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Management impacts on whole soil warming responses of CO_2 production and efflux in temperate climate

Md. Zulfikar Khan [a,b], Abad Chabbi [a,b,*], Caitlin E. Hicks Pries [c], Margaret S. Torn [d], Cornelia Rumpel [e]

[a] URP3F, Pluridisciplinaire prairies et plantes fourragères, Centre de recherche INRAE Nouvelle-Aquitaine-Poitiers, France
[b] UMR ECOSYS, Ecologie fonctionnelle et écotoxicologie des agroécosystèmes Université Paris-Saclay, INRAE, AgroParisTech, France
[c] Department of Biological Sciences, Dartmouth College, Hanover, USA
[d] Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
[e] CNRS, Institute of Ecology and Environmental Science-Paris (iEES-Paris), Sorbonne Université, Paris, France

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ABSTRACT

Although global warming has the potential to increase soil CO_2 efflux, the magnitude of these changes are uncertain, as CO_2 production rates in deep soil are poorly constrained. In particular, management effects on the warming responses at depth are unknown. Here, we conducted an *in-situ* soil warming experiment down to 2.0-m depth in an agricultural Cambisol to study the warming responses of (1) CO_2 production across different depths and (2) CO_2 efflux from topsoil in different seasons under two management practices. To this end, we measured whole-soil profile water content, CO_2 production and CO_2 efflux under continuous grassland and cropland in response to elevated temperature (+4°C).

Warming decreased soil water content for both management practices. We found contrasting warming effects on surface CO_2 efflux, depending on season and land management practices. Subsoil CO_2 production was more sensitive to warming than topsoil CO_2 production with grassland subsoil showing a greater warming response than cropland subsoil. Topsoil CO_2 production decreased in response to warming in the cropland but not the grassland. We concluded that warming responses of CO_2 production and efflux are affected by soil management practices. Their effect on biological processes (roots and microbial activity) and factors affecting gas diffusivity, such as soil water availability and soil physical organization need to be assessed to model warming effects on carbon exchange between soil and the atmosphere in agricultural systems.

1. Introduction

According to the Representative Concentration Pathways (RCPs) 8.5 scenario, the global soil temperature is expected to rise to $+4.5 \pm 1.1$°C above pre-industrial levels down to 1.0 m depth by the end of the 21st century (worst IPCC scenario) (Soong et al., 2020). These increasing temperatures will affect carbon (C) cycling in terrestrial ecosystems and possibly cause positive or negative feedbacks in terms of CO_2 exchange between the soil and atmospheric reservoirs (Carey et al., 2016; Davidson and Janssens, 2006). One of the most important mechanisms driving feedbacks to climate change is the increase in microbial activity in response to warming, which can increase the decomposition of soil organic carbon (SOC) and the soil CO_2 efflux to the atmosphere (Crowther et al., 2016). SOC is the largest biologically active C pool in terrestrial ecosystems, storing twice as much C as the earth's atmosphere and vegetation combined (up to 2500 Pg C) (Friedlingstein et al., 2020; IPCC, 2013). But it is still uncertain how this reservoir will respond to warming because the mechanisms controlling SOC turnover and microbial access to SOC are not fully understood (Bradford et al., 2016; Schmidt et al., 2011; Gestel et al., 2018).

In view of the international efforts to increase SOC stocks in agricultural systems through the development of sustainable agricultural practices (Rumpel et al., 2020; Smith et al., 2015), warming effects on C fluxes in managed agricultural systems are of crucial importance. Warming may affect the CO_2 soil efflux through its impact on the production and transport of CO_2 within and between individual soil depths. This was evidenced in recent *in-situ* whole soil warming (+4°C) experiments, in temperate and tropical forests, which found that warming

* Corresponding author at: URP3F, Pluridisciplinaire prairies et plantes fourragères, Centre de recherche INRAE Nouvelle-Aquitaine-Poitiers, France.
E-mail address: abad.chabbi@inrae.fr (A. Chabbi).

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caused substantial increases in soil CO_2 efflux due to the stimulation of soil profile CO_2 production (Hicks Pries et al., 2017; Nottingham et al., 2020). This increase was induced by the heterotrophic decomposition of SOC pools rather than autotrophic sources (Nottingham et al., 2020; Soong et al., 2021).

Rising temperatures are expected to stimulate CO_2 efflux by their effect on the plant-soil system (Bond-Lamberty and Thomson, 2010; Jochheim et al., 2022; Nottingham et al., 2020) and the magnitude of these responses are likely controlled by water availability (Védère et al., 2022). Water regulates plant and microbial activity, substrate availability, and soil gas diffusivity (Chen et al., 2016; McGrath et al., 2022; Wood et al., 2013). Also, seasonal climate variations affect soil temperature, soil water content, and plant phenology in temperate ecosystems (Vincent et al., 2006), leading to variable soil CO_2 efflux across time (Vanhala, 2002; Vincent et al., 2006). The controlling factors of CO_2 production and efflux, such as soil water content, microbial activity, root abundance and activity, which control substrate supply, and soil tortuosity are all influenced by soil management practices (Kuzyakov, 2006; Oertel et al., 2016; Pagenkemper et al., 2014; Vargas and Allen, 2008). Insight into how soil warming interacts with management to affect seasonal soil CO_2 efflux and its origin within the soil profile will enhance our ability to predict terrestrial C fluxes and C sink potential under future projected climate change.

The majority of publications addressing the effects of agricultural management on SOC turnover have focused on topsoil, ignoring the amount and climate vulnerability of SOC in deep soil layers (Voort et al., 2019; Yost & Hartemink, 2020; Moreland et al., 2021). It has been assumed that SOC stored in deep soil is relatively stable and unresponsive to agricultural practices. This assumption was mainly based on radiocarbon dating studies showing that subsurface C could be hundreds to thousands of years old (Hobley et al., 2017; Wang et al., 1999). Although decomposition rates in deeper soils are slower than in surface soils, recent studies have shown that part of subsoil C could turn over much faster due to preferential input of labile organic matter which could induce positive priming effects in subsoil (Chabbi et al., 2009; Min et al., 2020; Rumpel and Kögel-Knabner, 2011) and also be more responsive to changing abiotic conditions (Hicks Pries et al., 2017; Nottingham et al., 2020; Ofiti et al., 2021; Zhang et al., 2016) and agricultural management practices (Harrison et al., 2011; Osanai et al., 2020; Samson et al., 2021; Shahbaz et al., 2017) than previously assumed. Moreover, the microbial communities in subsoils are also quite different from those in surface soils, owing to lower SOC availability and more favorable conditions for oligotrophs due to nutrient-poor conditions (Ekelund et al., 2001; Fierer et al., 2003; Oertel et al., 2016; Scheffers et al., 2016; Stone et al., 2014; Zifcakova, 2020). Because of the soil depth profile with gradients of many abiotic and biotic factors affecting the mechanisms that control SOC input, loss, transformation, and stabilization, deep SOC is likely to respond differently to soil warming than surface SOC (Hicks Pries et al., 2023; Von Lützow and Kögel-Knabner, 2009). However, up to now it is unknown how deep soil C under different agricultural practices will respond to warming.

In this study, we thus aimed to provide *in-situ* experimental evidence on the SOC response to warming in managed agricultural soils down to 1.0 m depth. We used a whole-soil warming experiment established on an agricultural Cambisol to investigate how soil water content, CO_2 production, and CO_2 efflux respond to +4°C of warming under continuous grassland and temporary grassland in its cropland phase. In particular, we had the following study questions: (1) How does warming affect soil water content under contrasting land management?; (2) How does whole-soil warming affect the CO_2 efflux under contrasting management practices and seasons?; (3) How does the CO_2 production among differ depths respond to warming under contrasting land management? We hypothesized that in response to *in-situ* warming (H1) water content will decrease across all soil depths, because warming induces higher evapotranspiration, (H2) CO_2 efflux will increase year round in soils under continuous grassland but only seasonally in cropland soils, and (H3) CO_2 production will increase across the whole soil profile in grassland but not cropland soils, because grasslands show more root activity and root-derived C inputs throughout the year.

