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RESEARCH ARTICLE



Ancient and modern wheat varieties: A trade-off between soil CO₂ emissions and grain yield?

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Abstract

Introduction: Humanity is facing two great challenges: producing enough food for a growing population and mitigating greenhouse gas emissions. In this study, we investigated the choice of specific wheat varieties to improve carbon storage in soil while producing enough grain to assure food security. We hypothesize that ancient wheat varieties could store more carbon than modern ones, due to a likely bigger and deeper root system or to more recalcitrant root organic matter.

Materials and Methods: We conducted a field experiment with four modern and four ancient wheat varieties, on four different sites with contrasted soil properties. Root morphology was assessed by image analysis and potential CO₂ emissions by incubation for 60 days. Since in situ carbon storage differences between ancient and modern varieties were expected to be weak and not cumulated due to rotation, we estimated expected CO₂ emissions from root biomass and potential CO₂ emissions. The grain yield was also measured.

Results: The breeding type (ancient vs. modern varieties) affected root length in two of our four sites, with longer roots for ancient varieties, but it did not affect other root traits such as biomass. The breeding type also affected CO₂ emissions, with higher measured CO₂ emissions for modern than ancient varieties in Arenic Cambisol conditions (Morvan), and higher estimated (considering root biomass variations) CO₂ emissions for modern varieties in Rendzic Leptosol conditions (Saint Romain). Root traits and estimated CO₂ emissions were also dependent on the soil properties of the different sites. We did not find any significant differences in grain yield between ancient and modern varieties.

Conclusion: A possible trade-off between carbon storage and grain production was expected, but our results suggest that some types of soil can support both high grain yield and C storage, especially those with an important depth, a neutral pH and a fine texture.

KEYWORDS

ancient and modern wheat varieties, carbon storage, mineralization rate, root morphology, soil organic carbon

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1 | INTRODUCTION

Greenhouse gases (GHGs) emissions by humans, particularly carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O), play a direct role in climate change, with a major contribution of CO₂ (65% of global emissions) (Rodas-Zuluaga et al., 2021; Rogelj et al., 2018). This increase in atmospheric CO₂ concentration leads to an increased global mean temperature, accelerating climate change (Olivier & Peters, 2020; Stern, 2007). On the other hand, the world's demand for food is expected to increase by 25%–70% by 2050 (Hunter et al., 2017), which implies improving food production, defined as the biomass produced by time unit (the year for annual crops) (Ricklefs & Miller, 2000). At the same time the natural resources that sustain agriculture, such as soil, water and biodiversity, are impacted by climate change, making them increasingly scarce, degraded and vulnerable (World Bank, 2007). Humanity thus faces two great challenges: feeding 9–10 billion people by 2050 without exacerbating climate change (Godfray et al., 2010). Few studies to date have considered the interactions between these agronomical and pedological challenges (Smith et al., 2013).

Some agricultural practices, by adding high amounts of biomass to the soil, causing minimal soil disturbance, conserving soil and water, improving soil structure, enhancing activity and species diversity of soil fauna and strengthening mechanisms of elemental cycling, are known to stabilize or improve carbon (C) storage (Lal, 2004). But in some situations, mitigation solutions such as agroforestry or the reduction of synthetic chemical inputs may result in collateral negative consequences, like a decrease in grain yield due to the competition between trees and crops or reduced nutrient availability, respectively (Smith et al., 2013). Storing carbon in soils while maintaining a high crop production could indeed appear as a paradoxical goal. Carbon storage relies on the stabilization of organic matter (OM) in soils, through several processes, such as aggregation (Six et al., 2000). This supposes that an important amount of OM is not mineralized. Whereas in conditions with low chemical inputs, maintaining high grain yields requires reaching a sufficient rate of OM mineralization to ensure a good nutrient availability. In parallel, soil fertility also relies on a relatively stable OM to ensure a high cation exchange capacity and water storage (Lal, 2004). Based on these different mechanisms, for low input systems, a trade-off could exist between C storage and grain yield.

A solution could be found in changing the ratio between different C fractions with different turnover rates, to favour stabilization while keeping a good rate of mineralization (Rumpel et al., 2015). In this regard, several agricultural practices, such as no-tillage or straw feedback to the soil, have been found to participate in C storage in soils without decreasing grain yield (Shang et al., 2021; Sun et al., 2020).

An agricultural practice to store carbon in soils that have been poorly documented up to now is the choice of the cultivated variety. The diversity of varieties offers a large panel of traits with different performances regarding carbon storage and productivity, especially the root biomass and the shoot:root ratio. For example, wheat

produces 15–20 tons of biomass per ha (50% grains, 30% roots and 20% straw) (Arvalis, 2019). After harvest, straws can be exported for different uses, or incorporated into the soil, when roots are already in place. On a diversity of soils, measured values ranged from 7.5 to 10 tons of straw and roots corresponding to 1.1–1.5 tons of stable OM in the soil (Arvalis, 2019). This represents a stock of 450–600 kg of carbon, or 1650–2200 kg CO₂ eq per hectare (Arvalis, 2019). Since roots have a lower mineralization rate (Freschet et al., 2013), we will focus on root system mineralization in this study. Half of the carbon stored in soil is located below 0.3 m (Balesdent et al., 2018). Therefore, deep root systems could represent an opportunity to increase carbon storage. Among the cultivar diversity of wheat, farmers can choose between ancient or modern varieties, hereafter considered two 'breeding types'. Several studies showed that ancient varieties exhibit deeper root systems (Shaposhnikov et al., 2016; Subira et al., 2016) and show higher root biomass than modern ones (Pour-Aboughadareh et al., 2017; Waines & Ehdaie, 2007) in controlled conditions. Differences in the composition of plant tissues (Gotti et al., 2018; Iannucci et al., 2017) and root architecture (Beyer et al., 2019; Junaidi et al., 2018) between ancient and modern breeding types could also be responsible for reduced mineralization rates in ancient varieties, because of possible differences in recalcitrance to degradation or reduced surface for microbial access. Since the exudation profiles between ancient and modern varieties of the same species are supposed to differ (Beyer et al., 2019; Junaidi et al., 2018), microbial communities living in the vicinity of plant roots could also differ in structure and function, with potential consequences for carbon storage.

