfaces limits soil carbon sequestration. *Global Change Biology*, 30(12), e17950. https://doi.org/10.1111/gcb.17950

Poeplau, C., Jacobs, A., Don, A., Vos, C., Schneider, F., Wittnebel, M., Tiemeyer, B., Heidkamp, A., Prietz, R., & Flessa, H. (2020). Stocks of organic carbon in German agricultural soils—Key results of the first comprehensive inventory. *Journal of Plant Nutrition and Soil Science*, 183(6), 665–681. https://doi.org/10.1002/jpln.201900312

Poeplau, C., & Kätterer, T. (2017). Is soil texture a major controlling factor of root:shoot ratio in cereals? *European Journal of Soil Science*, 68(6), 964–970. https://doi.org/10.1111/ejss.12492

Poeplau, C., Kätterer, T., Bolinder, M. A., Börjesson, G., Berti, A., & Lugato, E. (2015). Low stabilization of aboveground crop residue carbon in sandy soils of Swedish long-term experiments. *Geoderma*, 237–238, 246–255. https://doi.org/10.1016/j.geoderma.2014.09.010

Poorter, H., & Nagel, O. (2000). The role of biomass allocation in the growth response of plants to different levels of light, CO2, nutrients and water: A quantitative review. *Australian Journal of Plant Physiology*, 27(12), 1191–1191. https://doi.org/10.1071/PP99173

Post, W. M., Emanuel, W. R., Zinke, P. J., & Stangenberger, A. G. (1982). Soil carbon pools and world life zones. *Nature*, 298(5870), 156–159. https://doi.org/10.1038/298156a0

Pribyl, D. W. (2010). A critical review of the conventional SOC to SOM conversion factor. *Geoderma*, 156(3–4), 75–83. https://doi.org/10.1016/j.geoderma.2010.02.003

Prout, J. M., Shepherd, K. D., McGrath, S. P., Kirk, G. J. D., & Haefele, S. M. (2021). What is a good level of soil organic matter? An index based on organic carbon to clay ratio. *European Journal of Soil Science*, 72(6), 2493–2503. https://doi.org/10.1111/ejss.13118

R Core Team. (2025). *R: A language and environment for statistical computing* (Version 4.4.1). R Foundation for Statistical Computing. https://www.R-project.org/

Rabot, E., Wiesmeier, M., Schlüter, S., & Vogel, H.-J. (2018). Soil structure as an indicator of soil functions: A review. *Geoderma*, 314, 122–137. https://doi.org/10.1016/j.geoderma.2017.11.009

Rasmussen, C., Heckman, K., Wieder, W. R., Keiluweit, M., Lawrence, C. R., Berhe, A. A., Blankinship, J. C., Crow, S. E., Druhan, J. L., & Hicks Pries, C. E. (2018). Beyond clay: Towards an improved set of variables for predicting soil organic matter content. *Biogeochemistry*, 137(3), 297–306. https://doi.org/10.1007/s10533-018-0424-3

Rasse, D. P., Rumpel, C., & Dignac, M.-F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269(1–2), 341–356. https://doi.org/10.1007/s11104-004-0907-y

Raza, S., Cooper, H. V., Girkin, N. T., Kent, M. S., Bennett, M. J., Mooney, S. J., & Colombi, T. (2025). Missing the input: The underrepresentation of plant physiology in global soil carbon research. *Soil*, 11(1), 363–369. https://doi.org/10.5194/soil-11-363-2025

Reinsch, S., Lebron, I., de Jonge, L. W., Weber, P. L., Norgaard, T., Arthur, E., Gomes, L., Pesch, C., Konstantinos, K., & Zalidis, G. (2025). The fraction of carbon in soil organic matter as a national-scale soil process indicator. *Global Change Biology*, 31(11), e70572. https://doi.org/10.1111/gcb.70572

Rennert, T. (2019). Wet-chemical extractions to characterise pedogenic Al and Fe species – A critical review. *Soil Research*, 57(1), 1–16. https://doi.org/10.1071/SR18334

Rennert, T., Antonova, S., & Dietel, J. (2026). Is selective identification of poorly crystalline aluminum hydroxides in soils of temperate latitude possible? *Soil Science Society of America Journal*, 90(1), e70177. https://doi.org/10.1002/saj2.70177

Revelle, W. (2015). *psych: Procedures for psychological, psychometric, and personality research* [R package]. https://CRAN.R-project.org/package=psych

Ritchie, H., & Roser, M. (2019). Half of the world's habitable land is used for agriculture. *Our World in Data*. https://archive.ourworldindata.org/20251125-173858/global-land-for-agriculture.html

Rowley, M. C. (2020). *Investigating calcium mediated accumulation of soil organic carbon at the Nant Valley alpage, Vaud Alps, Switzerland* [PhD thesis]. University of Lausanne. https://doi.org/10.13140/RG.2.2.11439.10403

Rowley, M. C., Grand, S., & Verrecchia, É. P. (2018). Calcium-mediated stabilisation of soil organic carbon. *Biogeochemistry*, 137(1–2), 27–49. https://doi.org/10.1007/s10533-017-0410-1

Sachs, J. D., Schmidt-Traub, G., Mazzucato, M., Messner, D., Nakicenovic, N., & Rockström, J. (2019). Six transformations to achieve the sustainable development goals. *Nature Sustainability*, 2(9), 805–814. https://doi.org/10.1038/s41893-019-0352-9

Salonen, A. R., de Goede, R., Creamer, R., Heinonsalo, J., & Soinne, H. (2024). Soil organic carbon fractions and storage potential in Finnish arable soils. *European Journal of Soil Science*, 75(4), e13527. https://doi.org/10.1111/ejss.13527

Sanderman, J., Hengl, T., & Fiske, G. J. (2017). Soil carbon debt of 12,000 years of human land use. *Proceedings of the National Academy of Sciences*, 114(36), 9575–9580. https://doi.org/10.1073/pnas.1706103114

Schlüter, S., Leuther, F., Albrecht, L., Hoeschen, C., Kilian, R., Surey, R., Mikutta, R., Kaiser, K., Mueller, C. W., & Vogel, H.-J. (2022). Microscale carbon distribution around pores and particulate organic matter varies with soil moisture regime. *Nature Communications*, 13, 674. https://doi.org/10.1038/s41467-022-28246-w

Six, J., Conant, R. T., Paul, E. A., & Paustian, K. (2002). Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. *Plant and Soil*, 241(2), 155–176. https://doi.org/10.1023/A:1016125726789

Sokol, N. W., Whalen, E. D., Jilling, A., Kallenbach, C., Pett-Ridge, J., & Georgiou, K. (2022). Global distribution, formation and fate of mineral-associated soil organic matter under a changing climate. *Functional Ecology*, 36(6), 1411–1429. https://doi.org/10.1111/1365-2435.14037

Stockmann, U., Adams, M. A., Crawford, J. W., Field, D. J., Henakaarchchi, N., Jenkins, M., Minasny, B., McBratney, A. B., de Courcelles, V. d. R., & Singh, K. (2013). The knowns, known unknowns and unknowns of sequestration of soil organic carbon. *Agriculture, Ecosystems & Environment*, 164, 80–99. https://doi.org/10.1016/j.agee.2012.10.001

Svensson, D. N., Messing, I., & Barron, J. (2022). An investigation in laser diffraction soil particle size distribution analysis to obtain compatible results with sieve and pipette method. *Soil and Tillage Research*, 223, 105450. https://doi.org/10.1016/j.still.2022.105450

Thornley, J. H. M. (1972). A balanced quantitative model for root:shoot ratios in vegetative plants. *Annals of Botany*, 36(2), 431–441. https://doi.org/10.1093/oxfordjournals.aob.a084602

Tian, Q., He, H., Cheng, W., Bai, Z., Wang, Y., & Zhang, X. (2016). Factors controlling soil organic carbon stability along a temperate forest altitudinal gradient. *Scientific Reports*, 6, 18783. https://doi.org/10.1038/srep18783

Totsche, K. U., Amelung, W., Gerzabek, M. H., Guggenberger, G., Klumpp, E., Knief, C., Lehndorff, E., Mikutta, R., Peth, S., & Prechtel, A. (2018). Microaggregates in soils. *Journal of Plant Nutrition and Soil Science*, 181(1), 104–136. https://doi.org/10.1002/jpln.201600451

Veerman, C., Pinto, T., Bastioli, C., Biró, B., Bouma, J., Cienciala, E., B., E., Frison, E., A., G., L., H., Kriauciuniene, Z., Pogrzeba, M., Soussana, J.-F., Vela, C., R., W., & Borsari, B. (2020). *Caring for soil is caring for life: Ensure 75% of soils are healthy by 2030 for food, people, nature and climate*. European Commission. https://ec.europa.eu/info/publications/caring-soil-caring-life_en

Vinther, F. P. (2006). Effects of cutting frequency on plant production, N-uptake and N_2 fixation in above- and below-ground plant biomass of perennial ryegrass–white clover swards. *Grass and Forage Science*, 61(2), 154–163. https://doi.org/10.1111/j.1365-2494.2006.00517.x

von Fromm, S. F., Hoyt, A. M., Lange, M., Acquah, G. E., Aynekulu, E., Berhe, A. A., Haefele, S. M., McGrath, S. P., Shepherd, K. D., & Sila, A. M. (2021). Continental-scale controls on soil organic carbon across sub-Saharan Africa. *Soil*, 7(1), 305–332. https://doi.org/10.5194/soil-7-305-2021

von Fromm, S. F., Hoyt, A. M., Sierra, C. A., Georgiou, K., Doetterl, S., & Trumbore, S. E. (2024). Controls and relationships of soil organic carbon abundance and persistence vary across pedo-climatic regions. *Global Change Biology*, 30(5), e17320. https://doi.org/10.1111/gcb.17320

Watson, R. T., Noble, I. R., Bolin, B., Ravindranath, N. H., Verardo, D. J., & Dokken, D. J. (2000). *Land use, land-use change, and forestry: A special report of the IPCC*. Cambridge University Press.

Weiglein, T. L., Strahm, B. D., Bowman, M. M., Gallo, A. C., Hatten, J. A., Heckman, K. A., Matosziuk, L. M., Nave, L. E., Possinger, A. R., SanClements, M. D., & Swanston, C. W. (2022). Key predictors of soil organic matter vulnerability to mineralization differ with depth at a continental scale. *Biogeochemistry*, 157(1), 87–107. https://doi.org/10.1007/s10533-021-00856-x

Wenzel, W. W., Golestanifard, A., & Duboc, O. (2024). SOC:clay ratio: A mechanistically-sound, universal soil health indicator across ecological zones and land use categories? *Geoderma*, 452, 117080. https://doi.org/10.1016/j.geoderma.2024.117080

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer. https://doi.org/10.1007/978-3-319-24277-4

Xu, J., & Juma, N. (1992). Above- and below-ground net primary production of four barley (Hordeum vulgare L.) cultivars in western Canada. *Canadian Journal of Plant Science*, 72(4), 1131–1140. https://doi.org/10.4141/cjps92-140

Yu, W., Weintraub, S. R., & Hall, S. J. (2021). Climatic and geochemical controls on soil carbon at the continental scale: Interactions and thresholds. *Global Biogeochemical Cycles*, 35(3), e2020GB006781. https://doi.org/10.1029/2020GB006781

Zhang, S., Wang, M., Zheng, J., & Luo, Z. (2026). A global dataset of soil organic carbon mineralization in response to various incubation conditions. *Earth System Science Data*, 18(1), 131–152. https://doi.org/10.5194/essd-18-131-2026

Popular science summary

Unless you've been living under a rock, you've probably heard that climate change affects us all. Earth's climate has always fluctuated. During the Paleolithic, human populations were sparse, and most societies lived as hunter–gatherers. Then came the Holocene — the period when the climate stabilized enough for people to settle and begin farming. Agriculture sparked innovation and growth, but it also triggered rapid population expansion, deforestation, and ultimately marked the dawn of the Anthropocene.

These transformations came at a cost. Forests that once stored vast amounts of carbon were cleared, and soils — worked more intensively and longer — lost organic matter. Greenhouse gas concentrations soared, giving rise to one of the greatest challenges of the 21st century: climate change. So, the question is: how can we restore soils while reducing the impacts of climate change?

The answer, at least in part, lies beneath our feet — in returning carbon to the soil while meeting the needs of local communities. Increasing soil carbon improves soil fertility and can support higher crop yields. After all, soils are the largest terrestrial carbon reservoir on Earth. Through photosynthesis, plants capture carbon dioxide from the atmosphere, use it to grow, and return much of that carbon to the soil when they die.

But that raises new questions: how much carbon can soils store, and what keeps it there? Soils aren't just passive storage vaults; they are living systems teeming with organisms. Beyond the earthworms you see after rainfall or the ants' carrying crumbs from your picnic, there are countless microorganisms breaking down dead plants for energy. In doing so, they release some of that carbon back into the atmosphere as carbon dioxide. The challenge, then, is to tip the balance — to maximize the carbon entering the soil while minimizing the carbon that escapes.

This is where my research comes in. I studied what we still don't fully understand or haven't measured well, so we can know how much carbon is stored and make smarter decisions about managing it. First, I studied roots — how they grow and how they're distributed across a field. Roots are vital because they're the main source of carbon that remains in the soil after harvest. Studies show that root-derived carbon is often stored more efficiently than carbon from above-ground plant parts. However, measuring roots directly is messy and time-consuming. Many researchers therefore estimate below-ground biomass using root-to-shoot ratios based on plant material above ground. It's convenient but misleading, since it assumes roots are evenly distributed across a field.

We decided to do the dirty work and found that this assumption of homogeneity rarely holds true. Even in uniformly managed fields, root-to-shoot ratios varied widely. Ignoring this variation increases the risk of drawing false conclusions.

Once roots die and become part of the soil, the next question is what controls whether that carbon remains protected, thus stored or is quickly mineralized. Traditional thinking highlights that soils rich in clay are better at protecting carbon. My findings, however, show that aluminum-bearing minerals formed during soil weathering are an even stronger predictor of carbon storage in the humid agricultural soils of Sweden. Aluminum, abundant in many weathered soils, forms bonds with carbon — effectively locking it in place.

But is aluminum truly the cause of this stabilization? When I examined the data more closely, the picture became more complex. While some carbon was clearly being protected, it wasn't necessarily by the aluminum-bearing minerals identified as the best predictors. Instead, the quality of carbon inputs (often represented by the carbon-to-nitrogen ratio) and total nitrogen content appeared to play important roles. It's possible that nitrogen exerts a confounding effect, influencing both the amount of protected carbon and the quality of inputs that are decomposed. This finding highlights the need to better understand the role of carbon-to-nitrogen ratio and nitrogen's role in carbon stabilization.

These insights are far from answering every question, but they bring us a step closer to understanding how soils can be part of the climate solution. The ideas shaping climate action today may not be as futile as they sometimes seem. There is reason for hope — and if you're looking for it, you might have to check under a rock. Some of the answers are literally in the ground beneath your feet.

Populärvetenskaplig sammanfattning

Om du inte har bott under en sten de senaste åren har du nog hört talas om att klimatförändringarna påverkar oss alla. Jordens klimat har alltid varierat. Under Paleolitikum var människorna få, och de flesta samhällen levde som jägare och samlare. Sedan kom Holocen – den period då klimatet stabiliserades tillräckligt för att människor skulle kunna bli bofasta och bedriva jordbruk. Jordbruket ledde till innovation och utveckling, men det satte också fart på snabb befolkningstillväxt, avskogning och markerade till slut början på Antropocen.

Dessa omvälvningar hade ett pris. Skogar som en gång lagrade enorma mängder kol höggs ner, och jordarna – som odlades mer intensivt och under längre perioder – förlorade organiskt material. Halterna av växthusgaser steg kraftigt och gav upphov till en av 2000-talets största utmaningar: klimatförändringen. Nu är frågan: Kan vi återställa jordens bördighet och samtidigt minska klimatpåverkan?

En del av svaret ligger, bokstavligen, under våra fötter – i att binda tillbaka kol i jorden samtidigt som vi möter lokala samhällens behov. Ökad kolhalt i jorden förbättrar dess bördighet och kan ge bättre skördar. Jorden är trots allt den största landbaserade kolförrådet på planeten. Genom fotosyntesen fångar växterna in koldioxid från luften, använder den för att växa och för sedan tillbaka en stor del av kolet till jorden när de dör.

Men det väcker nya frågor: hur mycket kol kan jorden egentligen lagra – och vad gör att det stannar kvar? Jorden är ingen passiv förvaringsplats, utan ett levande system fullt av organismer. Förutom daggmaskarna man ser efter ett regn och myrorna som bär iväg med smulor från picknicken finns där otaliga mikroorganismer som bryter ner döda växter för att få energi. I den processen släpper de en del av kolet tillbaka till atmosfären som koldioxid. Utmaningen är alltså att hitta rätt balans – att maximera mängden kol som binds in i jorden och minimera det som släpps ut igen.

Det är här min forskning kommer in. Jag har undersökt det vi ännu inte helt förstår eller har mätt tillräckligt noggrant, så att vi bättre kan veta hur mycket kol som lagras och fatta klokare beslut om hur vi ska förvalta det. Först och främst har jag studerat rötter – hur de växer och hur de fördelas i ett fält. Rötter är avgörande eftersom de är den främsta källan till det kol som finns kvar i jorden efter skörd. Studier visar att kol som härstammar från rötter ofta lagras mer effektivt än kol från växtens ovanjordiska delar.

Att mäta rötter direkt är dock ett tidskrävande, svårt och smutsigt arbete. Därför uppskattar många forskare mängden rotbiomassa utifrån så kallade *rot–skott-kvoter*, baserat på den växtmassa som är lättare att mäta ovan jord. Det är bekvämt men missvisande, eftersom det förutsätter att rötter är jämnt fördelade över fältet.

Vi valde att göra det verkliga fältarbetet och kunde visa att den förutsättningen sällan stämmer. Även i fält som sköts på samma sätt varierade rot–skott-kvoten kraftigt. Att ignorera den variationen ökar risken för att dra felaktiga slutsatser.

När rötterna dör och blir en del av jorden uppstår nästa fråga: vad avgör om kolet blir kvar i jorden eller snabbt bryts ner? Enligt traditionell kunskap är lerhaltiga jordar bättre på att lagra kol än jordar med låg lerhalt. Mina studier visar dock att mineraler som innehåller aluminium, och som bildas när jorden vittrar, är en ännu starkare indikator på kolinlagring i typiska svenska jordbruksjordar. Aluminium, som finns rikligt i vittrade jordar, kan binda kol och på så sätt ”låsa fast” det.

Men är det verkligen aluminium som *orsakar* den här stabiliseringen? När jag granskade data mer ingående blev bilden mer nyanserad. Ja, en del av kolet verkade skyddas – men inte nödvändigtvis av de aluminiumhaltiga mineraler som verkade bäst på att förutsäga kolhalten. I stället visade resultaten att kolkvaliteten (ofta uttryckt som kvoten mellan kol och kväve) och den totala kvävehalten kan spela en viktig roll. Det kan hända att kvävet påverkar båda processerna: dels mängden kol som stabiliseras, dels hur snabbt det bryts ner. Det här pekar på att vi behöver förstå kvävets roll i kolstabilisering bättre.

Dessa resultat besvarar långt ifrån alla frågor, men de tar oss ett steg närmare insikten om hur jorden kan bli en del av klimatlösningen. De idéer som formar klimatarbetet i dag är kanske inte så hopplösa som de ibland kan verka. Det finns skäl till hopp – och om du letar efter det, får du kanske titta under en sten. En del av svaren finns bokstavligen i marken under våra fötter.

