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Changes in soil N_2O emissions and nitrogen use efficiency following long-term soil carbon storage: Evidence from a mesocosm experiment

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ABSTRACT

Policy and market incentives are rapidly expanding to promote soil organic carbon (SOC) sequestration in global croplands. Evidence suggests that long-term increases in SOC can influence both crop yield and nitrogen (N) fertilizer requirements, with the potential to help address two important sustainability challenges. However, increases in SOC may also trigger higher soil nitrous oxide (N_2O) emissions, which would represent an important tradeoff for climate change mitigation. We tested the hypothesis that long-term increases in SOC are associated with higher crop yields and fertilizer N use efficiency (NUE), but at the cost of higher N_2O emissions. Wheat was grown in two soils (SOC_{low} and SOC_{high}) under three N fertilizer rates (0, 100, and 200 kg N ha^{-1}) in a mesocosm experiment. Soils were obtained (0–25 cm) from a 22-yr field experiment on no-till and cover cropping in California. Results indicate that total biomass and grain yield were higher for SOC_{low} than SOC_{high} at 100 kg N ha^{-1} but not the other N levels. Crop N uptake was also 28% greater for SOC_{low} at 200 kg N ha^{-1}, resulting in higher overall NUE. Soil N_2O emissions increased for SOC_{high} by 25–112% compared to SOC_{low}, likely due to long-term changes in labile C and N pools, microbial activity, and soil structure influencing porosity and gas diffusion. While there are well-documented crop and environmental benefits from enhancing SOC in agricultural soils, results from this study suggest that changes in soil N_2O emissions should be considered to accurately determine net GHG emission reductions.

1. Introduction

Efforts to reduce global greenhouse gas (GHG) emissions are increasingly focused on the ability of cropland soils to sequester carbon (C) from the atmosphere (Lal, 2010; Paustian et al., 2016). Enhancing soil organic carbon (SOC) stocks can help mitigate climate change while potentiallly increasing crop productivity and food security, soil ecology, and other critical ecosystem services (Blanco-Canqui et al., 2013; Horwath and Kuzyakov, 2018; Lal, 2004; Paustian et al., 2019; Schjønning et al., 2007). Improvements in SOC can be achieved through changes in land use or agricultural management practices such as agroforestry, no-till, cover cropping, biochar, organic amendments, and crop rotation among others, with rates of SOC storage ranging from 50 to 1000 kg C ha^{-1} yr^{-1} (Lal, 2004; Paustian et al., 2019; West and Marland, 2002). However, in the context of climate change mitigation, it is less often considered how changes in SOC will influence soil N_2O emissions, which can represent a large source of GHG emissions in cropping systems (Guenet et al., 2021). Due to tightly coupled biogeochemical C and N cycles, the possibility of higher N_2O emissions may offset some of the benefits of SOC sequestration, which represents an important tradeoff when considering net GHG emissions (Li et al., 2005; Lugato et al., 2018; Trost et al., 2013).

A recent analysis of N_2O emission factors showed that SOC was the largest relative driver of variation at global and regional scales compared to climate and management-related variables including fertilization, irrigation, and tillage (Cui et al., 2021). Soil organic carbon plays a key role in regulating microbial activity as well as soil moisture, oxygen (O_2) availability, labile carbon (C), and mineral nitrogen (N) concentrations, which together strongly influence N_2O emissions (Butterbach-Bahl et al., 2013; Li et al., 2022; Senbayram et al., 2012).

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Methods to increase SOC often involve C inputs in the form of root exudates or plant residue as well as N inputs from both organic and inorganic N sources (Blanco-Canqui et al., 2013; Van Groenigen et al., 2017). The main pathways for soil N_2O production, microbial nitrification and denitrification, are driven by the availability of soil C and N substrates, leading to concern that practices for increasing SOC can result in higher N_2O emissions (Guenet et al., 2021; Guo et al., 2014; Li et al., 2005).

Studies have shown that C and N availability increases microbial activity, promoting anoxic conditions and greater N_2O production via denitrification (Chen et al., 2013; Li et al., 2021; Senbayram et al., 2012). Changes in soil physical properties (e.g. hydraulic conductivity, water retention, macroporosity) can also influence N_2O emissions through altered soil moisture dynamics and gas diffusivity (Balaine et al., 2013; Blanco-Canqui and Lal, 2009; Wei et al., 2023). Within aggregates, elevated water content can further contribute to O_2 depletion, triggering denitrification processes (Cayuela et al., 2014; Li et al., 2022). At the same time, the development of larger pores with enhanced connectivity may facilitate upwards gas diffusion (Balaine et al., 2013). Studying soils where long-term management has resulted in elevated SOC is critical for investigating potential tradeoffs for N_2O emissions.

Crop yield has been shown to be positively impacted by higher SOC through direct and indirect pathways (Oldfield et al., 2019). Long-term studies have documented that management practices which increase SOC can increase yields due to changes in soil compaction, aeration, nutrient supply, aggregate stability, and water availability (Blanco-Canqui et al., 2013; King et al., 2020; Willoughby et al., 2023). As such, yield increases may be greater in marginal soils relative to those with improved nutrient supply and soil health, especially under suboptimal conditions like drought (Kane et al., 2021; Lal, 2006). In contrast, other studies have shown that yields either remained level or decreased under enhanced SOC (Oelofse et al., 2015; Oldfield et al., 2019; Swanepoel et al., 2018).

An important factor contributing to higher yields is the possibility of increasing the efficiency of external N fertilizer inputs. Increased SOC storage is accompanied by higher organic N stocks, leading to greater indigenous soil N supply and potentially lower N fertilizer demand (Bos et al., 2017; Todman et al., 2019). Moreover, improved soil structure and quality have been shown to increase yield potential and crop response to fertilizer, translating to gains in N use efficiency (NUE) (Ernst et al., 2020). Given that positive impacts on yield are not always observed with efforts to increase SOC, it is necessary to account for potential tradeoffs between GHG emission reductions and crop productivity (Xia et al., 2018; Shang et al., 2021).

Promoting yields of staple food crops such as wheat (*Triticum aestivum*) is critical from both an economic and food security perspective (Grote et al., 2021), especially under climate change with greater risks from weather extremes such as heat waves, droughts, and floods. Wheat is one of the most important global cereal crops and a main source of nutrition for approximately 30% of the world's population (Shiferaw et al., 2013). Research is necessary to balance the goals of enhancing SOC, which may have co-benefits for crop productivity and the efficiency of N fertilizer inputs, but without inadvertently increasing N_2O emissions. The objective of this study was to investigate changes in N_2O emissions, wheat yield, and NUE following long-term SOC storage. We hypothesized that wheat yields and NUE will increase with elevated SOC, but that altered soil C and N dynamics will also lead to higher N_2O emissions. Insights from this study will help determine the costs and benefits of increasing SOC for ecosystem processes related to climate regulation and food production.