2. Materials and methods

2.1. Study area description

The experimental field site is part of the long-term Observatory for Environmental Research: Agro-ecosystems, Biogeochemical Cycles and Biodiversity (SOERE ACBB, http://www.soere-acbb.com/index.php/fr/), hosted by the INRAE (French National Institute of Agricultural Research and Environment), situated in Lusignan, Nouvelle-Aquitaine (46°25′12.91″ N; 0°07′29.35″ E), western France. The climate of the experimental site is oceanic with mean annual precipitation of around 760 mm, with most of it occurring from November to March. The mean annual temperature is about 12°C, with a monthly maximum of 27.9°C in August and a monthly minimum of −3.1°C in January (data from Météo France, 2007 to 2021). The site is flat with a slight slope gradient (0.5 percent). The soils are complex because of their particular pedogenetic evolution (Ducloux and Chesseron, 1988). The soil is classified as a Cambisol (FAO soil group) with loamy texture in the upper horizons, and clayey texture at depth with a high content of oxides and kaolinite, classified as a Paleo-Ferralsol. Pedoclimatic characteristics are shown in Table 1.

2.2. Land management history

The long-term experiment (SOERE ACBB) started in 2005 on an area previously covered by oak forest and then devoted to conventional agroecosystem management (grassland, grain cropping, or temporary (ley) grassland) for at least the next 100 years. The aim of the experiment is to elucidate the impact of temporary grassland introduction into the cropping cycle (maize (*Zea mays* L.), winter wheat (*Triticum* spp.), and winter barley (*Hordeum vulgare* L.)) on biogeochemical cycling. The experiment is conducted with several treatments and two controls (continuous grassland and continuous cropland). Temporary (ley) grassland treatments differ in duration (3 or 6 years of ley), fertilization strategy (with or without N fertilization) and harvesting regime (cutting or pasture). Croplands are ploughed to a depth of 30 cm (using a mouldboard plough), and crop residues (straw and yield) are returned to the soil after harvesting. For grassland treatments, a mixture of perennial ryegrass (*Lolium perenne* cv. Milca), cocksfoot (*Dactylis glomerata* cv. Ludac), and tall fescue (*Festuca arundinacea* cv. Soni) is used. Grasslands are hayed three to four times per year depending on productivity or grazed by cattle. Plant root biomass is greater in the continuous grassland than in the ley grassland and cropland down to 90 cm depth (Table 2).

2.3. In-situ experimental soil warming

In 2019, we established an *in-situ* soil warming (+4°C) experiment in the continuous grassland and in the ley grassland that began its cropland phase in 2020 after 6 years of temporary grassland (Table 3 and Fig. 1). The treatments are called 'grassland' and 'cropland' hereafter.

The *in-situ* warming experiment heated the soil to +4°C above ambient temperature (°C) across 10 m^2 circular plots to a depth of 1.0 m with 2.0 m long resistance heating cables while retaining the natural temperature gradient within the soil profile based on Hicks Pries et al. (2017) and Hanson et al. (2011). The warming experiment consists of three ($n = 3$) replicated plot pairs: control (ambient temperature) and heated (ambient temperature +4°C). There was approximately a 10 m distance between the control and heated pair plots (Fig. 2b). Briefly, warming was maintained throughout the 3.5 m diameter circular plot and down to 1.0 m depth with twenty-two 2.0-m-long steel pipes, which were installed vertically around 0.50 m apart and 0.10 m beyond the

Table 1
Soil properties by horizon of the experimental site (Chabbi et al., 2009; Moni et al., 2010). Mean and coefficient of variation expressed as a percentage of the mean. Both grassland and cropland treatments are on the same soil type.

Horizons	Soil depth /cm	Bulk density /g cm^{-3}	$pH_{(H2O)}$	Particle size distribution			CEC	Base saturation /%	Oxides-Hydroxides			
				Sand	Silt	Clay	/cmol$_c$ kg^{-1}		Al_o	Fe_o	Fe_d	Al_d
				——/g kg^{-1} soil——					——/g kg^{-1} soil——			
Lp (n = 6)	0–30	1.43 ± 5%	6.3 ± 3%	105 ± 14%	727 ± 3%	168 ± 87%	7.08 ± 11%	0.98 ± 7%	1.20 ± 19%	3.22 ± 22%	20.97 ± 25%	3.08 ± 25%
S (n = 6)	30–59	1.45 ± 4%	6.6 ± 4%	95 ± 9%	594 ± 7%	311 ± 11%	8.6 ± 22%	0.94 ± 6%	1.65 ± 14%	1.53 ± 17%	27.19 ± 27%	5.11 ± 18%
S2 (n = 5)	59–84	1.60 ± 7%	6.9 ± 5%	103 ± 11%	520 ± 9%	377 ± 21%	10.8 ± 27%	0.94 ± 5%	2.01 ± 9%	1.82 ± 15%	45.27 ± 22%	7.20 ± 21%
C1 (n = 5)	84–143	1.59 ± 8%	6.6 ± 4%	98 ± 8%	330 ± 11%	572 ± 9%	11.6 ± 16%	0.93 ± 9%	1.95 ± 19%	2.03 ± 14%	62.79 ± 36%	7.42 ± 22%
C2 (n = 6)	>143	1.61 ± 6%	5.2 ± 3%	110 ± 10%	242 ± 13%	642 ± 12%	9.9 ± 17%	0.82 ± 10%	1.87 ± 15%	2.27 ± 11%	67.02 ± 32%	6.16 ± 27%

Here, CEC stands for cation exchange capacity; Fe_o and Al_o standas for amorphous forms of Fe and Al; Fe_d and Al_d stands for non-crystalline forms of Fe and Al.

Table 2
Plant root mass from whole soil profile (mean ± SE, $n = 5$) of the experimental site in the control plots with two different land management practice.

Field	Year	Root mass (kg ha^{-1}) in different soil depth		
		0–30 cm	30–60 cm	60–90 cm
Cropland	2019*	7160 ± 340	918 ± 26	222 ± 9
	2020	4250 ± 150	643 ± 8	314 ± 6
	2021	3560 ± 190	726 ± 7	258 ± 9
Grassland	2019	9850 ± 260	1200 ± 45	484 ± 8
	2020	11600 ± 1100	1250 ± 65	496 ± 10
	2021	12800 ± 1600	2000 ± 13	563 ± 9

*Data collected from temporary grassland in 2019, after that was in its cropland phase after 6 years of ley grassland (see Table 3).

edge of the plots (Fig. 2a). In warmed plots, self-regulating heating cables (TECHNITRACE (CAMT EA 35 W/m 230 V), France) were placed inside the pipes, which were then filled with sand, while control plots did not have that type of heating cable. We installed additional heating cables 5 cm below the soil surface in a horizontal zigzagging pattern across the circular plot, around 0.30 m apart, to compensate for surface heat loss (Fig. 2a). Similar unpowered heated cables were not installed in the control plots, modified from Hicks Pries et al. (2017). The heaters were powered by an electric power supply, which was controlled by a silicon-controlled rectifier (SCRs, Watlow, Missouri, USA) via a current-to-voltage converter with a unipolar multiplexer (1KOhms resistance). The amount of electricity (source of heating) supplied to the deep heaters was based on the temperature difference between control-heated paired thermistors at 50, 75, and 100 cm depths at 0.75 m radial distance from the center of the plot. Similarly, the temperature difference of thermistors at 15 and 30 cm depth at radial distances of 0 and 0.75 m from the center of the plot was used to calculate the power supplied to the surface heaters of each paired plot. We installed this *in-situ* soil warming experiment in two phases: (1) initial installation in 2019 and 2020, during which the warming system was turned on, and (2) conditioning in 2020 and 2021 before field data collection started in June 2021 (Fig. 2c). The conditioning phase was due to low soil warming with respect to our target of +4°C, and we reached our target after 1.5 years of turning on the warming system.

