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RESEARCH ARTICLE

Trade-offs between agronomic yields and sustainability in winter wheat cropping systems under climate change mediated by soil organic matter content

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Abstract

Empirical data is key to anticipate the impact of future climatic conditions on cropping systems and develop land management strategies that are sustainable while ensuring food security. Here, the combined effects of projected increases in temperature, atmospheric CO_2-concentrations, solar irradiation and altered precipitation patterns on winter wheat cropping systems were investigated using an Ecotron. Experimental plant-soil systems were subjected to three different meteorological conditions representing a gradient of ongoing climate change implementing the weather patterns of the years 2013, 2068, and 2085 respectively. In each climate, wheat plants were grown in soil monoliths from two differentially managed agricultural fields where one historically received twice as much organic matter (OM) as the other. Yields in the low-OM systems consistently increased across the three years and exceeded yields of the high-OM system notably in the future climates. Limited plant growth in the high-OM systems was possibly linked to increased nutrient immobilization in

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more complex belowground soil food webs and stronger plant-microbe competition. Moreover, modelling indicated lower CO_2 and N_2O-emissions for the low-OM systems in all climates, while reduced risk of nitrate leaching may make the high-OM systems more environmentally friendly. Together, these results support potential sustainability benefits of regenerative OM management, but also highlight areas of improvement, such as refinement of management practices to facilitate plant nutrient uptake and reduce greenhouse gas emissions. As shorter wheat growth cycles were observed in the future climates, one lever to replenish and mobilise soil nutrients and break disease cycles could be diversifying crop rotations and cover crops. Moreover, in both here studied soil types the wheat plants developed natural coping mechanisms against environmental stressors, such as enhanced root growth and increased levels of proline and silicon. Unravelling the molecular mechanisms that trigger such inherent plant defences is a further interesting target for breeding future crops.

Introduction

Climate change is expected to significantly impact winter wheat production in Central Europe over the next 100 years, with a theoretical potential for increased yields, but also an increased risk of crop failure following increased heat and water stress [1]. Wheat is currently the most cultivated cereal in Europe, representing 34% of global production, and is the third most cultivated cereal in the world after rice (*Oriza sativa* L.) and maize (*Zea mays* L.), with over 95% of wheat produced worldwide being bread wheat (*Triticum aestivum* L.) [2]. While wheat is a staple food in Europe which provides carbohydrates, protein, essential minerals like iron and zinc, and also vitamins like thiamine and pantothenic acid, its large-scale production is critical in terms of its environmental impact, notably nitrate pollution and greenhouse gas emissions [3–6]. Farmers therewith face a triple challenge: produce food for a growing world population, reduce the negative impact of cropping systems on the environment and adapt land management to more and more challenging climatic conditions.

The optimal growth temperature for common winter wheat (*Triticum aestivum* L.) varies by growth stage but generally falls between 15°C and 25°C. During vegetative stages (e.g., tillering and stem elongation), 15–20°C promotes robust growth, while slightly warmer temperatures (20–25°C) are ideal for heading and grain filling. Temperatures above 30°C or below 0°C during critical stages can stress the plant, reducing yield and quality [7–9]. Under the Representative Concentration Pathway (RCP) 8.5 scenario (8.5 W m^{-2}), Western Europe's climate by the end of the 21st century is projected to be warmer by approximately +3°C, experience an increase of +140 mm in annual precipitation with uneven distribution, and see atmospheric CO_2 concentrations rise by approximately 375 ppm above pre-industrial levels, reaching around 685–775 ppm, compared to the current level of just above 400 ppm [10]. While warmer temperatures might initially benefit yields, extreme heat events during critical growth phases (like flowering) can lead to heat stress and reduced yields [8,11]. Rising temperatures, especially combined with elevated atmospheric CO_2 concentrations are also going to affect growth cycles, potentially leading to earlier wheat maturation and shorter growth cycles [12]. This bears particular risks for winter wheat in central Europe as crops may be exposed to unfavourable weather conditions during their sensitive growth stages, for example heat waves during grain filling. Rising atmospheric carbon dioxide levels as such can have both beneficial and detrimental effects on crops. While increased CO_2 levels can initially benefit wheat growth through the CO_2-fertlisation effect, this is only observed under optimal temperature conditions. Beyond these conditions, the benefits diminish, and elevated CO_2 can decrease yields and protein levels [13,14]. Additionally, elevated CO_2 levels can promote rhizodeposition, which involves an increased release of root exudates intensifying microbial decomposition of soil organic carbon and potentially increasing CO_2-emissions from the soil [15]. Moreover, changes in rainfall, including both increased frequency of heavy rainfall and prolonged droughts, can negatively impact crop growth and ultimately yields, especially if wheats suffer from insufficient water supply in critical growth stages and/or excessive rainfall increases disease pressure and hinders field operations. In general, warmer temperatures and higher humidity levels can facilitate the spread of pests and diseases such as powdery mildew, septoria or take-all, which may lead to poor crop growth or even crop losses if not managed effectively. Similarly, changes in temperature and moisture influence soil microbial communities and nutrient cycling, potentially reducing soil health and fertility over time with negative consequences for the harvested crops.

A further key point to consider is disease propagation in winter wheat cropping systems under climate change, which is influenced by various factors including temperature, humidity, and pathogen biology [16,17]. Warmer temperatures can accelerate pathogen life cycles and increase disease severity, especially fungal diseases may become more prevalent. Altered precipitation patterns and higher humidity can also promote the growth of diseases such as powdery mildew and take-all [18,19]. With shifts to the timing of winter and spring, crop phenology and pathogen life cycles may face new combinations with currently unknown consequences for crop vulnerability towards pathogens. Integrated pest management strategies will be crucial for adapting to these changes, but these strategies depend on accurate information about the anticipated disease pressure.

To prevent devastating impacts of climate change on winter wheat cropping systems and anticipate negative consequences it is crucial to have accurate empirical data on future crop growth cycles, plant nutrient requirements and disease propagation. To date, most experiments focus on individual climate change factors such as elevated CO_2, however one of the cruxes of climate change is the multifactorial aspect of abiotic stresses combining elevated CO_2, altered precipitation patterns and rising temperatures at varying intensity. Here, an Ecotron facility was used to expose wheat plants growing in two soils with contrasting organic matter management to three climate change scenarios representing the meteorological conditions of the years 2013, 2068 and 2085 respectively. Above and belowground cropping system performance was monitored during the full growth cycle and thus unique insights to the agronomic performance and the environmental impact of the wheat of the future were obtained. The experimental insights provide new information about phenological shifts, disease propagation, plant adaptation strategies, plant nutrient uptake and yield, as well as nitrate leaching and greenhouse gas emissions.

The experiment addresses two main research questions: (i) how do future meteorological conditions impact winter wheat cropping systems and (ii) can low or high organic matter soil management strategies prevent some of the anticipated negative impacts of climate change on crop system performance and yield?

Methods

Time travelling with Triticum: Experimental set-up in the TERRA-Ecotron

The experiment was implemented in the TERRA-Ecotron (Gembloux Agro-Bio Tech, University of Liège, Belgium) [20]. The TERRA-Ecotron was built in 2018 and currently has six controlled environment rooms (CERs). The experiment was carried out in mesocosms, which have a soil compartment of 125 L each (cubes of 50x50x50cm), which allows to place nine mesocosms in each CER, resulting in a total of n = 54 experimental mesocosms. The first factor "climate" was implemented with three levels, i.e., wheat was grown under the meteorological conditions of the three years 2013, 2068 and 2085 respectively. The second factor crossed with “climate” was “soil management”, which had two levels that is low organic matter content (S1) and high organic matter content (S2). This resulted in a total of six modalities (2013.S1, 2013. S2, 2068.S1, 2068.S2, 2085.S1, 2085.S2). Each modality was implemented with eight replicates, half of which were kept untouched until final harvest for realistic estimation of yield components and the other half was sampled repeatedly during the experiment for destructive measurements such as root growth or leaf elemental composition, each time taking 3–5 plants. In addition, for each soil management type in each climate an unplanted control cube was kept to measure baseline soil processes. Having six CERs meant that each climate (2013, 2068, 2085) was replicated in two CERs and the replicate cubes of each of the two soil management type were randomly distributed amongst these CERs (Fig 1).