2. Materials and methods

2.1. Soil description and experimental design

Soils for this study were obtained from a long-term experiment on no-till and cover crops at the University of California West Side Research and Extension Center, which is located approximately 56 km southwest of Fresno, California USA (36.3419°N, 120.1103°W). Soils at the site are Panoche clay loam (fine-loamy, mixed superlative, thermic Typic Haplocambids) (Arroues, 2006). Selected soil properties are presented in Table 1. This long-term field experiment reflects typical summer irrigated crop rotations in the Central Valley of California, with sorghum (*Sorghum bicolor)* and garbanzo beans (*Cicer arietinum)* grown in previous years (Mitchell et al., 2022). A detailed description of management history, crop yields, and soil properties for this experiment are provided in previous studies (Mitchell et al., 2017, 2022).

For the present work, soil samples were obtained to 25 cm depth in October 2021 from two treatments representing the largest difference in SOC following 22 years of management (Table 1). Standard practice for the region includes conventional tillage without cover crops, which was designated SOC_{low}. Conversely, the treatment utilizing no-till and cover crops was designated SOC_{high}. The treatments SOC_{low} and SOC_{high} had SOC concentrations of 0.87 and 1.32% (which translates to 14.9 and 21.2 Mg C ha^{-1} when considering the 0–15 cm depth), respectively. Both no-till and cover crops are considered as important opportunities for enhancing SOC in croplands (Paustian et al., 2019). The most recent cover crop mixture consisted of triticale (*Triticosecale wittm.*), cereal rye (*Secale cereale L.*), common vetch (*Vicia sativa*), radish (*Raphanus sativus*), and clover (*Trifolium incarnatum*). The cover crop biomass had a C:N of 42:1 due to a higher ratio of triticale, radish and rye to legumes.

Soil properties for each treatment were previously determined as part of the Soil Health Institute's North American Project to Evaluate Soil Health Measurements, with full methods described by Norris et al. (2020). Briefly, SOC and total N concentrations were determined by elemental combustion. Active C was determined as permanganate oxidizable carbon digestion followed by colorimetric measurement. Potentially mineralizable N was determined via a 7-day anaerobic incubation followed by colorimetric measurement of NH_4-N. Soil water infiltration was determined using a 15 cm diameter ring inserted into the soil to 7.5 cm depth. The time required for infiltration of 400 mL water applied to the soil surface was recorded. In addition, soil nitrate (NO_3-N) was determined colorimetrically at the start of this study by extracting 6 g of homogenized and sieved soil (2 mm) with 30 mL of 0.5 M potassium sulfate.

Spatial and temporal variation in soil N_2O emissions under field conditions can be extremely high due to heterogeneous soil moisture and temperature conditions influencing microbial activity and labile C and N pools. Thus, to address our study objectives regarding the long-term effects of increasing SOC, wheat was grown in a controlled environment using intact soil cores (30 cm diameter by 25 cm depth, representing approximately 20 kg of soil). These large soil mesocosms were constructed using polyvinyl chloride (PVC) pipe following previous work (Castellano et al., 2010; Hansen et al., 2021). Undisturbed soil cores were obtained from random locations within each field replication. Soil moisture was very low (3.5%) at the time of field sampling.

Wheat was grown in the greenhouse under irrigation at the University of California, Davis, USA (38.5382°N, 121.7617°W). The experiment was arranged in a randomized split-plot design where soil C levels (SOC_{high} and SOC_{low}) were considered main-plots and inorganic N fertilizer rates as subplots (0, 100, and 200 kg N ha^{-1}). Treatments labels of SOC_{high} and SOC_{low} are subjective terms and only used to indicate relative differences in this study, and therefore should not be directly used for comparison with other work. Each treatment was replicated four times. Cover crop residue was removed from the soil surface in mesocosms to establish similar conditions for SOC_{high} and SOC_{low}, but remaining root biomass and smaller pieces of aboveground residues in SOC_{high} were left undisturbed. The N fertilizer was applied as urea (46% N) equally split between two wheat growth stages — initial emergence (3/7/2022 1.0=germination) and tillering (3.0–4.0= tiller formation) following recommended practices to increase plant uptake of applied N fertilizer for this region (Orloff et al., 2012). Urea granules were

Table 1
Selected soil properties for SOC_{high} and SOC_{low} (0–15 cm depth). Values followed by same letter within a column are not significantly different at $p<0.05$.

	SOC (%)	Total N (%)	Active C (mg kg^{-1})	Potentially mineralizable N (mg kg^{-1})	NO_3-N (mg kg^{-1})	Sand-silt-clay (%)	Bulk density (g cm^{-3})	Hydraulic conductivity (cm hr^{-1})
SOC_{high}	1.32 a	0.13 a	575 a	82.8 a	11.0 b	39–32–29	1.07 b	77.3 a
SOC_{low}	0.87 b	0.09 b	398 b	56.7 b	47.8 a	39–32–29	1.14 a	25.9 b

distributed across the soil surface followed by 4 mm of irrigation to ensure dissolution and subsurface incorporation of N fertilizer.

2.2. Wheat management and irrigation

Wheat was planted at a density of 86 plants m^{-2} using the variety AP Octane treated with Dividend Extreme (AgriPro Wheat Inc., Kansas, USA). Plant density followed recommendations for irrigated wheat in California, adjusting for the volume of soil in the mesocosm (Fan et al., 2016; UCANR, 2022). Four seeds were placed 2.5 cm below the soil surface in each well at 7.6 cm spacing. Plants were thinned after emergence to achieve a final population of 8 plants per mesocosm. Wheat was planted into moist soil to support germination and early growth.

Approximately 600 mm of cumulative irrigation was applied during the course of the study using deionized water (Fig. 1). Water was supplied to mesocosms through a combination of drip irrigation (daily) and five individual surface irrigation events. For drip irrigation, eight equally spaced drip spikes equipped with 1 L hr^{-1} flow emitters were placed at approximately 5 cm depth in mesocosms and controlled by an electronic timer to maintain uniform water application. To initiate the experiment, 70 mm of water was delivered over 8 days to increase soil moisture for planting (this included the first surface irrigation event of 28 mm during the first two days). Drip emitters were programmed to provide 3.6–7.2 mm of irrigation per day, with the rate increasing over the experiment. Irrigation volumes were based on monitoring soil moisture at 10 cm depth using a handheld probe. The second and third surface irrigations were 4 mm applied during each N fertilization event. Finally, two larger surface irrigation events (50 mm) were applied during reproductive growth (April 5 and 26, 41 and 62 days after seeding).

To evaluate surface soil conditions in relation to N_2O emissions, three ECH_2O 5TM Volumetric Water Content (VWC) and Temperature electronic sensors (Meter Group, Pullman, WA) were placed at 0–5 cm depth. Hourly soil temperature and VWC were recorded using two EM50 data loggers (Meter Group, Pullman, WA) and combined into a daily average.