2.4. Automated temperature and moisture data measurements

Portable dataloggers (CR1000, Campbell Scientific, Utah, USA) recorded continuous soil profile temperature and moisture data at 10-second intervals. In each plot, a PVC tube containing six temperature probes (OMEGA 44,007 thermistor) was placed at different depths (5, 15, 30, 50, 75, and 100 cm) with five replicates at 0.75 m radial distance from each other to monitor temperature, modified from Hicks Pries et al. (2017). The sensors at 15 and 75 cm depth were also used to regulate the surface and depth temperatures in order to ensure that the +4°C relative to the control is maintained throughout the soil profile. Another tube including five capacitance sensors equipped with enviroSCAN probes (Sentek, Australia) measured soil moisture at different depths (15, 30, 50, 70, and 90 cm) at a radial distance of 0.75 m from the center of each plot. The soil moisture readings were calibrated by comparing the sensor values at each depth to the volumetric water content recorded in the nearest (within 0.30 m) soil samples. We repeated this soil sampling two times over one year, in both dry and wet periods, to minimize the calibration errors.

2.5. Evaluation of in-situ soil warming (+4°C) performance

Our *in-situ* soil warming experiment shows a homogeneous temperature gradient (+4 ± 0.2°C for cropland and +4 ± 0.3°C for grassland) down to 1.0 m depth of the soil profile, except 0–15 cm depth, throughout the whole study period (Figs. 3a and 3b). The 0–15 cm depth showed a higher variability (+4 ± 0.5°C for cropland and +4 ± 0.4°C for grassland) concerning our target (+4°C) because there is no surface heating to compensate for the heat loss due to close contact of ambient air temperature and radiation compared to deep soils. However, the relative warming effect was consistent over the entire study period (Fig. 3a) and did not change with weather (seasonal fluctuations) or soil moisture conditions.

2.6. Leaf area index

During the growing season (March to June 2022), we measured leaf area (m^2) by scanning the leaf blades in a leaf area scanner (LI-2000, Li-

Table 3
Long-term land-use management history under an experimental site since 2005 in the Nouvelle-Aquitaine (Lusignan) region of western France.

Year:	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021	2022
Cropland:	Ley Grassland (harvested 3 to 4 times/year)						Maize	Wheat	Barley	Ley Grassland (harvested 3 to 4 times/year)						Maize	Wheat	Barley
Grassland:	Continuous Grassland (harvested 3 to 4 times/year) for annual forage production																	

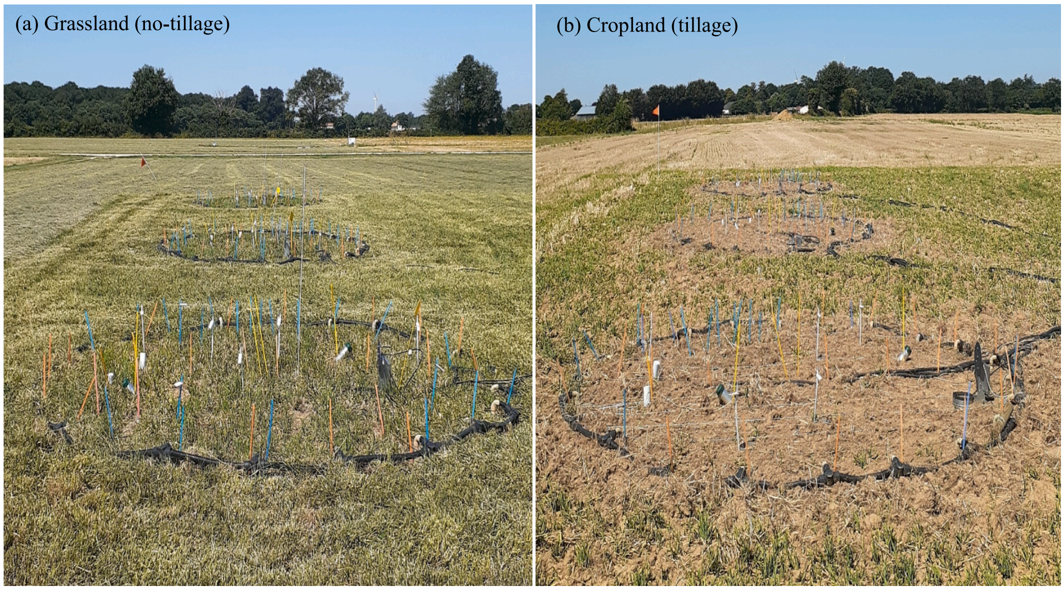

Fig. 1. *In-situ* whole-soil warming experiment under contrasting grassland management: (a) continuous grassland; and (b) cropland (cropland phase after 6 years of ley grassland) in a temperate region of western France.

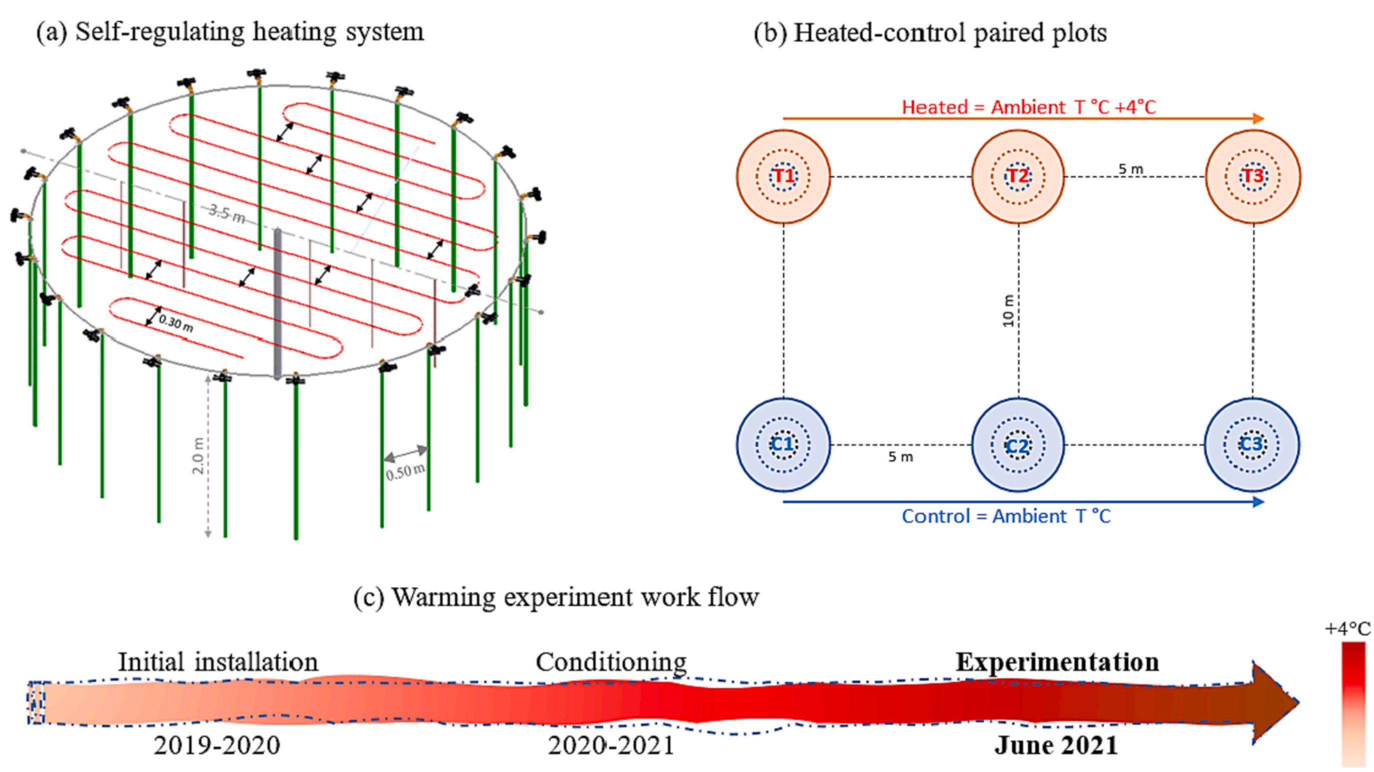

Fig. 2. *In-situ* soil warming experimental design under contrasting grassland management: (a) whole-soil warming methodology based on self-regulating heating cable down to 2.0 m soil profile (the red zigzag line represents the buried surface heating location at 5 cm depth while the green and gray bar represents the location of the deep heating system down to 2.0 m depth); (b) heated-control paired (replicates, $n = 3$) plots; and (c) warming experiment work-flow (after 1.5 years, we have +4°C, which has continued) in a temperate region of western France.