Three climate scenarios: 2013, 2068 & 2085

Historical data of continuous climate observations from the Ernage meteorological station (50°34’33“N, 4°43’1”E, Belgium, since 1980) was used as well as predicted future meteorological conditions using the Alaro-0 model [21]. The model ran for the Representative Concentration Pathway (RCP) scenario 8.5 W m^{-2} [22] and the two time periods 2040–2070 and 2070–2100 (Fig 2). The three years selected from these predictions (2013, 2068, 2085) align on a continuous gradient of increasing temperature, precipitation, hydrothermal index (HI) and atmospheric CO$_2$ concentrations (Fig 2). HI is a measure of the relationship between precipitation and temperature, calculated as the ratio of total precipitation to one-tenth of the sum of mean temperatures [23]. A higher HI indicates wetter and/or cooler conditions, suggesting more favourable moisture availability relative to temperature, which can benefit crops and vegetation. Conversely, a lower HI signifies drier

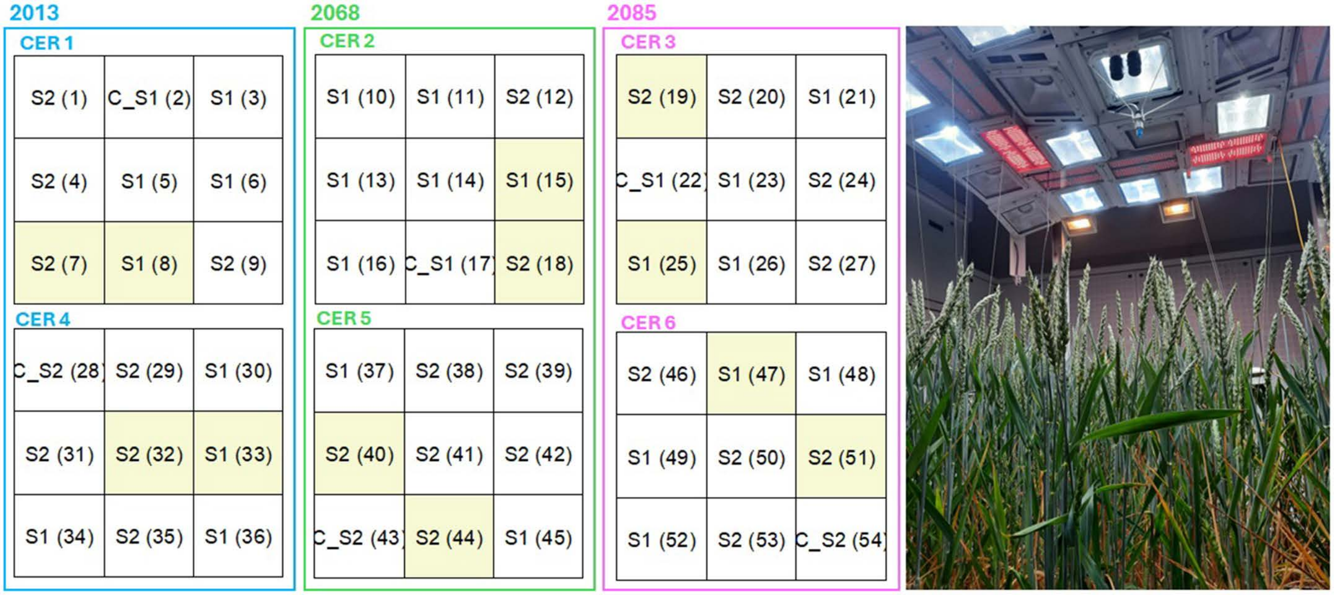

Fig 1. Experimental set-up. Left: Schematic representation of the TERRA-Ecotron which consists of six controlled environment rooms (CERs), in each of which n = 9 cubes are placed. Each cube measures 50x50x50cm and contains a soil monolith originating either from the field with low organic matter content (“S1”) or the field with high organic matter content (“S2”). In each CER one soil cube is unplanted (“C_”) while all other cubes are sown with *Triticum aestivum* var. Asory. In each of the CERs one meteorological condition is employed representing either one of the years 2013, 2068 or 2085, with each year being replicated in two CERs (2013: CER1, CER4, 2068: CER2, CER5, 2085: CER3, CER6). Darker shadows of the cubes indicate positioning of a scale underneath the cube. Right: View inside CER2 at 200DAS: Each CER is equipped with a lightening system combing plasma, halogen and LED lamps which can reach maximum photon fluxes of 1200 µmol m^{-2} s^{-1}. Sensors for photosynthetic active radiation (PAR) and irradiance are located at canopy height.

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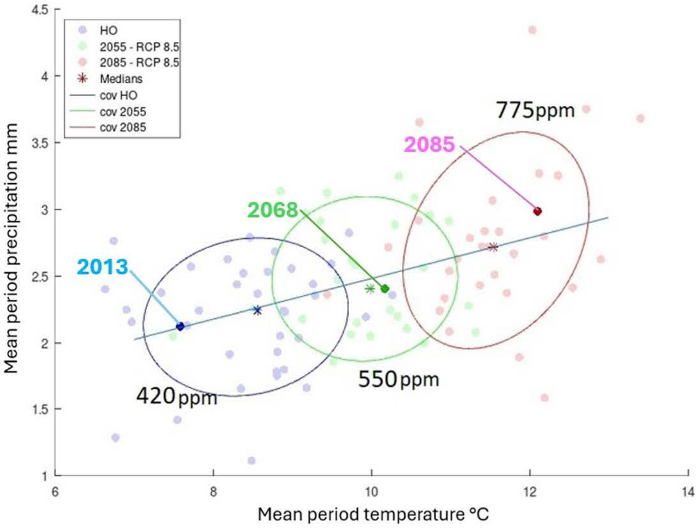

Climatic parameters	2013	2068	2085
Mean CO_2 ppm	420	550	775
Mean radiation µmol m^{-2} s^{-1}	51.81	53.98	54.49
Mean temperature °C d^{-1}	7.6	10.2	12.1
Mean precipitation mm d^{-1}	2.1	2.4	3
Hydrothermal index (rel.)	4	4.5	4.7
Maximum temperature °C	26.5	23.4	22.2
Minimum temperature °C	-7.6	-5.8	3.1
n days temperature ≤ 4°C	94	40	3
n days temperature ≥ 22°C	9	7	2
Maximum precipitation mm	46.3	39.0	47.3
Minimum precipitation mm	0.0	0.0	0.0
n days precipitation ≤ 0mm	135	4	3
n days precipitation ≥ 4mm	57	62	72

Fig 2. Climate scenarios. Left: Wheat agroecosystems were exposed to the meteorological conditions of three years representing the present climate (2013), the near future (2068) and a farther future (2085). The three years align on a continuous gradient of hydrothermal index with increasing temperature, precipitation and atmospheric CO_2-concentrations. The climate scenarios are based on continuous meteorological observations from the Ernage weather station (50°34'33"N, 4°43'1"E, Belgium, since 1980) and the predicted future climates were simulated using the Alaro-0 model. The historic observations (HO) cover the period 1981-2017 (blue) and the model ran for the Representative Concentration Pathway (RCP) scenario 8.5 W m^{-2} for the two time periods 2041-2070 (green) and 2070-2100 respectively (rosé). Each dot represents a year and the ellipses represent the 95% confidence interval of the three periods. Right: Table summarizing the key climatic parameter of the selected years.

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and/or warmer conditions, which may indicate drought stress or reduced water availability. The selection of the years 2013, 2068, and 2085 was made to represent a continuous gradient of HI as a robust measure of intensifying climate change. Using HI enables the identification of climate trends against the background noise of large variability in environmental parameters in some years along the timeline. In this experiment, 2013 served as a historical reference point capturing climate conditions close to the baseline used in climate models (e.g., 1986–2005 or early 21st-century averages) and enabling cross-validation of Ecotron, crop model and field-based data. The year 2068 represents a mid-century projection with moderate increases in temperature, precipitation and CO_2. The year 2085 represents a late-century projection, near the end of the standard climate modelling horizon (2100). By 2085, RCP 8.5 predicts substantial warming, as well as more intense rain and higher CO_2. Together, these three years form a continuous gradient spanning a broad timeline (past to future), with each year reflecting progressively higher values for temperature, CO_2, and precipitation, and corresponding to gradual shifts in HI. This allows to investigate how incremental changes affect cropping systems and soil health, to better understand the cumulative impacts of climate change and assess adaptation needs for wheat breeding and soil management.

