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The overlooked effects of environmental impacts on root:shoot ratio in experiments and soil-crop models

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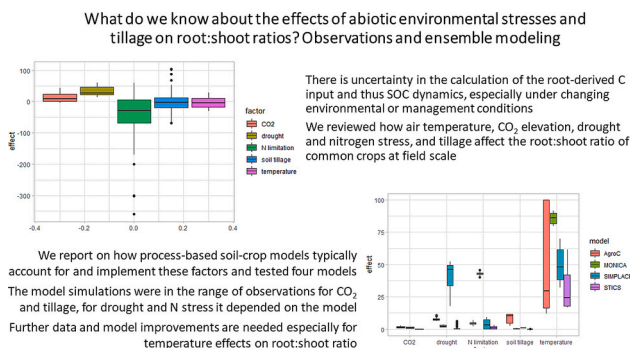[c] Drought Research Center, Shiraz University, Shiraz, Iran
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HIGHLIGHTS

- Predicting root-derived C inputs and SOC under varying conditions is challenging.
- We reviewed how various environmental factors affect root:shoot ratio at field scale.
- We compared soil-crop models simulations for environmental stress responses.
- Model simulations were in the range of observations for CO_2 enhancement and tillage.
- Temperature effects on root:shoot ratio require further data and model improvements.

GRAPHICAL ABSTRACT

What do we know about the effects of abiotic environmental stresses and tillage on root:shoot ratios? Observations and ensemble modeling

There is uncertainty in the calculation of the root-derived C input and thus SOC dynamics, especially under changing environmental or management conditions

We reviewed how air temperature, CO_2 elevation, drought and nitrogen stress, and tillage affect the root:shoot ratio of common crops at field scale

We report on how process-based soil-crop models typically account for and implement these factors and tested four models

The model simulations were in the range of observations for CO_2 and tillage, for drought and N stress it depended on the model

Further data and model improvements are needed especially for temperature effects on root:shoot ratio

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ABSTRACT

Process-based soil-crop models are becoming increasingly important to estimate the effects of agricultural management practices and climate change impacts on soil organic carbon (C). Although work has been done on the effects of crop type and climate on the root:shoot (biomass) ratio, there is a gap in research on the effects of specific environmental or management conditions such as drought, temperature, nutrient limitation, elevated CO_2 or tillage on the root:shoot ratio and thus, atmospheric C sequestration. In this study, we quantified the effects of these factors on the root:shoot biomass ratio by reviewing the current literature, presented common simulation approaches and performed model simulations using different examples. Finally, we identified different research gaps with respect to the root:shoot ratio with the aim of better estimating and predicting atmospheric C sequestration. A predominantly positive response of the root:shoot ratio was observed in case of elevated CO_2 (~12 %), low soil N levels (~44 %), and drought (~14 %). Soil tillage did not affect root:shoot ratio of the major field crops but increased it by ~15 % in case of wheat. There are only few field studies on air temperature increase and the results vary widely (mean − 48 %). The responses of tested models to the mentioned effects root:shoot ratio were slightly positive in case of CO_2 elevation (0 to 2 %) and tillage (0 to 8 %),

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slightly to clearly positive in the case of drought and N limitation depending on the model (1 to 40 %), and very variable in case of the air temperature scenarios. Our study reveals large model uncertainty (especially on temperature effects), particularly for below ground processes that highlight knowledge gaps in simulating root: shoot ratio. We advocate for the need of more model-oriented specific experiments under abiotic stresses to help model improvement. Such research effort would enable more robust and reliable root:shoot ratio simulations.

1. Introduction

Climate-smart use of agricultural soils has a great potential to become a managed sink for atmospheric CO_2. To increase soil organic carbon (SOC) stocks through agricultural activities is considered a negative emissions technology (Merante et al., 2017; Lal, 2019) and has led to the 4 per mille initiative launched at the COP21 aiming to increase SOC stocks by 0.4 % annually (Minasny et al., 2017). At the same time, climate change-driven SOC losses to the atmosphere might hinder such benefit (Riggers et al., 2021). In soils, root-derived C inputs (roots, exudates, secretes) in deep soil layers are a major stable source of SOC, due to limited microbial activity with increased soil depths (Chen et al., 2020; Yu et al., 2022). Other sources of C input besides roots are fertilizers (e.g., farmyard manure, compost), and above ground crop residues (e.g., stubbles, dead leaves) (Ranaivoson et al., 2017), which are incorporated mainly into the top soil.