Because the impact of agricultural practices on C storage and grain yield is dependent on the environmental context (Shang et al., 2021), assessing the potential of choosing modern or ancient varieties of wheat requires assessing it in different environmental contexts. Among soil properties, some are likely to affect root carbon mineralization, including soil texture, via its effect on water storage and physical protection due to adsorption on the solid-phase matrix (Baldock, 2007; Feng et al., 2013; Zhou et al., 2019), soil structure, via soil organic matter (SOM) protection due to aggregation and its relation to water fluxes, connectivity, or compaction (Balabane & Plante, 2004; Gupta & Germida, 1988; Six et al., 2004), soil pH, via the acid–base equilibrium and microbial activities (Kemmitt et al., 2006; Yang et al., 2019) and soil depth, via the volume available for storage (Jobbagy & Jackson, 2000; Richter & Markewitz, 1995; Swift, 2001). In this study, we thus investigated grain yield and root OM mineralization in different pedological contexts, but similar climatic conditions, to assess the potential of selecting specific varieties as a way to manage both grain production and OM stabilization.

In this study, both modern and ancient wheat varieties were grown in four different soils to test the possible trade-off between carbon storage and grain yield in the field. We measured, at different depths, root biomass, morphological root traits and root tissues elementary composition. We incubated roots and soils retrieved in the same plot at the same depth to assess CO₂ emission. This variable

was taken as a proxy for carbon storage, whose changes in 1 year are too weak to be detected in the field, and given than other heavier methods would have been difficult to apply on our multi-site experimental design. We also measured grain yield. Our hypotheses were that (1) ancient varieties can store more C in soil; (2) modern varieties present a better grain yield; (3) ancient varieties can be a good compromise between C storage and grain production.

2 | MATERIALS AND METHODS

2.1 | Study sites

This study was carried out in four agricultural sites located in the Bourgogne-Franche Comté administrative district (France), from October 2020 to July 2021. The four sites were selected in the same region to ensure minimal variability of climatic conditions (i.e. a temperate oceanic climate, [Cfb, Köppen-Geiger classification]) (Supporting Information: Table S1) and to cover different soil types (Supporting Information: Table S2).

2.2 | Wheat varieties

A group of eight winter common wheat (*Triticum aestivum*) varieties from two kinds of genotypes (ancient and modern varieties, hereafter called 'breeding types') was studied, among which four modern varieties, released after 1960 (<http://www.fiches.arvalis-infos.fr/>) and four ancient varieties, released before the Green Revolution (before 1960). Ancient varieties were provided by 'Graines de Noé', a nongovernmental organization (<http://www.graines-de-noe.org/>), which promotes the conservation of wheat landraces. Among their 200 varieties, we selected some with a local origin, mainly from the Bourgogne Franche-Comté administrative district (Table 1). They were and are still generally grown without agronomic inputs. Modern varieties were selected after the 60's in high-input systems. We chose some released after 2005 to ensure easy provisioning (Table 1).

2.3 | Experimental design

On each site, we set up plots with four modern and four ancient varieties, replicated three times ($n = 8 \text{ varieties} \times 3 \text{ replicates} = 24$ plots for each site). One square metre plots were separated from each other by 0.8 m. Grains were sown manually at a density of 300 seeds per square metre along seven rows (0.15 m apart) at 4 cm depth, between the 2 and 5 of November 2020. There was no agronomic input (such as fertilizer, herbicide or fungicide) application, to estimate the potential of varieties in the extreme scenario of agroecology, here defined as a reduction of inputs application.

2.4 | Root system and grain yield analyses

Root samples were collected between the 25 of May and the 3 of June, 2021 by using one soil core of 0.08 m diameter and 0.15 m length per plot, in the central row of each plot. Total sampled depth varies among sites, while cores of a 0.15 m depth were collected from soil surface until bedrock layer (Supporting Information: Table S1). Since the volume of the last core was not always the same, data were normalized per gram of soil. After sampling session, elutriation (Smucker et al., 1982), a method based on differential sedimentation (Fenwick, 1940) and adapted by Blouin et al. (2007), was used to separate the roots from soil mineral particles and dead OM: Afterward, root pieces were recovered and stored in water at 4°C for a week for further image analysis and incubations. To measure morphology parameters, roots were spread on a tray and scanned using an Epson GT2000 J151A (Epson America, Inc.). Images were analyzed with WinRhizo™ (Regent Instruments, Inc.). Different morphological traits were measured: length (cm g^{-1} soil), surface area (cm^2) and root average diameter (mm). Root biomass (mg g^{-1} of soil) was measured after image analysis and before taking some material for incubation, after drying at 50°C for 2 days.

At grain maturity when grain was below 15% humidity, between the 12 and the 16 of June 2021, plant stems were cut at the soil level. After a final air-drying for 10 days at room temperature, the grain was retrieved with a threshing machine and weighed (g m^{-2}). This weight

Breeding type	Variety	Year of release	Provider
Ancient	Automne Rouge	XIX th century	Graines de Noé
	Barbu du Mâconnais	XIX th –beginning XX th century	Graines de Noé
	Blé de Saône	Before 1960	Graines de Noé
	Blé du Jura	Before 1960	Graines de Noé
Modern	Alixan	2005	Limagrain
	Nemo	2015	Secobra
	Rubisko	2012	RAGT Semences
	Tulip	2011	Saaten Union

TABLE 1 Ancient and modern varieties selected for the experiment.

per plot was then converted to the weight of grain per hectare for analyses (t ha^{-1}).

2.5 | CO₂ emissions

Since we wanted to estimate potentially very small differences in CO₂ emissions from ancient and modern varieties that would have been likely impossible to detect in the field, we performed laboratory incubations. Given the frequent export of stubbles, we focused our analysis on CO₂ emissions from root system mineralization. To conserve, at least partially, the effect of root exudates on soil microbial communities and its potential consequences on CO₂ emissions, we incubated roots with their surrounding soil, which has been submitted to the influence of exudates during plant growth. The soil used for incubations was sieved at 2 mm and air-dried to adjust soil moisture for incubations (McGowen et al., 2018; Scheu & Parkinson, 1994). Two hundred and sixty-four microcosms (eight varieties, three replicates per breeding type, four sites and two to four depths per site) were set up in 37-mL flasks by placing 3 g of dry-weight soil together with 15 mg of dry-weight crushed roots, to avoid introducing variation due to root morphology. Soils were watered at 40% of the water holding capacity by adding sterile water. The soil microcosms were then incubated at 20°C in the dark for 60 days; these standard conditions, without seasonal or daily variations in temperature, humidity, and so on, were set up to improve our capacity to detect an effect of the breeding type. The gaseous phases of the microcosms were sampled at 3, 7, 14, 21, 44 and 60 days of incubation with a 1 mL air gas syringe and put in 10 mL airtight flasks for measurement of the CO₂ concentration. Microcosms were aerated after each sampling during the incubation period. CO₂ concentration was determined with the gas chromatograph, Agilent 7890B GC, equipped with a thermal conductivity detector coupled to an automatic sampler HS7697A (Agilent Technologies). We obtained the total CO₂ emitted after 60 days of incubation, that is, measured emissions.