Wheat growth stages were recorded using the Feekes Scale: 0=planting, 1.0=germination, 2.0=tillering, 3.0–4.0= tiller formation, 6.0= first node developed, 8.0= flag leaf developed, 10.0= booting, 10.5=heading, 11.1=milk, 11.3=hard kernel. Leaf chlorophyll measurements were obtained 57 days after seeding (10.5 = heading) using an atLeaf handheld meter (Zhu et al., 2012). Wheat was harvested when 90% of plants reached physiological maturity (Feekes 11.3–11.4). Aboveground biomass in each mesocosm was harvested by hand and separated into the spike and remaining straw portion (stems and leaves). Grain and straw samples were dried until a constant weight at 65 °C. Grain yield is reported on a dry basis. Total C and N concentrations of grain and straw were analyzed via combustion on a Leco TruSpec CN Analyzer (St. Joseph, MI, USA). Grain and straw N uptake are the product of their dry weight and N concentration and total N uptake is the sum of both fractions. Apparent nitrogen recovery efficiency (NRE) was calculated as the increase in total N uptake for fertilized treatments relative to the control, divided by N fertilizer rate (100 or 200 kg N ha^{-1}).

2.3. Soil N_2O emissions

Soil N_2O fluxes were measured following the closed static chamber method (Pitton et al., 2021; Parkin and Venterea, 2010). The chambers were constructed from PVC to include a chamber base (10 cm diameter) and a cylindrical, insulated, vented chamber lid (15 cm in height)

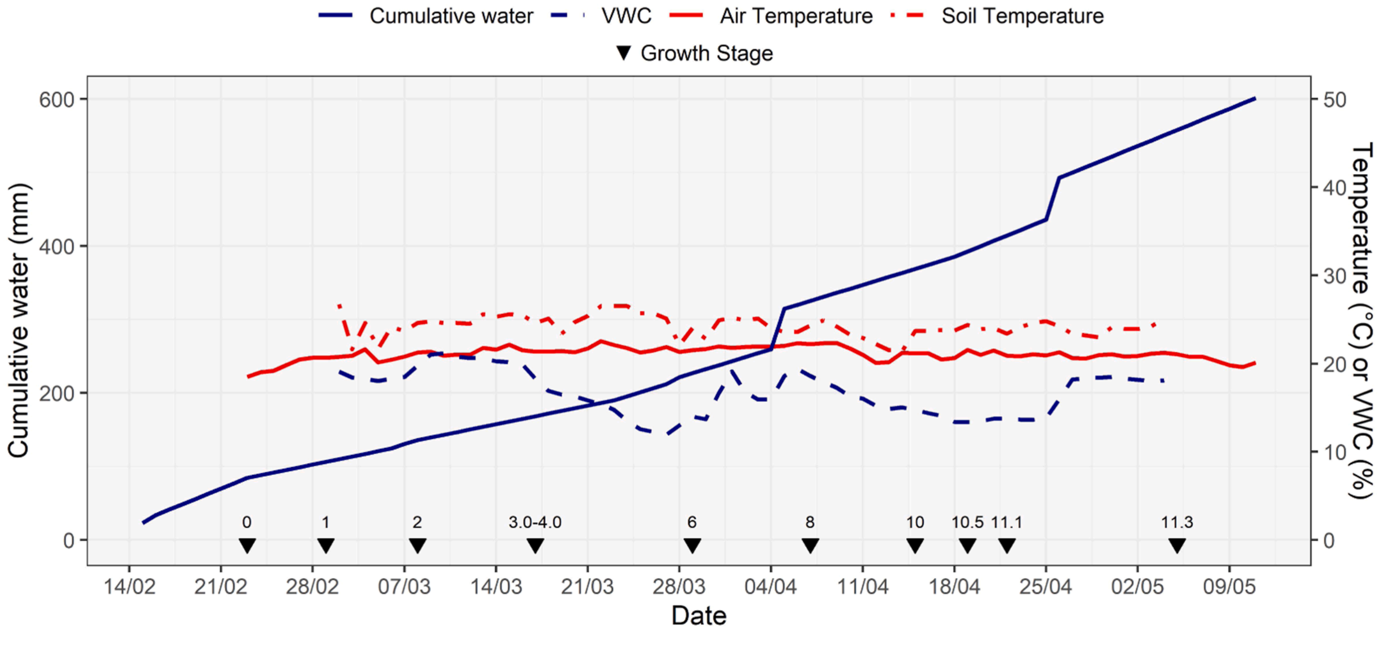

Fig. 1. Cumulative irrigation inputs (mm) and daily average air temperature, soil temperature, and soil volumetric water content (VWC) during the experiment. Wheat growth stages are denoted by black triangles using the Feekes Scale: 0=planting, 1.0=germination, 2.0=tillering, 3.0–4.0= tiller formation, 6.0= first node developed, 8.0= flag leaf developed, 10.0= booting, 10.5=heading, 11.1=milk, 11.3=hard kernel.

(Pitton et al., 2021). Bases were inserted to 5 cm soil depth in the middle of each mesocosm and remained in the same location for the duration of the study. During each sampling event, four gas samples were taken at 10-minute intervals (0, 10, 20, and 30 minutes). A syringe fitted with a needle was inserted into a rubber butyl septa (Labco Ltd., Lampeter, U.K.) on the chamber lid to remove 25 mL gas samples. Gas samples were immediately transferred into a previously evacuated 12 mL exetainers. The exetainers were sealed with butyl rubber stoppers (Labco Ltd., Lampeter, U.K.) and a clear silicone adhesive sealant to minimize leakage.

Gas sampling started two days after the initial irrigation event. Subsequent measurements were taken weekly, except for directly after N fertilizer events, during which additional gas samples were taken 1, 3, and 5 days post-application. Each sampling event occurred between 8:30–10:00 am. Samples were stored in exetainers until analysis using gas chromatography (GC) to determine N_2O concentration. The GC instrument was a Shimadzu GC-2014 fitted with an electron capture detector (Shimadzu Co., Kyoto, Japan) using helium as a carrier gas and certified N_2O calibration standards ranging from 0 to 9.95 ppm.

A restricted quadratic regression procedure was used to calculate daily N_2O fluxes as a function of increasing N_2O concentration in the chamber headspace over time (Venterea et al., 2020). This method was chosen in order to minimize the effects of measurement errors compared to standard nonlinear methods. Unlike linear regression models, the restricted quadratic procedure accounts for potential suppression of the vertical gas concentration gradient at the soil-atmosphere interface during chamber deployment (Venterea et al., 2020). A trapezoidal integration of flux versus time was used to estimate the cumulative area-scaled N_2O emissions during the entire study period (kg N_2O-N ha^{-1}).