Acknowledgements

"I am what I am because of who we all are."
Ubuntu

To my supervisors.

To Mats, who literary walked this path with me and saw beyond my limitations. I never imagined pursuing my studies in Sweden. From our first conversation, I felt unqualified due to my perceived shortcomings, yet you offered me the opportunity anyway. I once believed silence needed constant filling with affirmation or instruction, but you taught me its deeper value. In that silence, I grew, learned independence, and found space for my own voice. I may not have fully embraced that space at first, but your patience helped me mature.

Thank you for giving me room to grow, for your nurturing presence, and for always showing up (even in the field). Thank you also for challenging my words and ideas, pushing me toward new ways of thinking through constant feedback and endless support. Even when it was inconvenient, you provided a platform for my development. Most of all, thank you for your helping hand during the final, frantic days of writing this thesis. I could not have hoped for a better supervisor.

To Tino, thank you for embracing my uncertainties and confronting my fears. Thank you for the talks that reminded me of the light at the end of the tunnel, even when I couldn't see it. This journey was far more bearable because of your constant support. You provided the voice of reason when doubt echoed in my mind.

To Thomas, any doubt I had about belonging was swiftly vetoed by you. Your presence and efforts kept the work moving forward in the most encouraging way. Thank you for always showing up, for your availability, and for sharing insights I had been blind to. Above all, thank you for providing directions amid confusion.

To Claudia, thank you for leading with grace and deliberate clarity whenever I faced challenging concepts. Thank you for guiding my thoughts so clearly at any time. I can only aspire to your style of teaching. From the first day I sat in your class, I felt acknowledged. Thank you so much. Representation matters, and you exemplify this powerfully. I feel truly seen because of you. While it may not carry the same weight in the Swedish context, it did for me—and working with you has shown me exactly why. You have been a joy and an inspiration.

To my colleagues.

To my colleagues at SLU. The image of open glass doors captures the spirit of openness at this institute. Thank you for giving me the space to ask questions and for keeping your doors open whenever my own reasoning fell short. To Marie Spohn and the postdocs in your group, Björn Lindahl, Nicholas Jarvis, Jon Petter Gustafsson, Karolina Jörgensen, Anke Herrmann, and Björn Lindahl, thank you for keeping your doors open and generously sharing your insights. I would also like to thank Carin Sjöstedt and Johanna Wetterlind for their valuable support and assistance with the SMP dataset.

To the BGF group — both past and present, Nicholas Jarvis, Elisabet Lewan, Mats Larsbo, Elsa Coucheney, Anna Lindahl, David Nimblad Svensson — thank you for bringing me along on your journey. For the support that is visible in everyday interactions and the quiet support that comes from simply being included, I am forever grateful.

To the postdoc and PhD cohort — both past and present, and to those I have met at different times in classes, conferences, in the lunchroom, over fika, in corridors, the lab or in your office spaces — thank you for the support and walking this path with me. Hanna Sjulgård, David Nimblad Svensson, Jumpei Fukumasu, Emmanuel Ngonga, Erica Packard, Jeongyeon Yun, Péter Garamszegi, Rebecca Naomi Ter Borg, Tamlyn Gangiah, Ylva Bellander, Wiebke Mareile Heinze, Elsa Maria Arrazola Vasquez, Tove Florén, Louis Dufour, Samia Ghersheen, Evelin Pihlap, Oksana Valetska, Haichao Li, Getachew Gemtesa Tiruneh, Hui Liu, Lorena Chagas Torres, Jelena Rakovic, Louise Malmquist, Yaana Bruneel: the list is inexhaustible. I do not think anyone understands this journey quite like those who walk it with you, whether from the start or as they join along the way.

To Grace Pold and Katharina Meurer, thank you for reviewing the first draft of this thesis and offering your insights. To Nicholas Jarvis and the editorial committee, thank you for reading through the draft of this thesis and pointing out things I would otherwise have been blind to. Thank you for your advice and for taking the time and effort to review my work with genuine care.

To the administrative staff, thank you for keeping my employment at SLU running smoothly. Elisabet Lewan, Geert Cornelis, Josefine Agrell, and Sara Wassén, thank you for the support you have offered me each time I had questions about my employment and education. To Karin Blombäck and Helena Aronsson, thank you for your time and help when I needed it most, especially when my mental health failed me. Thank you for being the voice of reason when the voices in my head grew too loud.

To the laboratory staff and superintendents — both past and present — and to the cleaning staff, thank you for keeping the spaces I used running, whether in the lab or in the office. I am constantly in awe of the dedication and precision with which you do your work, and it helps me keep going. Thank you for your kindness.

I am sure there are countless more people at this institute whom I have encountered and who have, in one way or another, been instrumental in bringing me to this moment. This goes without saying — thank you, too.

To my parents.

To my ma, Rose Mweemba, who has walked this path alongside me: you deserve all the glory and praise. You were the first to believe in my dreams, even when no one else did, you truly saw me, both literally and figuratively. You loved me first and have supported me unwaveringly ever since. Thank you, Ma. This thesis is as much yours, as it is mine. Thank you for giving me the freedom to choose my own path, for your gentle guidance paired with ambitions I deeply admire. I could not be who I am today without you.

To my papa, Davison Chilipamshi, who always let me run wild: I was able to accomplish this because of you. If I can achieve even half of what you did, I will consider myself fortunate. I hope I have made you proud. I was unable to attend your funeral, but this thesis is my gift to you, Papa. This wasn't the plan—we were meant to do it together. Every day, I am reminded of your ambition, your love, and your belief in my dreams. I will always love you, and your memory will live on forever. Thank you for seeing me and creating a safe space for my curiosity. I will do my best to carry on the work you began and preserve your legacy for as long as I can. MYSRIP.

To my kin.

To my sister, Joy Chilipamushi: I do not know if I would have finished this journey without you. You almost died, and this thesis almost died with you. From November 2022 to September 2023, my life was on hold, but your fighting spirit kept me going. Thank you for being my voice of reason. This thesis is as much yours, as it is mine. I write this with tears in my eyes. May God continue to watch over you. You see me as I am and have nurtured me

into who I am today. Even when I feel misunderstood, your love keeps me grounded. Thank you for always checking up on me and cheering me on at every step, and for your prayers and words of encouragement.

To my siblings, Thandiwe Chilipamushi, Lydia Chilipamushi, Musonda Chilipamushi, Bertha Kasonde, and Linda Chilipamushi: thank you for being my family, my cheerleaders, and my anchor.

To my nephews and nieces, for whom I do this and who are a constant source of inspiration and joy: I am because we are.

To my nephew, Levi James: thank you for teaching me to be present and live in the moment. Your memory will forever be cherished. MYSRIP.

To my friends, who became family.

To Mwenya Mubanga: What a joy it has been to walk this path and encounter someone like you. You are an honorary member of my supervisors, even without the title. From the day I arrived in Sweden, I never felt alone—you literally met me at the airport, helped me settle in, and find my footing. This place almost feels like home because of the warmth you always extended to me. Thank you for showing up for me in countless ways. I hope God rewards you tenfold for what you have given. I will always be grateful.

To Sharon and Jeff Nkandu, Njelema Sanga, and Vito Laterza and Patience Mususa: Thank you for helping me realize my path. This road has felt far less bare because of you. You have become an extension of my family, bringing warmth to this place. Thank you for receiving me as I am and embracing me. I will always be grateful.

To Mwanja Rosemary Mwango and Joel Muke: Thank you for being there and traveling this road with me, even when it got hard. Thank you for your encouragement and support. I am forever grateful to you.

To Nisola Ayanfe and esethu monakali: Thank you for walking part of this journey with me. Nisola, thank you for all the hours we wrote together, for your feedback, and for your encouraging words. esethu, thank you for helping me find my way back to myself and reaffirming this journey.

To my church family (Keron Bwacha, Bosse and Ingrid Gustavsson, Marija Blazic, Cedric Kaneza, Mama Cedric, Lily, Elvirah Neza, Simon Okwir, Ellen, Shepherd Urenje, Christina and Bjorn Isaksson—the list is endless): Thank you for receiving me as I am and embracing me. Thank you for being the voice of reason when I could not. Thank you for making space for me to rest each week, for your prayers, and for your constant encouragement. Thank you for showing up at every milestone.

To Mr. and Mrs. Muke: Thank you for welcoming me into your family, for making room for me, and for consistently showing up since I moved to Sweden. I am forever grateful to you.

To the wonderful people I met and worked alongside on Focusmate, I would like to add my heartfelt thanks. I'm grateful for the encouragement from the many individuals I was randomly paired with from around the world—across all 1,943 sessions, totaling 1,619 hours, or 67.5 days of shared focus.

To my Lord and Savior, Jesus Christ.

All praise and glory belong to God (1 Samuel 2:1–3). Thank You for guiding me through these past years. When my physical and mental strength failed, You carried me. When my faith failed, You remained faithful. Every ounce of strength I had came from You. I am forever grateful that You have led me to this moment and have been my source of knowledge, wisdom, and understanding. I am because You reign.

I

Soil & Tillage Research 260 (2026) 107103

Contents lists available at ScienceDirect

Soil & Tillage Research

journal homepage: www.elsevier.com/locate/still

Within-field variation in root-to-shoot ratios and root traits in spring barley: Implications for estimating carbon inputs

Miyanda Chilipamushi [a,*], Claudia von Brömssen [b], Tino Colombi [a,c], Thomas Kätterer [d], Mats Larsbo [a]

[a] Department of Soil and Environment, Swedish University of Agricultural Sciences, Box 7014, Uppsala 750 07, Sweden
[b] Department of Energy and Technology, Swedish University of Agricultural Sciences, Box 7013, Uppsala 750 07, Sweden
[c] School of Biosciences, University of Nottingham, Sutton Bonington LE12 5RD, UK
[d] Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden

ARTICLE INFO

Keywords:
Allometric functions
Root-to-shoot ratio
Soil carbon inputs
Soil carbon modelling
Soil organic carbon monitoring
Temporal variability
Within-field variability

ABSTRACT

Roots are a major pathway for carbon (C) input into agricultural soils, yet field-scale measurements of below-ground C inputs and associated root traits remain limited. Consequently, many soil carbon models rely on fixed root-to-shoot ratios, and root trait variability is rarely considered. In this study, we quantified within-field variation in root-to-shoot ratios and root traits (root diameter, root length density and root tissue density) in spring barley (*Hordeum vulgare* L.) grown in southwestern Sweden in soil classified as Stagnic Eutric Cambisol, Eutric Stagnosol or Haplic Phaeozem according to the World Reference Base system. Roots (0–40 cm) and shoots were sampled during early to mid-reproductive stage, i.e. milking/early dough development stage, in a 50 × 50 cm grid at 11 sampling locations in the same field in two consecutive years. Shoot and root biomass were not correlated, resulting in variable root-to-shoot ratios (quartile coefficients of variation 7–18 %) and no consistent spatial pattern between years. Root traits displayed clear between year and depth variation, with coarser roots in the topsoil and root tissue densities and root length densities shifting across the profile, reflecting the highly plastic nature of root systems. The spatial variation in root properties in the field could not be explained by basic soil properties. Our findings call for a more mechanistic understanding of the drivers for root-to-shoot ratios and the plastic response of root traits to improve field-scale estimates of root-derived C inputs and SOC modelling accuracy.

1. Introduction

Changes in soil organic carbon (SOC) stocks in agricultural soils are monitored using repeated soil inventories or estimated with dynamic soil carbon models such as RothC (Coleman and Jenkinson, 2014), C-TOOL (Taghizadeh-Toosi et al., 2014), ICBM (Bolinder et al., 2019) and Yasso07 (Liski et al., 2005). In arable crops, about 25 % of the carbon fixed through photosynthesis is allocated to roots and rhizodeposition (Jacobs et al., 2020). Root-derived carbon inputs are particularly important for carbon balances, as they tend to form more stable SOC pools compared to input from above-ground plant residues (Rasse et al., 2005, Kätterer et al., 2011, Gasser et al., 2022). Hence, SOC input through roots needs to be properly accounted for in monitoring programs and modelling efforts. However, root sampling and analysis are labor-intensive, and root data are, therefore, often limited (Böhm, 1979, Cabal et al., 2021, Lux and Rost, 2012). Although above- and especially below-ground plant traits play a key role in determining SOC inputs, their influence on overall SOC balances remains insufficiently explored. Consequently, soil carbon models rely on simplifications such as fixed root-to-shoot ratios to estimate root-derived carbon inputs. This introduces uncertainty in modelled soil carbon inputs because, in reality, root-to-shoot ratios vary with soil properties, soil and crop management, soil nutrient status, soil moisture and climate (Bolinder et al., 2007, Taghizadeh-Toosi et al., 2020).

Previous studies have primarily focused on soil and crop management effects on root-shoot ratios using long-term plot-scale field experiments (Xu and Juma, 1992) and on inter-field and regional variability in root-to-shoot ratios (Bolinder et al., 2007, Mattila and Häkkinen, 2025, Hirte et al., 2018, Plaza-Bonilla et al., 2013, Heinemann et al., 2025) with little consideration of field scale heterogeneity.

* Corresponding author.
E-mail address: miyanda.chilipamushi@slu.se (M. Chilipamushi).

https://doi.org/10.1016/j.still.2026.107103
Received 17 September 2025; Received in revised form 1 February 2026; Accepted 3 February 2026
Available online 7 February 2026

Furthermore, it remains difficult to separate the effects of soil properties from the effects of management and climate in regional studies since this would require large amounts of data. For example, regional studies of annual crops have shown that root-to-shoot ratios may vary with soil texture (Poeplau and Kätterer, 2017; Mattila and Häkkinen, 2025) and weather conditions (Hirte et al., 2021).

Soil carbon sequestration is not determined by the quantity of root input only. The root system architecture (i.e., the spatial configuration of the root system), which encompasses features such as root length, spread, and diameter (Khan et al., 2016), influences microbial accessibility and, hence, root turnover. Despite the impact of above- and particularly below-ground plant traits for estimating SOC inputs, their impacts on SOC balances are understudied (Raza et al., 2025). Similar to root-to-shoot ratios, root architecture exhibits substantial variation in response to soil and crop management, soil properties and climate (Bao et al., 2014, Weemstra et al., 2022, Weemstra et al., 2021, Asefa et al., 2022, Durand-Maniclas et al., 2025). Soil-crop simulation models (e.g. USSF (Jarvis et al., 2024); DAISY (Hansen et al., 2012); APSIM (O'Leary et al., 2015)) are increasingly used to simulate SOC dynamics and other ecosystem processes under varying environmental and management conditions. These models integrate key biophysical processes such as crop growth, water and nutrient uptake, and carbon allocation, and often also consider, at least some aspects of root system architecture, such as root length density and diameter (Seidel et al., 2024, Dupuy et al., 2010). A deeper understanding of within-field variation in root architecture and its interaction with soil properties, as well as examining both between- and within-field variability in the root-to-shoot ratio and its underlying drivers, could enable improved process descriptions and parameterization of belowground components in soil and crop, and SOC models (Dupuy et al., 2010, Raza et al., 2025).

The objectives of this study were to i) quantify the within-field spatial and between year variation in shoot and root properties and corresponding root-to-shoot ratios, ii) quantify the within-field variation in root traits such as the root diameter, root length density and root tissue density, iii) test if soil properties could explain the variation in shoot and root properties, and iv) test if root biomass could explain the within-field variation in SOC in the topsoil. This was achieved by collecting shoot and root samples of spring barley during early to mid-reproductive stage, i.e. milking/early dough development stage from 11 sampling points during two consecutive years in a commercially managed field with large variation in soil texture and SOC content. This study moves beyond "average" rooting and biomass allocation by quantifying spatial heterogeneity within a single field and by linking root-to-shoot ratios and root traits to within-field variation in soil properties that are generally not considered in regional studies or in long-term plot-scale field experiments.

2. Methods and materials

2.1. Site description

The study area was a 46.9 ha conventionally-managed field in Bjertorp, Västergötland, in southwestern Sweden (58°14'00"N 13°08'00" E) with large spatial variations in soil texture and SOC content (clay content 9–45 % and SOC content 0.6–2.7 g kg^{-1} in the topsoil (0–20 cm) (Lindahl et al., 2008). Mean annual precipitation and temperature between 1961 and 2024 were 706 mm and 6.8°C, respectively. Depending on location, the soil in the field was classified either as Stagnic Eutric Cambisol, Eutric Stagnosol or Haplic Phaeozem according to the World Reference Base system (IUSS Working Group, 2015, Fukumasu et al., 2021). The field has been under continuous arable cultivation for more than 60 years (Lindahl et al., 2008, Fukumasu et al., 2021). The crop rotation has primarily consisted of winter wheat (*Triticum aestivum)*, barley (*Hordeum vulgare* L), oats (*Avena sativa*) and oilseed rape (*Brassica napus* L) as the main crops. The uppermost 20–25 cm has been mouldboard ploughed in the autumn, with a shallower plough depth in years when winter rapeseed was sown (Fukumasu et al., 2021). Fertilization has been applied with nitrogen, phosphorus, and potassium, with no addition of farmyard manure (Fukumasu et al., 2021). Fertilizers were applied at sowing between seeding rows at rates of 70, 26 and 44 kg ha^{-1} of nitrogen, phosphorus and potassium in 2023, and 70, 32 and 52 kg ha^{-1} of nitrogen, phosphorus and potassium in 2024. Additional nitrogen fertilizer was applied uniformly to the soil surface at 24 kg ha^{-1} in 2023 and 43 kg ha^{-1} in 2024.

2.2. Sampling design and analyzed variables

The sampling locations were selected to cover the variation in SOC content and soil texture (Fig. 1A, B). This selection was based on data from Fukumasu et al. (2021), who investigated the relationships between soil physicochemical properties, the reactive mineral phase, mean relative grain yield (as a proxy for carbon input) and SOC content in different soil fractions. From the initial 35 sampling points selected by Fukumasu et al. (2021), we applied systematic sampling at a fixed interval based on the SOC content analyzed by Fukumasu et al. (2021) to obtain the 11 representative sampling points shown in Fig. 1A, from which we collected samples for the analysis here. We sorted the SOC content measurements for the 35 points in ascending order and selected every third point.

Soil samples at the same sampling points were previously collected and analyzed by Fukumasu et al. (2021) for the variables listed in Table S1 at a depth of 3 – 13 cm. From the published dataset, we used SOC content, clay content, and elevation (Table 1). The elevation was between 88 and 94 m above sea level with a median slope of 0.3°. Loose soil was sampled at about 3 – 13 cm, dried at 38℃, crushed and sieved to < 2 mm, and SOC content was subsequently determined using a LECO Trumac CN analyzer according to SS-ISO 10694 (Fukumasu et al., 2021). Soil texture was also analyzed using the pipette method after organic matter oxidation according to Messing et al., 2024 in the data published in Fukumasu et al., 2021. A full description of the methods can be found in Fukumasu et al. (2021). Precipitation and temperature data at a daily resolution were obtained from a gridded map produced by the Swedish Meteorological and Hydrological Institute (SMHI) for the two years of our study (2023 and 2024).