To estimate the quantity that would have been emitted by the plot, hereafter called estimated emissions, measured emissions (based on 15 mg of roots) were weighed by the measured root biomass, summed on the different depths and extrapolated to the square metre plot.

2.6 | Soil and plant analysis

Samples were sent to analysis laboratories for soils (Laboratoire d'Analyses des Sols) and plants (Unité de Services et de Recherche en Analyses Végétales et Environnementales). The analyses performed for the soils were SOC (NF ISO 10694), total nitrogen (TN) (NF ISO 13878), C/N, Organic Matter, texture (NF X 31-107), pH (NF ISO 10390) and Cation Exchange Capacity (CEC) (NF ISO 23470) (Supporting Information: Table S2). The analyses carried out for the roots were total carbon (TC) and TN (Méthode Dumas).

2.7 | Statistical analysis

Analyses of root traits, incubations and grain yield data were performed with the Rstudio software (RStudio Team, 2020). Normality and homoscedasticity of the data were assessed using Shapiro and Bartlett test, respectively, using R default functions. Non-normally distributed data (Root Biomass, Average Diameter, Projected Area for all sites and Root Length for Dijon) were log-transformed.

Data were analyzed site by site in one-way analysis of variance (ANOVA), with the breeding type as a factor for estimated CO₂ emissions per square metre and grain yield (no relevance of depth), or in two-way ANOVA, with the breeding type and depth as factors, for root traits and measured CO₂ emissions. Data were also analyzed for all sites taken together in two-way ANOVA with the breeding type and site as factors, for estimated CO₂ emissions and grain yield. We also performed three-way ANOVA, with the breeding type, the depth and the site as factors. The data of root traits for all sites taken together were analyzed with the Scheirer-Ray-Hare test. These analyses were followed by a post-hoc Tukey's Honest Significant Difference test ($p < 0.05$, package 'agricolae', (De Mendiburu, 2017)).

To get an overview of the links between measured CO₂ emissions, plant traits and soil parameters (SOC, TN, C/N, Clay, Silt, Sand, pH and CEC), we performed a multivariate analysis (principal component analysis [PCA]) across sites. We also performed a second PCA for each site independently to get an overview of the covariation between some root tissues' elementary composition (percentage of C and N) with the other variables (root biomass, estimated CO₂ emissions and grain yield).

3 | RESULTS

3.1 | Root biomass and morphology

When sites were analyzed independently, the breeding type (ancient vs. modern varieties) had no significant effect on root biomass and root average diameter (Supporting Information: Table S3). Root length significantly varied breeding type for two sites: Morvan ($p = 0.014$) (Supporting Information: Table S3) and Breteniere ($p = 0.0046$) (Supporting Information: Table S3). The projected area was affected by the breeding type at Dijon ($p = 0.049$) (Supporting Information: Table S3). When all sites were considered together, the breeding type had no effect on any of the root morphological parameters (Supporting Information: Table S3). These parameters (root biomass, root average diameter, root length and root projected area) were impacted by the site (Supporting Information: Table S3). Whatever the study site, the observed trend is a decrease in root biomass with depth (Figure 1). The sites of Breteniere and Morvan presented a higher biomass within the first 0.15 m of soil (0.72 and 0.71 mg g^{-1} of soil, respectively) than those of Saint Romain and Dijon (0.53 and 0.39 mg g^{-1} of soil, respectively) (Figure 1). We also tested the specific root length (length of root per gram of dry root), on which the breeding type had no impact ($p = 0.27$, data not shown).