2.4. Data analysis

Considering the experimental methodology, results for wheat parameters are reported on an absolute basis (per mesocosm) while N_2O emissions are reported on an area basis (per ha) following similar work (Abbruzzini et al., 2019). Treatment effects were analyzed for each response variable using linear mixed models fitted in R software with the '*nlme*' package ('*lme*' function; Pinheiro et al., 2017). The model accounted for the split-plot treatment structure with soil (SOC_{high}, SOC_{low}), N rate (0, 100, 200 kg N ha^{-1}), and their interaction considered as fixed effects, whereas block was included as a random effect. Model residuals were inspected to assess normality assumptions and constant error variance. Analysis of variance was performed using the '*car*' package ('*Anova*' function; Fox and Weisberg, 2019) to test the significance of effects at $p < 0.05$. The Tukey test was used for mean comparisons with the '*multcomp*' package ('*cld*' function; Hothorn et al., 2008).

3. Results

3.1. Soil moisture and temperature

Daily average volumetric water content (VWC) at the soil surface (0–5 cm) was 16.7% over the study, ranging between 12.0% and 21.1% (Fig. 1). As drip irrigation spikes delivered water at 5 cm depth which is below the measurement area for surface soil moisture, VWC values deeper in the soil profile were higher than this range. The highest VWC was recorded early following wheat germination, particularly in the days following the initial application of urea. Soil VWC steadily declined between 20 and 35 days after seeding, reaching a low when wheat entered the tillering and booting growth stages (34 and 54 days after seeding, respectively). Notable increases in VWC corresponded with the two N fertilizer application events (where water was also applied to move fertilizer into soil), particularly in the week following the second N application (35–41 days after seeding). Soil VWC also increased rapidly following the two surface irrigation events later in the season.

Daily average air temperature remained mostly consistent throughout the course of the study. Soil temperatures fluctuated slightly more than average air temperatures, ranging from 21.4 to 26.7 °C. The highest soil temperatures occurred during the mid- to late-tillering growth stages, while the lowest soil temperatures occurred during the booting growth stage.

3.2. Soil N_2O emissions

Daily N_2O emissions were highest in the days immediately following surface irrigation and fertilization events (Fig. 2). However, the magnitude of this response varied with N rates. In the unfertilized control, N_2O emissions were highest on the first two sampling dates but remained below 20 g N_2O-N ha^{-1} d^{-1} for the rest of the study. Even when soil moisture increased following two surface irrigation events during reproductive growth, there was little to no increase in N_2O emissions. In the 100 kg N ha^{-1} treatment, there were three large peaks in N_2O emissions of similar magnitude, immediately following the initial irrigation as well as the two N fertilizer events. While similar trends in peak fluxes were observed at 200 kg N ha^{-1}, the magnitude of daily fluxes was higher and there were more frequent peaks resulting in 5–6 large emission events in total. These occurred following all five surface irrigation events: the initial irrigation, two N fertilizations, and two large surface irrigation events during reproductive growth. Interestingly, it was only in the 200 kg N ha^{-1} treatment that SOC_{low} had higher N_2O emissions than SOC_{high} on several sampling dates (the first N fertilization event and the second surface irrigation event).

Daily N_2O emissions were consistently greater for SOC_{high} compared to SOC_{low} across the experiment, both during peak emission events and on dates when fluxes were relatively low for both treatments. The increase in SOC_{high} relative to SOC_{low} for daily fluxes was most consistent without N fertilizer, followed by 100 kg N ha^{-1} and then 200 kg N ha^{-1}. Accordingly, cumulative N_2O emissions were significantly different for the two soils ($p=0.025$), with 51% greater emissions for SOC_{high} on a seasonal basis when averaged across N rates (941 vs. 624 g N ha^{-1}). Individual contrasts within each N rate showed that N_2O emissions were 112, 43, and 25% higher for SOC_{high} compared to SOC_{low} at 0, 100, and 200 kg N ha^{-1}, respectively (Fig. 3). For cumulative emissions, the effect of N rate was marginally significant ($p=0.062$), with 36% higher N_2O emissions for 200 kg N ha^{-1} compared to 0 kg N ha^{-1} (910 vs 671 g N ha^{-1}, respectively).

3.3. Plant productivity and NRE

There was a main effect of soil on straw and total biomass but not grain yield. Straw and total biomass were 16 and 12% higher, respectively, for SOC_{low} compared to SOC_{high} across N rates ($p=0.05$ and 0.06, respectively) (Table 2). However, the only difference in grain yield was for SOC_{low} compared to SOC_{high} at 100 kg N ha^{-1}. Higher N rates significantly increased straw, grain yield, and total biomass ($p=0.04$, 0.04, and 0.03 respectively), with 200 kg N ha^{-1} increasing yield by 23% compared to 0 kg N ha^{-1}. In-season measurement of leaf chlorophyll content was significantly affected by N rate ($p=0.048$), but not soil ($p=0.153$) (Table S1 in Supplementary Information). Chlorophyll content under 200 kg N ha^{-1} was significantly higher than 0 kg N ha^{-1}, but values for 100 kg N ha^{-1} were not different than the other two N rates.

Straw and grain N uptake were similarly affected by the treatments (Table 3), with N rate having a significant effect for grain N, straw N, and total N uptake ($p= <0.001$). The positive response to N fertilizer addition in both soils resulted in approximately a 40% increase in straw, grain, and total N uptake when comparing 200 kg N ha^{-1} to 0 kg N ha^{-1}. Although main effects of soil were not observed for straw, grain, and total N uptake, there was a significant soil by N rate interaction for these variables. When exploring these interactions, there was no significant effect of soil within 0 and 100 kg N ha^{-1} for straw, grain, or