2.3. Crops and growth conditions

Two-rowed spring barley (*Hordeum vulgare* L.) was grown in both 2023 and 2024 using different cultivars in the two years (Laureate in 2023 and Lexy in 2024). Plants were sampled during early to mid-reproductive stage, i.e. milking/early dough development stage (BBCH 71–83) in both years to capture root biomass after flowering, even though maximum biomass is often reported to occur at flowering (Gregory et al., 1996; Hoad et al., 2001) and to avoid the presence of extraneous organic matter (Hirte et al., 2017; Watt et al., 2008). Lexy and Laureate are similar malting barley cultivars; Lexy is distinguished by fine straw, while Laureate has a slightly shorter stalk (Lantmännen, 2025). In 2023, the plants were sown on 21st April. Root and shoot samples were collected on 25th and 26th July 2023. The mean temperature between sowing and sampling was 12.7 °C, and average daily precipitation during the same time was 2.6 mm, with a maximum daily precipitation of 37.3 mm. Cumulative precipitation in the preceding months was also relatively low compared to the peak in August (192.3 mm; Fig. 1D). Throughout the growing period, average monthly temperatures remained below 20 °C (Fig. 1C).

In 2024, plants were sown on 13th May. Root and shoot sampling were carried out on 29th and 30th July 2024 with a mean temperature of 12.7 °C and an average daily precipitation of 2.4 mm between sowing and sampling. Cumulative precipitation in April 2024 was approximately six times higher than in April 2023, and precipitation in the following two months was also larger in 2024 (Fig. 1D). Average monthly temperatures did not exceed 20 °C (Fig. 1C).

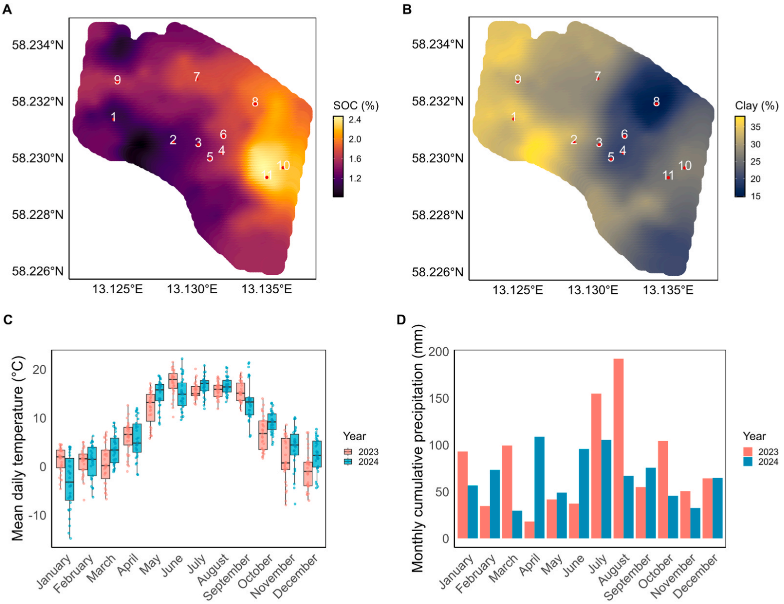


Fig. 1. Maps of the field in Bjertorp, Sweden, showing the sampled locations in 2023 and 2024 and the spatial variation in topsoil properties: (A) soil organic carbon content and (B) clay content at 3–13 cm depth. Box plots illustrate (C) mean daily temperature (each box shows the distribution of mean day temperatures for that month) and (D) monthly cumulative precipitation, based on interpolated gridded data from Swedish Meteorological and Hydrological Institute (SMHI).

Table 1
Descriptive statistics for the variables used for the 11 sampling locations used in the current study. Data was derived from Fukumasu et al. (2021) taken at 3 – 13 cm depth. SD is the standard deviation, and CV is the coefficient of variation.

Variable	Units	Means	SD	Minimum	Maximum	Median	CV
Soil organic carbon content	mg g^{-1}	16.9	4.3	11.8	24.3	15.1	25.2
Elevation	m (above sea level)	92.9	2.7	87.7	95.4	94.5	2.9
Clay content	%	28.1	7.6	16.5	38.8	30.3	26.9

2.4. Shoot and root sampling

Shoot samples were collected in one 50 cm × 50 cm area at each location using an electric clipper. The shoot samples were cut approximately 1 cm above the soil surface. The shoot samples were oven-dried at 60°C for 48 h within one day of collection. Root samples were taken at the depths 0–20 and 20–40 cm in the same grid as the shoot samples. Four sampling points were randomly chosen per sampling location: two samples between and two within the rows (Schuurman and Goedewaagen, 1971). Samples were taken using a metal auger with an inner diameter of 7 cm. Samples were stored in sealed polyethene bags at −20℃ until further processing.

2.5. Separation of roots and root biomass determination

Root biomass was determined using an adapted version of the method described in Mattila and Häkkinen (2025). Roots were first soaked overnight in a mixture of water and 100–200 mL of perfume-free liquid soap (Mölndal, Sweden) in closed buckets at 4°C. Following soaking, the soil was removed using a power hose, and remaining organic matter residues and any residual soil particles were repeatedly rinsed and sifted through a 1 mm sieve until all soil aggregates had disintegrated to minimize any losses (Böhm, 1979). Once all visible aggregates had been broken down, organic matter was separated from sand and gravel by density and transferred to a colorless container to which water was added. The mixture was continuously stirred, and floating organic matter was extracted using a 50 µm sieve. This process was repeated 5–10 times, depending on the volume of organic matter. The material collected on the 50 µm sieve was transferred to 70 % ethanol for storage until further analysis. Roots were then visually identified using a 127 mm glass lens magnifying lamp with a 570-lumen LED light by color and root architectural properties, and separated using tweezers (Böhm, 1979). Roots were stored in 70 % ethanol at 4°C until further analysis. All root fragments smaller than about 5 mm were excluded for practical reasons before scanning or removed from the images during post-processing. Finally, the roots were dried at 60°C for 48 h and weighed.

2.6. Root imaging and image processing

Roots were scanned in a flatbed scanner (Epson Perfection V850, Tokyo, Japan) at a resolution of 600 dpi. The roots were physically separated using plastic tweezers so that they did not exceed 1 cm of root length per cm^2 of tray area to minimize overlap (Delory et al., 2017). The final images were saved in tif-format and analyzed with RhizoVision Explorer Version 2.03 (Seethepalli et al., 2021) using the settings given in Supplemental Table S4. Root length and volume measurements acquired with RhizoVision were used to calculate root length density (cm root cm^{-3} soil) and root tissue density (g root cm^{-3} dry root biomass). In addition, the median root diameter was determined from RhizoVision, and roots were assigned to diameter classes (very fine: 0–0.2 mm, fine: 0.2–2 mm, and small to large: >2 mm).

2.7. Quantification of plant traits

We calculated the root biomass by summing root biomass within and between rows according to Frasier et al. (2016) and adapted by Hirte et al. (2021) as follows:

$$RB_{within} = \frac{M_{within}}{\pi * \left(\frac{d}{2}\right)^2} * \frac{d}{s} \tag{i}$$

$$RB_{between} = \frac{M_{between}}{\pi * \left(\frac{d}{2}\right)^2} * \frac{s-d}{s} \tag{ii}$$

where RB_{within} (g m^{-2}) and $RB_{between}$ (g m^{-2}) denote root biomass within and between rows respectively, M_{within} (g) and $M_{between}$ (g) denote the dry weight of roots extracted from the soil cores taken within and between rows respectively, d (m) is the inner diameter of the auger, and s (m) is the distance between rows. The shoot biomass per area, SB (g m^{-2}), was determined by:

$$SB = \frac{M}{A_Q} \tag{iii}$$

where M (g) is the dry weight of the shoots, and A_Q (m^2) is the sampled area. Measured shoot and root biomass (0–40 cm) data were then used to calculate root-to-shoot ratios.

2.8. Statistics and data visualization

We used non-parametric rank tests to analyse the data since the variables were generally not normally distributed, and the sample size was relatively small (n = 11) (Table S2). Spearman's rank correlation coefficients (ρ) were used to assess all correlations. Field variation was characterized with median values and the quartile coefficient of variation (QCV). The QCV was calculated as the ratio of the difference between the third and first quartiles to their sum, expressed as a percentage (Bonett, 2006). Comparisons between years were conducted using the Wilcoxon signed-rank test. To explore temporal trends, scatter plots were used for measurements taken at the same locations in both years, with a 1:1 reference line included to facilitate visual comparison. Additionally, the geostatistical interpolation in Fig. 1A-B was performed applying ordinary kriging at a spatial resolution of 10 m with SOC and clay content data from Lindahl et al. (2008) for the field.

All data processing and statistical analyses were conducted using R version 4.3.1 (R Core Team, 2023). Root image data extracted from RhizoVision were aggregated using weighted means using the "combinefeature" function (Seethepalli et al., 2024). Data processing and structuring were performed using "tidyverse" (Wickham et al., 2019) and "dplyr" (Wickham, Bryan., 2023). Data visualization was carried out using "ggplot2" (Wickham, 2016), with additional enhancements for statistical plots provided by "ggpubr" (Kassambara, 2023). Correlation matrices were visualized using custom functions built with the "corrplot" package (Wei and Simko, 2021). For geospatial analyses, vector data were managed using the "sf" package (Pebesma, 2018), and raster outputs were generated and masked to field boundaries using "terra" (Hijmans, 2023). Geostatistical interpolation was performed with "gstat" (Gräler et al., 2016). Field boundaries and the slope were digitized using Google Maps and Earth, respectively.

3. Results

3.1. Root and shoot biomass and the corresponding root-to-shoot ratio

Shoot biomass differed significantly between 2023 and 2024 ($p < 0.05$; QCV = 10 %; Fig. 2 A). Root biomass showed a similar pattern, with larger values in 2024 than in 2023 over the entire sampling depth (0–40 cm; Fig. 2B). Specifically, root biomass was 127 ± 24 g m^{-2} (median) in 2023 (QCV = 9 %; 0–40 cm; Fig. 2B) and 150 ± 40 g m^{-2} (median) in 2024 (QCV = 19 %; 0–40 cm; Fig. 2B). No significant differences in root biomass were found between years in the 20–40 cm layer or for the total 0–40 cm profile ($p > 0.05$; Fig. 2B). In contrast, root biomass in the top 20 cm was significantly larger in 2024 than in 2023 ($p < 0.05$; 0–20 cm; Fig. 2B). Across both years, 70–92 % of total root biomass was in the upper 20 cm, increasing from 2023 to 2024 (Fig. S1A). There was no significant overall effect of year on the root-to-shoot ratio ($p > 0.05$), with median values of 0.16 ± 0.04 in both years (Fig. 2 C). However, variation in root-to-shoot ratio was greater in 2023 (QCV = 18 %; Fig. 2 C) than in 2024 (QCV = 7 %; Fig. 2 C).

The shoot biomass, root biomass over the entire sampling depth, and root-to-shoot ratios in 2023 and 2024 were not correlated (Fig. 2D-F). Although there was a general tendency for both shoot and total root biomass to increase from 2023 to 2024, some locations showed notable decreases (Fig. 2 A, B). Relative increases were up to 70 and 200 % for shoots and total roots, respectively (Fig. S1A, B). Additionally, no consistent pattern was observed in the root-to-shoot ratio, with decreases up to 54 % and increases of more than 120 % (Fig. 2 F; Fig. S1C).

3.2. Root diameter, root tissue density and root length density

Root traits showed both notable within-field (QCVs up to 20 %; Table S2, S3) and temporal variation (Fig. 3A-C). Roots consistently had a higher median diameter in 2023 (QVC=4 %) than in 2024 (QVC=4 %) ($p < 0.05$; 0–40 cm; Fig. 3A). At 0–20 cm depth, the median root diameter was 0.29 ± 0.02 mm (QCV = 3 %; Fig. 3A) in 2023 and 0.27 ± 0.02 mm in 2024 (QCV = 4 %; Fig. 3A). A similar pattern was evident at 20–40 cm, where median root diameter decreased ($p < 0.05$) from 0.34 ± 0.02 mm in 2023 (QCV = 4 %) to 0.29 ± 0.04 mm in 2024 (QCV = 10 %). Across all depths and years, the majority (up to 98 %) of roots had diameters smaller than 2 mm, while roots thicker than 2 mm contributed less than 1 % to the total length (Fig. S3).

Root length density (RLD) exhibited notable variation within the field (QCV up to 24 %; Tables S2, S3) and differed significantly between years ($p < 0.05$; Fig. 3B). At 0–20 cm depth, median RLD was 13.0 ± 3.38 cm cm^{-3} in 2023 (QCV = 15 %) and was significantly smaller ($p < 0.05$) than in 2024, where values were 17.4 ± 5.33 cm cm^{-3} (QCV = 15 %). The same trend was observed at 20–40 cm depth as at 0–20 cm depth, with a wider variation in 2023 (QCV = 24 %) and 2024 (QCV = 16 %).

Root tissue density (RTD) also displayed considerable within-field variation (QCV up to 20 %; Tables S2, S3), with values ranging from 0.05 to 0.09 g cm^{-3} . However, no significant differences in RTD were observed between years ($p > 0.05$; Fig. 3C). At 0–20 cm depth, median RTD ranged from 0.07 ± 0.01 g cm^{-3} in 2023 (QCV = 7 %) and 0.07 ± 0.01 g cm^{-3} in 2024 (QCV = 9 %). Median RTD values were similar at the 20–40 cm depth.

Root diameter, root length density (RLD), and root tissue density (RTD) in 2023 and 2024 were not correlated to each other (Fig. 3D-F). Relative decreases in root diameter from 2023 to 2024 were up to 20 % (Fig. S2A), while RLD and RTD increased up to 200 and 30 %, respectively (Fig. S2B, C).

3.3. Correlations between soil properties and root traits across years in the top 20 cm

There were generally more significant correlations between soil

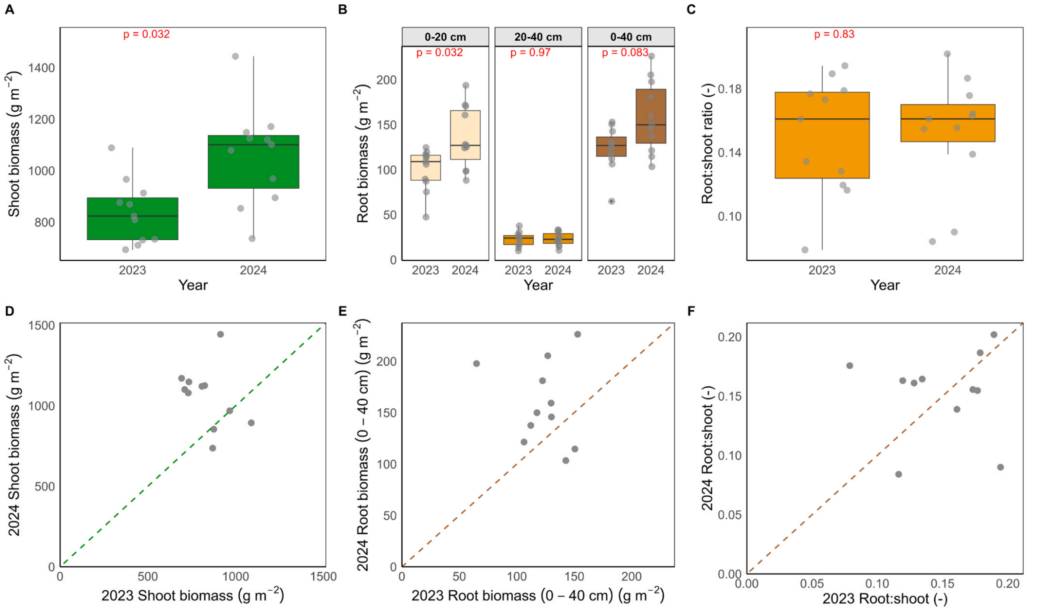


Fig. 2. (A) Total shoot biomass (g m^{-2}), (B) root biomass by depth (g m^{-2}), and (C) root-to-shoot ratio in study years 2023 and 2024. P-values indicate significance levels from the Wilcoxon signed-rank test. Between-year comparison of the (D) shoot biomass, (E) total root biomass and (F) root-to-shoot ratio, where the 1:1 line denotes equal values between years and deviations from this line illustrate the absence of a consistent relationship between 2023 and 2024 sampled at early to mid-reproductive stage, i.e. milking/early dough development stage (BBCH 71–83).

properties and plant traits in the wetter year 2024 compared to 2023 in the top 20 cm (Fig. 4A-B). In 2023, RLD was negatively correlated with SOC content, while in 2024, shoot biomass was negatively correlated with clay content and root diameter and RTD were positively correlated with clay content (Fig. 4A-B). The mean root biomass in the top 20 cm for the two years was also uncorrelated with SOC content (Fig. 4A-B).

4. Discussion

Observed median root-to-shoot ratios in our study (0.16) align with values reported for spring barley in southern Finland (0.14; Pietola and Alakukku 2005), values for small-grain cereals in Central European (0.07–0.18; Hirte et al. (2021)) and North American agro-ecosystems (~0.13; Bolinder et al. (2007)), indicating broad consistency in magnitude across regions and methods. Across both years, 70–92 % of root biomass was contained in the upper 20 cm of the soil profile (Fig. 2B). This depth distribution is broadly consistent with prior reports for small-grain cereals: spring barley allocated approximately 59 % of total (0–60 cm) root biomass to the 0–20 cm layer under Finnish conditions (Pietola and Alakukku, 2005), 70–75 % of spring barley roots were found within 0–20 cm of the 0–100 cm profile in experiments sensitive to nitrogen fertilization (Hansson and Andrén, 1987), and spring annual crops, on average, had allocated about 13–92 % of the root biomass to the 0–20 cm portion of the 0–40 cm profile across Finnish systems (Mattila and Häkkinen, 2025).

4.1. Root-to-shoot ratios show large within-field variation

Here, we found substantial within-field variation in root-to-shoot ratios across both sampling years. The quartile coefficient of variation (QCV) was 18 % in 2023 and 7 % in 2024, with no consistent spatial pattern emerging between years (Fig. 2 F). This indicates that above-ground biomass was a poor predictor of SOC input via roots, even under uniform management and climate. Previous studies have reported even larger variation in root-to-shoot ratios across sites and broader spatial scales, where differences have been attributed to tillage practices, soil texture, nutrient availability, crop genotype, and climate conditions. These findings highlight the multifactorial nature of belowground carbon allocation in annual cereals (Bolinder et al., 2007, Heinemann et al., 2023, Hirte et al., 2021, Hu et al., 2018, Mattila and Häkkinen, 2025, Xu and Juma, 1992).

For instance, the range of root-to-shoot ratios, including only roots in the 0–20 cm depth observed in our study (0.06–0.16 in 2023; 0.07–0.17 in 2024) was much narrower than the values reported for annual grain crops in a regional study from Finland (0.01–2.27; Mattila and Häkkinen, 2025). Similarly, when considering roots down to 40 cm, QCVs of 40 % in 2021 and 54 % in 2023 were found across multiple farms and spring crops in Mattila and Häkkinen (2025), again exceeding the variation observed within our field.

In the study of Mattila and Häkkinen (2025), the strongest predictors of root-to-shoot ratios were depth to a compacted layer and clay content. However, within our field, root-to-shoot ratios were not correlated with SOC content, clay content, or elevation (Fig. 4), suggesting that other unmeasured variables governed the observed within-field variation. Moreover, the lack of correlation between years (Fig. 2 F) indicates that different factors may have been important in the drier year 2023 compared with 2024. Alternatively, the same variables may have interacted differently with climatic conditions, so that their relative influence shifted between the years.