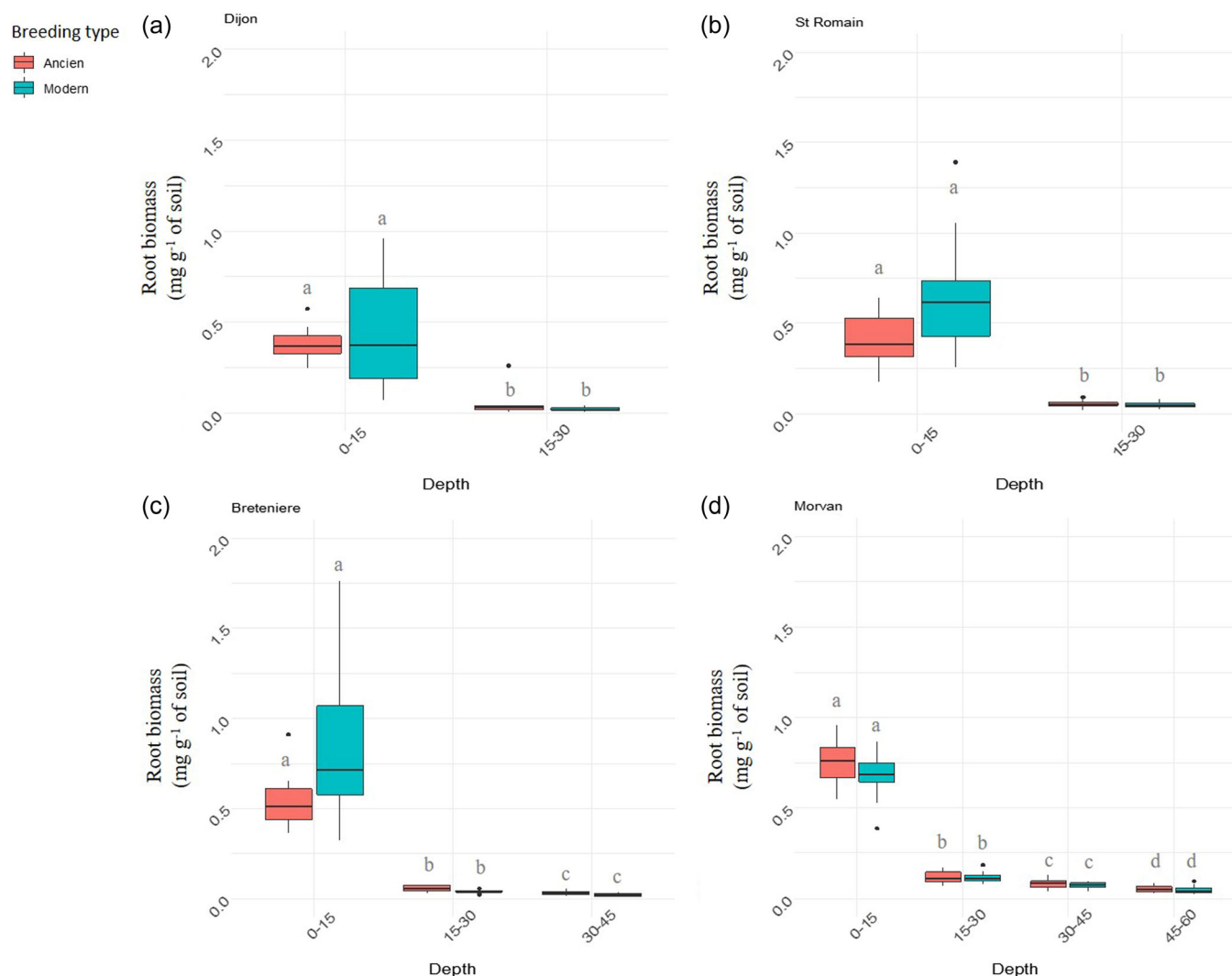


FIGURE 1 Root biomass (mg g^{-1} of soil) from modern (blue) and ancient (pink) varieties. Significant differences are represented by different letters, with $\alpha = 0.05$. Mean \pm se, $n = 12$ for each treatment.

3.2 | CO₂ emissions

The breeding type had no effect on measured CO₂ emission after 60 days for three of our sites (Breteniere, Saint Romain and Dijon), but it significantly impacted the emissions in Morvan ($p = 0.0003$) (Supporting Information: Table S4). When all sites were studied together, the breeding type had no effect, but measured CO₂ emissions were impacted by the site and the depth (Supporting Information: Table S4). The sites of Saint Romain and Morvan showed higher total CO₂ emissions after 60 days (for all breeding types taken together) (1075 and 962 $\mu\text{gC-CO}_2 \text{ g}^{-1}$ of soil at 0–0.15 m, respectively) than those of Dijon and Breteniere (598 and 555 $\mu\text{gC-CO}_2 \text{ g}^{-1}$ of soil at 0–0.15 m, respectively) (Supporting Information: Figure S1).

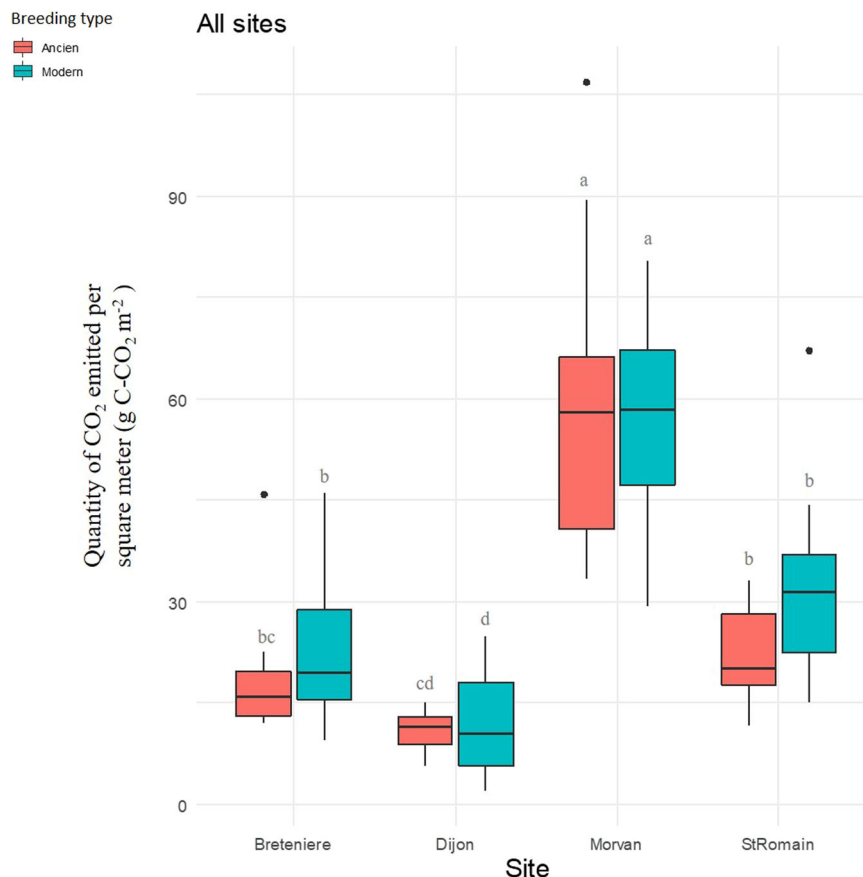
When analyzing the estimated emission of CO₂ emitted per square metre site by site (by integrating the actual root biomass, see Section 2), the breeding type had an effect only at Saint Romain (explaining 18% of the total variance, $p = 0.036$) (Supporting

Information: Table S5). When all sites were analyzed together, the site factor had a significant effect (explaining 66% of the total variance, $p < 2 \times 10^{-16}$), but not the breeding type (Supporting Information: Table S5). The Morvan was the site with the highest quantity of CO₂ emitted per square metre (for all breeding types taken together) (58.61 $\text{gC-CO}_2 \text{ m}^{-2}$), followed by Saint Romain and Breteniere (27.01 and 21.15 $\text{gC-CO}_2 \text{ m}^{-2}$, respectively) and by Dijon with the lowest CO₂ emissions (11.52 $\text{gC-CO}_2 \text{ m}^{-2}$) (Figure 2).