Cor, Lincoln, Nebraska, USA) to estimate the leaf area index (LAI, m^2 m^{-2}) based on ground cover (m^2).

2.7. Soil organic carbon content

In late May 2022, we collected soil samples from control-heated paired plots (n = 3) at different soil depths (0–15 cm, 15–30 cm, 30–50 cm, 50–70 cm, and 70–90 cm) before harvesting the vegetation cover, including cropland and grassland. To elaborate, soils were randomly sampled using a mechanical soil auger (8 cm in diameter) with five replicates (n = 5). Subsequently, all replicates were combined into a single composite sample for each plot and depth. These samples were then air-dried, sieved to 2 mm, and ground into a fine powder. Following this preparation, the concentration of soil organic carbon (SOC) was

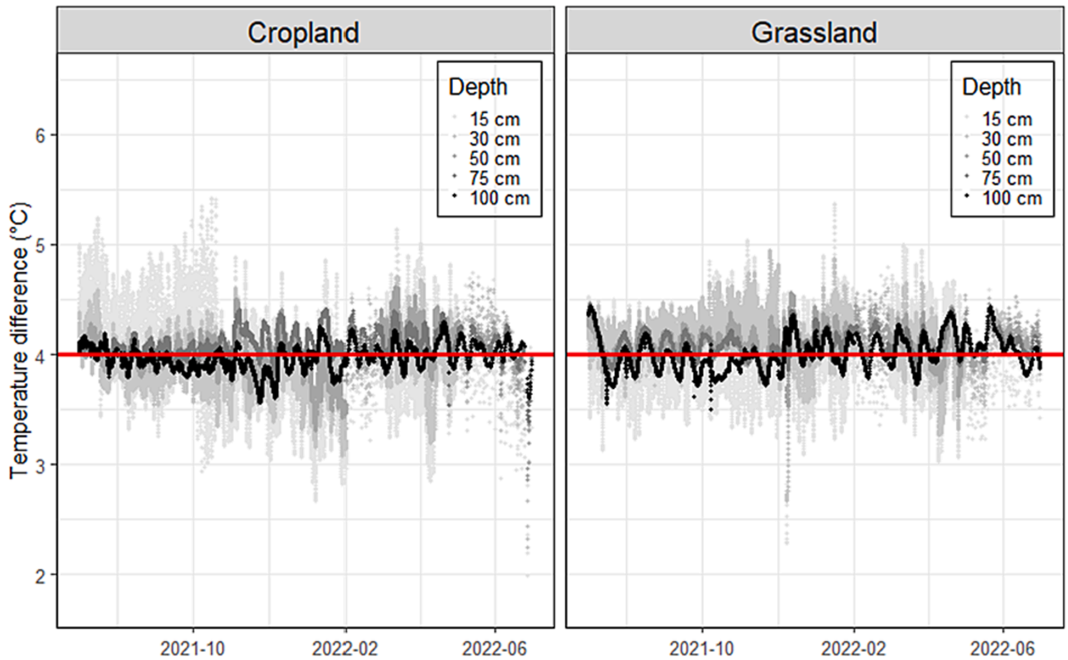

Fig. 3a. The average temperature difference between the control-heated pair plots ($n = 3$) at five depths over the study period (July 2021 to July 2022). The red line is the +4°C target. Discontinuities in warming (drops followed by sharp increases) were due to electrical outages.

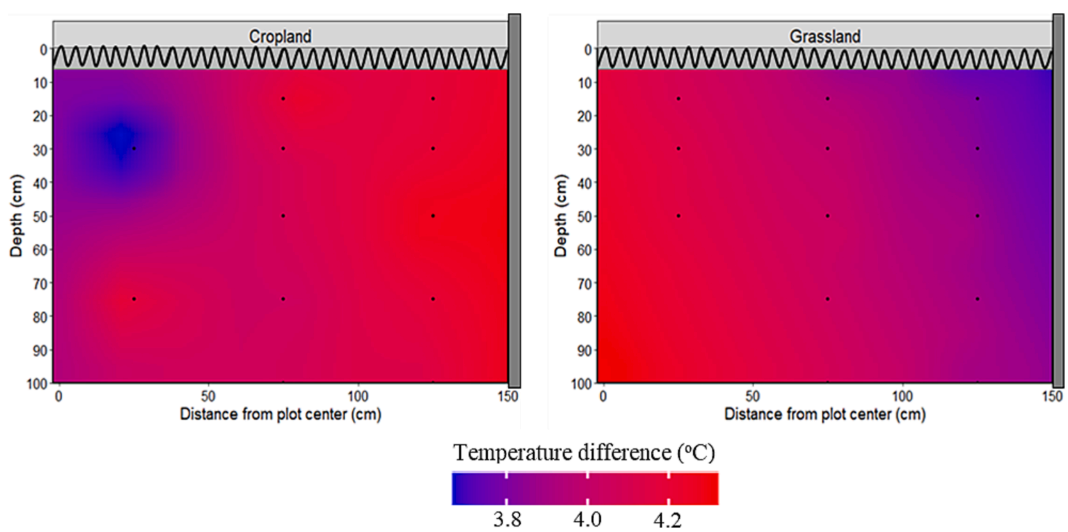

Fig. 3b. A radial cross-section of the study plot shows the average temperature difference ($n = 3$ plot pairs) from August to October 2021. The black dots represent the location of the temperature sensors. The horizontal zigzag line (black) is the location of the surface heaters and the vertical grey bar represents the 2.0 m long deep heaters, which are located 25 cm from the edge of the plot at 175 cm from the plot center. The data were interpolated using the automap package in R.

determined using a CHN auto-analyzer (Flash EA, Thermo Electron Corporation, Bremen, Germany).

2.8. Soil CO_2 efflux

Measurements of surface soil respiration (CO_2 efflux) were performed from July 2021 to June 2022 using soil respiration auto-chambers (8100A, LI-COR, Lincoln, Nebraska), which continuously measured the soil respiration fluxes every 90 min in each plot. During each flux measurement, the air temperature was also recorded using a temperature probe (OMEGA 44,007 thermistor), which was connected to the auto-chamber lid above the soil surface. The soil CO_2 efflux was calculated as follows:

$$f = \frac{dc}{dt} \times \frac{hMP}{RT} \quad (1)$$

Where f denotes the surface CO_2 efflux rates (μg m^{-2} s^{-1}), dc/dt is the rate of increase of the CO_2 concentration inside the chamber with time and is determined by the slope of linear regression; h is the height of the chamber; M is the molar mass of CO_2; P is the atmospheric pressure; R is the ideal gas constant; and T is the chamber air temperature in Kelvin. After that, the surface CO_2 efflux was converted to g C m^{-2} d^{-1} units.

To prevent CO_2 efflux from aboveground plant parts (leaves and stems), living plants inside the auto-chambers were manually eradicated once a week if they grew, and the removed plant material was left inside the chambers to die. Therefore, the CO_2 efflux measured in the soil did not include aboveground respiration from living plants (e.g., leaves and stems) but included belowground root respiration.

2.9. Soil profile CO_2 production

Gas measurements were carried out using a set of gas wells at 15, 30, 50, 70, and 90 cm depths of the soil profile, which had been installed at each plot at a distance of 0.20 m from the center. At 70 and 90 cm, the set up included two additional replicates to better account for deep soil heterogeneity. The gas wells were 6.35 mm (diameter) stainless steel tubes inserted at a 45° angle into the soil to the desired depth and topped with straight swage pipe-fittings with septa at the distal end (TECHNITRACE, France). We collected soil gas samples every fifteen days during six months (January 2022 to June 2022). Samples were collected from the gas wells with a 60 ml syringe, after clearing the headspace in each well. For gas analysis, 3, 20 ml samples were immediately injected into a portable infrared gas analyzer (EGM-5, PP Systems, USA) in the field and stored the gas concentration (ppm) reading with a nonvolatile semiconductor memory (TECHNITRACE, France). In addition, the actual CO_2 concentration from the EGM-5 data was calculated using a four-point standard calibration curve ranging from 0 to 20,000 ppm.