The Ecotron reproduces the simulated weather conditions at a very high temporal resolution, where the key environmental parameters such as sun light intensity and temperature are adjusted every five minutes. By these means, diurnal and seasonal variabilities are accurately reproduced, and plant behaviour can be studied under realistic climate scenarios. For example, the irradiation includes natural sun rise and sun set patterns. The main climatic components that were manipulated for each year in this experiment were atmospheric CO_2 concentration, temperature and precipitation. In line with the HI gradient, CO_2 concentrations also gradually increased for the three years, from 420 ppm in 2013, to 550 ppm in 2068 and 775 ppm in 2085. The historic reference year 2013 was characterised by a mean temperature of 7.59°C during the wheat growth cycle, with a mean precipitation of 2.12 mm d^{-1} (HI = 3.99). Interestingly, this year is the most extreme in terms of maximal and minimal temperature (26°C, -7.6°C), and also the year with the longest periods outside the optimum range for wheat in terms of cold and hot days (n = 94 days below 4°C and n = 9 days above 22°C). The year had a long cold winter from approximately 51–176 days after sowing, during which the soil was frozen and therewith the water present in the soil was not readily available to plants. The year 2013 also had the largest number of rain-free days (n = 135), but the lowest number of rainy days (n = 57 days with precipitation >=4mm). The 2068 climate was characterised by mean temperature higher than 2013 with 10.17°C but still had a significant winter period with n = 40 days where temperatures dropped below 4°C. Mean precipitation was slightly higher than in 2013 with 2.4 mm d^{-1} and only n = 4 days without rain, but more rainy days (n = 62). The climate of the year 2085 was the smoothest in regards of temperatures around 12.1°C and very rarely below 4°C or above 22°C. The winter period was short with only n = 3 days below 4°C. In regards of precipitation, 2085 was the wettest scenario with n = 72 days of rain (>=4mm). Interestingly, all three years experience at least one day with very high rain (>30mm), though these maximum rain events occurred at different moments during the season: in March for 2068, in May for 2085 and in July for 2013.

Two soil types with different management history

The experiment tests two soils which are very closely related in terms of pedogenesis, both originating from the Walloon Brabant in Belgium (0°38'35.1474"N, 4°37'22.0123"E ("S1"), 50°39'12.8668"N, 4°38'10.7664"E ("S2"), Fig A in S1 File). In this area limestone formations are prevalent and soils are often clay-rich, which helps retain moisture and nutrients making them very suitable for agriculture [24]. Both soils are classified as Aba(b)0 in the Belgian soil classification system and characterised as silty loam [25]. Both soils are from fields that are under agricultural management since generations and implement the regular local crop rotations with winter wheat and root vegetables mainly. In recent years, cover crops with plants such as phacelia, oats, radish and clover have always been grown between two main crops in S2. In both fields standard and reduced tillage was applied regularly, as well as commercial fertilisers, green and brown manure and occasionally herbicides (Table A and B in S1 File). The main differences between the two soils is that soil two (S2) has received significantly higher quantities of organic matter than soil one (S1). While the soils have similar C:N of 10.5 and pH just above 8, these higher organic matter inputs left S2 with more than doubled humus, carbon (C), nitrogen (N), and extractable phosphorous (P), potassium (K), magnesium (Mg) and calcium (Ca) contents as compared to S1 (Table 1). Another difference is in the soil texture, which is sandier for the low organic matter content soil S1. In each field, a total of n = 27 cubes were sampled in November 2022 and moved to the Ecotron. Soils were sampled as undisturbed soil monoliths (50x50x50cm) with a surface of 0.25 m^2 and each weighing approximately 200 kg. Monoliths were taken to realistically represent field conditions in the Ecotron, avoid disturbance of sensitive soil organisms and keep the soil structure intact. One cube of each soil type in each CER was placed on a scale to monitor the weight of the cubes and improve estimates of evapotranspiration.

Crop management and monitoring

During an initial acclimatisation period of three weeks, the soil cubes were kept under respective climates in the CERs of the Ecotron. At the time of the monolithic sampling for the Ecotron trial the S2 field was pre-cropped with a radish mix,

Table 1. Physicochemical characterisation of the two soils, both classified as silt loam (Aba(b)0) at the beginning of the experiment, one composite sample per soil type, sampling depth: 0-20 cm. Abbreviations: OM: organic matter, C: carbon, N: nitrogen, P: phosphorous, K: potassium, Mg: magnesium, Ca: calcium. Extractant for P, K, Mg, Ca was ammonium-acetate 0.5N EDTA 0.02 M, pH 4.65.

	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	C/N	P ($mg\ kg^{-1}$)	K ($mg\ kg^{-1}$)	Mg ($mg\ kg^{-1}$)	Ca ($mg\ kg^{-1}$)	pH (H_20)	Humus (%)	Clay (%)	Silt (%)	Sand (%)
Soil One (S1) "low OM"	9.92	0.94	10.5	136.0	312.0	83.7	2183.1	8.04	1.98	12.15	67.13	20.72
Soil Two (S2) "high OM"	22.01	2.09	10.5	397.9	725.1	147.0	5344.2	8.08	4.23	13.55	78.85	7.60

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in grass cover with a dense layer of mulch in the sub-surface (wheat straw). There was no cover crop sown in the S1 field prior to sampling the cubes, but a straw layer had also been incorporated to the soil before the sampling. The soils in all cubes were weeded and surface tillage (raking to 15 cm depth) was applied during the acclimatisation period. On 23/12/22, which corresponds to 01/11 Ecotron date, 54 cubes were planted with winter wheat (*Triticum aestivum* (L.) var. Asory) at a density of 308 seeds m^{-2} (77 seeds per cube). Cubes were weeded manually when needed and no herbicides were applied. At the beginning of the experiment, metaldehyde pellets were applied to control molluscs. The pellets were placed in the reversed lids of 50 ml Falcon tubes which were then placed on the soil to minimise impact on soil chemistry and other soil organisms [26,27]. After germination, plant development was closely monitored and several agronomic and environmental parameters were regularly recorded (Fig 3, Table D in S1 File). For the aboveground compartment, plant BBCH growth stages, plant height and leaf area index (LAI) were measured to quantify plant growth and maximum quantum efficiency of photosystem II (Fv/Fm) was measured as an indicator of plant performance [28,29]. At three time points (BBCH30/50/80) foliar silicon and foliar proline were determined as important molecules in plant stress response [30,31]. For the belowground compartment, soil microbial biomass and total root length were measured at the same time points and root infestation with the fungus *Gaeumannomyces tritici* (take-all disease) was quantified once at 230 DAS [32–34]. Unless prevented by drought conditions, interstitial soil pore water was extracted weekly to quantify freely available nitrate in aqueous soil solution and glucose equivalents as indicators of root exudation [35,36]. During the experiment, both soils in all climates were fertilised with ammonium nitrate (N: 27%), which was applied in three doses according to plant growth stage, namely at the end of tillering/stem-elongation, 2. node and flag leaf in each climate respectively. The quantities of N-fertiliser varied between 150 and 205 kg N ha^{-1} for the different soils and climates as a function of the mineral N measured in the different soils at the end of winter, with S1 receiving approximately 50 kg N ha^{-1} more than S2 (Table C in S1 File). Plants were harvested when fully ripe (BBCH89) and for each cube aboveground biomass was determined (straw/leaves/heads), as well as number of heads, grain fresh weight, grain humidity, grain yield at 14% moisture, thousand grain weight and grain nitrogen content.

DNDC model

DNDC (i.e., DeNitrification-DeComposition) is a process-based computer simulation model of carbon and nitrogen biogeochemistry in agro-ecosystems [37,38]. DNDC predicts soil environmental factors, C sequestration, and emissions of C and N gases primarily based on microbe-mediated biogeochemical processes, including decomposition, nitrification, denitrification, fermentation, and methanogenesis [39–41]. DNDC simulates these processes based on the activity of different functional groups of microbes under different environmental conditions including temperature, moisture, pH, redox potential (Eh) and substrate concentration gradients in soils. For example, nitrification is modelled as first-order process based on soil ammonium concentration (NH_4^+) under aerobic conditions and nitrous oxide production (N_2O) is modelled as a fraction of the overall nitrification rate. Soil Eh is calculated with the Nernst equation at a daily time step following soil saturation and then used to determine anaerobic microbial group activity under a given set of soil conditions. Anaerobic microbial group activity is then modelled using standard Michaelis-Menten-type kinetics. The DNDC model has been extensively evaluated against datasets of trace gases fluxes that were measured worldwide [37,38]. To access the accuracy of the model for this experiment, the model's predicted outputs were compared with measured Ecotron variables and the coefficient of determination (R^2) was used as a measure of goodness of fit (Fig B in S1 File).