3.3 | Relationships between root parameters, measured CO₂ emissions and soil properties

The PCA performed on the whole data set showed that the two first axes explained 67% of the total variance (Supporting Information: Figure S2). Axis 1 (38% of the total variance) was apparently associated with soil texture and root morphology (root biomass, root average diameter and root length) and measured CO₂ emissions to a

FIGURE 2 Estimated CO₂ emissions per square metre, calculated by weighing measured CO₂ emissions by the actual quantity of root biomass of all depths, from modern (blue) and ancient (pink) varieties. Significant differences are represented by different letters, with $\alpha = 0.05$. Mean \pm se. $n = 12$ for each treatment.



lesser extent. A higher proportion of sand or a lower proportion of clay, silt or a lower pH, were thus associated with better root development and higher measured CO₂ emissions. Axis 2, which captured 28% of the variance, was more difficult to interpret, but likely related to a gradient of soil fertility (OM, N and C contents) and root development. Three of the four ellipses representing the different sites (Dijon, Breteniere and Saint Romain) were very close or superposed, which means that no major differences were observed between those sites. The fourth ellipse (Morvan) was clearly separated from the others, this site is characterized by soil properties that differ from the three others, especially in terms of texture (sandy loam, United States Department of Agriculture texture class) and pH (acidic soil). We also observe an elongation of the ellipses which may be due to the soil depth effect for each site.

3.4 | Grain yield

No differences in grain yield were observed between ancient and modern varieties, either when considering the sites independently or simultaneously (Supporting Information: Table S6). However, modern varieties tended to have a higher grain yield at each site (Figure 3), with an 18% increase for modern varieties (3.49 t ha⁻¹) as compared with ancient ones (2.96 t ha⁻¹). Breteniere was the site with the higher grain yield (7.04 t ha⁻¹), followed by Saint Romain (3.00 t ha⁻¹), Dijon (1.98 t ha⁻¹) and Morvan (1.32 t ha⁻¹) (Figure 3). Shoot

biomasses (straw and leaves) were collected for one single site (Breteniere), and did not vary the breeding type. Dry shoot biomass was 21% higher for ancient varieties than for modern ones, but this difference was not significant ($p = 0.43$, data not shown).

3.5 | Relationship between CO₂ emissions and productivity

The PCA showed that Axes 1 and 2 explained respectively 41.6% and 29.3% of the total variance for Dijon (Figure 4a), 42.7% and 32.9% for Saint Romain (Figure 4b), 44.7% and 20.2% for Breteniere (Figure 4c) and 37.4% and 30.8% for the Morvan (Figure 4d). For the sites of Dijon, Saint Romain and Morvan, roots with the highest C concentration were associated with high measured CO₂ emissions (Figure 4a,b,d), but it was not the case for Breteniere (Figure 4c). For Saint Romain, high root C concentration and high measured CO₂ emissions were also correlated with a higher grain yield. The arrows of root N concentration and grain yield were orthogonal and even slightly opposed for all sites (Figure 4). For the sites of Dijon, Saint Romain and Breteniere, arrows that represent root N concentration and root biomass are opposed, these variables seem negatively correlated (Figure 4a,b,c). For three sites out of four (Dijon, Saint Romain and Morvan), grain yield and measured CO₂ emissions seem positively correlated on the plan formed by Axes 1 and 2.

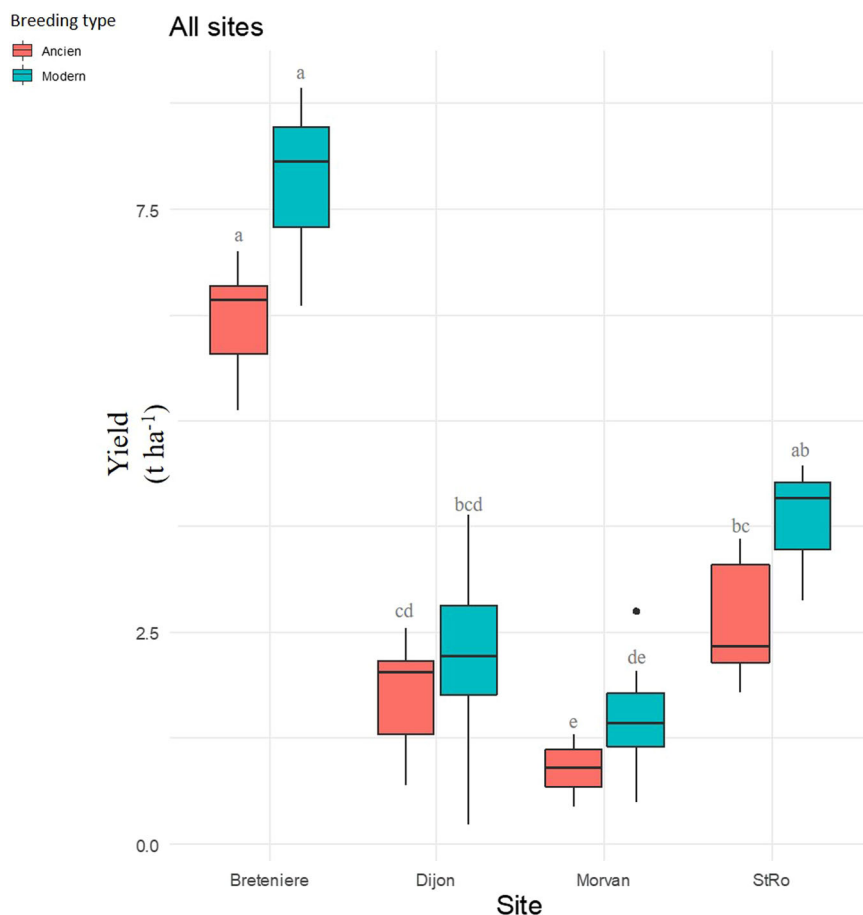


FIGURE 3 Grain yield (t ha⁻¹) of modern (blue) and ancient (pink) varieties. Significant differences are represented by different letters, with $\alpha = 0.05$. Mean \pm se. $n = 12$ for each treatment, except for St Romain with $n = 3$ for modern varieties and $n = 7$ for modern ones.

We then analyzed the correlation between grain yield and estimated CO₂ emissions. Results from the correlation test (Pearson method) showed that grain yield and expected CO₂ emissions are not correlated (Supporting Information: Table S7). When focusing on the data of estimated CO₂ emissions and grain yield, we can observe three 'groups' (Figure 5). Morvan showed high estimated CO₂ emissions with low yields, Dijon and Saint Romain formed a second group with low grain yields but also low estimated CO₂ emissions, and Breteniere presented low estimated CO₂ emissions with high grain yields (Figure 5).