On average, plants allocate 76 % of C stocks to shoots and only 24 % to roots (Mathew et al., 2017). Only few studies that have investigated the quantitative relationship between plant C and SOC (Mathew et al., 2017). According to Kuzyakov and Domanski (2000), cereals transfer 20–30 % of total assimilated C to the soil. Half of this amount is subsequently found in the roots and about one third in the CO_2 extracted from the soil by root respiration and microbial utilisation of root organic matter (Kuzyakov and Domanski, 2000). Based on experimental data of the Swedish Ultuna long-term continuous soil organic matter experiment, Kätterer et al. (2011) reported that root-derived C contributes more to relatively stable soil C pools than the same amount of above-crop residue-derived C. In their meta-analysis, Mathew et al. (2017) compared data of 389 field trials to determine allocation of biomass and C in plants and SOCs under fields of different crop types considering long-term mean annual precipitation and mean annual temperature, geographical location and soil properties (clay content, bulk density and pH). Grasses and cereals had the highest potential for C sequestration. Furthermore, the authors stated that the highest C sequestration would be expected to occur in tropical climates. Beside crop type and climate, agricultural management can affect soil C input dynamics in agricultural soils (Stockmann et al., 2013).

The application of dynamic carbon models to report changes in SOC stocks is becoming increasingly important (Jacobs et al., 2020; Keel et al., 2017; Riggers et al., 2019; Riggers et al., 2021). However, there is a large uncertainty in soil carbon modelling related to method of calculating of plant C input in agricultural systems (Keel et al., 2017). Most process-based multi-compartment SOC models such as ROTH-C, Yasso, Candy carbon balance, or IPCC equation describe SOC decomposition by first order kinetics and define different SOC qualities represented by interacting SOC pools (Farina et al., 2021). C-pool decomposition rates are modulated by external factors, such as soil temperature, soil moisture (sometimes aeration), or soil texture (mostly clay content). These SOC models use crop-specific coefficients to quantify soil C inputs for above- and below-ground plant residues including exudates and dead roots (Keel et al., 2017). Additionally, these models assume either a linear relationship between yield and C input, or use a yield-independent C input (Keel et al., 2017), which increases the uncertainty when calculating C inputs as the methods selection can lead to different results. This approach also constrains the modelling to soil processes and excludes the simulation of shoot and root growth responses to changes in the environment.

Process-based one-dimensional field-scale soil-crop models are composed of different sub-modules for certain processes related to crop growth and soil-nutrient and water dynamics in response to atmospheric conditions and management practices. Biomass increment can be affected by water and nutrients (mainly nitrogen N) availability in a given physical environment (Ittersum et al., 2003). Drought stress effects on crop growth are often quantified by the ratio between actual and potential transpiration and often lead to an increased dry matter allocation to root biomass while reducing leaf biomass (Ittersum et al., 2003). Current model intercomparisons have shown that root simulations, and how roots impact SOC formation via root biomass residues, largely diverge among models (Couëdel et al., 2024). Process-based crop models simulate several of the above mentioned C inputs and related processes such as shoot and root biomass production of main and catch crops, fertilizer input (including organic fertilizers like manure with defined C contents), and plant residue return to the soil. Several process-based crop models simulate also SOC turnover including soil respiration and microbial activity and microbial biomass production. Currently, only very few crop models consider root exudates such as AgroC (Klosterhalfen et al., 2017) as a source of C to the soil. Several crop models also simulate the effect of tillage practices on soil states (Maharjan et al., 2018). Therefore, crop models can potentially capture in season stress effects on the root:shoot ratio (calculated by dividing the total root biomass by the shoot biomass) and yield and long-term feedbacks (legacy effects in crop rotations, C sequestration) of environment and management practices on total biomass and soil C input.

However, the simulation of effects of extreme climate events such as heat, drought, and excess water on crop growth, which are expected to become more frequent in the future, are not always well considered in crop models (Kim et al., 2024; Webber et al., 2022), therefore, predicting agronomic management impacts (e.g., fertilization, crop rotation) on agroecosystem performance under future environments poses an additional challenge (Peng et al., 2020). Although the effects of crop type and climate on atmospheric carbon sequestration have been studied (Bolinder et al., 1997, 2007; Kuzyakov and Domanski, 2000; Mathew et al., 2017), there is a lack of knowledge about the effects of atmospheric CO_2 elevation, air temperature change, drought, N deficiency and conventional tillage on the root:shoot ratio, which is also reflected in the modelling approaches and simulation capabilities.