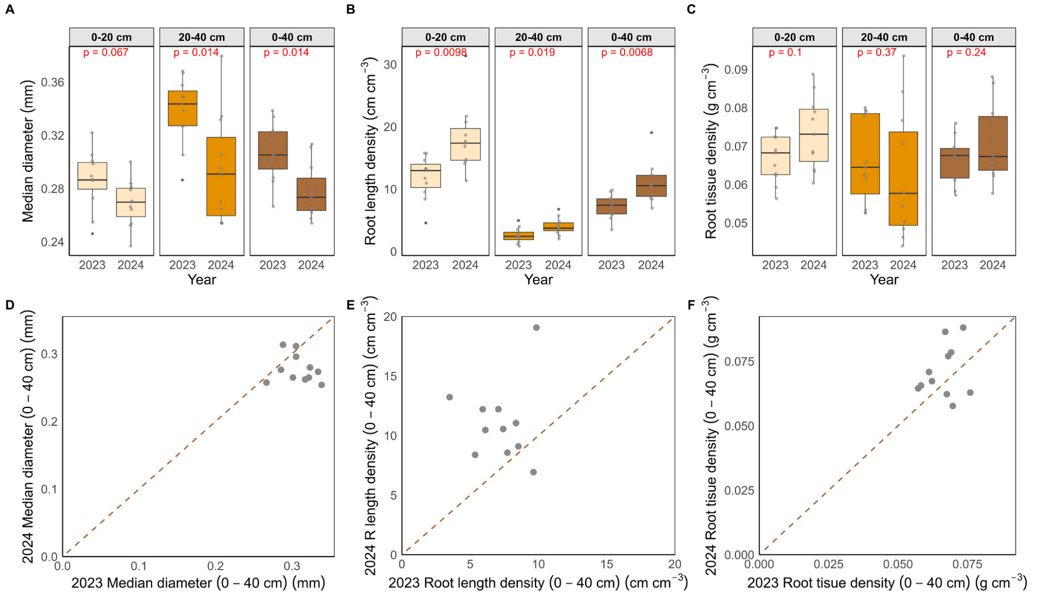


Fig. 3. A) Median root diameter, B) root length density, and C) root tissue density. P-values indicate significance levels from the Wilcoxon signed-rank test. Between-year comparison of the (D) shoot biomass, (E) root biomass and (F) root-to-shoot ratio, where the 1:1 line denotes equal values between years and deviations from this line illustrate the absence of a consistent relationship between 2023 and 2024 sampled at early to mid-reproductive stage, i.e. milking/early dough development stage (BBCH 71–83).

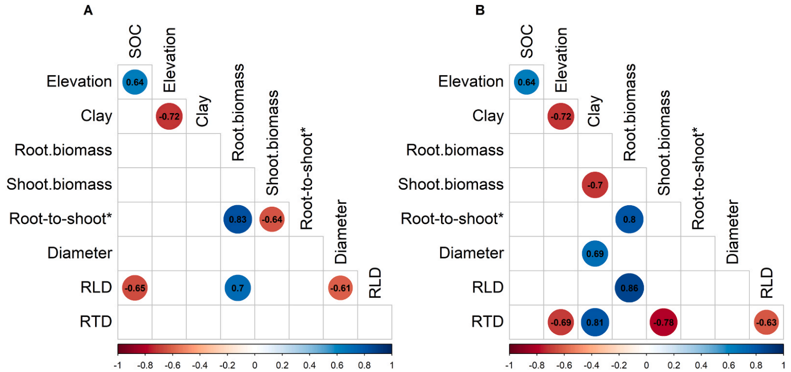


Fig. 4. Spearman rank correlation coefficients (ρ) between selected soil and site parameters measured in 2017 at 3–10 cm depth (Fukumasu et al., 2021) and root parameters at 3–10 cm for (A) 2023 and (B) 2024. Only statistically significant correlations ($p < 0.05$) are shown. SOC, soil organic carbon content; RLD, root length density; RTD, root tissue density. Root-to-Shoot* denotes the root-to-shoot ratio calculated using root biomass across the full measured depth (0–40 cm).

4.2. Shoot and root biomass differed between years

Inter-annual differences were evident in both shoot biomass and root biomass in the top 20 cm (Fig. 2 A, B), with topsoil biomass increasing from 2023 to 2024. These differences coincided with lower cumulative precipitation between April and June in 2023 (97.1 mm) compared with 2024 (254 mm), while mean temperatures were similar (~12 °C; Fig. 1C, D). The drier conditions in 2023 likely contributed to the reduced shoot and root biomass in the topsoil. In April 2023, the sowing month, had the lowest precipitation during the growing season (18.1 mm; Fig. 1D), which may have impaired crop productivity (Kaushal and Wani, 2016).

Although there was no significant overall effect of year on the root-to-shoot ratio, patterns varied considerably among sampling points (Fig. 2 F). This suggests that root-to-shoot ratio responses depended on field location, indicating interactive effects between site-specific soil properties and year-to-year weather conditions. Similar inter-annual effects have been reported elsewhere: in a four-year Danish study, variation in root-to-shoot ratios of cereals was strongly linked to weather conditions, with dry springs associated with reduced topsoil root biomass and deeper root distribution (Hu et al., 2018). Likewise, Mattila and Häkkinen (2025) found that the proportion of roots in subsoil layers was partly determined by the number of early-season moisture stress days, with more subsoil allocation occurring in the year with higher moisture stress.

It remains uncertain whether differences in barley cultivars between the two years (Laureate in 2023 and Lexy in 2024) and the differences in the growth stage at the time of sampling (i.e. early to mid-reproductive stage at milking/early dough development stage) contributed to the observed inter-annual variation in shoot and root biomass and, thus, the root-to-shoot ratio. For instance, the effect of timing on root-to-shoot ratios has been documented in western Canada, producing a wide range of root-to-shoot ratios with time (Xu and Juma, 1992). However, this is unlikely to explain the differences observed here, as both cultivars (Lexy and Laureate) were sampled at similar growth stages. Additionally, cultivar-dependent variation at ripening ranged from 0.08 to 0.11 among four barley cultivars (Abee, Harrington, Bonanza and, Samson) (Xu and Juma, 1992), which may have contributed to the variation observed between Lexy and Laureate in this study. However, other studies have found root-to-shoot ratios to be broadly consistent among barley cultivars (Leger, Chapais and Codac) (Bolinder et al., 1997). In wheat, by contrast, considerable genotypic variation expressed in different cultivars and varieties has been reported, with coefficients of variation up to 45 % in spring wheat and 25 % in winter wheat (Heinemann et al., 2023).

4.3. Implications of the observed within-field variation in root and shoot data on SOC content

Although the majority of root biomass was concentrated in the upper 20 cm of the soil profile, we found no correlation between soil organic carbon (SOC) content and root biomass in either study year (Fig. 4) or when data from both years were averaged (Fig. S4). Previous research has established that root-derived inputs are among the most important factors in building up SOC (e.g., (Bolinder et al., 2007, Ogle et al., 2012, Börjesson et al., 2018). However, in our study, root inputs measured at the 0–20 cm depth did not explain SOC content in the topsoil. Three main factors likely contributed to this result:

First, there was substantial year-to-year variation in root biomass at most field locations, and two years of sampling were insufficient to generate representative mean values of root inputs. For comparison, a previous long-term study at this site found a correlation (ρ=0.49) between SOC and mean relative yield (the ratio of site-specific grain yield to the field's average yield, used as a proxy for total plant carbon inputs from both roots and above-ground residues) for 14 years in the period 1997–2016 (Fukumasu et al., 2021). Notably, mean relative yield correlated negatively with both elevation and clay content, suggesting reduced carbon inputs in lower-lying, clay-rich areas due to sub-optimal crop growth. In contrast, our measurements of root and shoot biomass did not reveal similar patterns. Second, we did not account for carbon inputs from rhizodeposition, such as sloughed-off root cells and exudates, which can amount to roughly 65 % of below-ground carbon (Bolinder et al., 2007). Third, SOC contents are not only determined by carbon inputs but on the long-term balance between input and losses, primarily through microbial decomposition.

Despite pronounced variation in clay content, SOC, and elevation across the field (Fig. 1A–B), the sources of variation in root-to-shoot ratios remain unresolved. These ratios were uncorrelated between years (Fig. 2 F), suggesting that unmeasured local properties played an important role and that their effects on root-to-shoot ratios varied between the two seasons, which experienced contrasting early-season precipitation.

4.4. Root diameter, root tissue density and root length density varied between years and soil depth

Root tissue density (RTD) showed within-field variation (QCV 6–20 %) across years. Although no significant interannual differences were detected, differences in changes per sampling location were observed (Fig. 3F). Notably, in the wetter year of 2024, but not in 2023, RTD in the top 20 cm was positively associated with clay content and negatively correlated with elevation (Fig. 4A-B). This suggests that RTD was affected by interactive effects between the weather and localized soil conditions. Median root diameters showed limited within-field variation (QCV = 4 %) and were larger during the drier year of 2023, ranging from 0.27 to 0.34 mm, compared to 2024 (0.25–0.31 mm) and tended to become larger with depth (Fig. 3B and E). These results suggest that the increase in diameter was a response to increased soil mechanical resistance, which typically increases in drier soil and in lower soil layers with greater bulk density (Vanhees et al., 2022, Potocka and Szymanowska-Pułka, 2018).

Similarly, the larger mean root diameter in the topsoil at sites with higher clay content in 2024 (Fig. 4) likely reflects greater mechanical resistance in soils with higher clay content. Increased penetration resistance also decreases root branching (Potocka and Szymanowska-Pułka, 2018, Lynch, 2022). Both root thickening and reduced branching lead to increased mean root diameter. In our study, we cannot separate these two possible effects. Such variation and the plastic nature of root diameter, even at this scale, are critical for trait-to-trait conversions, such as RTD and specific root length, as well as for robust model parameterization (Pagès and Kervella, 2018, Rose, 2017, Freschet et al., 2020, Jarvis et al., 2024, Hansen et al., 2012).

Root length density ranged from 3.5 to 9.9 cm cm^{-3} in 2023 and increased twofold in 2024 (Fig. S1B) and showed considerable within-field variation with a QCV of 16–24 %. Our data from 2023 align with reported values for spring barley under medium and high sowing densities and other temperate cereals (Gregory, 2006). The range of RLD values in 2024 (6.9–19 cm cm^{-3}) was comparable to grasses that have an RLD of about 20 cm cm^{-3} or more (Stokes et al., 2009). Improved understanding of the source of this variation in the RLD, could improve the parametrization of SOC models. In these predictive models, such as the USSF model (Jarvis et al., 2024), RLD is modelled to dictate where organic matter is supplied within the soil profile, especially when it is combined with the root depth distribution (Freschet et al., 2020, Coucheney et al., 2024, Poirier et al., 2018).

5. Conclusions

The large within-field variability in shoot and root biomass, root-to-shoot ratios and root traits at early to mid-reproductive stage, together with differences in both mean values and spatial patterns between the two study years, indicate that the use of fixed root-to-shoot ratios for estimating root carbon inputs may introduce substantial uncertainty into SOC model predictions. The observed variability in root biomass and root traits highlights their plasticity in response to environmental conditions. Recognizing and accounting for spatial heterogeneity in root traits is crucial, as these dynamics should be reflected in SOC model parameterization, even at the scale of individual fields. The current scarcity of comprehensive root trait datasets that demonstrate plasticity in response to environmental conditions is a key limitation in SOC modelling, reinforcing the need for expanded empirical research.

CRediT authorship contribution statement

Tino Colombi: Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Thomas Kätterer:** Writing – review & editing, Validation, Supervision. **Mats Larsbo:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Miyanda Chilipamushi:**

Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Claudia von Brömssen:** Writing – review & editing, Validation, Supervision, Methodology.

Funding sources

This study was financed by the FORMAS (grant no. 01326, 2020). TC also acknowledges funding from the University of Nottingham (Nottingham Research Fellowship) and TK from FORMAS (grant no. 00214, 2022).

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used Perplexity in order to edit the grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Acknowledgments

We would like to thank Kjell Carlsson at Lantmännen for support with sampling in Bjertorp. We would also thank Nick Jarvis for valuable comments on the first draft of this manuscript. We also extend our gratitude to Sajani Hansana and Keron Bwacha for their assistance with root selection and scanning. We would also like to thank Tuomas Mattila for generously making his data available for comparison with our study.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2026.107103.

Data availability

Data will be made available on request.

References

Asefa, M., Worthy, S.J., Cao, M., Song, X., Lozano, Y.M., Yang, J., 2022. Above- and below-ground plant traits are not consistent in response to drought and competition treatments. Ann. Bot. 130, 939–950. https://doi.org/10.1093/aob/mcac108.

Bao, Y., Aggarwal, P., Robbins, N.E., Sturrock, C.J., Thompson, M.C., Tan, H.Q., Tham, C., Duan, L., Rodriguez, P.L., Vernoux, T., Mooney, S.J., Bennett, M.J., Dinneny, J.R., 2014. Plant roots use a patterning mechanism to position lateral root branches toward available water. Proc. Natl. Acad. Sci. U. S. A. 111, 9319–9324. https://doi.org/10.1073/pnas.1400966111.

Böhm, W., 1979. Methods of studying root systems. Ecol. Stud. https://doi.org/10.1007/978-3-642-67282-8.

Bolinder, M., Angers, D., Dubuc, J., 1997. Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. Agric. Ecosyst. Environ. 63, 61–66. https://doi.org/10.1016/S0167-8809(96)01121-8.

Bolinder, M., Menichetti, L., Lundblad, M., Kätterer, T., 2019. Implementing a new version of ICBM in NIR. ⟨https://urn.kb.se/resolve?urn=urn:nbn:se:naturvardsverket:diva-8932⟩.

Bolinder, M., Janzen, H., Gregorich, E., Angers, D., VandenBygaart, A., 2007. An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in Canada. Agric. Ecosyst. Environ. 118, 29–42. https://doi.org/10.1016/j.agee.2006.05.013.

Bonett, D.G., 2006. Confidence interval for a coefficient of quartile variation. Comput. Stat. Data Anal. 50, 2953–2957. https://doi.org/10.1016/j.csda.2005.05.007.

Börjesson, G., Bolinder, M.A., Kirchmann, H., Kätterer, T., 2018. Organic carbon stocks in topsoil and subsoil in long-term ley and cereal monoculture rotations. Biol. Fertil. Soils 54, 549–558. https://doi.org/10.1007/s00374-018-1281-x.

Cabal, C., De Deurwaerder, H.P.T., Matesanz, S., 2021. Field methods to study the spatial root density distribution of individual plants. Plant Soil 462, 25–43. https://doi.org/10.1007/s11104-021-04841-z.

Coleman, K., Jenkinson, D., 2014. RothC – A model for the turnover of carbon in soil. Model description and users guide (Windows version, updated June 2014). ⟨https://repository.rothamsted.ac.uk/item/98xv8/rothc-a-model-for-the-turnover-of-carbon-in-soil-model-description-and-users-guide-windows-version-updated-june-2014⟩.

R. Core Team, 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org⟩.

Coucheney, E., Herrmann, A.M., Jarvis, N., 2024. A simple model of the turnover of organic carbon in a soil profile: model test, parameter identification and sensitivity. EGUsphere 2024 1–22. https://doi.org/10.5194/egusphere-2024-3883.

Delory, B.M., Weidlich, E.W.A., Meder, L., Lütje, A., Van Duijnen, R., Weidlich, R., Temperton, V.M., 2017. Accuracy and bias of methods used for root length measurements in functional root research. Methods Ecol. Evol. 8, 1594–1606. https://doi.org/10.1111/2041-210X.12771.

Dupuy, L., Gregory, P.J., Bengough, A.G., 2010. Root growth models: towards a new generation of continuous approaches. J. Exp. Bot. 61, 2131–2143. https://doi.org/10.1093/jxb/erp389.

Durand-Maniclas, F., Heinemann, H., Seidel, F., Ciulla, F., Bárcena, T.G., Camenzind, M., Corrado, S., Csűrös, Z., Czakó, Z., Eylenbosch, D., Ficke, A., Flamm, C., Herrera, J.M., Horáková, V., Hund, A., Lüddeke, F., Platz, F., Poós, B., Rasse, D., Hirte, J., 2025. Linking root length and surface area to yield: variety-specific root plasticity in winter wheat across contrasting European environments. Ann. Bot. https://doi.org/10.1093/aob/mcaf155.

Frasier, I., Noellemeyer, E., Fernández, R., Quiroga, A., 2016. Direct field method for root biomass quantification in agroecosystems. MethodsX 3, 513–519. https://doi.org/10.1016/j.mex.2016.08.002.

Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimešová, J., Lukac, M., McCormack, M. L., Meier, I.C., Pagès, L., Poorter, H., Prieto, I., Wurzburger, N., Zadworny, M., Bagniewska-Zadworna, A., Stokes, A., 2020. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. N. Phytol. 232, 1123–1158. https://doi.org/10.1111/nph.17072.

Fukumasu, J., Poeplau, C., Coucheney, E., Jarvis, N., Klöffel, T., Koestel, J., Kätterer, T., Svensson, D.N., Wetterlind, J., Larsbo, M., 2021. Oxalate-extractable aluminum alongside carbon inputs may be a major determinant for organic carbon content in agricultural topsoils in humid continental climate. Geoderma 402, 115345. https://doi.org/10.1016/j.geoderma.2021.115345.

Gasser, A.A., Diel, J., Nielsen, K., Mewes, P., Engels, C., Franko, U., 2022. A model ensemble approach to determine the humus building efficiency of organic amendments in incubation experiments. Soil Use Manag 38, 179–190. https://doi.org/10.1111/sum.12699.

Gräler, B., Pebesma, E., Heuvelink, G., 2016. Spatio-temporal interpolation using gstat. R. J. 8, 204–218. https://doi.org/10.32614/RJ-2016-014.

Gregory, P., 2006. Roots, rhizosphere and soil: the route to a better understanding of soil science? Eur. J. Soil Sci. 57, 2–12. https://doi.org/10.1111/j.1365-2389.2005.00778.x.

Gregory, P.J., Palta, J.A., Batts, G.R., 1996. Root systems and root:mass ratio – carbon allocation under current and projected atmospheric conditions in arable crops. Plant Soil 187, 221–228. ⟨http://www.jstor.org/stable/42947907⟩.

Hansen, S., Abrahamsen, P., Petersen, C.T., Styczen, M.E., 2012. Daisy: model use, calibration, and validation. Trans. ASABE 55, 1317–1335. https://doi.org/10.13031/2013.42244.

Hansson, A.C., Andrén, O., 1987. Root dynamics in barley, lucerne and meadow fescue investigated with a mini-rhizotron technique. Plant Soil 103, 33–38. https://doi.org/10.1007/BF02370664.

Heinemann, H., Hirte, J., Seidel, F., Don, A., 2023. Increasing root biomass derived carbon input to agricultural soils by genotype selection – a review. Plant Soil 490, 19–30. https://doi.org/10.1007/s11104-023-06068-6.

Heinemann, H., Durand-Maniclas, F., Seidel, F., Ciulla, F., Bárcena, T.G., Camenzind, M., Corrado, S., Csűrös, Z., Czakó, Z., Eylenbosch, D., Ficke, A., Flamm, C., Herrera, J.M., Horáková, V., Hund, A., Lüddeke, F., Platz, F., Poós, B., Rasse, D., Don, A., 2025. Optimising root and grain yield through variety selection in winter wheat across a European climate gradient. Eur. J. Soil Sci. 76. https://doi.org/10.1111/ejss.70077.