Statistical analysis

The effects of climate and soil type on the empirically measured parameters were assessed using linear mixed-effects models (LMM) with climate and soil as fixed effects, and random intercepts for time and CER to account for the within-subject correlation of repeated measures and replicate rooms. Post-hoc comparisons using estimated marginal means (EMMs) were used where appropriate to elucidate differences between the levels of each fixed effect, i.e., the interaction between climate and soil (2013/2068/2085xS1/S2). For yield components (Table 2, Fig 3Q) and take-all index (Fig 3L) analysis of variance (ANOVA) was used to identify differences between climate and soil type. The parameters derived from the DNDC model, that is upscaled budgets of CO_2, N_2O, N leaching and transpiration, have only one observation per modality (Fig 3R-T). They are descriptive but were indicatively compared via Krustkal-Wallis test for climate and soil individually. To reduce the overall dimensionality of the dataset to better understand what the core characteristics

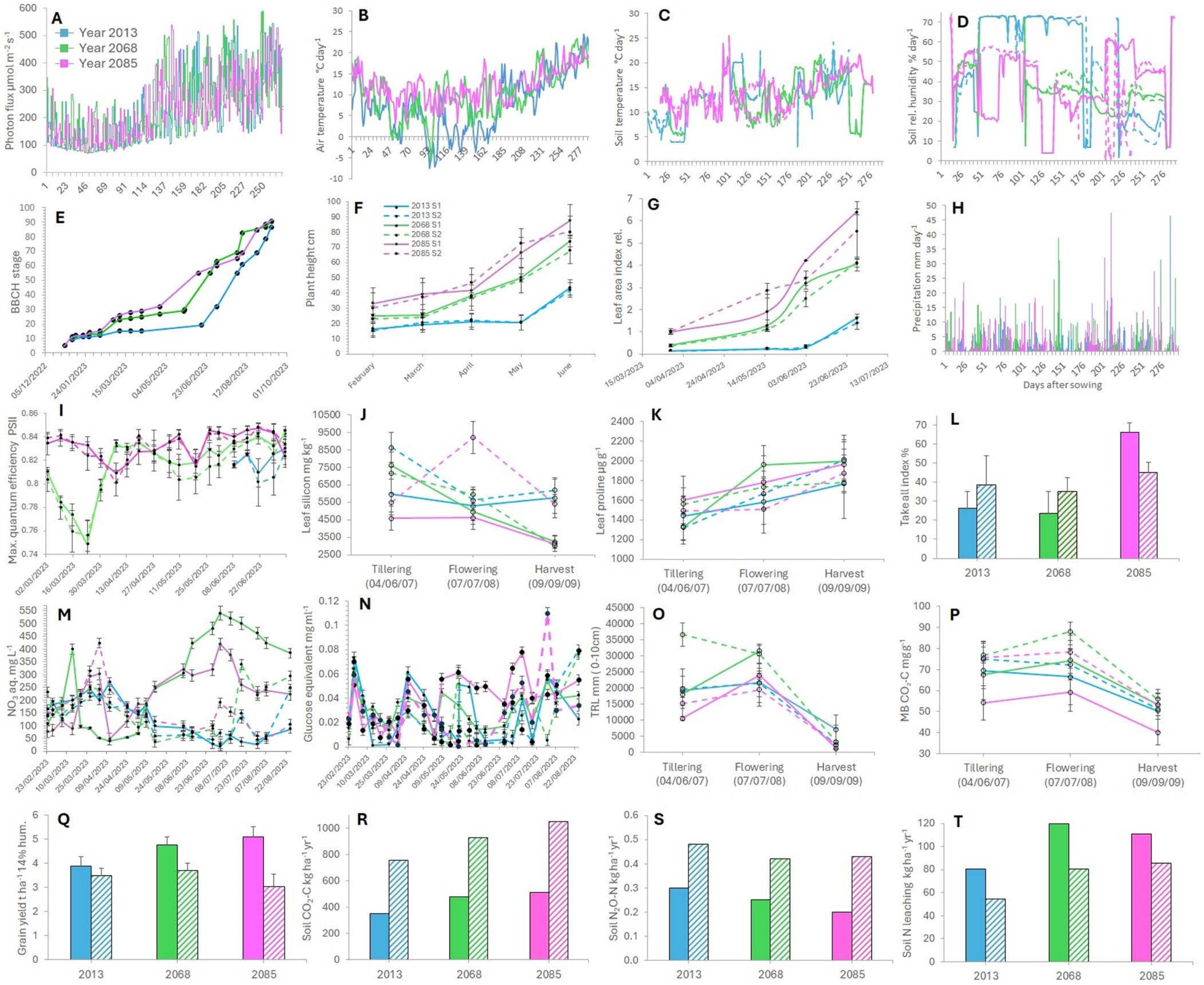

Fig 3. Environmental, crop and soil parameters of two management systems (S1: continuous line/fill and S2: dotted line/hatched area) in the meteorological conditions of the years 2013 (blue), 2068 (green) and 2085 (rosé). Details of each measurement method and replication for each parameter in Table D in S1 File. A: Photon flux µmol m^{-2} s^{-1}, B: Air temperature °C day^{-1},C: Soil temperature °C day^{-1}, D: Soil relative humidity % day^{-1}, E: BBCH scale plant growth stages, F: Plant height cm, G: Leaf area index (LAI), H: Precipitation mm day^{-1}, I: Maximum quantum efficiency of photosystem II (Fv/Fm), J: Leaf silicon mg kg^{-1}, K: Leaf proline µg g^{-1}, L: Take-all index (% *Gaeumannomyces tritici* infestation), M: Nitrate (NO_3) mg L^{-1}in aqueous soil solution, N: Glucose equivalent in aqueous soil solution mg ml^{-1}, O: Total root length (TRL) mm for 0-10 cm soil depth, P: Microbial biomass (MB) CO_2-C mg g^{-1}, Q: Grain yield t ha^{-1} at 14% grain humidity, R: Annual soil CO_2-C budget kg ha^{-1} yr^{-1}, S: Annual soil N_2O-N budget kg ha^{-1} yr^{-1}, Annual soil N leaching kg ha^{-1} yr^{-1}, A-D, H: Daily measurements, E: BBCH growth stages evaluated for all cubes and only one value noted per modality, F-G, I-Q: Dots represent means ± SD of n = 4 or n = 8, R-T: Data modelled with DNDC and only one value per modality.

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Table 2. Yield components for winter wheat (*Triticum aestivum* var. Asory) grown in two differentially managed soil types (low OM content S1 and high OM content S2) in the meteorological conditions of the years 2013, 2068 and 2085. F-statistic and probability values provided for two-way analysis of variance with asterisks indicating significance levels at <0.001*, ≤ 0.01**, ≤ 0.05*, > 0.05 not significant.**

	2013		2068		2085		F-statistic, p-value		
	S1	S2	S1	S2	S1	S2	soil x climate	soil	climate
Grain yield t ha^{-1}	3.79 ±0.51	3.50 ±0.34	4.76 ±0.37	3.71 ±0.32	5.09 ±0.50	3.05 ±0.59	1.912, 0.177	9.449, 0.007**	0.920, 0.417
Thousand grain weight g	31.12 ±2.3	30.45 ±6.85	35.62 ±2.77	47.13 ±8.48	45.18 ±1.95	41.29 ±3.98	5.126, 0.017*	1.350, 0.260	14.445, <0.001***
Grain nitrogen (%)	2.26 ±0.20	2.25 ±0.18	2.00 ±0.11	1.87 ±0.11	2.11 ±0.39	1.97 ±0.22	0.237, 0.792	1.129, 0.302	4.155, 0.033*
Number of heads cube^{-1}	108 ±20	108 ±19	111 ±11	88 ±9	118 ±20	101 ±27	1.513, 0.247	4.632, 0.045*	0.222, 0.803
Total fresh weight straw g cube^{-1}	121.54 ±17.53	131.74 ±52.51	176.55 ±22.84	186.71 ±40.81	327.29 ±71.40	206.21 ±49.92	5.366, 0.015*	3.169, 0.092	18.629, <0.001***

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of each cropping system in each climate are, probabilistic principal component analysis (pPCA) was performed (Fig 4). pPCA extends traditional PCA by incorporating a probabilistic framework, which allows the estimation of principal components to identify underlying latent structures in the presence of noise [42]. Subsequently, Bayesian network analysis was performed to gain further insights to links between agronomic yields and other cropping system components in the two contrasting soil types [43]. In particular, we were interested in whether we could detect potential trade-offs between cropping systems given very distinct edges and edge weights occurring among relevant drivers of crop yield. Each analysis included 12 variables (nodes) identified by pPCA to describe the emerging properties of the cropping systems (Fig 5). Prior distributions were fitted according to Bernoulli distributions with prior probability of edge inclusion set to 0.5 and 3 degrees of freedom for G-Wishart distribution for the prior of the edge weights [44,45]. The Bayes factor for inclusion of an edge was set to a conservative $BF_{10} > 15$.

Statistical analysis was carried out using R 4.4.1 [46] with the additional packages car [47], easybgm [43], emmeans [48], ggplot2 [49], lmerTest [50], missForest [51] and multcompView [52].