4 | DISCUSSION

CO₂ emission in laboratory incubations was taken as an estimate of C storage in soil. We assumed this methodological choice since the expected annual variations in soil C amount due to different wheat varieties is very weak and because the need for crop rotation prevents repeating the experiment for several years at the same place. In addition, CO₂ emissions were estimated in controlled conditions with constant temperature, humidity and soil water content, whereas it is well known that these parameters, which vary in the field, influence CO₂ emissions. In addition, we used destructured soil to fix the amount of root biomass added for incubation despite a documented effect showing that the sieving of

soil leads to an increase of CO₂ emissions (Salomé et al., 2010). Our study is however a first attempt to determine if there is a trade-off between grain yield and carbon mineralization, in situations contrasted by the type of wheat variety and soils.

4.1 | CO₂ emissions and storage potential

Carbon storage results from the balance between the inputs of OM and the outputs of C (as CO₂ emissions) in and from the soil (Wiesmeier et al., 2019). Increasing the input of organic carbon in soil could be achieved by bigger root systems (Olson & Al-Kaisi, 2015). But in our study, the breeding type had no significant effect on root biomass. Since we studied four ancient and four modern varieties across four sites, including sites with deep soils, we can conclude that these varieties are not differing by the size of their root system. By comparing the set of varieties selected in this experiment, we can assume that the dwarfism gene introduced in modern varieties of wheat does not seem to induce changes in root system size of modern varieties, as it did on the shoot size. Another explanation could be that the ancient varieties that we have selected have particularly small root systems. This differs from what has been observed in other studies conducted in laboratory experiments (Subira et al., 2016), we can thus imagine that the use of unstructured soil in laboratory experiments, generally by sieving, can be

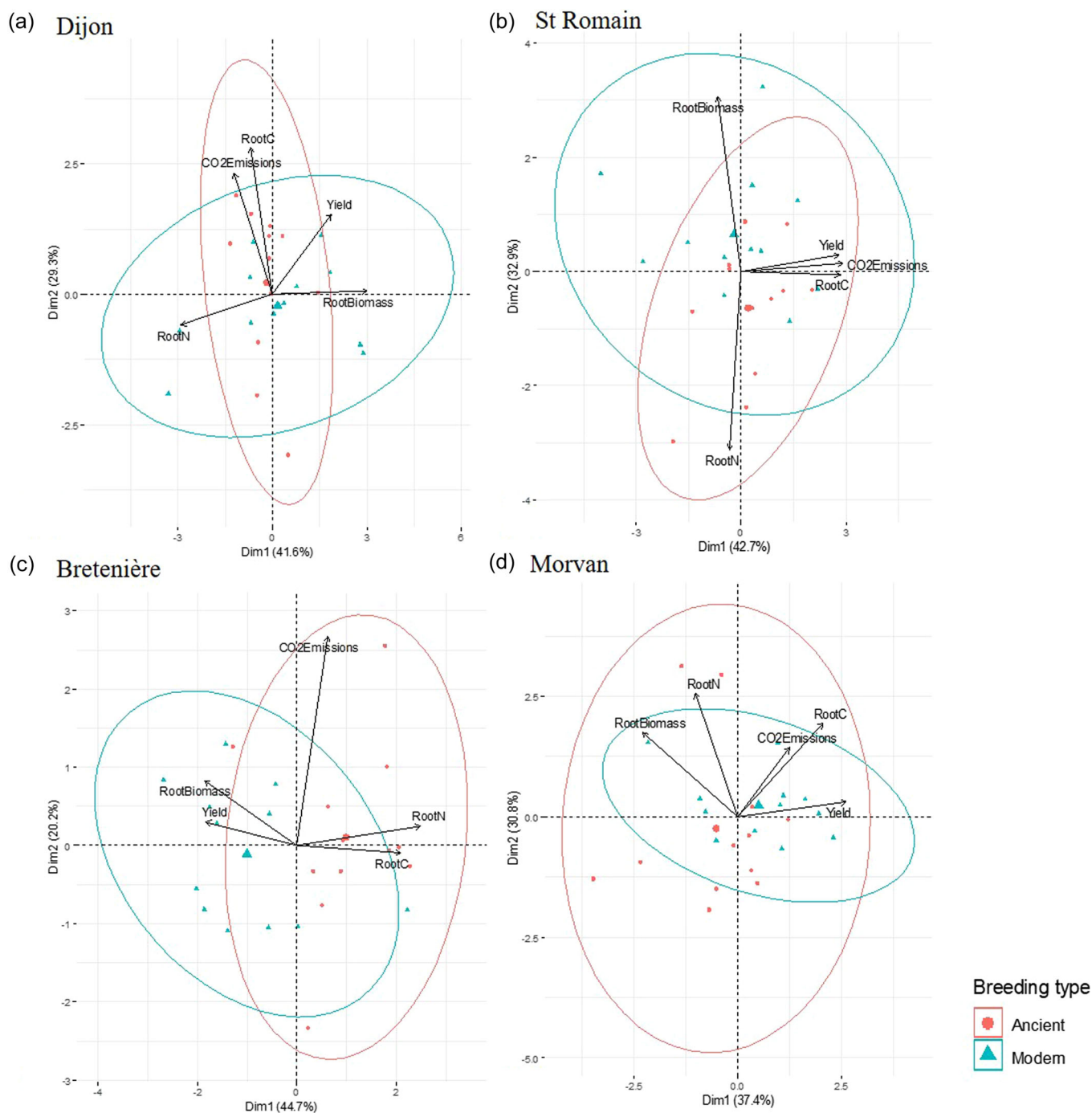


FIGURE 4 Principal component analysis using chemical root traits (root C and N), root biomass, its mineralization (CO₂ emissions) and grain yield for the four sites.

responsible for a better development of the root system of ancient varieties, which is not observed in the field (White & Kirkegaard, 2010).