Hijmans, R.J., 2023. terra: Spatial data analysis. ⟨https://rspatial.org⟩.

Hirte, J., Leifeld, J., Abiven, S., Oberholzer, H.R., Hammelehle, A., Mayer, J., 2017. Overestimation of Crop Root Biomass in Field Experiments Due to Extraneous Organic Matter. Mar 1 Front Plant Sci. 8, 284. https://doi.org/10.3389/fpls.2017.00284.

Hirte, J., Leifeld, J., Abiven, S., Oberholzer, H., Mayer, J., 2018. Below ground carbon inputs to soil via root biomass and rhizodeposition of field-grown maize and wheat at harvest are independent of net primary productivity. Agric. Ecosyst. Environ. 265, 556–566. https://doi.org/10.1016/j.agee.2018.07.010.

Hirte, J., Walder, F., Hess, J., Büchi, L., Colombi, T., van der Heijden, Mayer, J., 2021. Enhanced root carbon allocation through organic farming is restricted to topsoils. Sci. Total Environ. 755, 143551. https://doi.org/10.1016/j.scitotenv.2020.143551.

Hoad, S.P., Russell, G., Lucas, M.E., Bingham, I.J., 2001. The management of wheat, barley, and oat root systems. Adv. Agron. 74, 193–246. https://doi.org/10.1016/S0065-2113(01)74034-5.

Hu, T., Sørensen, P., Wahlström, E.M., Chirinda, N., Sharif, B., Li, X., Olesen, J.E., 2018. Root biomass in cereals, catch crops and weeds can be reliably estimated without considering aboveground biomass. Agric. Ecosyst. Environ. 251, 141–148. https://doi.org/10.1016/j.agee.2017.09.024.

IUSS Working Group, W.R.B., 2015. World Reference Base for Soil Resources 2014, update 2015. In: International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports, 106. FAO, Rome.
Jacobs, A., Poeplau, C., Weiser, C., Fahrion-Nitschke, A., Don, A., 2020. Exports and inputs of organic carbon on agricultural soils in Germany. Nutr. Cycl. Agroecosyst 118, 249–271. https://doi.org/10.1007/s10705-020-10087-5.
Jarvis, N., Coucheney, E., Lewan, E., Klöffel, T., Meurer, K.H.E., Keller, T., Larsbo, M., 2024. Interactions between soil structure dynamics, hydrological processes, and organic matter cycling: a new soil–crop model. Eur. J. Soil Sci. 75. https://doi.org/10.1111/ejss.13455.
Kassambara, A., 2023. ggpubr: 'ggplot2' based publication ready plots. R package version 0.6.0. 〈https://CRAN.R-project.org/package=ggpubr〉.
Kätterer, T., Bolinder, M.A., Andrén, O., Kirchmann, H., Menichetti, L., 2011. Roots contribute more to refractory soil organic matter than above-ground crop residues, as revealed by a long-term field experiment. Agric. Ecosyst. Environ. 141, 184–192. https://doi.org/10.1016/j.agee.2011.02.029.
Kaushal, M., Wani, S.P., 2016. Rhizobacterial–plant interactions: strategies ensuring plant growth promotion under drought and salinity stress. Agric. Ecosyst. Environ. 231, 68–78. https://doi.org/10.1016/j.agee.2016.06.031.
Khan, M., Gemenet, D.C., Villordon, A., 2016. Root system architecture and abiotic stress tolerance: current knowledge in root and tuber crops. Front. Plant Sci. 7, 1584. https://doi.org/10.3389/fpls.2016.01584.
Lantmännen, 2025. Inför vårsådd 2025: Vårutsäde, vallfrö, majs, mellan- och fånggrödor för svenska odlingsförhållanden. 〈https://www.lantmannenlantbrukmaskin.se/siteassets/om-oss/vara-tjanster/broschyrtorg/spannmal-och-vaxtodling/infor-varsadd-2025_.pdf〉 (accessed 28 January 2026).
Lindahl, A.M., Söderström, M., Jarvis, N., 2008. Influence of input uncertainty on prediction of within-field pesticide leaching risks. J. Contam. Hydrol. 98, 106–114. https://doi.org/10.1016/j.jconhyd.2008.03.006.
Liski, J., Palosuo, T., Peltoniemi, M., Sievänen, R., 2005. Carbon and decomposition model Yasso for forest soils. Ecol. Model 189, 168–182. https://doi.org/10.1016/j.ecolmodel.2005.03.005.
Lux, A., Rost, T.L., 2012. Plant root research: the past, the present and the future. Ann. Bot. 110, 201–204. https://doi.org/10.1093/aob/mcs156.
Lynch, J.P., 2022. Harnessing root architecture to address global challenges. Plant J. 109, 415–431. https://doi.org/10.1111/tpj.15560.
Mattila, T.J., Häkkinen, L., 2025. Exploring the effects of soil structure, nutrients, and farm management on crop root biomass and depth distribution. Field Crops Res 327, 109909. https://doi.org/10.1016/j.fcr.2025.109909.
O'Leary, G., Liu, D., Ma, Y., Li, F., McCaskill, M., Conyers, M., Dalal, R., Reeves, S., Page, K., Dang, Y., 2015. Modelling soil organic carbon. 1. The value of long term agronomic experimental data. 〈https://www.cabidigitallibrary.org/doi/10.5555/20183347100〉.
Messing, I., Soriano, A.M.M., Svensson, D.N., Barron, J., 2024. Variability and compatibility in determining soil particle size distribution by sieving, sedimentation and laser diffraction methods. Soil Tillage Res 238, 105987. https://doi.org/10.1016/j.still.2023.105987.
Ogle, S.M., Swan, A., Paustian, K., 2012. No-till management impacts on crop productivity, carbon input and soil carbon sequestration. Agric. Ecosyst. Environ. 149, 37–49. https://doi.org/10.1016/j.agee.2011.12.010.
Pagès, L., Kervella, J., 2018. Seeking stable traits to characterize the root system architecture. Study on 60 species located at two sites in natura. Ann. Bot. 122, 107–115. https://doi.org/10.1093/aob/mcy061.
Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. R. J. 10, 439–446. 〈https://journal.r-project.org/archive/2018/RJ-2018-009〉.
Pietola, L., Alakukku, L., 2005. Root growth dynamics and biomass input by Nordic annual field crops. Agric. Ecosyst. Environ. 108, 135–144. https://doi.org/10.1016/j.agee.2005.01.009.
Plaza-Bonilla, D., Álvaro-Fuentes, J., Hansen, N.C., Lampurlanés, J., Cantero-Martínez, C., 2013. Winter cereal root growth and aboveground–belowground biomass ratios as affected by site and tillage system in dryland Mediterranean conditions. Plant Soil 374, 925–939. https://doi.org/10.1007/s11104-013-1926-3.
Poirier, V., Roumet, C., Munson, A.D., 2018. The root of the matter: linking root traits and soil organic matter stabilization processes. Soil Biol. Biochem 120, 246–259. https://doi.org/10.1016/j.soilbio.2018.02.016.
Potocka, I., Szymanowska-Pułka, J., 2018. Morphological responses of plant roots to mechanical stress. Ann. Bot. 122, 711–723. https://doi.org/10.1093/aob/mcy010.
Rasse, D.P., Rumpel, C., Dignac, M., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant Soil 269, 341–356. https://doi.org/10.1007/s11104-004-0907-y.
Raza, S., Cooper, H.V., Girkin, N.T., Kent, M.S., Bennett, M.J., Mooney, S.J., Colombi, T., 2025. Missing the input: the underrepresentation of plant physiology in global soil carbon research. SOIL 11, 363–369. https://doi.org/10.5194/soil-11-363-2025.
Rose, L., 2017. Pitfalls in root trait calculations: how ignoring diameter heterogeneity can lead to overestimation of functional traits. Front. Plant Sci. 8, 898. https://doi.org/10.3389/fpls.2017.00898.
Schuurman, J.J., Goedewaagen, M.A.J., 1971. Methods for the examination of root systems and roots. Pudoc, Wageningen.
Seethepalli, A., Dhakal, K., Griffiths, M., Guo, H., Freschet, G.T., York, L.M., 2021. RhizoVision Explorer: open-source software for root image analysis and measurement standardization. AoB Plants 13, plab056. https://doi.org/10.1093/aobpla/plab056.
Seethepalli, A., Ottley, C., Childs, J., Cope, K.R., Fine, A.K., Lagergren, J.H., Kalluri, U., Iversen, C.M., York, L.M., 2024. Divide and conquer: using RhizoVision Explorer to aggregate data from multiple root scans using image concatenation and statistical methods. N. Phytol. 244, 2101–2108. https://doi.org/10.1111/nph.20151.
Seidel, S.J., Ahmadi, S., Weihermüller, L., Couedel, A., Lopez, G., Behrend, D., Kamali, B., Gaiser, T., Hernández-Ochoa, I., 2024. The overlooked effects of environmental impacts on root:shoot ratio in experiments and soil-crop models. Sci. Total Environ. 955, 176738. https://doi.org/10.1016/j.scitotenv.2024.176738.
Stokes, A., Atger, C., Bengough, A.G., Fourcaud, T., Sidle, R.C., 2009. Desirable plant root traits for protecting natural and engineered slopes against landslides. Plant Soil 324, 1–30. https://doi.org/10.1007/s11104-009-0159-y.
Taghizadeh-Toosi, A., Christensen, B.T., Hutchings, N.J., Vejlin, J., Kätterer, T., Glendining, M., Olesen, J.E., 2014. C-TOOL: a simple model for simulating whole-profile carbon storage in temperate agricultural soils. Ecol. Model 292, 11–25. https://doi.org/10.1016/j.ecolmodel.2014.08.016.
Vanhees, D.J., Schneider, H.M., Sidhu, J.S., Loades, K.W., Bengough, A.G., Bennett, M.J., Pandey, B.K., Brown, K.M., Mooney, S.J., Lynch, J.P., 2022. Soil penetration by maize roots is negatively related to ethylene-induced thickening. Plant Cell Environ. 45, 789–804. https://doi.org/10.1111/pce.14175.
Watt, M., Magee, L.J., McCully, M.E., 2008. Types, structure and potential for axial water flow in the deepest roots of field-grown cereals. N. Phytol. 178, 135–146. https://doi.org/10.1111/j.1469-8137.2007.02358.x.
Weemstra, M., Freschet, G.T., Stokes, A., Roumet, C., 2021. Patterns in intraspecific variation in root traits are species-specific along an elevation gradient. Funct. Ecol. 35, 342–356. https://doi.org/10.1111/1365-2435.13723.
Weemstra, M., Valverde-Barrantes, O.J., McCormack, M.L., Kong, D., 2022. Root traits and functioning: from individual plants to ecosystems. Oikos 2023, e09924. https://doi.org/10.1111/oik.09924.
Wei, T., Simko, V., 2021. corrplot: visualization of a correlation matrix. R. Package Version 0. 92. 〈https://github.com/taiyun/corrplot〉.
Wickham, H., 2016. Programming with ggplot2. ggplot2: Elegant graphics for data analysis. Springer, Cham, pp. 241–253. https://doi.org/10.1007/978-3-319-24277-4_12.
Swedish Meteorological and Hydrological Institute (SMHI). Gridded Precipitation and Temperature Data (PTHBV). 〈https://www.smhi.se/data/ladda-ner-data/griddade-nederbord-och-temperaturdata-pthbv〉 (accessed 25 August 2025).
Wickham, H., Bryan, J., 2023. R packages. O'Reilly Media, Sebastopol, CA.
Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D.A., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Softw. 4, 1686. https://doi.org/10.21105/joss.01686.
Xu, J.G., Juma, N.G., 1992. Above- and below-ground net primary production of four barley (Hordeum vulgare L.) cultivars in western Canada. Can. J. Plant Sci. 72, 1131–1140. https://doi.org/10.4141/cjps92-138.

II

Geoderma Regional 44 (2026) e01038

Contents lists available at ScienceDirect

Geoderma Regional

journal homepage: www.elsevier.com/locate/geodrs

Oxalate-extractable aluminium is a key predictor of organic carbon content in Swedish agricultural topsoils

Miyanda Chilipamushi [a,*], Claudia von Brömssen [b], Tino Colombi [a,c], Thomas Kätterer [d], Mats Larsbo [a]

[a] Department of Soil and Environment, Swedish University of Agricultural Sciences, Box 7014, 750 07 Uppsala, Sweden
[b] Department of Energy and Engineering, Swedish University of Agricultural Sciences, Box 7013, 750 07 Uppsala, Sweden
[c] School of Biosciences, University of Nottingham, Sutton Bonington LE12 5RD, UK
[d] Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden

ARTICLE INFO

Keywords:
Soil organic carbon
Oxalate extractable aluminium
Soil monitoring
Carbon storage
Humid climate

ABSTRACT

Previous research has shown the importance of oxalate-extractable aluminium (Alox) for predicting soil organic carbon (SOC) contents across diverse geographical regions. However, studies using data from humid continental climates are scarce, and the data used in these studies have not been statistically representative for larger scales. Our study aimed to 1) evaluate the influence of soil physical and geochemical properties (specifically Alox), farm management, and climate on the spatial distribution and storage potential of SOC in Swedish agricultural soils and 2) to assess whether estimates of aggregation, assumed to influence the protection of soil organic matter, could improve predictions. We analyzed a statistically representative subset of mineral soils with pH < 7 from the Swedish soil and crop monitoring program, which covers the country's agricultural land. We identified the most important predictors for topsoil SOC contents using a random forest model. We employed partial dependence plots to visualize and interpret the interactions between key variables and SOC contents. Results showed that Alox was the most important predictor for SOC contents, as evidenced by its high relative importance score and the increased out-of-bag error when removed from the model. Notably, SOC content reached a plateau at Alox contents of about 3.5 g kg^{-1}, suggesting the possibility of SOC under-saturation. Climatic variables were of secondary importance, while farm management did not emerge as a significant predictor. Surprisingly, silt-sized aggregation was not identified as an important variable for predicting SOC content. Our findings emphasize the importance of incorporating geochemical properties, particularly Alox, in addition to soil texture, in predictive modelling and monitoring efforts for enhanced soil carbon management in humid climates.

1. Introduction

Carbon storage in agricultural soils may help mitigate climate change and, at the same time, make soils more adapted to a changing climate (Lal, 2008; Sanderman et al., 2017). Soil is the largest terrestrial soil organic carbon (SOC) pool. About 65 % of this SOC is considered to be contained in mineral-associated organic matter and thereby partly protected from microbial decomposition (Heckman et al., 2022; Sokol et al., 2022). The clay fraction (<2 μm) has often been considered an indicator of SOC storage capacity in mineral soils (Feng et al., 2013; Salonen et al., 2024; Solly et al., 2020; Wiesmeier et al., 2019). Finer particles, such as clay, have a larger specific surface area and, therefore, a large capacity to adsorb soil organic matter (SOM) (Rabot et al., 2018; Sollins et al., 1996). Based on this understanding, it has been suggested that soils have a finite capacity to store SOC and that this storage capacity depends on the clay content (Feng et al., 2013; Hassink and Whitmore, 1997; Salonen et al., 2024). The point at which this capacity is reached has been referred to as '*carbon saturation*' (Hassink, 1997). When soils are not saturated, soil and crop management changes that increase organic matter inputs can increase the mineral-associated SOC pool (Castellano et al., 2015; Guillaume et al., 2022; Hassink, 1997). Agricultural soils, especially deeper soil layers, are typically '*carbon under-saturated*' (Georgiou et al., 2022; Sanderman et al., 2017).

According to the Swedish soil and crop monitoring program (SMP; accessible at https://miljodata.slu.se/mvm/aker), there has been an increase in SOC concentrations in Swedish agricultural soils, equivalent

* Correspondence author.
E-mail address: miyanda.chilipamushi@slu.se (M. Chilipamushi).

https://doi.org/10.1016/j.geodrs.2025.e01038
Received 18 February 2025; Received in revised form 24 October 2025; Accepted 4 December 2025
Available online 10 December 2025

to a relative increase of 0.38 % yr^{-1} during the last decades (Henryson et al., 2022; Poeplau et al., 2015). This increase has been attributed to changes in land use, with an increase in the area under ley and a corresponding decrease in annual crops as the main driver (Henryson et al., 2022; Poeplau et al., 2015). Data from the same monitoring program and data from the Swedish Farm Register also showed that SOC contents were larger in dairy farms than in arable farms (Henryson et al., 2022). These changes were attributed to a larger proportion of ley and higher use of animal manure in dairy farms (Henryson et al., 2022; Poeplau et al., 2015). This shows that Swedish agricultural soils may have the potential to store more SOC.

However, clay content alone does not determine SOC storage since it does not fully account for the surface area or presence and abundance of reactive minerals (Bailey et al., 2018; Farrar and Coleman, 1967; Rasmussen et al., 2018; Totsche et al., 2018). Other soil properties besides clay content, are needed to estimate a soil's SOC storage capacity (Bailey et al., 2018; Solly et al., 2020), and the clay saturation concept could be replaced by a soil's mineralogical capacity to store SOC (Poeplau et al., 2024). The mineralogical capacity should not be viewed as a threshold since a soil's capacity to store SOC can also be influenced by management and climate (i.e. the '*ecosystem capacity*' (Poeplau et al., 2024)).

In order to explain the mineralogical capacity, reactive mineral phases containing Al and Fe can be leveraged since they are considered to associate with SOM through organo-metal complexation and/or co-precipitation and thereby regulate microbial and enzymatic accessibility SOM (Kleber et al., 2015). It has also been suggested that interactions between clay, reactive metal phases, and SOM facilitate soil aggregation (Schlüter et al., 2022; Tisdall and Oades, 1982; Totsche et al., 2018). Aggregates are assumed to protect SOM by physically limiting microbial and enzymatic accessibility (Hall and Thompson, 2021; Matus et al., 2014). Since SOC is mainly associated with the silt and clay fraction, aggregation in silt- and/or clay sizes may be more important than macro-aggregation for SOM protection (Totsche et al., 2018; Wiesmeier et al., 2019). Furthermore, SOC has been shown to correlate with the volume of released clay particles upon SOM removal (Jensen et al., 2019; Fukumasu et al., 2021).

Indeed, positive correlations between oxalate-extractable aluminium (Alox) and iron (Feox) (assumed to represent the reactive mineral fraction of these metals) and SOC contents have been reported on national scales in the United States, New Zealand, and Chile in different climates (Beare et al., 2014; Hall and Thompson, 2021; Matus et al., 2006; Rasmussen et al., 2018). For example, Rasmussen et al. (2018) showed, using data from the U.S. Department of Agriculture's National Cooperative Soil Survey, that SOC contents increased with increasing Alox and Feox under humid conditions in acidic to neutral soils. Fukumasu et al. (2021) showed for a limited dataset from the Nordic countries and Canada that Alox was positively correlated with topsoil SOC contents. Alox was also the strongest predictor for topsoil SOC for a dataset of arable soils from southern Finland (Salonen et al., 2024). However, it is unclear how statistically representative these datasets are for Sweden and other regions with humid continental climates and soils formed from quaternary deposits.

In this study, we used a statistically representative sub-sample of the data contained in the SMP, which covers all agricultural land in Sweden, to identify the strongest predictors for SOC contents across a humidity gradient. These data were combined with new measurements of oxalate extractable Al, Fe and P and silt-sized aggregation. Our objectives were i) to quantify the relationships between soil physical and geochemical properties, farm management, climatic variables, and topsoil SOC contents in Sweden and ii) to assess whether estimates of aggregation, assumed to influence the protection of SOM, could improve predictions.