Results

Phenological advance in future meteorological conditions

Warmer temperatures and more intense rain, but overall less stressful weather with higher atmospheric CO_2 concentrations meant that crops grew faster and bigger the further in the future the climate scenario was (Fig 3E-G). The phenological advance manifested from February onwards, with plants maturing faster in 2068 and 2085 (BBCH $p < 0.0001$). There was a significant effect of soil type in interaction with climate for plant height ($p < 0.0001$), with taller plants the further in the future the climate scenario. Notably, plants in 2085 were almost twice as high as in 2013 (Fig 3F) and plant height was one of the main characteristics of the 2085 cropping systems on both soil types in the ordination (Fig 4, Table E in S1 File). In 2013, plants in S2 grew taller than plants in S1 (2013.S1: 19.3 ± 0.445, 2013.S2: 20.8 ± 0.476). The soil type effect was reversed for the two future climates where plants grew taller in S1 compared to S2 and (2068.S1: 25.6 ± 0.445, 2068.S2: 24.0 ± 0.445, 2085.S1: 39.4 ± 0.445, 2085.S2: 37.2 ± 0.445). Small leaf area index (LAI) was one of the main characteristics of the 2013 cropping systems, particularly S2 (Fig 3G, Fig 4, Table E in S1 File) and considerably increased in the future climates ($p < 0.0001$).

Early harvest and yield components

The phenological advance entailed earlier harvests in the future years, with approximately two weeks between each of the climate scenarios. Plants in 2068 were harvested first in early July, followed by 2085 in late July, while 2013 was

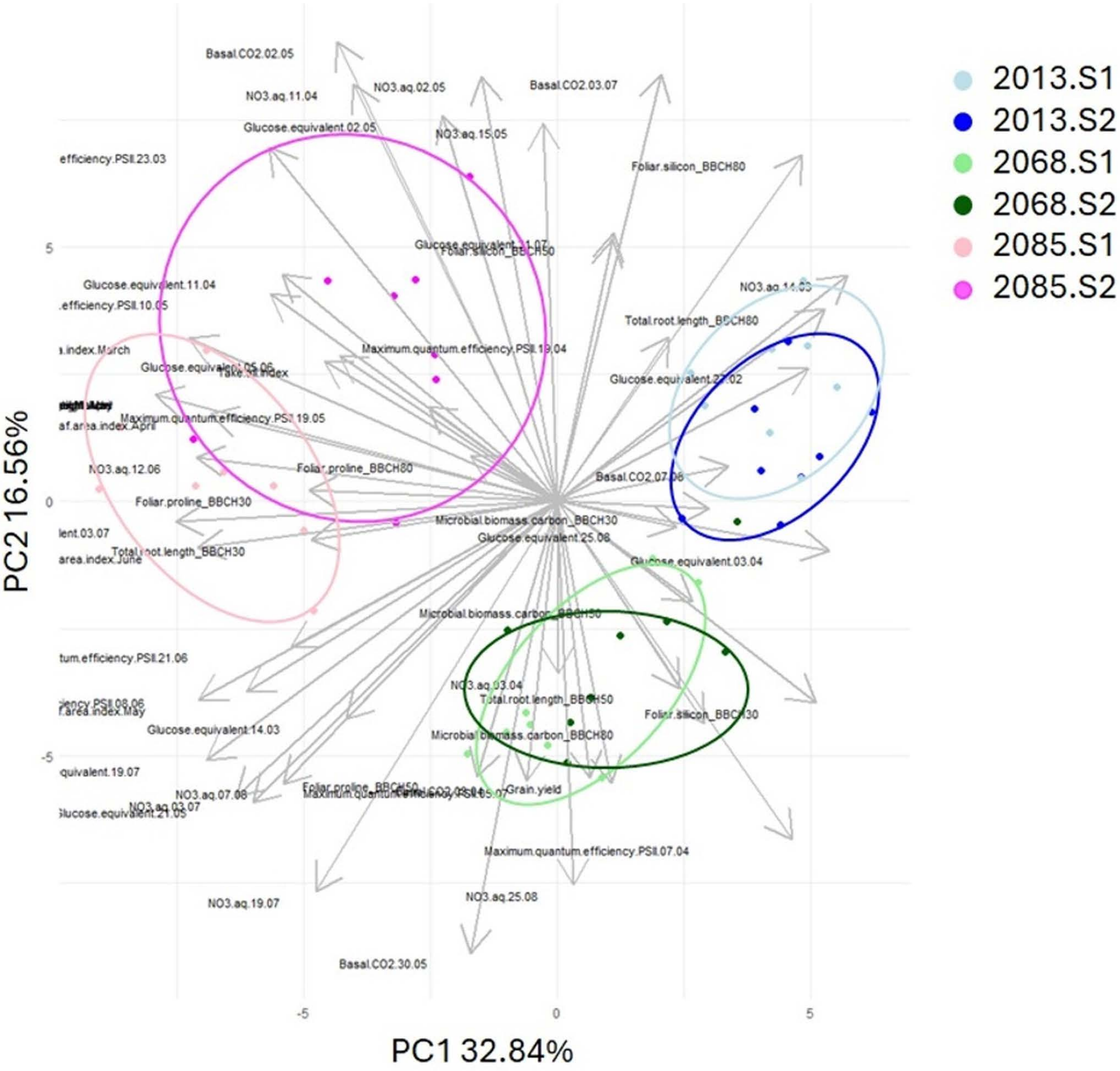

Fig 4. Ordination of agronomic and environmental parameters in probabilistic principle component analysis (pPCA) and clustering by simulated year and soil type. Main parameters which distinguish the groups: 2013.S1: glucose equivalent, take-all index; 2013.S2: leaf area index; 2068.S1: foliar proline, microbial biomass carbon, total root length; 2068.S2: basal CO_2, maximum quantum efficiency PSII; 2085.S1: plant height, aq. NO_3, total root length; 2085.S2: foliar silicon, plant height (detailed vector loadings in Table E in S1 File).

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harvested beginning of August (all dates refer to Ecotron months). Visually distinguishable differences in plant developmental stages between the two soil types were minor and plants from both soils were harvested simultaneously once all grains were fully ripened for the respective year.

Grain yield was always higher in S1 as compared to S2, with an overall significant soil type effect ($p = 0.007$) and minor differences between climate scenarios (Fig 3Q, Table 2). Most notably, yield increased proportional to the increasing hydrothermal index across the three years for S1, meaning that for this soil type the further in the future the climate scenario, the higher the yield. The globally highest aboveground biomass and also highest grain yield were achieved for S1 in 2085, while the lowest grain yield was recorded for S2 in 2085. Thousand grain weight was also significantly affected by soil and climate ($p < 0.001$) with lowest values in 2013 and highest values for S2 in 2068 (Table 2). Grain nitrogen was lower in the two further climates ($p = 0.03$).

Plant health

The maximum quantum efficiency of photosystem II, represented as Fv/Fm (Fig 3I), is a crucial parameter in plant physiology with values around 0.8 considered optimal and lower values indicating stress leading to impaired PSII efficiency [29,53]. Fv/Fm is measured at leaf level and requires significantly wide leaf area, which is why the measurement was initially not possible in 2013. For the data available, Fv/Fm was not significantly different between soil types, but significantly different between climates ($p < 0.002$), with on average higher Fv/Fm in 2085 than in 2068 (than in 2013 when measured). A notable drop in Fv/Fm was recorded for 2068 compared to 2085 at the beginning of the experiment (March Ecotron month) and overall lowest Fv/Fm was measured for S2.2068 which distinguished this cropping system (Fig 4, Table E in S1 File).

Leaf silicon and proline levels as key indicators of plant stress and adaptation mechanisms were also characterised (Fig 3J, 3K). There was notably elevated foliar silicon in S2.2085 at BBCH50 and elevated proline in S1.2068 at BBCH80 (Fig 4, Table E in S1 File). Overall, leaf silicon levels were most distinguished 2085 ($p = 0.02$) with the lowest levels for S1.2085 and the highest foliar silicon for S2.2085 (Fig 3J). Foliar silicon tended to be globally higher in S2 than in S1