We modeled depth-resolved CO_2 production (μmol m^{-3} s^{-1}) from soil CO_2 concentrations (ppm) using Fick's first Law as a flux gradient approach (Davidson et al., 2006; Hicks Pries et al., 2017; Vargas et al., 2010):

$$F = -D\frac{dC}{dz} \tag{2}$$

Where F denotes the flux density of CO_2 across a horizontal surface on each depth of soil (μmol m^{-2} s^{-1}), D indicates the diffusion coefficient (mm^2 s^{-1}) of air into soil pores, and the change in CO_2 mol fraction at each depth is represented by dC/dz, which was calculated using the first derivative of a curve fit to the depth profile of CO_2 mol fraction. For each depth and time interval, the diffusion coefficient (D) was calculated as follows:

$$D = D_o{}^*\xi \tag{3}$$

$$D_o = D_{ao}\left(\frac{T}{293.15}\right)^{1.75}\left(\frac{101.3}{P}\right) \tag{4}$$

Where D_o is the diffusion coefficient of CO_2 in the air at the soil temperature (T) and local air pressure (P), D_{ao} is a reference value for CO_2 in the air (15.7 mm^2 s^{-1}), and ξ is the dimensionless tortuosity factor. Tortuosity was estimated using six different equations (Jassal et al., 2005; Millington, 1959; Moldrup et al., 2001; Moyes and Bowling, 2013), and we picked the equation that resulted in the best match between the measured surface flux and the estimated surface flux from soil profile data. The most effective equation was determined by an empirical relationship (Hicks Pries et al., 2017; Moyes and Bowling, 2013):

$$\xi = 0.95\varepsilon^{1.93} \tag{5}$$

Where ε is the calculated air-filled porosity (m^3 m^{-3}) from the total soil porosity (based on dry soil bulk density and solid particle density) and volumetric water content at each soil depth and measurement time. Finally, CO_2 production (μmol m^{-3} s^{-1}) was calculated from a given depth interval by subtracting the difference in flux densities (μmol m^{-2} s^{-1}) across that interval and dividing by the depth (m) increment. After that, the CO_2 production was converted to g C m^{-3} d^{-1} units.

2.10. Statistical analysis

To evaluate the impacts of the warming treatment on various measured responses, we ran mixed effects models in RStudio (R Core Team, 2022) using the *nlme* package (Pinheiro et al., 2017) and restricted maximum likelihood with blocks ($n = 3$) as a random effect. Using Q-Q plots and residual histograms, we visually examined all models for homoscedasticity and normality of distribution, and we used a log transformation to meet model assumptions when necessary. Afterward, we used slightly different statistical model structures owing to the varied data structures of SOC concentration, soil water content, CO_2 production and CO_2 efflux. Plots were utilized as random effects to examine the fixed effects of treatment, depth, and their interaction on SOC content within the soil profile. This analysis was conducted separately for cropland and grassland.

To test the fixed effects of treatment, depth, and their interaction on soil water content, we used plots crossed with the sampling date as random effects (to account for violations of independence), separately for cropland and grassland. For surface soil CO_2 efflux, we used a different model that included treatment, seasons, and their interaction as fixed effects, and plots crossed with sampling date as random effects, to test the treatment and seasonal effects on surface soil CO_2 efflux, separately for cropland and grassland. To test the fixed effects of treatment, depth, and their interaction on soil CO_2 production from within the soil profile, we used plots crossed with the sampling date as random effects, separately for cropland and grassland. Besides that, we used treatment, field, and their interaction as fixed effects, and plots crossed with sampling date as random effects, to test the treatment and management effects on leaf area index. Also, a pairwise mean comparison test was performed using the *emmeans* package in RStudio (Searle et al., 2023) when significant differences were observed for any response variables from mixed effect models.

We also calculated the warming response for each block at each sampling date, to test whether warming affected whole-soil profile CO_2 production and surface CO_2 efflux. The warming response was expressed as a percentage difference between warmed and control conditions, which was normalized by the control values of soil CO_2 production and surface CO_2 efflux. A similar warming response was also tested for SOC concentrations.

$$Warmingresponse(\%) = \frac{Warm - Control}{Control} \times 100 \tag{6}$$

3. Results

3.1. Warming effects on soil profile water content

In control plots, annual average soil water contents across the different soil depths ranged from 23.7 to 26.4% in cropland and 24.3 to 28.5% in grassland (Fig. 4). The soil water content significantly ($p \le 0.05$) decreased in most depths with *in-situ* warming for grassland, and a decreasing trend was noted for cropland, which was only statistically significant at 50 cm ($p \le 0.05$). In addition, we observed a significant interaction between warming treatment and depth ($p < 0.001$) for both cropland and grassland. Indeed, grassland showed a stronger warming response than cropland, as warming reduced the water content under grassland by 9.7 to 22.9% and by 0.35 to 13.2% under cropland compared to control plots. The greatest differences between the two management practices were found at 30 cm depth with warming, where soil water content was strongly decreased for grassland and slightly decreased for cropland (Fig. 4).

The depth-wise soil water content also depended on the season (significant, $p < 0.001$) for both land management practices (supplementary Fig. S1). During the winter season, topsoil (0–15 cm) showed higher water content, while during other seasons deeper soils had a higher water content for both cropland and grassland. Despite the seasonal variations, *in-situ* warming reduced soil water content throughout the year for both land management practices.

3.2. Warming effects on seasonal CO_2 efflux

The mean surface CO_2 efflux (g C m^{-2} d^{-1}) in the four seasons is presented in Fig. 5. In control plots, CO_2 efflux ranged from 0.52 to 1.35

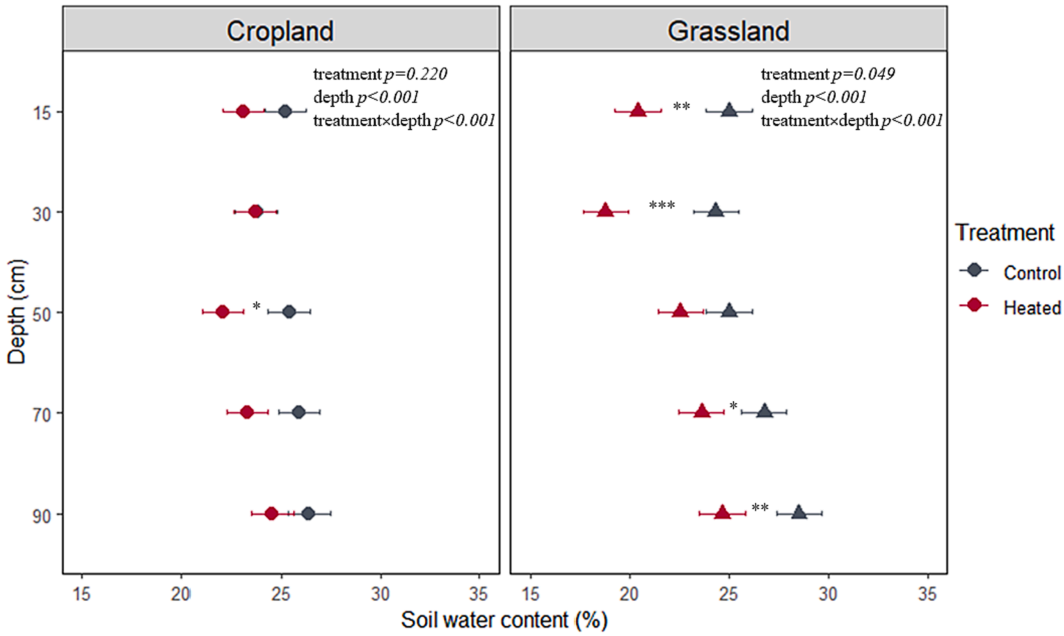

Fig. 4. Mean soil water content (%) in the control and heated plots (mean ± SE, $n = 3$) throughout the 1.0 m depth of soil profile over the study period (July 2021 to June 2022). In the figure, the *p*-values denote the statistically significant effects of treatment, depth, and their interaction (treatment × depth). The asterisk indicates any significant treatment effect within depth as determined by post hoc analysis (*$p \leq 0.05$; **$p \leq 0.01$; ***$p \leq 0.001$).