2. Methods and materials

2.1. Inventory design and data sets

We used stored topsoil samples from the Swedish soil and crop monitoring program (SMP) of arable land (Eriksson, 2021). The SMP includes measured data on soil chemical and physical variables and information on farm type and is, therefore, suitable for gaining insights into which variables best explain variations in soil organic carbon (SOC) contents. Soil samples have been collected repeatedly from these sites since 1988, with sampling occurring every ten years. For this study, we exclusively utilized data from the third inventory cycle (Inventory III), which was conducted between 2011 and 2017. After sampling, the samples were air-dried, sieved through a 2-mm sieve, and stored in airtight plastic containers in a temperature-controlled room. All soil samples from the SMP had previously been analyzed for the variables listed in Table S1. We only used the SOC content, texture, pH and exchangeable cations (Ca, K, Mg, and Na) (Eriksson, 2021). We selected these variables based on evidence from large-scale studies, which have demonstrated their significant influence on SOC contents (Rasmussen et al., 2018; von Fromm et al., 2025) and to limit overfitting and avoid adding noise. Element concentrations were analyzed using the 200.8 method (ICP SFMS). Soil pH (H_2O) was determined according to SS-ISO 10390. Carbon content was determined using a LECO Trumac CN analyzer according to SS-ISO 10694. Soil texture was analyzed using the pipette method after organic matter oxidation (Messing et al., 2024).

2.2. Selection of sampling points

To limit the number of samples used for further chemical analysis, we selected 100 samples from the 2039 topsoil samples contained in Inventory III. Since SOC has previously been shown to correlate with the contents of short-range order (SRO) phases and organo-metal complexes (i.e. the reactive mineral fraction estimated from Alox and Feox) for mineral acidic soils (Fukumasu et al., 2021; Hall and Thompson, 2021), we selected samples that represented mineral acidic soils. We first excluded samples with pH >7 (n = 258). In line with previous studies distinguishing between mineral and organic soils, we excluded organic soils, defined as those with SOC content greater than 70 g kg^{-1} (n = 147), from our analysis (Andrén et al., 2008; Poeplau et al., 2015). The pH of the remaining samples (n = 1624) was between 4.5 and 6.9, and SOC content was between 10 and 70 g kg^{-1} soil. To obtain a representative sub-sample, we stratified the remaining samples into four groups: high pH-high SOC (n = 276), high pH-low SOC (n = 477), low pH-high SOC (n = 477) and low pH-low SOC (n = 394). The first twenty-five samples were selected from each group after randomization. The amount of soil left in storage was insufficient for one of the selected samples. This sample was replaced by the 26th sample from the same group. In this manner, we merged the advantages of ensuring representation across key subgroups through stratification with the statistical benefits of random sampling within each stratum (Neyman, 1992).

The geographical distribution of the sampling locations for the selected samples was checked against the distribution of locations for the whole dataset (Fig. 1A). Distributions of SOC content and pH for our subsample were representative of the distributions for all data from Inventory III, again excluding samples with SOC contents >70 g kg^{-1} and pH >7 (Fig. 1B and C). The density curves were achieved using the Kernel density estimation, which produced smooth curves of pH and SOC (Wickham and Wickham, 2016). Fig. S1 shows that our subsample was also representative of the SMP concerning soil and crop farm management.

2.3. Oxalate extraction

In addition to the variables selected in the SMP, we carried out ammonium oxalate extractions to estimate Alox, Feox and Pox contents.

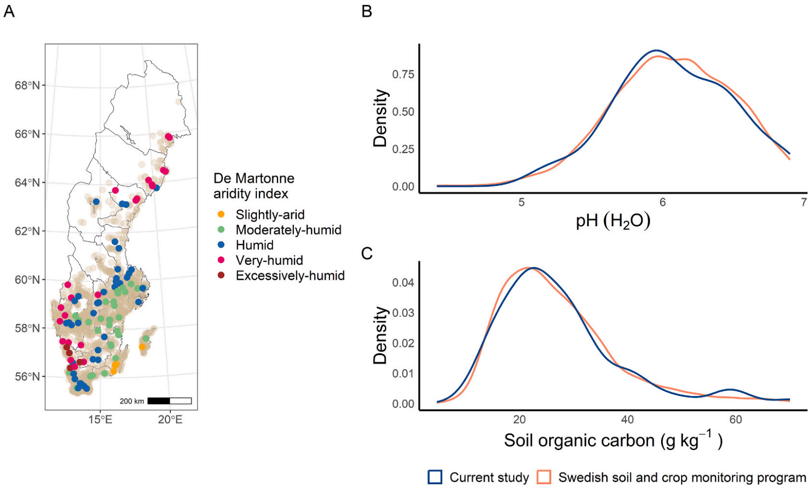


Fig. 1. A) The geographical distribution of sampling points in the Swedish soil and crop monitoring program (SMP) brown and the selected sampling points for the current study visualized according to the De Martonnes aridity index, B) Distributions of soil pH and C), soil organic carbon content at 0–20 cm depth for samples from the SMP and the sub-sample used in this study. Samples with pH > 7 and SOC contents >70 g kg^{-1} were excluded for both cases.

The Al and Fe extracted with oxalate originate from short-range order (SRO) aluminosilicates, poorly crystalline hydrous oxides and organic-mineral complexes (Hall and Thompson, 2021; Matus et al., 2008). The Pox would represent extracted inorganic and organic phosphorus fractions (Fransson, 2001). Approximately one gram of air-dried soil, sieved through a 2-mm mesh, was mixed with 100 mL of 0.2 mol L^{-1} acid ammonium oxalate solution. This solution was prepared by combining diammonium oxalate monohydrate ($[NH_4]_2C_2O_4 \cdot H_2O$) and oxalic acid dihydrate ($C_2H_2O_4 \cdot 2H_2O$), with the pH adjusted to 3.0. The mixture was shaken for four hours on an orbital shaker (GFL orbital shaker, Vortexers, *Germany*) with as little exposure to light as possible to minimize photochemical oxidation. The suspension was centrifuged for 15 min at 4000 rpm. The supernatant was then filtered through a 0.2 μm micro filter (Sarstedt™, *Germany*) using a syringe, again with as little exposure to light as possible. The filtrate was diluted with water at a 1:3 ratio. Alox, Feox and Pox concentrations were analyzed using Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES) on a Perkin Elmer 5300 DV instrument (*Ontario, Canada*).

2.4. Silt-sized soil aggregation

The volume of (<2 μm) particles released upon chemical dispersion of the silt-sized aggregates was used as a measure of soil aggregation (Fukumasu et al., 2021). This volume was estimated from the difference in the volume of clay-sized particles after chemical dispersion and mechanical dispersion. Mechanically dispersed soil was assumed to contain primary particles and micro-aggregates, while chemically dispersed soil contained only primary particles.

For mechanical dispersion, 5 g of air-dried soil was mixed with water, shaken overnight, and sieved through a 63-μm sieve. The particle size distribution of the suspension was then determined using the methods described by Svensson et al., 2022. For chemical dispersion, the soil was treated with hydrogen peroxide, boiled, cooled, and rinsed. Then 1 mL of a chemical dispersant (sodium carbonate, Na_2CO_3 7 g L^{-1} and sodium metaphosphate, $(NaO_3P)_n$ 33 g L^{-1}) and distilled water were added, resulting in a final volume of ca. 40 mL. The mixture was shaken overnight and sieved before analyzing the particle size distributions. Particle size distributions for chemical dispersion and mechanical dispersion were determined through laser diffraction measurements using a Horiba Partica LA-90 V2 (Svensson et al. (2022).

2.5. Statistical analysis

We used a random forest model (RFM) to predict SOC contents for selected explanatory variables (Friedman, 2001). The selected explanatory variables included four categorical farm management variables, nine geochemical variables, measured concentrations of Alox, Feox and Pox, three measured physical properties and three climatic variables (Table 1). The weather data was obtained by averaging observed records from 1961 to 2017 provided by the Swedish Meteorological and Hydrological Institute (Swedish Meteorological and Hydrological Institute, 2025). These data were derived from gridded analysis models, which interpolate observed climate records for enhanced spatial accuracy. From these data, we calculated the De Martonne aridity index (DMAI), a measure of humidity and aridity (De Martonne, 1925):

$$\mathrm{DMAI} = \frac{\mathrm{MAP}}{\mathrm{MAT} + 10} \tag{1}$$

where MAP (mm) is the mean annual precipitation and MAT (°C) is the mean annual temperature. For visualization purposes, DMAI was divided into seven classes (Table S2) (Pellicone et al., 2019).

We selected the most influential variables based on previous knowledge related to SOC predictions (Solly et al., 2020; Von Fromm et al., 2021; Yu et al., 2021). Summary statistics for all included variables are presented in Table S3. Note that all variables were logarithmically transformed in the analysis to reduce skewness. MAT was first transformed by subtracting each value from the maximum MAT value and adding 1 to ensure that all values were positive before the logarithmic transformation. All farm management variables were included as categorical variables (yes/no), according to the answers in an SMP farmer questionnaire.

Initial data exploration was conducted using Spearman's rank correlation coefficients (ρ) to examine pairwise relationships between all untransformed non-normal variables. In cases where tied ranks occurred, p-values were approximated as exact computation is not possible with ties. From the RFM, we determined the variable

Table 1
Variables used for the Random forest analysis. SMHI is the Swedish meteorological and hydrological institute. SMP is the Swedish soil and crop monitoring program.

Type	Variable	Unit	Abbreviation	Source
Climate	Mean annual temperature (1961–2017)	°C	MAT	SMHI
	Mean annual precipitation (1961–2017)	mm	MAP	SMHI
	De Martonne aridity index	–	DMAI	De Martonne (1925); SMHI
Geochemical properties	pH (H_2O)	–	pH	SMP
	Exchangeable magnesium	g kg^{-1} soil	Mg	SMP
	Exchangeable manganese	g kg^{-1} soil	Mn	SMP
	Exchangeable calcium	g kg^{-1} soil	Ca	SMP
	Exchangeable potassium	g kg^{-1} soil	K	SMP
	Oxalate extracted aluminium	g kg^{-1} soil	Alox	Ammonium oxalate extraction
	Oxalate extracted iron	g kg^{-1} soil	Feox	Ammonium oxalate extraction
	Oxalate extracted phosphorus	g kg^{-1} soil	Pox	Ammonium oxalate extraction
Soil physical properties	Clay (<2 μm)	%	Clay	Chemical dispersion
	Silt (2–63 μm)	%	Silt	Chemical dispersion
	Silt-sized aggregation (Volume of primary particles in aggregates)	% of <2 μm particles in <63 μm aggregates	Aggregation	Chemical and mechanical dispersion
Farm management	Practice	–	I. Organic (Yes/No) II. Conventional (Yes/No)	SMP
	Operation	–	I. Crop (Yes/No) II. Mixed (Yes/No) III. Animal (Yes/No) IV. No.farming (Yes/No)	SMP
	Rotation	–	I. Mostly.crops.without.ley (Yes/No) II. Crops.and.several.years.of.ley (Yes/No) III. Almost.only.ley (Yes/No) IV. Other.rotation (Yes/No)	SMP
	Manuring	–	I. Regular.manure.application (Yes/No)	SMP

importance based on the increase in the mean square error (IMSE) when a variable was removed from the model. We used the Boruta algorithm to select the relevant variables with respect to the response variable (Kursa and Rudnicki, 2010). In addition, we used partial dependency plots (PDP) to illustrate how individual explanatory variables contributed to the variation in SOC while other variables were kept constant (Friedman, 2001; Pearson, 2017). The model performance was evaluated using the out-of-bag (OOB) error (OOBE), which is the mean square error for the data points not included in each bootstrap sample. This estimate provides internal validation without requiring a separate test set to mitigate the risk of overfitting (Breiman, 2001).

We compared the RFM with the results of a linear regression model (LRM) as a benchmark model. We used the method of comparing the RFM and the LRM described by Jeong et al. (2016) to ensure that the two models were comparative. We trained an optimized RFM (based on the Boruta feature selection algorithm) and LRM (based on a backward selection using the model with the lowest Akaike information criterion score) on 50 % of the data and tested both models on the remaining data. We used the root mean square error (RMSE) to assess how well the model fitted the measured data.

Data processing and analysis were carried out using R version 4.3.1 (R Core Team, 2023). We used the “RandomForest” R package (Friedman, 2001; Liaw and Wiener, 2002) and the “partial” function in the “PDP” R package to determine the partial dependence of each variable (Greenwell, 2017). The LRM analysis was conducted with the “lm” function in R (R Core Team, 2023) and the “relaimpo” R package (Groemping, 2006) to show the relative variable importance in the LRM. In addition, we also used the packages “ggplot2” (Wickham, 2016), “ggspatial” (Dunnington, 2023) and “ggtern” (Hamilton & Ferry, 2018) for graphical and geographic illustrations. The base shape files used for the maps to create Swedish administrative borders were from the 2011 annual stock block data from the Swedish Board of Agriculture (Jordbruksverket, 2025).

3. Results

3.1. SOC content in relation to geochemical and physical properties, farm management and climate

Soil organic carbon content was between 10 and 70 g kg^{-1} (Table S3) with a mean C:N ratio of 11.5 ± 2.7. Alox and Feox concentrations were 0.4 to 4.3 g kg^{-1} and 1.2 to 13 g kg^{-1} soil, respectively (Table S3). Soil texture covered ten different classes, with clay contents in the range of 1.4–52 % and silt contents in the range of 9.6–95 % (Fig. S1). The fraction of clay contained in silt-sized aggregates was between 0 and 38 %. Climate data indicated conditions from slightly arid (30 ≤ DMAI≤35; Table S2) to excessively humid (60 ≤ DMAI≤187; Table S2) (Fig. 1A). The northern parts of Sweden were characterized by very humid to humid conditions, while the southern parts were slightly arid to excessively humid. The central regions were characterized by moderately humid (35 ≤ DMAI≤40; Table S2) to humid conditions (40 ≤ DMAI≤50).Of the selected samples, 43 % were from crop farms, 31 % from animal farms, 24 % from mixed farms, and 2 % reported no specific farming activities (Fig. S1). Forty-six percent of the samples were from fields where manure was regularly applied. Additionally, 34 % of the samples were from fields with annual crops without ley, 31 % annual crops with several years of ley, and 27 % almost exclusively ley.

The geographical distributions of SOC content co-varied with Alox concentrations (Fig. S2) but not with Feox concentrations or pH (Fig. S3). The clay content was generally higher in the central part of Sweden compared to the southern and northern parts (Fig. S5), whereas the silt content was higher in the northern parts compared to the central and southern parts of Sweden (Fig. S5). Spearman rank correlation coefficients (ρ) confirmed the above-described relationships (Fig. 2). The strongest correlation with SOC content was found for Alox (ρ = 0.6) (Fig. 2). SOC content was not significantly correlated with Feox or clay content but weakly positively correlated with other geochemical variables (exchangable Ca and Pox) and climatic variables (DMAI). SOC content was also weakly positively correlated with regular application of manure and mixed framing. Notably, DMAI was high when the rotation was dominated by ley (ρ = 0.29) and low when the rotation was dominated by annual crops without ley. Silt-sized aggregation was strongly positively correlated with clay content (ρ = 0.7).

3.2. Key predictors of SOC across a humidity gradient

The random forest model (RFM) reproduced the measured SOC contents (RMSE = 0.32 g kg^{-1}) slightly better than the linear regression model (LRM) (RMSE = 0.34 g kg^{-1}; Fig. S5). Our model showed that Alox was the most important predictor, with an increase in mean square error (MSE) of approximately 21 % when excluded from the RFM, followed by DMAI with an increase in MSE of approximately 9 %. Other important variables selected by the Boruta algorithm were Mn, Pox, Silt, exchangable Ca, MAT and MAP, with an increase in MSE ranging from 6 to 9 % when excluded from the model.

The RFM with all relevant variables included (Fig. 4A) had a lower prediction error than the model without Alox (Fig. 4B). Excluding Alox from the RFM increased the OOBE with 10 % compared to the model containing all key predictors (Fig. 4). Both models underestimated SOC contents for values larger than 40 g kg-1, while values smaller than approximately 20 g kg^{-1} were overestimated. Both models showed a greater propensity for underestimation than overestimation.

The partial dependence plots (PDPs) in Fig. 5A illustrate that predicted SOC content increase with higher Alox concentrations, with the largest increases observed between 2 and 3.5 g kg^{-1}. Further increases in Alox beyond this range had a limited effect on predicted SOC content. Similar trends were observed for DMAI and Pox, where SOC content increased and then plateaued at higher values of these variables (Fig. 5B, C). For DMAI, this plateau was evident under very humid (50 ≤ DMAI ≤ 60) and excessively humid (60 ≤ DMAI ≤ 187) conditions. Predicted SOC generally decreased with increasing exchangable Mn (Fig. 5D) but increased with higher proportions of silt-sized particles, and exchangable Ca (Fig. 5E, F). MAT and MAP had opposing effects. MAT decreased with predicted SOC content (Fig. 5G). For MAP, predicted SOC contentwas lowest at values around 600–700 mm, increased with higher MAP, and plateaued above approximately 800 mm (Fig. 5H).

4. Discussion

4.1. General modelling results

The random forest model generally reproduced the measured SOC contents better compared to the LRM. The RFM was more robust and better at capturing the complex relationships between the predictors and SOC contents. In both models, oxalate-extractable aluminium (Alox) was the most important predictor (Fig. 3, S6). However, SOC contents in the RFM were overestimated for values smaller than 20 g kg^{-1}, while values larger than 40 g kg^{-1} were underestimated. Only 11 and 26 % of the samples had SOC contents <20 and > 40 g kg^{-1}, respectively. This imbalance could have resulted in overfitting in the 20–40 g kg^{-1} range at the expense of poorer fit to measured data at lower and higher SOC contents. Expanding the dataset for these ranges might have improved model performance, as was the case for Jeong et al. (2016). Even though RFM can sometimes be overly specialized to training data, which potentially leads to overfitting, using out-of-bag error (OOBE) helps to reduce this risk.

4.2. Geochemical predictors of spatial variation in SOC contents in Swedish agricultural soils

Geochemical properties, particularly Alox, emerged from the RFM model as the most important predictors for SOC contents for Swedish agricultural soils with pH lower than 7. This was shown both by the relative importance scores and the fact that the model, by including Alox, resulted in smaller out-of-box errors (OOBE; Fig. 4). This result is in line with previous studies in temperate and humid climatic zones such

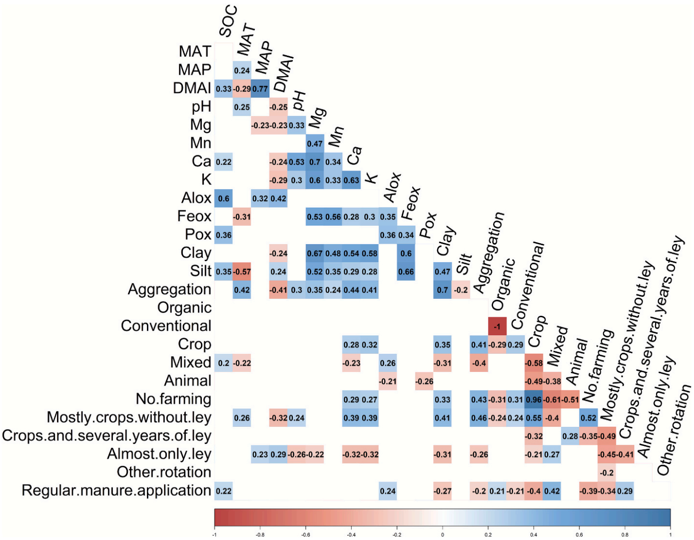


Fig. 2. Spearman rank correlation coefficients (ρ) for the relationships between all variables. Correlations with *p*-values below 0.05 are shown.