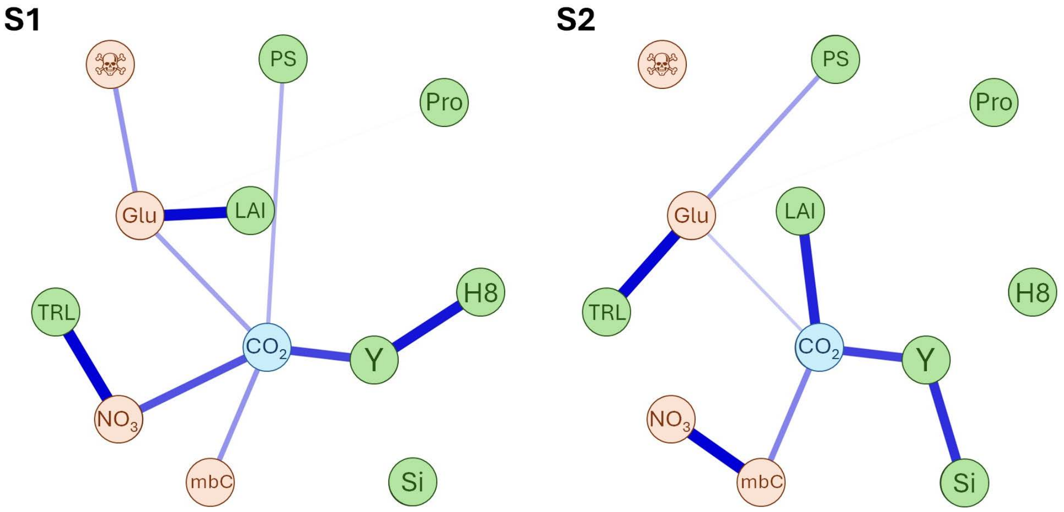

Fig 5. Network analysis of the crop system components in the two soil types (S1: low OM, S2: high OM). Networks of emerging cropping system properties were constructed based on interactions between the discriminant variables Y: Yield, TRL: Total root length, LAI: Leaf area index, H8: Plant height, PS: Photosynthesis (quantum efficiency of PSII), Si: Foliar Silicon, Pro: foliar prolin, mbC: Microbial biomass carbon, ☠: Pathogen *G.tritici*, Glu: Glucose, NO_3: Nitrate (aq.), CO_2: soil-emitted carbon dioxide. Variables are represented by nodes (circles), and the interactions between the variables are represented by edges (lines). The thickness of the edges corresponds to the value of the edge weights, in this case all interactions with evidence for inclusion represent positive relations (blue edge). Edge evidence plots for inclusion or exclusion and network evaluation criteria are shown in Fig C, Table F and G in S1 File.

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($p = 0.095$). Foliar proline also stood out in 2085 ($p = 0.07$), with an opposite trend to silicon, having lowest values in S2.2085 and highest in S1.2085 together with S1.2068 (Fig 3K).

Take-all disease is a common struggle in winter wheat plantations [54] and was quantified at BBCH80 in this experiment (Fig 3L). Symptoms of root infestation with the fungus *Gaeumannomyces tritici* (take-all index) were increased in 2085, especially in S1, but overall no significant climate or soil effect was detected ($p = 0.06$).

Rhizosphere processes and environmental impact

Decreased total root length (TRL) was amongst the main characteristics of the two future cropping systems on S1 in the ordination (Fig 3O, Fig 4). TRL differed particularly at the early stages of plant development where it was higher in S2 compared to S1, but TRL was not significantly different ($p = 0.08$). Microbial biomass in the root zone was quantified at three time points corresponding to BBCH 30/50/80 (Fig 3E), where it was always higher in S2 compared to S1 ($p = 0.03$). Microbial biomass was one of the main characteristics of the S1.2068 cropping system, together with glucose equivalent (Fig 3P, Fig 3N, Fig 4). Detectable glucose levels averaged around 0.038 mg ml^{-1} in all modalities and were one of the main characteristics of the S1.2013 cropping system (Fig 4). There was a periodical variation in glucose concentrations with a common low level during winter and then varying peaks according to climate and soil type (Fig 3N). The overall lowest levels of glucose were detected in S1.2013. Later in the experiment, the largest spikes were detected in the 2085 climate, with the all-time highest peak at the beginning of August in S2.2085 (Fig 3N). Freely available nitrate presented high temporal variation just as did glucose levels (Fig 3M), yet nitrate in soil solution was overall significantly higher in the two future climates ($p = 0.02$) and globally not significantly different between soil types. Most notable spikes in free nitrate were detected in S1.2068 and S1.2085 (Fig 3M) and according to the DNDC model, the risk of nitrate leaching was always higher in S1 compared to S2 (Fig 3T), but not statistically significant for soil nor climate. The DNDC model also predicted both higher soil CO_2 emissions and higher soil N_2O emissions for S2 compared to S1 (both $p = 0.05$). Comparing predicted GHG emissions (e.g., CO_2 and N_2O) across the three climate scenarios revealed an overall trend towards decreasing soil N_2O and increasing soil CO_2 emissions with increasing hydrothermal index (Fig 3R,3S).

Discussion

Yield, soil organic matter and synthetic fertiliser: Less is more?

The future climates accelerated the yield gap between S1 and S2, which was minor in 2013 (-0.29 t ha^{-1} (-8%) in S2, $p = 0.65$), in 2068 summed to a difference in grain yield of one ton per hectare (-22% in S2, $p = 0.07$) and in 2085 amounted to two tons per hectare less in S2 (-40%, $p = 0.03$) (Fig 3Q, Table 2). This yield gap may partly relate to the fact that the S1 soil received ¼ more mineral N fertiliser than S2; however the S2 soil was characterised by 2x higher total C and N contents than S1 and fertilisation was adjusted to provide equal amounts of nitrate in all soils at the end of respective winter periods (Table C in S1 File). Given that the theoretically equal amounts of N are not reflected in equal plant performance in the two soils in the future climate scenarios suggests a negative impact of climate change on nutrient cycling and plant nitrogen availability in high-OM soil. Under climate change, the high soil OM content may limit the yield potential of winter wheat due to enhanced nutrient immobilization in larger and more active belowground food webs (Fig 4, 5). Nutrient immobilisation can occur when microbes incorporate mineral elements into their cells during catabolic processes, temporarily locking them away from plants [55]. Moreover, in complex soil food webs, nutrients like nitrogen and phosphorus can be immobilized within higher trophic levels (e.g., protozoa, nematodes), which can hinder plant growth, especially in nutrient-poor soils or during early growing seasons when plant demand is high [56–58]. For example, in systems with high carbon-to-nitrogen (C:N) ratio inputs (e.g., straw), microbes may outcompete plants for nitrogen, causing temporary deficiencies in N for plants [59,60]. Balanced organic inputs (e.g., mixing high C:N materials with low C:N materials like legumes) and timing applications to match plant growth stages can minimize N-immobilization [61]. Accordingly, in this experiment soil nitrate (NO_3) was positively correlated with total root length (TRL) in S1, but with microbial biomass in S2 (Fig 5). In line with this observation, one factor which likely further contributed to the higher yields in the low OM input system (S1) compared to the high OM input system (S2) is the contrasting C-limitation and N-mobility in the two systems. In the S1 soil, which is characterised by lower SOC and microbial biomass than S2, plant C-inputs are cycling faster through the belowground food web than in S2 because S1-microbes have high qCO_2 which is inversely correlated with CUE (Fig F in S1 File) [62]. Consequently, proportionally less N is bound in the build-up of microbial and meso-fauna biomass belowground in S1 than in S2, meaning the available N-pool can be relatively more accessible to plants in S1. Plant N-uptake in S2 on the other hand competed with a larger belowground food web and microbes with higher CUE, therefore possibly requiring a larger plant C-input to generate a nutrient surplus from the soil food web and/or from SOM via positive priming effects [55,56,60,61,63–65]. The lower return-on-investment for plant-C inputs due to C-buffering and nutrient retention belowground in S2 possibly contributed to the reduced yield observed in the S2 soil, but at the same time potentially reduced the risk of N-leaching (Fig 3Q, 3T).

Overall, the proportional increase in yield with the hydrothermal index for S1 supports previous findings that optimal moisture and temperature conditions can lead to substantial yield improvements for winter wheat in the future [66,67]. In this study, yields in the high OM soil S2 increased in the near future scenario of 2068, but in the far-future scenario of 2085 yields decreased strongly. In contrast, yields constantly increased for S1 across the climates and were always higher than in S2 (Fig 3Q, Table 2). The better realisation of the yield potential in future climates with higher CO_2 and warmer temperatures in S1, but not in S2, aligns with a mesocosm experiment in California which also found that higher soil organic carbon does not relate to higher wheat yields [68] and with a survey of European farms which found a poor association between soil organic matter and crop yields [69]. The observation in this experiment that high soil OM content can limit the yield potential of winter wheat especially in future climate confirms one of the major concerns of regenerative agriculture, which provides many ecosystem services, but often lags behind in agronomic yield, especially in systems using mixed approaches and still regularly applying mineral N-fertiliser [70–73].

Given that soil properties play a key role in wheat productivity, especially as climate conditions fluctuate [74], future studies could investigate how nutrient retention and release in belowground food webs under higher SOC affects cropping systems in the long-term, and how we need to adjust fertilisation schemes to account for the impact of climate change on nutrient cycling to leverage the full potential of belowground biodiversity in connection with plant performance.

Should we consider GHG-emissions when using soil organic matter as indicator of "soil health"?