Root morphology is another variable to consider since the shape of the root system can affect the surface available for microbial mineralization. In our study, root length was longer for ancient than modern varieties in Morvan (+18.2% at 0–0.15 m) and Bretenière (+12.9% at 0–0.15 m). However, no differences were observed for root average diameter, specific root length or root projected area

(except an effect of the breeding type on the projected area in Dijon). In the literature, results on the impact of root morphology on decomposition rate are heterogeneous. Birouste et al. (2012) showed that morphological traits did not explain differences in decomposition rates. Poirier et al. (2018) show that the relationships between specific root length or fine root diameter and decomposition rate can be species-specific: they can relate negatively, positively or not relate to root decomposition. Root morphology could also influence the mineralization rate by modifying OM stabilization processes, such as

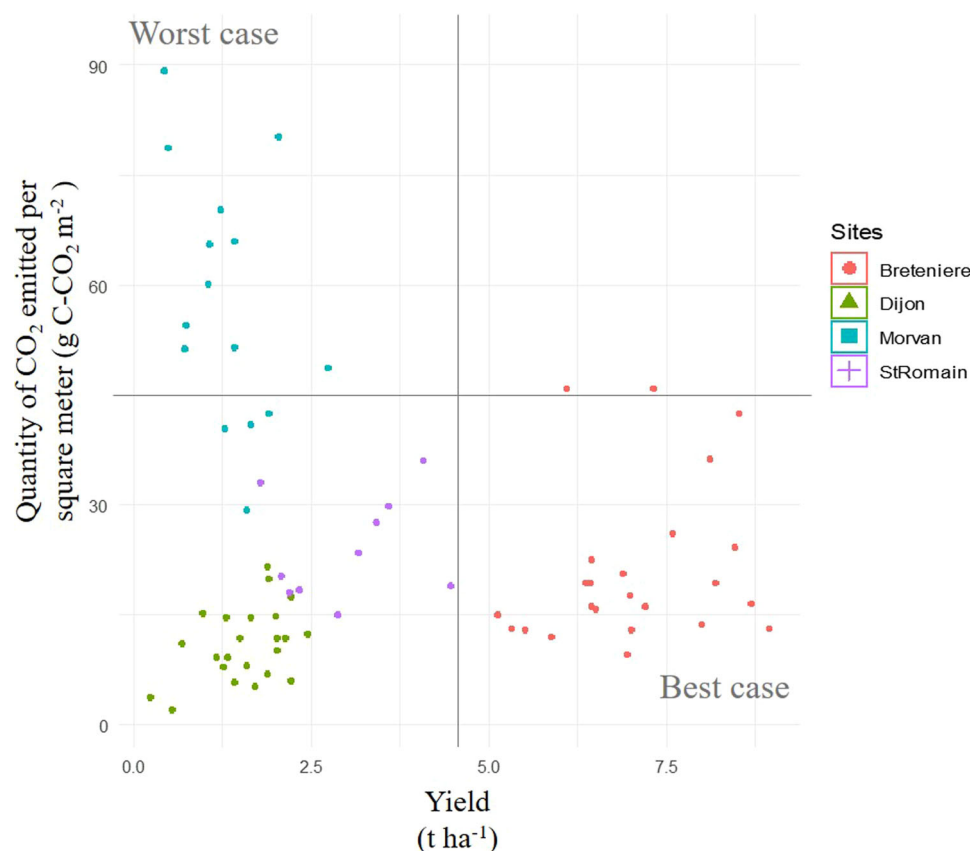


FIGURE 5 Relationship between estimated CO₂ emissions and grain yield. mean \pm se. $n = 24$ for Breteniere and Dijon, $n = 15$ for Morvan and $n = 10$ for St Romain.

the formation of stable aggregates. But results are also contrasted: for Erktan et al. (2016) macroaggregation is increased by a high root diameter, whereas for Poirier et al. (2017) the mass of stable macroaggregates increased with a smaller root diameter. The review of Poirier et al. (2018) concludes that there is no clear relation between morphological traits commonly measured, such as root diameter, and SOM stabilization. If a relation exists, it could be necessary to distinguish between the different hierarchical orders (primary axes, secondary ramifications...), which often differ in structure and function (Poirier et al., 2018).

C inputs to the soil via root biomass, and root morphology which could modify the access of microorganisms to this material, did not differ between ancient and modern varieties. The physical, chemical and biological—especially microbiological—properties of soils from the four different sites could thus be responsible for different CO₂ emission rates. We found that the site had an effect on measured CO₂ emissions, with the highest emissions for Morvan and the lowest for Breteniere and Dijon.

When we integrated the measured value of root biomass in the field on all depths to estimate CO₂ emissions per square metre, the highest emissions were also observed for Morvan and the lowest for Breteniere and Dijon. This site-dependent effect could be due to the texture or to the pH, since the soil of Morvan is the one with the lowest pH (pH=5.47 at 0–0.15 m) and the highest proportion of sand (61% vs. 18% of clay),

whereas the lowest measured CO₂ emissions were found for Dijon and Breteniere, where the soil presents a fine texture (35% and 42% of clay, respectively) and a higher pH (pH=8.28 and 7.64 at 0–0.15 m, respectively). These two sites also present the lowest SOC concentration (Supporting Information: Table S2). The amount of C in soils is indeed positively correlated with the mineralization process (Fang & Moncrieff, 2005; Parton et al., 1987). Texture can also play a role in OM stabilization. Clay and fine silt particles have bigger specific surface areas to absorb and protect OM (Gu et al., 1994), this offers physical protection. Clay and fine silt particles thus help to stabilize SOM (Baldock & Skjemstad, 2000). In this line, Hassink (1992) shows that the process of mineralization of organic C is more important in coarse-textured soils (with more than 60% of sand; FAO [2006]) compared with fine-textured ones (with more than 35% of clay; FAO, 2006).

Regarding the breeding type, we found higher emissions for modern varieties (+4.9% at 0–0.15 m) only for the Morvan soil, when incubating a fixed amount of root biomass in the soil in which it has grown (i.e. respecting the site, plot and depth). This difference in the intensity of CO₂ emissions between varieties in this specific soil are likely not due to physical and chemical properties of the soil of Morvan, otherwise it would have been observed for the two breeding types, neither to root tissue composition, otherwise the difference would have been observed in several soils. Thus, an interaction between genotypes and soils is more likely. We suspected that in this specific soil, root exudates of modern and

ancient varieties could recruit microbial communities with different catabolic activities, resulting in a more pronounced degradation of roots made by modern varieties. The breeding type had no effect on estimated CO₂ emissions (which takes into account differences in root biomass production), except for Saint Romain (Supporting Information: Table S5) where there was an increase of 46.7% of estimated CO₂ emissions for modern varieties compared with ancient ones. Although we did not observe a significant effect of the breeding type on root biomass (see above), combining both the variations of the mineralization rate with depth and small differences in root biomass allows detecting an effect of the breeding type on estimated CO₂ emissions in Saint-Romain, whereas this effect disappears in Morvan despite a difference in mineralization intensity.