g C m^{-2} d^{-1} under cropland and 0.50 to 2.47 g C m^{-2} d^{-1} under grassland (Fig. 5). The response of CO_2 efflux to warming depended on the season (Fig. 5). Comparing the different seasons for the grassland, our results show that *in-situ* warming only increased (non-significantly) surface CO_2 efflux in winter, while warming significantly ($p \leq 0.05$) reduced CO_2 efflux in other seasons (Fig. 5). In contrast, *in-situ* warming had no effect on surface CO_2 efflux in cropland during the summer and winter, while in autumn and spring warming reduced CO_2 efflux (non-significantly) (Fig. 5). Overall, the whole-soil warming response of annual surface CO_2 efflux was reduced by 21.8% under cropland (from 399 g C m^{-2} y^{-1} in control plots to 312 g C m^{-2} y^{-1} in heated plots) and by 20.6% under grassland (from 528 g C m^{-2} y^{-1} in control plots to 419 g C m^{-2} y^{-1} in heated plots).

3.3. *Warming effects on soil profile CO_2 production*

The CO_2 production in the different soil depths, which was measured during six months, is presented in Fig. 6. In control plots, CO_2 production ranged from 0.54 to 4.68 g C m^{-3} d^{-1} under cropland and 0.84 to 5.21 g C m^{-3} d^{-1} under grassland (Fig. 6). In grassland, the CO_2 production significantly ($p \leq 0.05$) increased with *in-situ* warming in subsoil (below 30 cm), while statistically non-significant differences were observed between the two treatments in topsoil (0–30 cm) (Fig. 6). In contrast, in cropland, the CO_2 production significantly ($p \leq 0.05$)

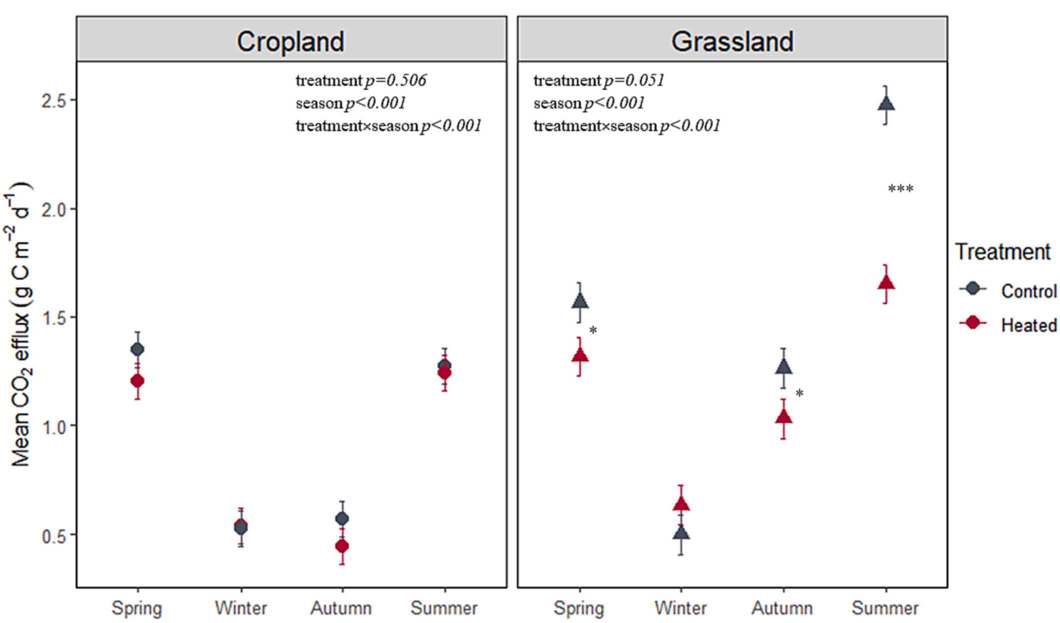

Fig. 5. Mean seasonal variations of soil CO_2 efflux (g C m^{-2} d^{-1}) in the control and heated plots (mean ± SE, $n = 3$) from the whole-soil profile over the study period (July 2021 to June 2022). In the figure, the *p*-values denote the statistically significant effects of treatment, season, and their interaction (treatment × season). The asterisk indicates any significant treatment effect within season as determined by post hoc analysis (*$p \leq 0.05$; ***$p \leq 0.001$).

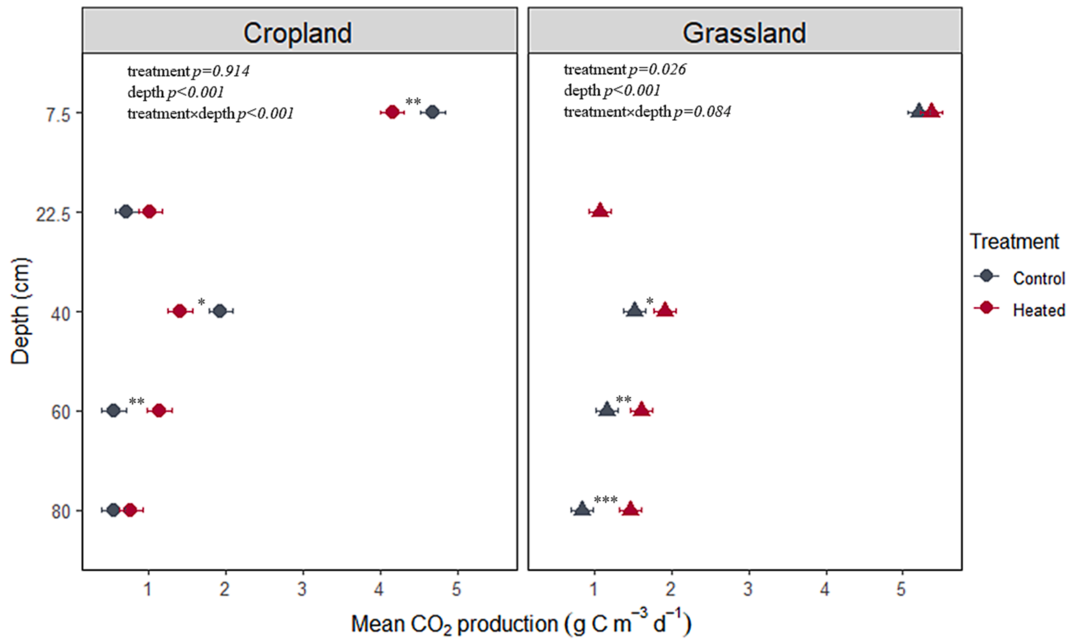

Fig. 6. Mean CO_2 production (g C m^{-3} d^{-1}) in the control and heated plots (mean ± SE, *n* = 3) with depth increment (0–15, 15–30, 30–50, 50–70, and 70–90 cm) over the study period (January 2022 to June 2022). In the figure, the *p*-values denote the statistically significant effects of treatment, depth, and their interaction (treatment × depth). The asterisk indicates any significant treatment effect within depth as determined by post hoc analysis (*$*p \le 0.05$; $**p \le 0.01$; $***p \le 0.001$).*

decreased with *in-situ* warming at the 0–15 cm and 30–50 cm depths, but an increasing trend was also noted below 50 cm (Fig. 6). The interaction between treatment and depth was significant ($p < 0.001$) for cropland but not for grassland ($p = 0.084$).