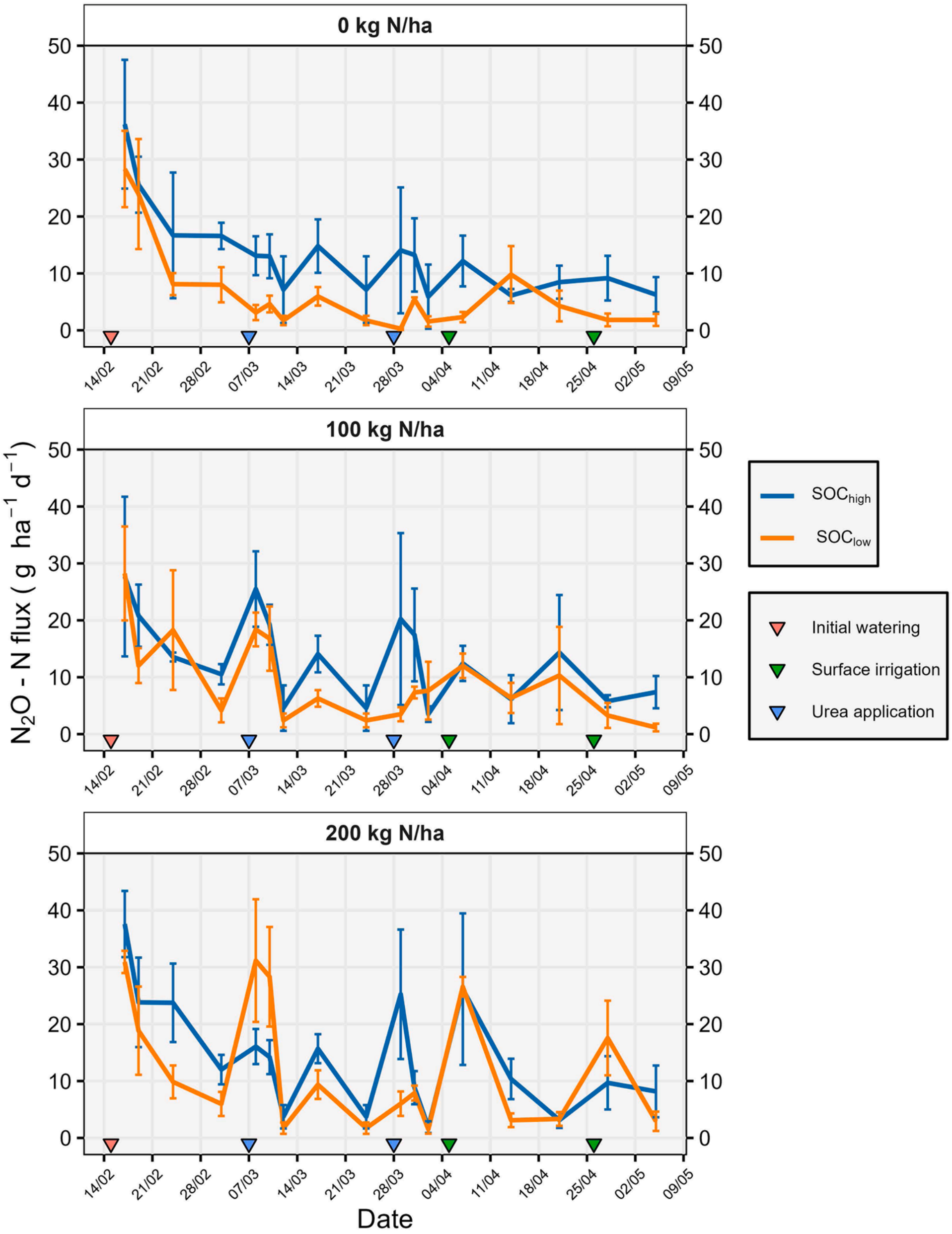

Fig. 2. Daily soil N_2O emissions (g N_2O-N ha^{-1} d^{-1}) for SOC$_{high}$ and SOC$_{low}$ under three N fertilizer rates (0, 100, and 200 kg N ha^{-1}). Colored triangles depict initial and surface irrigation events and the split N fertilizer addition. Error bars represent the standard error of the mean (n=4).

total N uptake. However, SOC$_{low}$ had significantly greater straw, grain, and total N uptake than SOC$_{high}$ at 200 kg N ha^{-1}.

Owing to the different patterns of crop N uptake described above, soil had a significant impact on NRE (p=0.014). There was a 3.5-fold increase in NRE for SOC$_{low}$ compared to SOC$_{high}$. The greatest difference in NRE between the two soils was at 100 kg N ha^{-1} (p=0.029), while a 2.6-fold increase in NRE was observed between soils at 200 kg N ha^{-1}.

4. Discussion

4.1. Soil N_2O emissions

Cumulative N_2O emissions from SOC$_{high}$ were 25–112% higher than SOC$_{low}$ across N rates, confirming the hypothesis that increasing SOC can lead to higher N_2O emissions (Fig. 3). This finding aligns with a growing body of evidence indicating that improvements in SOC may contribute to higher N_2O fluxes (Guenet et al., 2021; Li et al., 2005; Todman et al., 2019). Some common practices for building SOC are focused on C inputs such as manure or compost, which can trigger higher N_2O emissions compared to the relative increase in SOC, limiting the potential for net GHG reductions (Bos et al., 2017; Charles et al., 2017; Zhou et al., 2017). Similarly, straw return helps promote SOC accumulation but was found to increase reactive N losses in other work, including higher N_2O emissions (Xia et al., 2018). In contrast, Abdalla et al. (2019) found that cover crops were successful at increasing SOC without having significant effects on N_2O emissions, thus providing net GHG mitigation of approximately 2 Mg CO_2-eq ha^{-1} yr^{-1}. Given the multiple benefits SOC provides in terms of ecosystem services and soil productivity (Bos et al., 2017; Lal, 2010), greater emphasis is needed to determine the degree to which elevated N_2O emissions may offset SOC benefits, thereby influencing the magnitude of net GHG reductions (Lugato et al., 2018).

Several mechanisms likely explain the consistent increase in N_2O

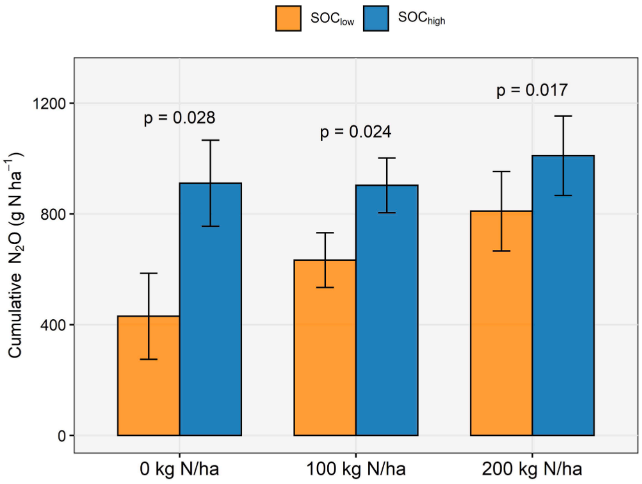

Fig. 3. Cumulative soil N_2O emissions (g N ha^{-1}) for SOC_{high} and SOC_{low} under three N fertilizer rates (0, 100, and 200 kg N ha^{-1}). Error bars represent the standard error of the mean (n=4). P-values represent comparisons between SOC_{low} and SOC_{high} within each N rate.

emissions both in the presence and absence of added N fertilizer (Figs. 2 and 3). The concentration of SOC and total N were 52 and 44% greater for SOC_{high} following two decades of management (Table 1). Soil C is a key driver of N_2O emissions due to its combined influence on soil chemical, biological, and physical properties including enhanced microbial activity, C and N substrate availability, and gas diffusion pathways (Chen et al., 2013; Cui et al., 2021). Similar to C and N concentrations, active C and potentially mineralizable N were 44–46% greater for SOC_{high} (Table 1). These labile C and N pools likely stimulated higher microbial activity (Mitchell et al., 2022; Schmidt et al., 2018), enhancing soil organic matter turnover and nitrification- and denitrification-derived N_2O production (Butterbach et al., 2013). The observed increase in N_2O emissions for SOC_{high} across the different N rates is particularly noteworthy considering the relatively high initial NO_3-N concentration for SOC_{low}. This finding suggests that changes in soil microbial activity associated with increased SOC may impact N_2O emissions to a greater extent than differences in inorganic soil N concentrations. Denitrification rates have been shown to increase with higher soil C and N content as well as microbial biomass (Li et al., 2022), especially when strong biological O_2 demand leads to the formation of anaerobic microsites.