4.2 | Grain yield

The site with the highest grain yield was Breteniere (7.04 t h⁻¹), with a grain yield more than two times higher than for the other sites (3.00 t ha⁻¹ for Saint Romain, 1.98 t ha⁻¹ for Dijon and 1.32 t ha⁻¹ for the Morvan). The average grain yield in the region Bourgogne Franche-Comté for the year 2021 was 6.7 t h⁻¹ (Terre net, 2021). The grain yield gap observed between Morvan, Dijon and Saint-Romain versus the average grain yield in the region could be due to the absence of inputs in our experiment. This absence of inputs was likely compensated in Breteniere due to the deep soil, which can increase the availability of water and nutrients (Hirzel & Matus, 2013). But other site-specific factors can be mentioned to explain the importance of the grain yield gap: (i) the wheat did not emerge very well in Dijon for an unknown reason; (ii) in Saint Romain, boars damaged the experiment; (iii) in Morvan, pH was low (5.47 at 0–0.15 m) and texture was very sandy, which is not favourable to wheat grain productivity (Nouri et al., 2016). So even if the soil depth was relatively important for this latter site, other soil characteristics negatively impacted the grain yield.

The breeding type had no significant effect on grain yield at any site, but a trend to be higher with modern varieties (+18%). This result is in accordance with previous observations, for example, Voss-Fels et al. (2019) observed a good correlation between the age of a variety (from 1966 to 2013) and the grain yield ($n = 191$). This could be explained by the choice of the ancient varieties, released before 1960 and chosen for their local origin. Unpublished data show that the difference between our ancient and modern varieties in a given soil could be observed in some years but not others, suggesting the importance of climatic or biotic conditions.

4.3 | A trade-off between CO₂ emission and grain yield?

The meta-analysis from Shang et al. (2021) raised the issue that there is a lack of studies focusing on the interactions between cropland management practices for GHG mitigation and productivity. This study stresses the importance of carefully managing croplands to

stabilize SOC without sacrificing the grain yield (Shang et al., 2021). Our study brings knowledge of a particular management practice, that is, the choice of the breeding type, by comparing the performance between CO₂ emission and grain yield in four sites.

When analyzed separately for each site, grain yield and estimated CO₂ emissions seemed positively correlated for three of the four sites (Figure 4), but it was really the case only in Dijon ($p = 0.05$, Supporting Information: Table S7). However, when all sites were taken together, no correlation between estimated CO₂ emissions and grain yield was observed (Figure 5), despite a nonsignificant trend for a negative correlation ($p = 0.10$, Supporting Information: Table S7). In a meta-analysis, Soussana et al. (2019) compiled 32 field studies and showed that grain yield and SOC stocks are significantly allied: an increase of SOC stock by 0.4% was coupled with a 1.4% gain in grain yield. Since we were not able to assess an actual variation of SOC stock, it is difficult to compare our results with those of the meta-analysis. Measured CO₂ emission from incubation is only a proxy for C storage in soil, used to evaluate the small effect of the breeding type in standard conditions without seasonal or daily variations in temperature, humidity..., during a single year of growth. It remains difficult to determine if the breeding type can change SOC stabilization in the long term, as it can be done with other agricultural practices more directly linked with SOC. Keeping this in mind, several recommendations can be drawn from our results.

For managers, the worst-case scenario is a situation with high CO₂ emissions and low grain yield, because it indicates a failure to feed people and mitigate climate change. On the contrary, the best-case scenario is low CO₂ emissions with high grain yield, implying a high performance for food production and climate regulation. In our study, the site of Morvan represented the worst-case scenario, whereas the site of Breteniere represented the best case (Figure 5). Despite a low number of sites investigated due to the complexity of the experimental design, our results suggest that some soil properties could be beneficial for productivity and climate regulation, such as an important depth, a pH close to neutrality and a fine texture. But of course, these soils are in general already used for agriculture.

As far as the choice between ancient and modern varieties is concerned, we found significantly higher expected CO₂ emissions with modern as compared with ancient varieties in the site of Saint-Romain. It could be expected that deep soils are a prerequisite for a higher C storage by ancient varieties, due to the space available for root development. But apparently, this is not the case: ancient varieties can be unable to store more carbon in deep soils such as Morvan, and more performant in storing C even in 0.30 m-depth soils such as Breteniere. This soil is very rich in clay and with a neutral pH. Choosing another panel of soils with a wide range of decorrelated clay content, pH and depth could help in validating this expectation.

5 | CONCLUSION

We emitted the hypothesis that ancient varieties of wheat could help in storing more carbon in the soil, especially due to bigger and deeper root systems and tested it in the field, in four soils with contrasting

properties. We observed significant differences between ancient and modern varieties in terms of root biomass production or measured CO₂ emissions in one of our four sites. In the soil of the Morvan, longer roots and lower CO₂ emissions of ancient varieties were observed, suggesting that ancient varieties could store more C than modern ones in specific edaphic conditions. When considering the root biomass for estimated CO₂ emissions, the site of Saint Romain showed a high difference between ancient and modern varieties, with higher emissions for modern ones. We did not notice any differences in grain yield between ancient and modern varieties during the year of the experiment. The relationship between CO₂ emissions and grain yield was site-dependent. Some soil properties seemed to favour both carbon storage and grain yield, such as an important depth, a pH close to neutrality and a fine texture. The choice among wheat varieties was thus not a good predictor of carbon storage potential when considered alone. It has to be considered together with soil characteristics.

AUTHOR CONTRIBUTIONS

Manuel Blouin, Laly Rouch and Stéphane Follain conceived the research. Eric Pimet and Laly Rouch carried out the experiment. Laly Rouch, Eric Pimet and Florian Bizouard retrieved the soil and roots in the field. Laly Rouch performed root morphology measures, Laly Rouch, Elodie Cognard and Olivier Mathieu performed the incubations and the CO₂ emissions analyses. Laly Rouch wrote the paper with significant inputs from Manuel Blouin and Stéphane Follain. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The authors confirm that they have adhered to the ethical policies of the journal.

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SUPPORTING INFORMATION

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

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