Overall, we found that warming-induced CO_2 production in subsoil was higher for both grassland and cropland as compared to their controls, with a larger increase in grassland (42%) than in cropland (10%). In contrast, the warming-induced CO_2 production rate in topsoil (0–30 cm) differed between grassland and cropland: warming increased CO_2 production by 2.4% in grassland but decreased CO_2 production by 4.2% in cropland. However, it should be noted that the depthwise CO_2 production measurements occurred during the winter and spring seasons, while we do not have data for the summer and autumn seasons. The warming response on cumulative CO_2 production from the whole-soil profile during six months was increased by 1.2% under cropland (from 84 g C m^{-3} $half.y^{-1}$ in control plots to 85 g C m^{-3} $half.y^{-1}$ in heated plots) and by 16.3% under grassland (from 98 g C m^{-3} $half.y^{-1}$ in control plots to 114 g C m^{-3} $half.y^{-1}$ in heated plots).

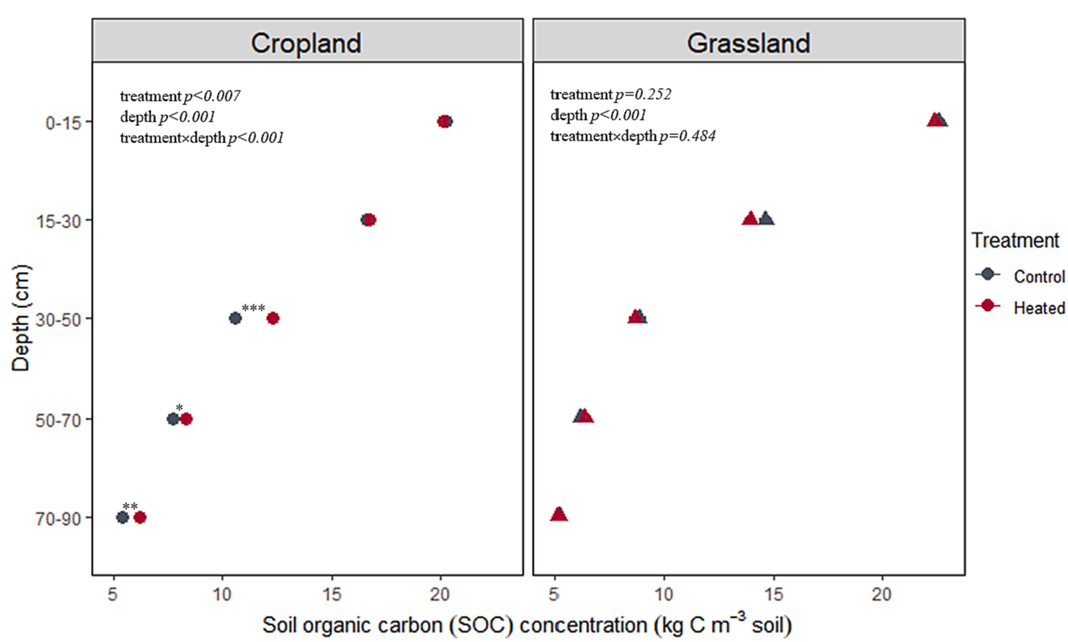

Fig. 7. Soil organic carbon (SOC) concentration (kg C m^{-3} soil) in the control and heated plots (mean ± SE, *n* = 3) with depth increment (0–15, 15–30, 30–50, 50–70, and 70–90 cm), sampled in May 2022, one year after the onset of *in-situ* warming. In the figure, the *p*-values denote the statistically significant effects of treatment, depth, and their interaction (treatment × depth). The asterisk indicates any significant treatment effect within depth as determined by post hoc analysis (*$*p \le 0.05$; $**p \le 0.01$; $***p \le 0.001$).*

3.4. Warming effects on soil profile carbon content

In the control plots, SOC concentrations varied across different soil depths, ranging from 20.24 to 5.42 kg C m^{-3} soil in cropland and from 22.59 to 5.20 kg C m^{-3} soil in grassland (Fig. 7). *In-situ* warming did not affect the topsoil SOC content under both land management practices. However, a divergent response to warming was observed in the subsoil (>30 cm): it significantly increased under cropland but not under grassland (Fig. 7). The interaction between treatment and depth was found to be significant ($p < 0.001$) for cropland but not for grassland ($p = 0.484$).

Overall, we observed that the warming-induced SOC content in subsoil was higher in cropland (12.7%) but lower in grassland (0.09%). In contrast, the warming-induced SOC content in topsoil decreased for both cropland (0.05%) and grassland (2.42%) compared to their respective controls. Over the course of one year, the warming response on SOC content across the entire soil profile increased by 4.9% in cropland (from 60.6 kg C m^{-3} in control plots to 63.6 kg C m^{-3} in heated plots) and decreased by 1.6% in grassland (from 57.4 kg C m^{-3} in control plots to 56.5 kg C m^{-3} in heated plots).

3.5. Warming effects on leaf area index

In control plots, the leaf area index was 3.2 under cropland and 3.4 under grassland (Table 4). It significantly increased with *in-situ* warming for grassland ($p < 0.01$) and also showed an increasing, but non-significant trend for cropland (Table 4).

4. Discussion

4.1. Negative warming effects on whole-soil profile water content under the two land management practices

Our findings revealed that *in-situ* warming had a negative effect on soil water content in the whole-soil profile for both land management practices (Fig. 4). These results are in agreement with a recent *meta*-analysis by Xu et al. (2013), which showed that warming generally leads to soil drying in agricultural ecosystems. The two main processes of water loss from the soil reservoir include evaporation from the soil surface and transpiration by plants (Chapin et al., 2002). Both may be affected by land management practices (Liancourt et al., 2012). In this study, we showed that grassland soil was more vulnerable to soil water loss under *in-situ* warming compared to cropland. Despite the lack of air warming, warming-induced reduction in soil water content could be attributed to increased plant growth and transpiration processes with a higher leaf area index (Table 4), as also found by other authors (Chen et al., 2021a; Wan et al., 2002; Xia et al., 2010). However, the plants' effects on soil water might be species- or management-and/or site-specific (Wang et al., 2012). In particular, in grassland with a complex root system exploring deeper soil layers it might be stronger than croplands. Indeed in grasslands, perennial plants could respire throughout the year involving (i) transpiration by plant leaves and (ii) water consumption by plant roots for their physiological and metabolic activities (Du et al., 2011). In contrast, cropland soil is characterized by periods of bare soil, plant regrowth and harvest, involving less root production (Table 2) (Hu & Chabbi, 2021) and consequently probably much less water consumption by plant roots and transpiration. As soil water becomes depleted under *in-situ* warming, this could alter the plants' C allocation strategies depending on land management practices, thereby affecting the C inputs and turnover in the soil profile (Li et al., 2019; Mokany et al., 2006; Védère et al., 2022).

Table 4
Warming response of leaf area index (mean ± SE, $n = 3$) under the two different land management practices during the plant growing season (March to June 2022) with different treatments (control: heated).

	Leaf area index (m^2 m^{-2})	
Field	Control	Heated
Cropland	3.2 ± 0.2^{b}	3.6 ± 0.2^{ab}
Grassland	3.4 ± 0.2^{b}	4.6 ± 0.2^{a}

Here, different letters indicate the statistically significant effects of treatment and field interaction, as determined by post hoc analysis ($p < 0.01$).

4.2. Contrasting warming response of seasonal CO_2 efflux under the two land management practices

Our data indicated that *in-situ* warming suppressed surface CO_2 efflux for both land management practices in the spring and autumn, whereas the other seasons (winter and summer) showed a contrasting warming response of surface CO_2 efflux (Fig. 5). *In-situ* warming could be a constraint for the spring and autumn seasons by slowing the processes that lead to both autotrophic and heterotrophic respirations that are controlled by precipitation and soil moisture determining plant growth (Miao et al., 2020; Quansah et al., 2015). In contrast, the different warming responses of soil CO_2 efflux in the winter and summer for both land management practices might be related to the continuous rhizodeposition supplied by the perennial root systems in grassland while cropland soil is bare during these periods (Hu & Chabbi, 2022; McGowan et al., 2019). In grassland, the warming response was negative in summer but positive in winter, which could be due to the warming-induced lower soil water content and seasonal fluctuation of plant growth and their root activity (Du et al., 2019; Hu et al., 2017). For example, the combination of high soil temperature and low soil water content might constrain root and microbial activity under summer warming, while in winter adequate moisture fuels greater microbial activity (supplementary Fig. S1) (Davidson et al., 1998; Vincent et al., 2006). In cropland, *in-situ* warming did not affect surface CO_2 efflux during summer or winter, which could be because the plants are only actively growing in the spring, providing evidence for plant activity as a control (Chen et al., 2021b).