Long-term changes in soil structure with elevated SOC can also contribute to increased N_2O emissions due to differences in water holding capacity, compaction, or gas diffusion (Balaine et al., 2013; Cayuela et al., 2014; Charles et al., 2017; Li et al., 2005; Steinbach and Alvarez, 2006). Araya et al. (2022) previously showed that improved soil aggregation and pore size distribution in the SOC_{high} treatment enhanced water infiltration rate, water retention, and water availability following irrigation. However, these changes in soil hydraulic properties can also influence relative gas diffusivity which is a strong predictor of N_2O emissions (Balaine et al., 2013), especially if larger pores with improved connectivity facilitate upwards gas diffusion and soil-surface N_2O fluxes. While improved pore connectivity would also increase O_2 diffusion into soil, Wei et al. (2023) documented how quickly soil O_2 concentrations decrease following N fertilization, making O_2 concentration a primary control on soil N_2O production relative to other factors. Therefore, co-existing processes occurring at different scales (microsites vs macropores) can interact to trigger higher N_2O emissions, leading Wei et al. (2023) to conclude that "a mix of oxygenated and anaerobic soil sites, are a prerequisite to stimulating soil N_2O production, while at the same time allowing for significant diffusion to the soil surface, resulting in high soil surface N_2O fluxes".

The largest N_2O peaks followed surface irrigation and N fertilizer events in both soils, as expected (Fig. 2). Surprisingly, the highest N_2O fluxes occurred with the initial irrigation at the start of experiment, which was prior to N fertilizer addition (this period accounted for over 40% of cumulative N_2O emissions in both soils). Soil N_2O emissions tend to be highest when water filled pore space is above 70% (Butterbach-Bahl et al., 2013; Guo et al., 2014). Previous research has attributed these large N_2O pulses after rewetting events primarily to the release of substrates which can fuel microbial denitrification and nitrification processes (Fierer and Schimel, 2002; Guo et al., 2014). Prior to N fertilizer addition, it is likely that greater microbial activity and substrate availability as a result of rewetting caused higher N_2O fluxes in SOC_{high}, despite much greater NO_3-N availability in SOC_{low} (Table 1). These apparent differences in biological activity are also supported by the higher potentially mineralizable N observed for SOC_{high}. While soil N concentration is often viewed as an important control on N_2O emissions, our comparison of soils with contrasting SOC levels indicates that N_2O

Table 2
Main effects of soil and N fertilizer rate on wheat grain yield, straw yield, and total biomass (g per mesocosm). Values followed by same letter within a column are not significantly different at $p<0.05$.

Soil	N rate (kg N ha^{-1})	Grain yield (g)	Straw yield (g)	Total biomass (g)
SOC_{high}		40.6	39.5	80.1
SOC_{low}		44.6	45.8	90.4
	0	38.5b	39.4 b	77.8b
	100	42.0ab	41.2 ab	83.2ab
	200	47.4a	47.3 a	94.7a
P-VALUES				
Soil		0.1473	0.05137	0.05819
N rate		0.0309	0.04666	0.03506
SOC_{high}	0	36.2	73.2	37.0
SOC_{low}		42.5	82.5	40.0
SOC_{high}	100	37.7	76.8	39.0
SOC_{low}		44.7	89.7	45.0
SOC_{high}	200	44.5	90.4	45.8
SOC_{low}		50.1	99.1	49.0
P-VALUES				
0		0.3463	0.5836	0.1584
100		0.0029	0.0000	0.0331
200		0.2274	0.2087	0.2531

Table 3
Main effects of soil and N fertilizer rate on wheat N content (grain N, straw N, total N uptake) and N recovery efficiency (NRE). Due to a significant interaction for plant N parameters, the effect of soil within each N rate is also displayed. Values followed by same letter within a column are not significantly different at $p<0.05$.

Soil	N rate (kg N ha^{-1})	Grain N (g)	Straw N (g)	Total N uptake (g)	NRE (%)
SOC_{high}		0.78	0.39	1.17	13.8 b
SOC_{low}		0.92	0.46	1.38	48.7 a
	0	0.71	0.36 b	1.07 b	-
	100	0.82	0.40 b	1.23 b	30
	200	1.02	0.51 a	1.53 a	32.5
P-VALUES					
Soil		0.2288	0.2203	0.2222	0.01431
N rate		$p < 0.001$	$p < 0.001$	$p < 0.001$	0.720
SOC_{high}	0	0.712	0.367	1.08	-
SOC_{low}		0.699	0.354	1.05	-
SOC_{high}	100	0.736	0.354	1.09	9.4
SOC_{low}		0.912	0.45	1.36	50.5
SOC_{high}	200	0.895	0.44	1.34	18.1
SOC_{low}		1.14	0.576	1.72	46.9
P-VALUES					
0		0.935	0.857	0.91	-
100		0.202	0.122	0.17	0.029
200		0.005	0.045	0.015	0.009

production in SOC_{low} may have been more limited by C substrates and microbial activity rather than NO_3-N availability.

The influence of soil moisture on N_2O emissions was not the same across N levels. Surface irrigation events had less effect under N-limited conditions (unfertilized control) but triggered high N_2O emissions in both treatments when N was plentiful (200 kg N ha^{-1}). This resulted in fewer peaks of smaller magnitude following surface irrigation in the absence of added N fertilizer (1–2 vs 5–6 peaks for the highest N rate) (Fig. 2). Hence, increased microbial activity and labile C and N pools increased N_2O emissions the most for SOC_{high} relative to SOC_{low} in the unfertilized control (Fierer and Schimel, 2002; Trost et al., 2013). This finding highlights that management of C and N cycles cannot easily be separated, and one important consequence of increasing SOC is that benefits for one may result in tradeoffs for another (Abdalla et al., 2019; Chen et al., 2014; Xia et al., 2018; Zhou et al., 2017).