Most anthropogenic CO_2-emissions (86%) originate from fossil fuels, fossil carbonates such as in cement manufacturing, and other industrial processes including production of chemicals and fertilizers. Land use change and land management on the other hand are the main contributors to long-lived N_2O-emissions. Currently, 10–20% of total agricultural GHG emissions originate from soil, where the magnitude depends on region and farming practices [10]. CO_2 is the major contributor to these emissions (74%), but it has a lower radiative forcing than N_2O [75]. In this study, modelling results suggest that the contribution of soil-emitted GHGs (CO_2 and N_2O) could significantly increase under future climates (Fig 3R, 3S), which has important implications for future management practices related to net zero goals. High SOC and microbial biomass are generally considered to indicate healthy, fertile soils with robust ecosystem services [76]. However, nuances and potential trade-offs should be carefully considered, such as the here and elsewhere observed potential for higher GHG-emissions from high-OM soils due to enhanced biological activity [77,78], a tendency which can be even more amplified under global warming [79,80]. Depending on pedo-climatic context, high soil OM also bares the risks of clay dispersion and surface crusting due to ionic imbalances following organic amendments [81]. The here observed risk of increased levels of soil-emitted CO_2 and N_2O from enhanced activity of soil organisms in the high OM soil (S2) especially in the far-future scenario of 2085 is in line with kinetic theory, which predicts that the higher the particulate organic carbon (POC) and microbial biomass contents of a soil, the higher the rates of microbial respiration, even more so when mineral-associated organic carbon (MAOC) is saturated and under higher temperatures [82–85], and further supported by the results of the DNDC-model (Fig 3R, 3S, Fig E in S1 File). While the CO_2 observations are based on simplified respiration assays [32] and CO_2 and N_2O budgets are based on modelling only [37], they also align with field experiments using respiration chambers to compare CO_2 emissions in conventional and organically amended fields, which indicate up to more than 2x more CO_2 emitted in the latter [77,78,86]. Similar observations have been made in comparison of different tillage systems, where no-tillage increases SOM and the abundance of belowground organisms as compared to standard tillage, but also increases soil-emitted CO_2 up to 3x and often associates with lower yields [58,87]. Therewith, the here and elsewhere observed tendency for higher soil CO_2 emissions in high OM soils indicate a potential for saturation of MAOC and high reactivity of POC [88,89], which together with the tendency for lower crop yields in high-OM soils (Fig 3Q) [78] presents a potential trade-off associated with SOC-increasing strategies which deserves to be considered. A full assessment of environmental impact however requires multi-year data across various crop rotations and life cycle assessments (LCA) including comprehensive C and N balances, as for example enhanced soil CO_2 losses could be compensated by increased SOC formation and lower C-exports in aboveground biomass and negative balances for other GHGs [86,90,91]. In the same sense, microbial biomass and respiration are nuanced indicators of soil health to be used with care because i) microbial respiration alone doesn't allow to distinguish between activity of beneficial or harmful microbes and ii) soil-emitted CO_2 is a two-sided coin as it's enhancement can have negative impacts on global warming [79,80,92–94]. Using microbial respiration as soil health indicator means applying double standards: a positive connotation for increased microbial activity, and a negative connotation when excessive CO_2 losses from soils, which can undermine carbon sequestration goals and fuel global warming. For instance, in tropical soils or disturbed systems, high microbial activity can lead to repeated breakdown and renewal of organic matter, which results in rapid organic matter cycling potentially offsetting carbon storage benefits [95]. This is no minor issue, since it is estimated that greenhouse gas emissions from soil alone already account for 15% of the entire global increase in climate warming, with carbon dioxide being the most important gas emitted from soil (74% of total soil-derived warming), followed by nitrous oxide (17%) and methane (9%) [75]. To develop reliable and unambiguous soil health indictors, it is therefore critical to consider multi-indicator systems combining soil carbon content with physical (e.g., bulk density, water holding capacity) and biological (e.g., enzyme or gen activity) metrics for holistic assessments of the relationship between soil carbon, belowground food webs and nutrient cycling, as these links are fundamental to understanding soil health and its role in biogeochemical cycles and cropping system performance [61,96]. For example, soil organic carbon (SOC) was originally proposed as critical measure to assess soil restoration, but cannot be used as a stand-alone indicator of C-sequestration because soil C sequestration requires free mineral binding sites which are not found in particulate organic matter (POC) and mineral binding sites can be saturated [64,88]. Therefore, the soil C indicator has been modified to a threshold-based parameter aiming at a SOC-to-clay ratio of >1:8 [97,98] or the emergent effective MAOC capacity [89]. The difficulties arise because SOC-to-clay ratios can be sensitive to clay content and disproportionately flag clay-rich soils as degraded, in addition to inconsistent results compared to national GHG inventory data and failure to account for climate, land use, or management practices [99].

Importance of multi-scale performance indicators beyond agronomic yield

To provide a more holistic, sustainable, and realistic assessment of agricultural systems, it is important to evaluate performance indicators beyond agronomic yields. While yield is a key metric, system longevity, sustainability and equity also depend on economic, social and resilience parameters. For example, in this study resource retention belowground did not benefit crop yield in S2 in neither climate scenario, but increased the systems' capacity to defeat the root pathogen *G. tritici* in the far-future scenario in S2, possibly linked to plant cells strengthened by silicon (Fig 5). This increase in disease resistance is an important ecosystem feature and could become even more vital in more extreme crop seasons. However, it also must be noted that the overall abundance of fungal pathogens was higher in S2 than in S1, which could have contributed to the reduced yields in S2 as the plants had to allocate more C into pathogen defence rather than aboveground biomass (Fig H in S1 File). Similarly, soils fertilised with on-farm produced materials or their by-products reduce dependence on external inputs and their higher biodiversity above and belowground can increase resilience against environmental and biological stressors [100,101]. Environmental indicators such as water use efficiency provide insight into the ecological integrity of the system, with efficient water and nutrient use not only preserving resources but also minimising pollution risks [102,103]. Similarly, resilience indicators assess the system's capacity to withstand and recover from disturbances such as drought, pests, or market fluctuations. These include yield stability across seasons, diversity in crop species, and the system's ability to maintain function under stress. For example, a diversified cropping system may buffer against pest outbreaks and climatic extremes better than a monoculture [70,100]. Together, environmental and socio-economic indicators provide a more nuanced understanding of system performance and can help recognize vulnerabilities and design interventions that enhance both productivity and sustainability over time. Focusing on these indicators is critical for adapting agriculture to climate change and resource constraints.

Quality of harvested grains

To prevent malnutrition, it will also be important to determine the nutritious value and technological properties of the harvested grains [104]. In this study, grain nitrogen content was not statistically different between soil types or climates, but tended to decrease the further in the future the climate scenario (Table 2). This could be due to the flexibility of the multiple biological belowground nitrogen sinks and sources which can buffer variability in exogeneous N-input and thus stabilise the plant-available N-pool to a certain extend [63]. Accordingly, the grains harvested in this experiment were not N-depleted as previously observed in FACE-experiments, suggesting that either belowground N-buffering, increased nitrogen use efficiency at plant-level and/or N-remobilization during ripening can to a certain extend compensate dilution effects from CO_2-fertilisation [105–107]. Interestingly, in this study thousand grain weight (TGW), which is an important component of crop yield linked to potential flour yield [108], increased in parallel to the overall yield for the future climate scenarios, but had no consistent relation with soil type (Table 2). This presents a potential opportunity for breeding programs, as elevated TGW is linked to the stress resilience of wheat plants and can prevent premature ripening, while also positively influencing seedling vigour in the next generation [109]. However, developing a soil management plan to target these traits requires more empirical data to establish consistent trends between soil management practices and nutrient redistribution during grain filling, taking the shorter growth cycle in the future climates into account.

Naturally balancing the nitrogen cycling?

N_2O is a relevant greenhouse gas with much higher global warming potential than CO_2 [10,22]. Agricultural land is one of the main N_2O sources and as higher temperatures stimulate mineralization and nitrification processes and therewith substrate availability for denitrification, increases in N_2O emissions are expected in the future [110]. However, depending on local conditions such as soil moisture and N availability, reductions in soil N_2O emissions are also possible [111,112]. In this study, the DNDC model predicted an overall decrease in soil N_2O emissions for future climates, with higher N_2O-emissions in S2 compared to S1, while the difference between S1 and S2 regarding N_2O-emissions did not change between the years (Fig 3S). As the future years were smoother in the rainfall distribution, the soils were overall drier (Fig 3D,H) and therewith the risk of waterlogging and anaerobic conditions was reduced, limiting denitrification and N_2O production [113]. Moreover, there was no indication of limited plant nitrogen uptake in the future climates (Table 2), which could indicate that the increased soil mineralisation did not lead to nutrient losses in GHGs, but instead nitrogen was taken up by the growing plants. Another mechanism which could have successfully prevented gaseous N-losses could be associated with greater N immobilization belowground, with surplus inorganic NO_3-N and NH_4-N being incorporated into microbial biomass, supporting greater N recycling and retention [65,114,115]. The process of enhanced nutrient immobilisation in microbial biomass could also explain the decreased risk of nitrate leaching predicted for S2 as compared to S1, which has higher microbial biomass, while the sandy texture of S1 likely contributed to its higher susceptibility to nutrient leaching [116]. This means that while low organic matter input may be a soil management strategy to reduce GHG-emissions without compromising yield, soils with higher drainage may experience greater nitrate loss through leaching due to the soils' reduced capacity to retain nutrients effectively. To reduce the environmental impact of high-yielding cropping systems especially on sandy soils it could therefore be interesting to identify soil management practices which allow nutrient and water buffering and increase of SOC without necessarily adding large quantities of composted organic matter or manure to limit a negative GHG footprint, where alternative options could include biochar, clay amendments, cover crops, fertigation or biological nitrification inhibition (Fig G in S1 File).