The contrasting warming response of seasonal CO_2 efflux leads to an overall reduction in whole-soil warming annual surface CO_2 efflux, depending on land management practices. Our findings differ from those found in various terrestrial ecosystems where warming stimulated soil CO_2 efflux (Hicks Pries et al., 2017; Lin et al., 2011; Luo et al., 2010; Ofiti et al., 2021; Schindlbacher et al., 2009; Yan et al., 2022). Nevertheless, our data are consistent with studies reporting reduced soil and microbial respiration under warming in an old-field grasslands (Wan et al., 2007), in some seasons in tallgrass prairie (Verburg et al., 2005), and in an alpine meadow (Saleska et al., 1999). However, one recent *meta*-analysis demonstrated that on average, global soil will be a source of C to the atmosphere under a future warmer climate (Wang et al., 2022), supporting the expectation of positive SOC loss as a warming feedback (García-Palacios et al., 2021). In our study, warming-induced reductions in soil water content may be strongly influencing surface CO_2 efflux, through its influence on microbial communities and their functionalities, which are temperature- and moisture-dependent (Curiel Yuste et al., 2007; Davidson and Janssens, 2006). Water availability is a critical factor that can affect plant and microbial respiration. When water is limited, plants slow down photosynthesis to conserve water (Wang et al., 2018), leading to a decrease in plant contributions to soil respiration (Ribas-Carbo et al., 2005). Similarly, water limitation can reduce microbial activity and their contribution to respiration as insufficient water can impede substrate diffusion to microbial cells (Lehmann et al., 2020; Moyano et al., 2013; Védère et al., 2022). Moreover, *in-situ* warming may reduce the contribution of seasonal fine root respiration as a source of surface CO_2 efflux. In warmer climates, grassland ecosystems may increase their total root system length but lose a proportion of fine roots growing in the superficial layer of soil (Pilon et al., 2013).

4.3. Warming alters soil CO_2 production along soil depths under the two land management practices

Our results showed greater positive effects of warming on subsoil CO_2 production than in topsoil for both agricultural practices (Fig. 6). This is consistent with previous whole-soil warming observations in a temperate forest (Hicks Pries et al., 2017), but not in a tropical forest (McGrath et al., 2022). The stronger warming effect on CO_2 production in subsoil than in topsoil could be due to a contrasting response of microbial metabolisms and/or root respiration in both parts of the soil profile. In subsoil, microbial activity is generally much lower than in topsoil (Rumpel and Kögel-Knabner, 2011), which was explained by the absence of fresh organic matter input (Fontaine et al., 2007). Under warming, energy input into subsoil through root growth and dissolved organic matter could be increased and stimulate copiotrophic populations at greater depths, leading to CO_2 production through decomposition of fresh root litter (Müller et al., 2016; Sanaullah et al., 2016; Soong et al., 2021). Root growth deeper in the soil profile could be stimulated by lower soil water content in warmed soil, which forces plants to explore deeper soil horizons (Joslin et al., 2000; Sotta et al., 2007).

Warming effects on CO_2 production were contrasting in the two management systems. Subsoil CO_2 production was more pronounced under warming of grassland soil compared to cropland. This might be explained by greater root production and activity under grassland than cropland, as indicated by the greater standing root biomass in this agroecosystem (Table 2). Conversly, we observed that warming-induced subsoil SOC content was significantly higher in cropland but slightly lower in grassland. These findings suggest that the turnover or accumulation of subsoil SOC, as well as the subsequent mechanisms for CO_2 production under warming conditions, may vary based on different management practices. For instance, if warming leads to an increase in above-ground biomass, soil disturbance caused by tillage might be advantageous. This disturbance helps in transferring crop residues, dead roots, and topsoil C into subsoil layers where C accumulates, as shown in studies by Yang et al. (2022). Consequently, this process results in higher subsoil SOC content in cropland. Additionally, the organic materials added through this process could serve as a food source for microorganisms, potentially leading to increased CO_2 production in the short term.

In contrast, warming might cause a greater allocation of belowground C in grassland compared to cropland. This allocation is primarily derived from rhizodeposition provided by the perennial root system, as indicated in Table 2 (Hu & Chabbi, 2022; McGowan et al., 2019). Consequently, continuous interactions between living root systems and subsoil microbes could have contributed to higher CO_2 production in grassland. This is supported by the negligible SOC loss observed under warming conditions.

In topsoil, warming-induced CO_2 production was differently affected by management. Under grassland, increased CO_2 production in topsoil could be attributed to a greater contribution of plant roots and rhizosphere microbes or saprotrophic microorganisms under warming conditions, which are the primary contributors to SOC decomposition (Schindlbacher et al., 2009; Zhou et al., 2007), as evidenced by lower SOC content under warming conditions. While decreasing CO_2 production in response to warming in cropland may be attributed to a double effect of both warming and tillage-induced soil disturbance (ploughing horizon at 30 cm depth), which can lead to shifts in soil microbial community and function due to lower plant root biomass (Table 2), resulting in lower CO_2 production and less sensitivity to warming-induced SOC decomposition, as evidenced by negligible SOC loss.

4.4. Future prospects

Although an increase in CO_2 production in subsoil is well documented in this study (Fig. 6) and supported by another whole-soil warming study in a temperate forest (Hicks Pries et al., 2017), the biotic fixation and movement of CO_2 in the context of projected global warming under different agricultural management practices are still unknown. Despite a few recent studies confirming that soil microbes can fix CO_2 in temperate soils (Nel and Cramer, 2019; Spohn et al., 2020). Moreover, warming might change the microbial community composition and in particular increase fungal contribution, leading to the formation of more stable pore structures (Miller and Jastrow, 2000). These effects may depending on soil management, as there is lower fungal contribution in cropland than in grassland due to ploughing events (Schnoor et al., 2011). In order to get a complete picture of soil responses, heterotropic respiration should in future studies be distinguished from autotropic respiration.

Additionally, CO_2 flux within the soil profile may also be influenced by its microstructural properties. Indeed, a recent study found that grassland soil has a larger macropore diameter due to the presence of large biopores that are periodically destroyed in cropland (Schlüter et al., 2022). The processes affecting soil structure may have an impact on soil gas diffusivity, which determines whether CO_2 produced at depth is lost to the atmosphere or fixed in situ (Liao et al., 2023). Thus, we propose that for understanding and modeling the effects of soil warming on CO_2 efflux under different agricultural management practices, the parameters influencing CO_2 diffusivity, such as soil architecture need to be taken into account in addition to factors affecting CO_2 production such as root activity and microbial community composition.

5. Conclusion

In this study we investigated seasonality of whole soil warming responses of CO_2 efflux. Moreover, we compared CO_2 production across soil depths down to 1 m. We conclude that *in-situ* soil warming led to soil drying, the extent of which depended on soil management. Soil drying was more pronounced in grassland compared to cropland, supporting our initial hypothesis (H1). We also found contrasting seasonal dynamics of surface CO_2 efflux. While our findings indicate that *in-situ* warming suppressed surface CO_2 efflux for both land management practices in the spring and autumn, winter and summer showed greater increases and decreases in response to warming, respectively, under grassland compared to cropland. These findings reject our second hypothesis (H2), which states that CO_2 efflux would increase year round in response to warming under continuous grassland but only seasonally in cropland soils.

Subsoil (>30 cm) CO_2 production was more vulnerable to warming than in the topsoil, and this increase due to warming was more pronounced in grassland compared to cropland, confirming our last hypothesis (H3). In topsoil (0–30 cm), warming decreased CO_2 production in cropland but not in the grassland. Overall, land management had a significant impact on CO_2 production throughout the soil profile, which may driven by both autotrophic and heterotrophic sources. Thus, we suggest that management influences the warming responses of CO_2 production and efflux by its effects on soil physical organization in addition to plant and microbial activity with root carbon input.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2023.116725.

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