For given inputs, variability in soil-crop model simulations arises from variability in the model equations (structure) and the used parameter values (Wallach et al., 2024; Wang et al., 2024). To our knowledge, dry matter partitioning as main sources of uncertainty in climate change impact assessment for agricultural crop yield has not been investigated before. Consequently, there is an urgent need to evaluate and improve the simulation of the root biomass-derived soil C input, and therefore, atmospheric C sequestration potential considering environmental conditions and (changing) agricultural management practices.

In this study, we focused on testing the sensitivity of model equations to the different inputs for fixed model parameters. We i) review how the root:shoot ratio and the root biomass-derived C input via root biomass of common arable crops are affected by atmospheric CO_2 elevation, air temperature change, drought, N deficiency, and conventional tillage; ii) report how process-based soil-crop models account for these factors in their equations, and iii) compare and evaluate the sensitivity of four process-based soil-crop models to simulate the impacts of these factors on root:shoot ratio and absolute root biomass input in the soil in a scenario analysis.

2. Materials and methods

2.1. Observed effects of abiotic factors and tillage on root:shoot ratio of crops

In total, we found and reviewed 12 articles on the effects of atmospheric CO_2 elevation (3 of them were meta-analysis or reviews), 7 of air temperature variation, 7 of drought (3 reviews), 13 of N deficiency, and 29 articles of soil tillage effects (no-tillage vs. conventional or reduced tillage) on root:shoot ratio of common agricultural crops observed under field conditions (or semi-natural conditions) (sources see supplementary material). The major outcomes of these factors on root:shoot ratios are presented in the following sub-sections.

2.1.1. Elevated atmospheric CO_2 levels

Enhanced atmospheric CO_2 generally leads to increased biomass growth and root:shoot ratios due to improved water use efficiency, which indicate a proportional stimulation of below-ground biomass production, though the magnitude of the response can vary among crop species (Fig. 1) (Vanuytrecht et al., 2012). A review by Rogers et al. (1995) showed substantial variation in root:shoot ratio response to enhanced CO_2 for various crops, with a mean positive response of 7 % (12 % for <580 ppm). In 59.5 % of the cases, the root:shoot ratio increased, whereas in 37.5 % of the cases it decreased, and in only 3 % of the cases it remained unchanged. However, most experiments were conducted under controlled conditions. Results from a meta-analysis on agricultural crops showed that above ground biomass and root:shoot ratio increased substantially, by 15 % and 14 %, respectively, for elevated CO_2 between 541 and 580 ppm, and further increased by 35 % when CO_2 ranged between 581 and 620 ppm (Vanuytrecht et al., 2012). Another meta-analysis in a wide range of ecosystems reported a significant root:shoot ratio increase of 12 % for agricultural crops (Nie et al., 2013).

With regards to wheat, we identified only four field FACE studies that provide data on root:shoot ratio. Kou et al. (2007) used two atmospheric CO_2 concentration levels (350 and 550 ppm) and high or low N fertilizer. The reported root:shoot ratio declined between 2 (low N) and 8 % (high N) in all treatments. In contrast, Ma et al. (2007) reported about 20 % (low N) and 25 % (high N) higher wheat root:shoot ratio under elevated

CO_2, with the strongest increase observed between jointing to heading stages. As for spring wheat, Wall et al. (2006) reported increased of root:shoot ratio due to elevated CO_2 (ambient 370 ppm vs. ambient +180 ppm) by 10 and 3 % under dry and wet conditions, respectively. But, during another growth period, elevated atmospheric CO_2 led to about 3 % (dry conditions) and 7 % lower (wet conditions) root:shoot ratio. In two open top chamber experiments with elevated CO_2, Rønn et al. (2003) reported a 2 % decrease of root:shoot ratio, whereas Qiao et al. (2010) reported an increase of root:shoot by 22.8 % and of 9.1 % under well-watered and drought conditions, respectively. Considering these six FACE and open chamber wheat studies, a mean positive response of

Table 1

Effect of factors on observed (obs) root:shoot ratio (mean, minimum, and maximum differences) of common agricultural crops and of winter wheat observed under field conditions and semi-natural controlled conditions in case of low data availability. Simulated values are ranges of the applied models where each value represents the mean of the daily difference in % from end of tillering to end of flowering of winter wheat of the scenarios with the highest difference.