The methods of our greenhouse experiment do not represent field conditions and values reported here should only be interpreted as relative differences. Measurement of soil N_2O emissions is an intrusive process and there are important limitations, with previous research concluding that most reported flux values are biased and poorly represent actual emissions (Rochette and Eriksen-Hamel, 2008). While some aspects of our mesocosm could have caused unnaturally high fluxes (e.g. irrigation regime), the range of daily flux values and cumulative emissions reported here is similar or lower than previous field experiments on wheat in California (Zhu-Barker et al., 2015). Similarly, cumulative emissions in our study (even with N fertilizer addition) were all lower than a recent global analysis reporting background soil N_2O emissions for cropland of 1.10 kg N_2O-N ha^{-1} $year^{-1}$ (Yin et al., 2021). The relative differences observed in our greenhouse study should be corroborated under field conditions focusing on representative crops, management practices, and weather conditions for different regions.

4.2. *Grain yields and NUE*

We observed no main effect of soil on grain yield across N rates in this study (Table 2), disproving our hypothesis that yields would increase with higher SOC. In fact, total crop biomass and yields increased in SOC_{low} compared to SOC_{high} at 100 kg N ha^{-1}, which is in contrast to the results of other studies. A recent global meta-analysis found that yields were 1.2 times greater in soils with 1.0 vs 0.5% SOC (Oldfield et al., 2019). Other findings are mixed on whether SOC directly contributes to yield increases (Blanco-Canqui et al., 2012; Lorenz et al., 2019), with relatively fewer studies assessing crop productivity after building SOC (Lal, 2006, 2010; Swanepoel et al., 2018; Xu et al., 2019).

At the start of our experiment, inorganic N concentrations were higher in SOC_{low} than SOC_{high} which likely influenced the crop yield response to applied N fertilizer. Leading up to the field sampling when there was no active plant growth, higher microbial activity and labile C availability in SOC_{high} could be associated with greater N immobilization, with surplus inorganic NO_3-N being incorporated into microbial biomass, supporting greater N recycling and retention (Cao et al., 2021). In contrast, while repeated soil disturbance with tillage in SOC_{low} likely promoted SOC mineralization, when coupled with lower microbial N demand, this may have contributed to a buildup of soil NO_3-N prior to field sampling. This higher soil NO_3-N for SOC_{low} at the start of the experiment substantially increased the total inorganic N supply (soil + fertilizer), which likely explains the observed increase in total biomass, grain yield, and crop N uptake for SOC_{low} compared to SOC_{high} at 100 or 200 kg N ha^{-1} (Tables 2 and 3). At the same time, lower yields or N uptake in SOC_{high} may have been caused by immobilization of applied N fertilizer due to higher labile C availability, as noted above (Alijani et al., 2012; Cao et al., 2021; Senbayram et al., 2012).

Despite greater inorganic NO_3-N availability for SOC_{low} at the start of the experiment, an interesting finding is that unfertilized yields for both soils were similar. This suggests there were important differences in both the timing and source of plant-available N supply for SOC_{high} due to long-term changes in organic N pools and microbial activity. Most notably, total N stocks and potential N mineralization rates were significantly higher for SOC_{high} (Table 1), providing a consistent release of plant-available N throughout the growing season. In contrast, the unfertilized SOC_{low} treatment had higher initial mineral NO_3-N, which provided a burst of available N to support early vegetative growth, but may have experienced relatively less SOC mineralization occurring during later stages of crop growth and grain filling. As a result, the higher organic N supply in SOC_{high} likely offset the difference in mineral NO_3-N for SOC_{low} at the start of experiment. Accordingly, because SOC_{high} relied more on indigenous soil N supply to meet crop N demand, SOC_{high} had lower NRE for applied N fertilizer compared to SOC_{low} (Table 3). However, it should be noted that only N fertilizer was included in the calculation of NRE, not total inorganic N inputs (soil

NO_3-N + N fertilizer).

An important consideration is that previous field research at this long-term experimental site found similar or higher yields with SOC_{high}, although results depended on crop and year (Mitchell et al., 2015, 2022). A primary contributor to higher yields was improved soil health and water dynamics resulting from the combination of no-till and cover cropping, particularly increased aggregation, water infiltration rate and water retention, and total N stocks and potentially mineralizable N (Mitchell et al., 2022; Araya et al., 2022). Lower yields were attributed to high levels of surface residue and compaction that impeded crop establishment in some years. Surface residues can breakdown slowly, leading to N immobilization and consequently decreased yields (Alijani et al., 2012).

One difference in our study compared to prior field results is that relatively steady soil moisture conditions were maintained in order to assess the potential for increased N_2O emissions. However, this is different than field conditions where significant variation in soil water levels occurs between irrigation events, potentially causing crop water stress when air temperatures are high. We acknowledge this as a limitation, as previous studies have shown the potential for elevated SOC to mitigate water stress and provide yield benefits under hot, dry conditions (Lal, 2006; Oldfield et al., 2019; Swanepoel et al., 2018). Moreover, since water and N supply are co-limiting factors to crop growth, improved soil water availability under field conditions would also lead to more crop N uptake, especially when water is limiting. As maintaining steady soil moisture in this study may have masked the benefits of improved soil water dynamics (Araya et al., 2022), future research should incorporate heat or drought stress to better reflect field conditions and future climate scenarios.

For the range of N rates studies here, our hypothesis that elevated SOC can decrease N fertilizer requirements and increase NUE was not confirmed. Expected NRE in wheat typically falls within the range of 40–50% (Ladha et al., 2005), indicating that NRE for SOC_{high} was extremely low (9–18%). This was because grain yield and total N uptake increased substantially for SOC_{low} at 100 and 200 kg N ha^{-1} but to a smaller extent for SOC_{high} (Table 3). Oelofse et al. (2015) summarized twenty years of data on wheat and barley and also found that NUE decreased with increasing SOC. As noted above, lower total N uptake in SOC_{high} may have been caused by lower soil NO_3-N availability at the start of the experiment or immobilization of applied N fertilizer due to higher labile C levels (Alijani et al., 2012; Senbayram et al., 2012). An important option for decreasing N fertilizer requirements is when similar yields can be achieved with lower N inputs. Considering the differences in initial soil NO_3-N availability which increased total inorganic N supply for SOC_{low}, the lack of yield effects at 200 kg N ha^{-1} suggests a lower N fertilizer requirement for SOC_{high}. Yet an accurate understanding of how much N fertilizer can be reduced requires future work, as yields for SOC_{high} at 100 kg N ha^{-1} did not match those of SOC_{low} at 200 kg N ha^{-1}. Experiments focusing on crop N response often include smaller N rate increments (e.g. 50 kg N ha^{-1}), so it is also possible that yield differences between the two soils could exist between the range of 100 and 200 kg N ha^{-1}.