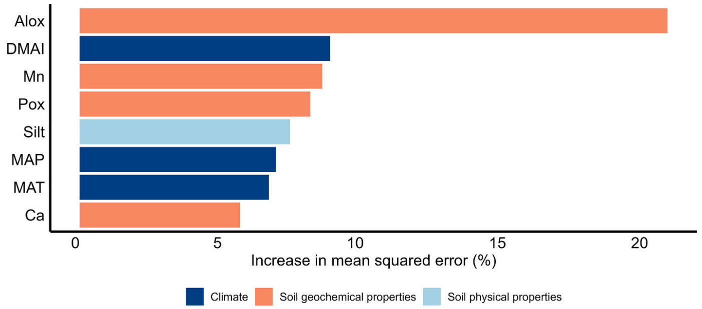


Fig. 3. Variable importance, expressed as the increase in mean squared error (MSE) upon removal of each predictor from the random forest model for soil organic carbon (SOC) content. Variables are grouped by category: climate, soil geochemical properties, and soil physical properties.

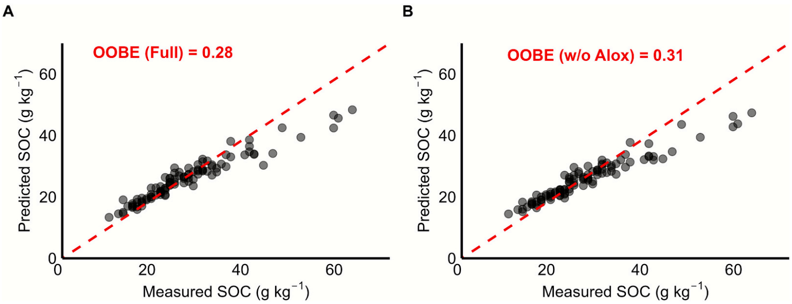


Fig. 4. Predicted soil organic carbon (SOC) contents from the random forest model plotted against measured SOC contents for A) all predictor variables selected by the Boruta algorithm and B) all predictor variables except Alox. OOBE is the out-of-bag error.

as those in New Zealand, the United States and Finland (Beare et al., 2014; Hall and Thompson, 2021; Salonen et al., 2024). For example, Hall and Thompson (2021) demonstrated that Alox was the strongest predictor for SOC contents in climates ranging from temperate to tropical in North America, Puerto Rico, Alaska, and Hawaii (NEON, 2020; Yu, 2021). We, thereby, confirmed results from studies based on smaller datasets or with more limited geographical coverage for humid continental climates (Fukumasu et al., 2021; Salonen et al., 2024). For example, Salonen et al. (2024), found that Alox explained 21 % of the variation in SOC contents in Finnish arable soils with clay contents between 2 and 68 %.

The underlying mechanisms behind our findings likely involve: (1) Sorption: Short-range order mineral phases represented in Alox provide abundant reactive surfaces for the sorption (via hydrogen bonds and covalent bonds (Ahmad and Martsinovich, 2023)) of organic carbon compounds (e.g., carboxylic acids and cellulose), hereby, also promoting aggregation (Kleber et al., 2021; von Fromm, 2025). This reduces the accessibility of SOC to microbial decomposition, thereby increasing SOC persistence in soil. (2) Formation of organometal co-precipitates and complexes: Aluminium oxides can form strong complexes with organic matter, particularly with ligands containing carboxyl and phenolic groups. These complexes decrease the solubility and mobility of organic carbon, further promoting SOC retention (Hall & Thompson, 2025). In our study, the measurement of total Alox encompasses both short-range order mineral phases and organometal complexes, making it difficult to distinguish the specific contributions of each to SOC stabilization. However, the role of Alox in aggregation as suggested in the first mechanism is questionable, as aggregation was not correlated with Alox (Fig. 2).

Exchangeable cations can act as binding agents for SOC and are closely associated with enhanced aggregate stability, thereby contributing to SOC stabilization (Bronick and Lal, 2005; Phocharoen et al., 2018; Slimani et al., 2022; Totsche et al., 2018). This stabilization may be partly attributed to the formation of cation bridges with SOC (Huang et al., 2019) and ionic bonds with organic substrates, resulting in immobilisation and stabilization of SOC (Solly et al., 2020; Kunhi Mouvenchery et al., 2012). Our findings support this mechanism, as we observed increased SOC concentrations with higher levels of exchangeable Ca (Fig. 5F) and a positive correlation between exchangeable Ca and Aggregation ($\rho = 0.44$; Fig. 2). The abundance of Ca cations in Swedish agricultural soils likely reflects the widespread presence of lime-rich glaciofluvial deposits and calcareous soils, particularly in Götaland, as well as in the western, southern, and central regions of Sweden, and in southwestern mountainous areas under cultivation (Clason & Granström, 1992). In contrast, the decrease in SOC content with increasing exchangeable Mn concentration (Fig. 5D) may be related to the catalytic role of Mn in SOM decomposition, where Mn facilitates the breakdown of complex organic molecules into simpler compounds (Li et al., 2021).

Rasmussen et al. (2018) proposed that the principal controls on SOC storage are determined by soil pH and water availability. Specifically, in water-limited, alkaline soils, calcium, and to a lesser extent, clay content, are the dominant factors influencing SOC storage. In contrast, in more humid and acidic environments, iron and aluminium minerals, particularly their complexes and oxyhydroxides, play a greater role. Based on these findings, it is plausible that under less humid conditions, exchangeable Ca is the most important factor for SOC stabilization, whereas under more humid conditions, oxalate-extractable aluminium

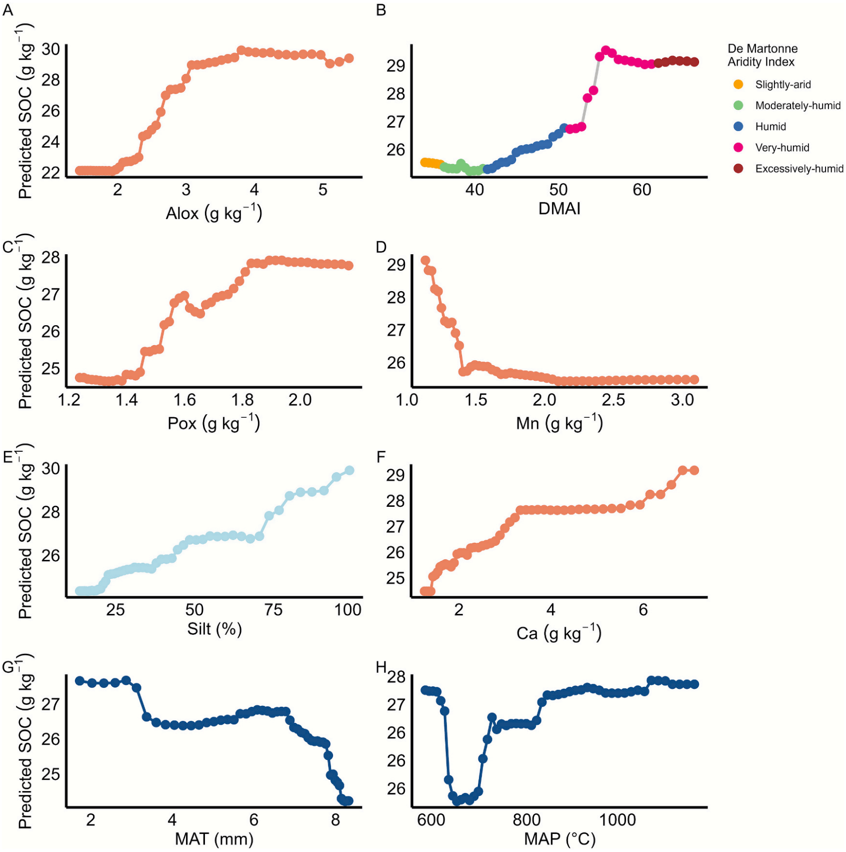


Fig. 5. Partial dependence plots (PDPs) for the predictor variables with the highest relative importance scores, as identified by the Boruta algorithm, in the random forest model (RFM) for soil organic carbon (SOC). A) oxalate-extractable aluminium (Alox), B) De Martonne aridity index (DMAI), C) oxalate-extractable phosphorus (Pox), D) exchangeable manganese (Mn), E) silt-sized soil particles (2–63 μm), F) mean annual temperature (MAT), G) exchangeable calcium (Ca), and H) mean annual precipitation (MAP).

(Alox) may assume greater importance.

Surprisingly, in contrast to the findings of Fukumasu et al. (2021), who reported that SOC stabilization via physical protection was associated with silt-sized aggregates and particles in the topsoil of Swedish agricultural fields, our study found that silt-sized aggregation was not a strong predictor of SOC content. This suggests that aggregation played a relatively minor role in protecting SOM from microbial decomposition in the soils we examined. Notably, silt-sized aggregation was positively correlated with clay content (Fig. 2), consistent with the well-documented influence of clay on soil aggregation (Boix-Fayos et al., 2001; Kemper and Koch, 1966; Rivera and Bonilla, 2020). Clay content is frequently incorporated into pedotransfer functions to predict aggregate stability (Wu et al., 2017). Beyond the sorption of SOM onto clay surfaces, aggregates smaller than 20 μm are thought to consist of flocculated clay particles held together by van der Waals forces, hydrogen bonding, and Coulombic interactions (Tisdall and Oades, 1982).

The observed increase in predicted SOC content with increasing Pox can be attributed to the intrinsic properties of SOM. A substantial proportion of organic phosphorus is associated with SOM (Kleber et al., 2007; Spohn, 2020). Organic phosphorus compounds, which typically contain one or more phosphate groups, exhibit a high affinity for adsorption to mineral surfaces (Spohn, 2024). Accordingly, Pox is expected to correlate positively with both SOC and Alox, which was confirmed in our study (Fig. 2, Fig. 5C). Pox also includes a fraction of inorganic phosphorus forms, often associated with Alox and Feox in acidic soils (Fransson, 2001). The combined contributions of organic and inorganic phosphorus to Pox likely explain the similar trends observed in the PDPs for Alox and Pox (Fig. 5A, C), as well as its positive correlation with SOC ($\rho = 0.36$; Fig. 2).

In contrast to our results, Feox content was a significant predictor in the regression models used by Salonen et al. (2024), and the sum of clay and silt contents was a significant predictor in one of their models. However, the effect of Feox was insignificant for soils with clay content smaller than 30 %. In our data, the range of clay contents was not as wide (1–52 %), and 75 % of the samples had clay contents smaller than 30 %. It is possible that the limited effects of soil texture and Feox contents in our dataset compared to Salonen et al. (2024) were due to these differences in soil texture. Another possibility is that the effects of increased surface area with increasing clay content were cancelled out by increased soil moisture. Soils with high clay content are more prone to create partially anaerobic microsites, which limits microbial degradation (Keiluweit et al., 2017; Noël et al., 2024). Also, Feox, which was positively correlated with clay content (Fig. 2), may have been affected by soil moisture. Under anaerobic conditions, Fe(III) may be reduced to Fe(II), which is a less reactive form of iron (Chen et al., 2020; Fukumasu et al., 2021). Nonetheless, our findings agreed well with previous large-scale studies (e.g., Hall & Thompson 2022; Rasmussen et al., 2018; von Fromm et al., 2025; Yu et al., 2021).

4.3. Limited influence of climate and farm management on SOC predictions compared to geochemical properties

In line with previous studies, our results show that climate variables and farm management practices were of secondary importance to geochemical properties (Doetterl et al., 2015; Van De Vreken et al., 2016). However, previous national-scale studies, which were based, at least partly, on the same data as we used, have shown that differences in farm management also led to changes in SOC contents (Henryson et al., 2022; Poeplau et al., 2015). Furthermore, the data from Eriksson (2021) showed higher SOC contents on animal farms (Table S5) due to a higher degree of pastures, regular manure application, and crop rotations that included ley. Both Poeplau et al. (2015) and Henryson et al. (2022) used SOC data from the SMP. However, unlike the method used by Poeplau et al. (2015), who conducted their analysis at the county scale, in the approach taken here, we used data from individual fields for which the farmers reported farm management data. Henryson et al. (2022) based their farm management data on the Swedish Farm Register. The data in the Swedish Farm Register are based on information on land use and the number of animals reported by farmers to the Swedish Board of Agriculture. The data on land use are uncertain due to unclear definitions (Glimskär and Skånes, 2015). It should be noted that differences in SOC content between ley-dominated rotations and other rotations were smaller for our subset compared to the complete data from Inventory III, which may explain the differences in our results (Table S5).

Climate influences both carbon inputs to soil, via its effect on net primary productivity (NPP), and the turnover of SOM (Poeplau et al., 2024; Wiesmeier et al., 2019). Yet, the complex interactions among soil physical properties, management practices, and climate introduce uncertainty in interpreting these relationships. Despite these challenges, our findings align with global-scale analyses (Jobbágy and Jackson, 2000; Hansen et al., 2023; von Fromm, 2025).

In this study, mean annual temperature (MAT) emerged as a significant predictor of soil organic carbon (SOC), with SOC decreasing as MAT increased (Fig. 3; 5F). This contrasts with Salonen et al. (2024), who observed no significant effect of MAT in a climate similar to Sweden's, likely due to the narrower MAT range in their dataset. The relationship between predicted SOC content and mean annual precipitation (MAP) was non-linear, showing an initial sharp decrease followed by a rapid increase, which is difficult to interpret (Fig. 5D). Our study would have benefited from evaluating geochemical predictors within pedo-climatically uniform sub-regions, as demonstrated by Wenzel et al. (2024). However, when MAT and MAP were integrated into the DMAI index, a general increase in predicted SOC content was observed with increasing wetness (Fig. 5C). These results suggest that higher soil moisture and lower temperature may limit microbial turnover of SOM and/or enhance NPP, thereby increasing SOC.

4.4. Assessing the SOC saturation state in Swedish agricultural soils across a humidity gradient

The partial dependence plots (PDP) show that SOC content increased gradually until it reached a plateau at higher Alox contents (Fig. 5A). A similar pattern was observed for multiple ecosystem types for the National Ecological Observatory Network dataset with sampling points across North America (Yu et al. (2021). Yu et al. (2021) suggested that this plateau indicates a potential for further SOC accrual. In other words, soils with high Alox contents may not have reached their *mineralogical capacity*. For Sweden, previous studies on the effects of changes in farm management on SOC contents have indicated that further changes should be possible if the input of SOM were increased (Eriksson, 2021; Henryson et al., 2022; Poeplau et al., 2015). It is plausible to assume that such changes should mainly occur for soils with higher Alox contents where the *ecosystem capacity* may be a limiting factor for attaining the mineralogical capacity.

Soil organic carbon content did not continue to increase with DMAI in very humid and extremely humid conditions (DMAI>53) (Fig. 5C). Aside from the limitation on C inputs, we do acknowledge other possible mechanisms that can result in the lower protection of SOC. For instance, as Alox content increases, the dominant stabilization mechanism may shift toward surface sorption, where organic molecules adsorb directly onto metal oxide surfaces from co-precipitation, providing proportionally less carbon protection per unit of metal (Wagai and Mayer, 2007). The effect of DMAI suggests a limited influence on NPP for the two wettest humidity classes. The sampling points with higher DMAI are mainly located on the west coast in the south of Sweden and in the north of Sweden. In the north, NPP is limited due to short growing seasons. At the same time, humid conditions also promote weathering, which creates new mineral surfaces that may help to stabilize SOM and decrease soil pH, leading to slower SOM turnover (Meier and Leuschner, 2010; Doetterl et al., 2015).

5. Conclusions

We found that the variations in SOC contents in Swedish agricultural soils could mainly be predicted by soil geochemistry. Especially oxalate-extractable aluminium (Alox) emerged as a key predictor. Based on these results and previous studies highlighting the importance of reactive aluminium phases in soils for SOC stabilization, we suggest that Alox measurements should be included in future soil inventories. The relationship between SOC contents and Alox suggests a potential for additional carbon storage in Swedish arable soils with large amounts of Alox. Farm management and climate variables were of secondary importance for predicting SOC contents. This study also highlights the need to explicitly include Alox in process-based models for predicting SOC storage in humid climates rather than relying solely on clay and silt content.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2025.e01038.

Declarative statement on the use of AI-assisted technologies

During the preparation of this work, the MC used Grammarly and Perplexity in order to improve the readability and language of the manuscript. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

CRediT authorship contribution statement

Miyanda Chilipamushi: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Claudia von Brömssen:** Writing – review & editing, Validation, Supervision, Software, Methodology, Formal analysis, Conceptualization. **Tino Colombi:** Writing – review & editing, Visualization, Validation, Supervision, Conceptualization. **Thomas Kätterer:** Writing – review & editing, Validation, Supervision, Investigation, Conceptualization. **Mats Larsbo:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Funding sources

This study was financed by the FORMAS (grant no. 01326, 2020). TC also acknowledges funding from the University of Nottingham (Nottingham Research Fellowship) and TK from FORMAS (grant no. 00214, 2022).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to extend our gratitude to Ana Maria Mingot Soriano, who oversaw the soil physical laboratory methods at the time of collecting data, and to David Nimblad Svensson for his assistance in setting up the laser particle size analyzer experiment. We also acknowledge Jan Fiedler and Mina Spångberg from the Soil and Plant Laboratory at the Department of Soil and Environment for their invaluable help in setting up the oxalate extractions. Special thanks to Carin Sjöstedt, Johanna Wetterlind, and Jan Eriksson for their support in accessing the data and samples selected from the Swedish soil and crop monitoring program. We are grateful to Evelin Pihlap and Mwenya Mubanga for their comments on the first draft of this manuscript and to Jon-Petter Gustafsson for fruitful discussions. Lastly, we thank Karin Blombäck for granting us access to the data on oxalate-extracted phosphorus.

Data availability

Comprehensive data from the Swedish soil and crop monitoring program are openly available at https://miljodata.slu.se/mvm/aker. The specific dataset used in this study can be made available by the authors upon request.

References

Ahmad, A., Martsinovich, N., 2023. Atomic-scale modelling of organic matter in soil: adsorption of organic molecules and biopolymers on the hydroxylated α-Al2O3 (0001) surface. Phil. Trans. R. Soc. A 381, 20220254. https://doi.org/10.1098/rsta.2022.0254.

Andrén, O., Kätterer, T., Karlsson, T., Eriksson, J., 2008. Soil C balances in Swedish agricultural soils 1990–2004, with preliminary projections. Nutr. Cycl. Agroecosyst. 81, 129–144. https://doi.org/10.1007/s10705-008-9177-z.

Bailey, V.L., Bond-Lamberty, B., DeAngelis, K., Grandy, A.S., Hawkes, C.V., Heckman, K., Lajtha, K., Phillips, R.P., Sulman, B.N., Todd-Brown, K.E., 2018. Soil carbon cycling proxies: understanding their critical role in predicting climate change feedbacks. Glob. Chang. Biol. 24 (3), 895–905. https://doi.org/10.1111/gcb.13926.