Stimulating natural plant acclimatisation to mitigate stress

Plants in the future climatic conditions were more prone to stress because of their changed phenology and a higher potential for disease propagation. For example, leaf area index (LAI) increased significantly under future climate scenarios, which not only indicates increased rates of photosynthesis, but a larger leaf area also allows for greater stomatal conductance, which facilitates more water vapor loss through transpiration and may thus stress plants and increase the water requirements of the cropping system [102]. Therewith, plants with larger LAI are more vulnerable to drought spells which can be detrimental for yields [117,118]. Similarly, taller growing plants as observed in the future climates in this experiment are more vulnerable to physical damage from wind and require better rooting systems and stronger cell walls to withstand high wind speeds [74,119,120]. In addition, plant health is expected to worsen under climate change when autumns and winters become milder and wetter which favours water logging and the spread of fungal diseases which may ultimately pose severe risks to food production systems [17]. In this study, the pathogenic root fungus *Gaeumannomyces tritici,* which causes take-all disease, was enhanced in the two future climates, most notably in the 2085 climate, and there particularly in S1, but the pathogenic root infestation did eventually not threaten the yields (Fig 3L, 3Q). This indicates that the plants could trigger successful stress mitigation mechanisms to combat the pathogen. Two factors which could have contributed to the plants' successful defence are proline and silicon. The increase in production of these two factors imply that wheat plants may have evolved adaptive plasticity responses to cope with pathogenic infections. If that would be the case, plant management strategies to increase plant acclimation rates in response to infections could be advisable. Proline functions as a potent antioxidant, scavenging reactive oxygen species (ROS) and reducing oxidative damage, which can help protect cellular structures and macromolecules during stress conditions [30]. Moreover, exogenous proline application has been shown to improve photosynthetic parameters such as chlorophyll content, stomatal conductance, and PSII efficiency in stressed plants [121] and proline accumulation is associated with increased resistance to various pathogens acting as a signalling molecule triggering defence responses and the production of antimicrobial compounds [122]. Silicon on the other hand can contribute to plant health by impregnating cell walls and thus forming a barrier that impedes pathogen penetration, while it also physically strengthens plant stems which could benefit crops that grow taller and are expose to higher wind speeds [31]. Silicon has also been shown to improve drought tolerance which could become even more important in the future as crops grow with larger leaf area like in this study [123] and like proline has been related to oxidative stress mitigation [124].

Implications of phenological advance for farming practices

Plants use various signals to plastically respond to environmental changes, including solar signals which determine the photoperiod, past seasonal experiences like winter chilling, and current conditions such as temperature and moisture [125]. The advancement in harvest date of approximately two weeks between each climate scenario observed in this study reflects this response and aligns with trends observed in other experiments which report that warmer temperatures accelerate crop development and lead to earlier maturity dates, and that in spring photoperiod and winter chilling work together to determine plant growth [125,126]. The here observed phenological advance in future meteorological conditions has significant implications for agricultural management, for example harvesting winter wheat up to four weeks earlier requires adapting the crop rotation cycle including sowing dates and identifying wheat varieties with genetically determined shorter maturation cycles which could be potentially better preadapted to regional climate, soil conditions, and farming goals. For example, short-cycle varieties are preferable in warmer, drought-prone regions of Western Europe (e.g., southern France, Spain) where avoiding summer heat and drought is critical. However, a reduced crop growth season may lower SOC inputs and potentially decrease microbial biomass over time, especially if residue decomposition accelerates under warmer conditions (+3°C). Therefore, faster wheat rotations ideally could be paired with cover crops to offset belowground C-losses and maintain SOC. Longer-cycle varieties on the other hand may be better suited in cooler, wetter regions (e.g., northern Germany, UK), where milder winters and higher HI support extended growth, and benefits from CO_2-fertilisation could be maximized. Higher biomass from extended growth supports SOC accumulation and microbial activity, but late-season drought or heat could reduce residue quality, and elevated CO_2 may increase microbial respiration, releasing CO_2 and reducing SOC stability. A balanced strategy could involve diverse varieties within rotations—short-cycle for riskier years/regions and longer-cycle for optimal conditions—combined with adaptive management (e.g., precision irrigation, adjusted sowing).

Another observation in this experiment was that plants in 2085 reached heights nearly double those recorded in 2013, which is in line with other studies [127]. These taller plants may require more physical protection against wind by means of hedges or trees and harvesting equipment may need to be adapted to the higher positioning of the grains [128]. Overall, the projected advances in crop maturity and plant height could have profound implications for agricultural practices and as climate conditions continue to evolve, further research will be needed to refine models predicting phenological responses and to develop adaptive strategies for sustainable agricultural practices in changing environments.

Ecotron constraints

While Ecotrons are unique tools to study agroecosystems under climate change, they are a compromise operating at an intermediate scale between simplistic microcosm experiments and real-world ecosystems, which still cannot fully replicate the complexity of natural environments [20,129]. It is therefore vital to cross-validate observations from Ecotron experiments with data from field experiments and to replicate experiments sufficiently. A further challenge to Ecotron experiments is the timescale, as exposing soil and miniature agroecosystems to future meteorological conditions without several generations of adaptive changes occurring implies a very abrupt change in climate conditions. In this experiment for example, soil monoliths sampled in November 2022 had about one month to acclimate to the conditions of the simulated November 2085 rather than slowly evolving adaptations through 63 years of climate change. However, the experiment looking at plastic and potentially adaptive responses remains realistic, especially for wheat as a plant with a long growth cycle in a crop rotation, because even in current meteorological conditions, year-to-year climatic variability can result in substantial shifts in meteorological conditions between two wheat seasons (Fig 2). Future experiments could look at how the accumulation of several more extreme seasons affects cropping systems and how the occurrence of individual more extreme events within one growing season impacts crop performance.

Conclusion

This study provides new insights into the complex interplay between climate change, soil organic matter content, and winter wheat performance. The observed phenological advances, increased yields in low organic matter soils (S1) as compared to high organic matter soil (S2), and potentially adaptive mechanisms to cope with stress such as proline and silicon accumulation highlight the capacity of crops to respond to future climate conditions. However, additional research is needed to better understand why in some soil conditions (like S2 in this study) the CO_2-fertilization effect remains limited, and yields decrease under more distant future climates. This may be linked to higher nutrient immobilisation in high organic matter systems compared to low organic matter systems, which could also explain the lower risk of nitrate leaching in S2. To ensure sustainable performance of future cropping systems it would therefore be key to further develop management practices that take the risk of saturation of mineral-associated organic carbon (MAOC) and the high reactivity of particulate organic carbon (POC) into account, and allow more gentle increase of SOC and improved nutrient cycling, such as cover crops (e.g., legumes) or biochar application. Fertigation or biological nitrification inhibition could be tested under future meteorological conditions to assess their potential to optimise nutrient availability and use efficiency in agroecosystems. This study further highlights the need to investigate links between altered soil processes and plant diseases under future climates, where shorter cropping cycles may provide an opportunity to break disease cycles and restore soil nutrient stocks with inter-cropping.

Supporting information

S1 File. Table A: Management history field 1 50°38'35.1474"N, 4°37'22.0123"E (S1). Table B: Management history field 2 50°39'12.8668"N, 4°38'10.7664"E (S2). Fig A: Soil monolith sampling. Table C: Details of mineral N fertiliser applied during the Ecotron experiment. Table D: Empirical and modelled parameter to quantify agronomic performance and environmental impact. Fig B: Correlation between empirical and modelled parameter estimates. Table E: Loadings for the main vector of each modality (Year.Soil). Fig C: Edge evidence plot showing the evidence for inclusion or exclusion. Table F: Edge evidence probability tables for S1 and S2. Table G: Edge evidence probability tables for S2. Fig D: Centrality plot. Table H: Centrality measures per variable. Fig E: Basal and exudate-induced soil respiration measured in situ. Fig F: Metabolic quotient (qCO2) and multiple substrate-induced respiration (MSIR) measured under standardised laboratory conditions. Fig G: Conceptual framework of carbon and nitrogen pools and fluxes in the two soil types S1 and S2. Fig H: Relative abundance of known fungal pathogens in the two soils S1 and S2 in the three climates 2013, 2068 and 2085, each measured at three time points.
(PDF)

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