To achieve higher NUE in crop production, research efforts are often focused on increasing grain yield response to N fertilizer addition under different management practices (Ernst et al., 2020; King et al., 2020). However, it is also important to understand how yields for the unfertilized control may change, especially under elevated SOC because this can increase the inherent soil N supply and reduce the need for external N inputs, having strong implications for NUE. While higher soil C and N stocks are likely to increase inherent soil productivity (i.e. crop yields without fertilizer), high rates of external N fertilizer can still make up the difference in soils with lower SOC to meet crop N demand and produce equivalent or higher yields (Oelofse et al., 2015; Oldfield et al., 2019). There was evidence of N deficiency across the different N rates both during the growing season (chlorophyll measurements) and for grain yield and total biomass at harvest, resulting in a 40% increase in crop N uptake at 200 kg N ha^{-1} (Table 3). However, the increase in crop N uptake at 200 kg N ha^{-1} was primarily evident in SOC_{low} rather than SOC_{high}. An important point is that even if SOC_{high} increased NUE, this does not automatically correspond with lower N_2O losses. In a meta-analysis, Xia et al. (2018) found that straw return increased crop N uptake and NUE by 11 and 15%, respectively, but N_2O emissions were still 22% higher. While enhancing SOC is often considered a key strategy for boosting crop productivity, further investigation is required to determine if sustainability co-benefits such as improved NUE can be achieved without a corresponding increase in N_2O emissions (Bos et al., 2017; Li et al., 2005; Todman et al., 2019).

4.3. *Net GHG emissions*

Assessment of net GHG mitigation strategies must account for both changes in SOC and non-CO_2 emissions such as N_2O contributing to climate change, recognizing the potential for tradeoffs (Xia et al., 2018; Shang et al., 2021). Even if N_2O emissions increase with elevated SOC, this may still be worthwhile for climate change mitigation if the gains in SOC outweigh the change in N_2O emissions on the basis of CO_2-equivalents (CO_2-eq) (Li et al., 2005). Across N rates in our study, there was an average increase of 0.317 kg N_2O-N ha^{-1} for SOC_{high} – equivalent to 0.140 Mg CO_2-eq ha^{-1} yr^{-1}. When comparing this value to the long-term SOC storage rate observed in the field experiment that served as the basis for the present work (0.324 Mg C ha^{-1} yr^{-1} or 1.187 Mg CO_2-eq ha^{-1} yr^{-1}), the measured increase in N_2O emissions from our mesocosm study would offset annual SOC storage by roughly 12% per year. Fertilizer-induced emission factors can provide another estimate of this relationship based on relative rather than absolute changes in N_2O emissions. Assuming wheat is fertilized with 150 kg N ha^{-1} yr^{-1}, a baseline estimate for direct N_2O emissions from SOC_{low} using a 1% emission factor would be approximately 0.698 Mg CO_2-eq ha^{-1} yr^{-1}. If emissions increased by 51% for SOC_{high} as observed in this study (1.05 Mg CO_2-eq ha^{-1} yr^{-1}), the additional release of 0.355 Mg CO_2-eq ha^{-1} yr^{-1} would offset annual SOC storage by around 30% per year.

These calculations involve many assumptions and determining net GHG emissions should be a priority for future work. For example, if N fertilizer requirements were reduced with SOC_{high}, this would likely decrease the tradeoff for N_2O emissions because avoiding excess N inputs is a key factor for minimizing N_2O losses (Hoben et al., 2011; McSwiney and Robertson, 2005). Likewise, SOC storage will reach a limit at some point due to saturation, after which the impacts of higher N_2O emissions on CO_2-eq will hold increased importance (Guenet et al., 2021; Lugato et al., 2018). A recent meta-analysis reported that practices for promoting SOC storage tended to reduce net GHG emissions without impacting yields but outcomes were highly dependent on N rate, temperature, and crop residue management (Shang et al., 2021). Long-term biogeochemistry modeling across soils in Europe found that despite higher N_2O emissions, practices for SOC sequestration can achieve net mitigation for 20–30 years, though around half of locations become a net source of GHG emissions by 2060 (Lugato et al., 2018). To better reflect the contribution of agriculture in emission inventories, efforts are also underway to develop revised IPCC emission factors which better capture the long-term effects of different soil and crop management practices on N_2O emissions. This could enable more accurate national GHG inventories related to changes in SOC, for example by improving N_2O emission factors for residue management which contributes to SOC storage (Olesen et al., 2023) or using higher N_2O emission factors for soils with higher SOC concentration (Hergoualc'h et al., 2021).

The global emphasis on promoting SOC sequestration to mitigate climate change has led to new agricultural initiatives and market incentives. One example is the "4 per mil" (4p1000) initiative launched in 2017 by France, attributing its name to the target of increasing soil C stocks by 0.4% annually. The 4p1000 Initiative states that practice recommendations must account for non-CO_2 emissions "to ensure that net greenhouse emissions do not exceed the offset benefit from increased SOC sequestration" (Rumpel et al., 2020). While management practices aiming to increase SOC stocks have been extensively studied (Paustian et al., 2016), empirical research quantifying potential synergies or tradeoffs between SOC storage and N_2O losses in the same study are scarce for different regions (Guenet et al., 2021). Although the potential for increased N_2O emissions is generally not enough to negate the benefits of SOC sequestration, this offset must be accounted for to accurately determine best practices for mitigating net GHG emissions, especially considering the growing emphasis on carbon markets and financial incentives in agriculture.

5. Conclusion

Recent studies have highlighted the possibility that practices contributing to SOC gains can increase N_2O emissions, partially offsetting the reduction in net GHG emissions. However, improvements in soil structure and fertility associated with elevated SOC may provide other important sustainability benefits, particularly related to crop productivity and N fertilizer requirements. We tested the hypothesis that long-term increases in SOC can improve wheat yield and NUE, yet N_2O emissions will also be higher. In this study, cumulative N_2O emissions significantly increased regardless of N fertilizer rate. This was likely due to changes in biogeochemical processes contributing to N_2O production, such as microbial activity and labile C and N availability, as well as modifications to soil structure, hydraulic properties, and gas diffusion. Crop yields did not increase with elevated SOC while total N uptake decreased at 200 kg N ha^{-1}, leading to an overall decrease in NRE. These results suggest the benefits of SOC for crop productivity may be more related to soil water dynamics than N supply. However, the conditions of this experiment did not include crop water stress, which is more typical under field conditions and should be evaluated in future work. In light of growing policy and market incentives promoting climate change mitigation in agriculture, our results add to a growing body of evidence showing it is necessary to quantify potential increases in N_2O emissions when determining net GHG reductions associated with practices for SOC sequestration.

CRediT authorship contribution statement

Lindsey A. Kelley: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Amélie C.M. Gaudin:** Writing – review & editing, Conceptualization. **Cameron M. Pittelkow:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Mark E.:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Jeffrey P Mitchell:** Writing – review & editing, Supervision, Conceptualization. **Zhenglin Zhang:** Writing – review & editing, Methodology, Investigation. **Santiago Tamagno:** Writing – review & editing, Methodology, Formal analysis, Data curation.

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109054.

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