Beare, M., McNeill, S., Curtin, D., Parfitt, R., Jones, H., Dodd, M., Sharp, J., 2014. Estimating the organic carbon stabilization capacity and saturation deficit of soils: a New Zealand case study. Biogeochemistry 120 (1), 71–87. https://doi.org/10.1007/s10533-014-9982-1.

Boix-Fayos, C., Calvo-Cases, A., Imeson, A., Soriano-Soto, M., 2001. Influence of soil properties on the aggregation of some Mediterranean soils and the use of aggregate size and stability as land degradation indicators. Catena 44 (1), 47–67. https://doi.org/10.1016/S0341-8162(00)00176-4.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32. https://doi.org/10.1023/A:1010933404324.

Bronick, C.J., Lal, R., 2005. Soil structure and management: a review. Geoderma 124 (1–2), 3–22. https://doi.org/10.1016/j.geoderma.2004.03.005.

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 (9), 3200–3209. https://doi.org/10.1111/gcb.12982.

Chen, C., Hall, S.J., Coward, E., Thompson, A., 2020. Iron-mediated organic matter decomposition in humid soils can counteract protection. Nat. Commun. 11 (1), 1–13. https://doi.org/10.1038/s41467-020-16071-5.

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., 2015. Soil carbon storage controlled by interactions between geochemistry and climate. Nat. Geosci. 8 (10), 780–783. https://doi.org/10.1038/ngeo2516.

Eriksson, J., 2021. Tillståndet i svensk åkermark och gröda: data från 2011-2017. Current status of Swedish arable soils and cereal crops Data from the period, pp. 2011–2017. https://pub.epsilon.slu.se/23486/1/eriksson_j_210514.pdf.

Farrar, D., Coleman, J., 1967. The correlation of surface area with other properties of nineteen British clay soils. J. Soil Sci. 18 (1), 118–124. https://doi.org/10.1111/j.1365-2389.1967.tb01493.x.

Feng, W., Plante, A.F., Six, J., 2013. Improving estimates of maximal organic carbon stabilization by fine soil particles. Biogeochemistry 112 (1), 81–93. https://doi.org/10.1007/s10533-011-9679-7.

Fransson, A.-M., 2001. Evaluation of oxalate/oxalic acid for extracting plant available phosphorus in unfertilized acid soils. Commun. Soil Sci. Plant Anal. 32 (15–16), 2469–2484. https://doi.org/10.1081/CSS-120000385.

Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. Ann. Stat. 1189-1232. https://doi.org/10.1214/aos/1013203451.

Fukumasu, J., Poeplau, C., Coucheney, E., Jarvis, N., Klöffel, T., Koestel, J., Kätterer, T., Svensson, D.N., Wetterlind, J., Larsbo, M., 2021. Oxalate-extractable aluminum alongside carbon inputs may be a major determinant for organic carbon content in agricultural topsoils in humid continental climate. Geoderma 402, 115345. https://doi.org/10.1016/j.geoderma.2021.115345.

Georgiou, K., Jackson, R.B., Vindušková, O., Abramoff, R.Z., Ahlström, A., Feng, W., Harden, J.W., Pellegrini, A.F., Polley, H.W., Soong, J.L., 2022. Global stocks and capacity of mineral-associated soil organic carbon. Nat. Commun. 13, 3797. https://doi.org/10.1038/s41467-022-31540-9.

Glimskär, A., Skånes, H., 2015. Land Type Categories as a Complement to Land Use and Land Cover Attributes in Landscape Mapping and Monitoring. Land Use and Land Cover Semantics-Principles, Best Practices and Prospects. CLC Press/Taylor & Francis, Boca Raton. https://doi.org/10.1201/b18746-9.

Greenwell, B.M., 2017. Pdp: an R package for constructing partial dependence plots. R J 9 (1), 421. https://doi.org/10.32614/RJ-2017-016.

Groemping, U., 2006. Relative importance for linear regression in R: the package relaimpo. J. Stat. Softw. 17 (1), 1–27. https://doi.org/10.18637/jss.v017.i01.

Guillaume, T., Makowski, D., Libohova, Z., Bragazza, L., Sallaku, F., Sinaj, S., 2022. Soil organic carbon saturation in cropland-grassland systems: storage potential and soil quality. Geoderma 406, 115529. https://doi.org/10.1016/j.geoderma.2021.115529.

Hall, S.J., Thompson, A., 2021. What do relationships between extractable metals and soil organic carbon concentrations mean? Soil Sci. Soc. Am. J. https://doi.org/10.1002/saj2.20343.

Hassink, J., 1997. The capacity of soils to preserve organic C and N by their association with clay and silt particles. Plant Soil 191 (1), 77–87. https://doi.org/10.1023/A:1004213929699.

Hassink, J., Whitmore, A.P., 1997. A model of the physical protection of organic matter in soils. Soil Sci. Soc. Am. J. 61 (1), 131–139. https://doi.org/10.2136/sssaj1997.03615995006100010020x.

Heckman, K., Hicks Pries, C.E., Lawrence, C.R., Rasmussen, C., Crow, S.E., Hoyt, A.M., von Fromm, S.F., Shi, Z., Stoner, S., McGrath, C., 2022. Beyond bulk: density fractions explain heterogeneity in global soil carbon abundance and persistence. Glob. Chang. Biol. 28 (3), 1178–1196. https://doi.org/10.1111/gcb.16023.

Henryson, K., Meurer, K.H., Bolinder, M.A., Kätterer, T., Tidåker, P., 2022. Higher carbon sequestration on Swedish dairy farms compared with other farm types as revealed by national soil inventories. Carbon Manag. 13 (1), 266–278. https://doi.org/10.1080/17583004.2022.2074315.

Huang, X., Jia, Z., Guo, J., Li, T., Sun, D., Meng, H., Yu, G., He, X., Ran, W., Zhang, S., Hong, J., Shen, Q., 2019. Ten-year long-term organic fertilization enhances carbon sequestration and calcium-mediated stabilization of aggregate-associated organic carbon in a reclaimed Cambisol. Geoderma 355, 113880. https://doi.org/10.1016/j.geoderma.2019.113880.

Jensen, J.L., Schjønning, P., Watts, C.W., Christensen, B.T., Peltre, C., Munkholm, L.J., 2019. Relating soil C and organic matter fractions to soil structural stability. Geoderma 337, 834–843. https://doi.org/10.1016/j.geoderma.2018.10.034.

Jeong, J.H., Resop, J.P., Mueller, N.D., Fleisher, D.H., Yun, K., Butler, E.E., Timlin, D.J., Shim, K.-M., Gerber, J.S., Reddy, V.R., 2016. Random forests for global and regional crop yield predictions. PLoS One 11 (6), e0156571. https://doi.org/10.1371/journal.pone.0156571.

Jordbruksverket, 2025. Inspire-tjänster, kartor och GIS. https://jordbruksverket.se/e-tjanster-databaser-och-appar/e-tjanster-och-databaser-stod/kartor-och-gis#h-Laddanerkartskikt assesed 22 May 2024.

Keiluweit, M., Wanzek, T., Kleber, M., Nico, P., Fendorf, S., 2017. Anaerobic microsites have an unaccounted role in soil carbon stabilization. Nat. Commun. 8 (1), 1–10. https://doi.org/10.1038/s41467-017-01406-6.

Kemper, W.D., Koch, E.J., 1966. Aggregate Stability of Soils from Western United States and Canada: Measurement Procedure, Correlations with Soil Constituents. U.S. Department of Agriculture, Agricultural Research Service, U.S.

Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. Biogeochemistry 85, 9–24. https://doi.org/10.1007/s10533-007-9103-5.

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.

Kunhi Mouvenchery, Y., Kucerik, J., Diehl, D., Schaumann, G.E., 2012. Cation-mediated cross-linking in natural organic matter: a review. Rev. Environ. Sci. Biotechnol. 11 (1), 41–54.

Kursa, M.B., Rudnicki, W.R., 2010. Feature selection with the Boruta package. J. Stat. Softw. 36, 1–13. https://doi.org/10.18637/jss.v036.i11.

Lal, R., 2008. Soil carbon stocks under present and future climate with specific reference to European ecoregions. Nutr. Cycl. Agroecosyst. 81, 113–127. https://doi.org/10.1007/s10705-007-9147-x.

Li, H., Santos, F., Butler, K., Herndon, E., 2021. A critical review on the multiple roles of manganese in stabilizing and destabilizing soil organic matter. Environ. Sci. Technol. 55 (18), 12136–12152. https://doi.org/10.1021/acs.est.1c00299.

Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. R news 2 (3), 18–22.

Matus, F., Amigo, X., Kristiansen, S.M., 2006. Aluminium stabilization controls organic carbon levels in Chilean volcanic soils. Geoderma 132 (1–2), 158–168. https://doi.org/10.1016/j.geoderma.2005.05.005.

Matus, F., Garrido, E., Sepúlveda, N., Cárcamo, I., Panichini, M., Zagal, E., 2008. Relationship between extractable Al and organic C in volcanic soils of Chile. Geoderma 148 (2), 180–188. https://doi.org/10.1016/j.geoderma.2008.10.004.

Matus, F., Rumpel, C., Neculman, R., Panichini, M., Mora, M., 2014. Soil carbon storage and stabilization in andic soils: a review. Catena 120, 102–110. https://doi.org/10.1016/j.catena.2014.04.008.

Meier, I.C., Leuschner, C., 2010. Variation of soil and biomass carbon pools in beech forests across a precipitation gradient. Glob. Chang. Biol. 16 (3), 1035–1045. https://doi.org/10.1111/j.1365-2486.2009.02074.x.

Messing, I., Soriano, A.M.M., Svensson, D.N., Barron, J., 2024. Variability and compatibility in determining soil particle size distribution by sieving, sedimentation and laser diffraction methods. Soil Tillage Res. 238, 105987. https://doi.org/10.1016/j.still.2023.105987.

Neyman, J., 1992. On the two different aspects of the representative method: The method of stratified sampling and the method of purposive selection. In: Breakthroughs in Statistics: Methodology and Distribution. Springer, pp. 123–150. https://doi.org/10.1007/978-1-4612-4380-9_12.

Noël, V., Boye, K., Naughton, H.R., Lacroix, E.M., Aeppli, M., Kumar, N., Fendorf, S., Webb, S.M., 2024. X-ray chemical imaging for assessing redox microsites within soils and sediments. Front. Environ. Chem. 5, 1329887. https://doi.org/10.3389/fenvc.2024.1329887.

Pearson, R., 2017. Interpreting predictive models using partial dependence plots. Apr 15, 16.

Pellicone, G., Caloiero, T., Guagliardi, I., 2019. The de martonne aridity index in Calabria (southern Italy). J. Maps 15 (2), 788–796. https://doi.org/10.1080/17445647.2019.1673840.

Phocharoen, Y., Aramrak, S., Chittamart, N., Wisawapipat, W., 2018. Potassium influence on soil aggregate stability. Commun. Soil Sci. Plant Anal. 49 (17), 2162–2174. https://doi.org/10.1080/00103624.2018.1499752.

Poeplau, C., Bolinder, M.A., Eriksson, J., Lundblad, M., Kätterer, T., 2015. Positive trends in organic carbon storage in Swedish agricultural soils due to unexpected socio-economic drivers. Biogeosciences 12 (11), 3241–3251. https://doi.org/10.5194/bg-12-3241-2015.

Poeplau, C., Dechow, R., Begill, N., Don, A., 2024. Towards an ecosystem capacity to stabilize organic carbon in soils. Glob. Chang. Biol. 30 (8), e17453. https://doi.org/10.1111/gcb.17453.

R Core Team, R, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria.

Rabot, E., Wiesmeier, M., Schlüter, S., Vogel, H.-J., 2018. Soil structure as an indicator of soil functions: a review. Geoderma 314, 122–137. https://doi.org/10.1016/j.geoderma.2017.11.009.

Rasmussen, C., Heckman, K., Wieder, W.R., Keiluweit, M., Lawrence, C.R., Berhe, A.A., Blankinship, J.C., Crow, S.E., Druhan, J.L., Hicks Pries, C.E., 2018. Beyond clay: towards an improved set of variables for predicting soil organic matter content. Biogeochemistry 137 (3), 297–306. https://doi.org/10.1007/s10533-018-0424-3.

Rivera, J.I., Bonilla, C.A., 2020. Predicting soil aggregate stability using readily available soil properties and machine learning techniques. Catena 187, 104408. https://doi.org/10.1016/j.catena.2019.104408.

Salonen, A.R., de Goede, R., Creamer, R., Heinonsalo, J., Soinne, H., 2024. Soil organic carbon fractions and storage potential in F innish arable soils. Eur. J. Soil Sci. 75 (4), e13527. https://doi.org/10.1111/ejss.13527.

Sanderman, J., Hengl, T., Fiske, G.J., 2017. Soil carbon debt of 12,000 years of human land use. Proc. Natl. Acad. Sci. 114 (36), 9575–9580. https://doi.org/10.1073/pnas.1706103114.

Schlüter, S., Leuther, F., Albrecht, L., Hoeschen, C., Kilian, R., Surey, R., Mikutta, R., Kaiser, K., Mueller, C.W., Vogel, H.-J., 2022. Microscale carbon distribution around pores and particulate organic matter varies with soil moisture regime. Nat. Commun. 13 (1), 1–14. https://doi.org/10.1038/s41467-022-29605-w.

Slimani, I., Barker, X.-Z., Lazicki, P., Horwath, W., 2022. Reviews and syntheses: Iron: a driver of nitrogen bioavailability in soils? Biogeosci. Discuss. 2022, 1–40. https://doi.org/10.5194/bg-2022-194.

Sokol, N.W., Whalen, E.D., Jilling, A., Kallenbach, C., Pett-Ridge, J., Georgiou, K., 2022. Global distribution, formation and fate of mineral-associated soil organic matter under a changing climate: a trait-based perspective. Funct. Ecol. 36 (6), 1411–1429. https://doi.org/10.1111/1365-2435.14040.

Sollins, P., Homann, P., Caldwell, B.A., 1996. Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74 (1–2), 65–105. https://doi.org/10.1016/S0016-7061(96)00036-5.

Solly, E.F., Weber, V., Zimmermann, S., Walthert, L., Hagedorn, F., Schmidt, M.W., 2020. A critical evaluation of the relationship between the effective cation exchange capacity and soil organic carbon content in Swiss forest soils. Front. For. Glob. Chang. 3, 98. https://doi.org/10.3389/ffgc.2020.00098.

Spohn, M., 2020. Increasing the organic carbon stocks in mineral soils sequesters large amounts of phosphorus. Glob. Chang. Biol. 26 (8), 4169–4177. https://doi.org/10.1111/gcb.15154.

Spohn, M., 2024. Preferential adsorption of nitrogen- and phosphorus-containing organic compounds to minerals in soils: a review. Soil Biol. Biochem. 109428. https://doi.org/10.1016/j.soilbio.2024.109428.

Svensson, D.N., Messing, I., Barron, J., 2022. An investigation in laser diffraction soil particle size distribution analysis to obtain compatible results with sieve and pipette method. Soil Tillage Res. 223, 105450. https://doi.org/10.1016/j.still.2022.105450.

Swedish Meteorological and Hydrological Institute, 2025. Gridded Precipitation and Temperature Data (PTHBV). Retrieved from. https://www.smhi.se/data/ladda-ner-data/griddade-nederbord-och-temperaturdata-pthbv. accessed 15 August 2024.

Tisdall, J.M., Oades, J.M., 1982. Organic matter and water-stable aggregates in soils. J. Soil Sci. 33 (2), 141–163. https://doi.org/10.1111/j.1365-2389.1982.tb01755.x.

Totsche, K.U., Amelung, W., Gerzabek, M.H., Guggenberger, G., Klumpp, E., Knief, C., Lehndorff, E., Mikutta, R., Peth, S., Prechtel, A., 2018. Microaggregates in soils. J. Plant Nutr. Soil Sci. 181 (1), 104–136. https://doi.org/10.1002/jpln.201600451.

Van De Vreken, P., Gobin, A., Baken, S., Van Holm, L., Verhasselt, A., Smolders, E., Merckx, R., 2016. Crop residue management and oxalate-extractable iron and aluminium explain long-term soil organic carbon sequestration and dynamics. Eur. J. Soil Sci. 67 (3), 332–340. https://doi.org/10.1111/ejss.12343.

Von Fromm, S.F., Hoyt, A.M., Lange, M., Acquah, G.E., Aynekulu, E., Berhe, A.A., Haefele, S.M., McGrath, S.P., Shepherd, K.D., Sila, A.M., 2021. Continental-scale controls on soil organic carbon across sub-Saharan Africa. Soil 7 (1), 305–332. https://doi.org/10.5194/soil-7-305-2021.

von Fromm, S.F., Jungkunst, H.F., Amenkhienan, B., Hall, S.J., Georgiou, K., Hicks Pries, C., Montaño-López, F., Quesada, C.A., Rasmussen, C., Schrumpf, M., Singh, B., Thompson, A., Wagai, R., Fiedler, S., 2025. Moisture and soil depth govern relationships between soil organic carbon and oxalate-extractable metals at the global scale. Biogeochemistry 168 (20). https://doi.org/10.1007/s10533-025-01208-9.

Wagai, R., Mayer, L.M., 2007. Sorptive stabilization of organic matter in soils by hydrous iron oxides. Geochim. Cosmochim. Acta 71 (1), 25–35. https://doi.org/10.1016/j.gca.2006.08.047.

Wenzel, W.W., Golestanifard, A., Duboc, O., 2024. SOC: clay ratio: a mechanistically-sound, universal soil health indicator across ecological zones and land use categories? Geoderma 452, 117080. https://doi.org/10.1016/j.geoderma.2024.117080.

Wickham, H., Wickham, H., 2016. Data analysis. Springer. https://doi.org/10.1007/978-3-319-24277-4_9.

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Lützow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Ließ, M., Garcia-Franco, N., 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, X., Wei, Y., Wang, J., Wang, D., She, L., Wang, J., Cai, C., 2017. Effects of soil physicochemical properties on aggregate stability along a weathering gradient. Catena 156, 205–215. https://doi.org/10.1016/j.catena.2017.04.017.

Yu, W., Weintraub, S.R., Hall, S.J., 2021. Climatic and geochemical controls on soil carbon at the continental scale: interactions and thresholds. Glob. Biogeochem. Cycles 35 (3). https://doi.org/10.1029/2020GB006781 e2020GB006781.

Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 2026:18

Soil organic carbon (SOC) storage plays an important role in supporting vital ecosystem services, but current estimates remain too uncertain to guide informed decisions on carbon management. This thesis investigated the factors influencing SOC storage. Root-to-shoot ratios varied within the study field, and while soil geochemistry was a strong predictor of SOC content, it did not account for the mineralization of SOC. These findings offer important insights that could be considered when conceptualizing SOC storage processes for improved SOC estimates.

Miyanda Chilipamushi earned her graduate degree from the Department of Soil and Environment at SLU. She holds a Master of Science in Sustainable International Agriculture, a joint program offered by the University of Göttingen and the University of Kassel in Germany.

Acta Universitatis Agriculturae Sueciae presents doctoral theses from the Swedish University of Agricultural Sciences (SLU).

SLU generates knowledge for the sustainable use of biological natural resources. Research, education, extension, as well as environmental monitoring and assessment are used to achieve this goal.

ISSN 1652-6880
ISBN (print version) 978-91-8124-215-7
ISBN (electronic version) 978-91-8124-235-5