Factor	Obs root:shoot of common crops	Obs root:shoot of winter wheat	Simulated in this study
Elevated CO_2[1]	+12 %, +14 %, +12 % (−11 % to +47 %)[1]	+5 (−5 % to +16 %)[2]	0 to +2 %
Drought occurence	13.5 % (+13 to +59 %)[3]	+21 % to +27 %[4]	+1 to +40 %
Nitrogen deficiency	+44 % (−22 % to +121 %)[5]	+64 % (+40 % to 84 %)[5]	+1 to +43 %
Air temperature increase [5]	−20 % to +26[6]	−20 % to −30 %[6]	−30 to −86 %
Soil tillage	0.5 % (−104 % to 69 %)[7]	2.4 % (−25 % to 45 %)[7]	0 to +8 %

[1]Considering Rogers et al. (1995) and Vanuytrecht et al. (2012) with CO_2 increase <580 ppm with 12 % and Nie et al. (2013); [2] Considering only the six FACE and open top chamber studies; [3] Based on the review of Zhou et al. (2018); [4] Based on Fang et al. (2017); [5] based on Lopez et al. (2023); [6] Air temperature increase compared to normal conditions/ control. Based on Füllner et al. (2012) and Rehman et al. (2019); [7] On average, CT (conservative and conventional tillage) increased root:shoot ratio in wheat by 14.8 % compared to NT (no-tillage) based on 8 studies with $n = 16$ data pairs. Considering only winter wheat, the increased root:shoot ratio is only 2.4 % (4 studies, 9 pairs).
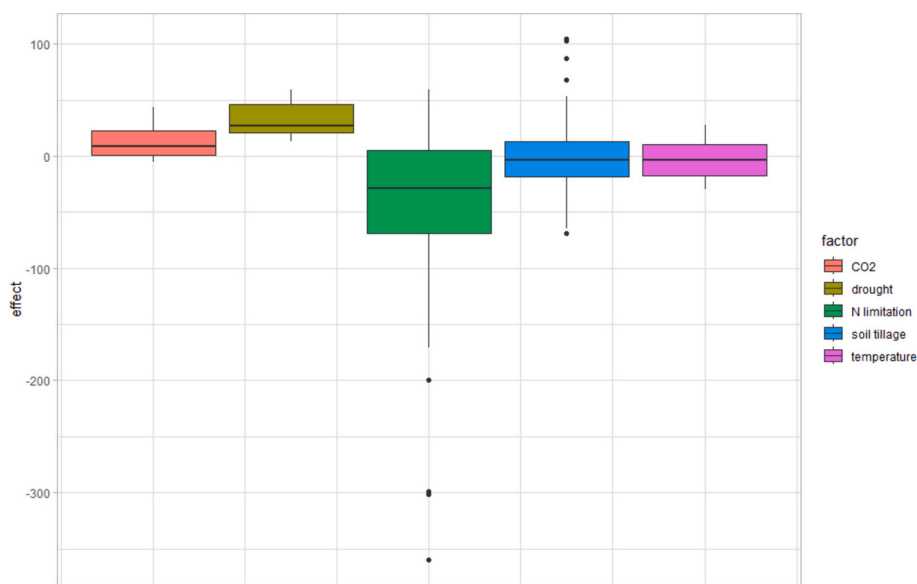

Fig. 1. Effect of abiotic factors on observed root:shoot ratios of common agricultural crops under field and semi-natural controlled conditions in case of low data availability. The data show the percentage effect of ambient CO_2 elevation (number of data points $n = 15$), drought stress ($n = 7$), nitrogen (N) limitation ($n = 191$), increasing air temperature ($n = 10$) and conventional soil tillage (vs. no-tillage or conservative tillage, $n = 68$). The data source can be found in the supplementary material.

5 % on root:shoot ratio to elevated CO_2 was observed (Table 1, range: −5 % to +16 %, $n = 9$). However, the root:shoot response of wheat, and other agricultural crops, to elevated CO_2 experiments is contradictory as evidenced by the wide range of results obtained from different studies. Additionally, CO_2 may interact with other factors such as water and nutrient supply, genotype, plant age. For instance, legumes, root and tuber crops are expected to have a greater response to elevated CO_2 (Butterly et al., 2015; Rogers et al., 1995), with increased response under well-watered (23 %) than under drought conditions (9 %) (Qiao et al., 2010). In general, it was found that root:shoot ratio increased when increasing ambient CO_2 levels by a mean of 12–14 % (Table 1).

2.1.2. Water supply and drought

Drought is one of the main abiotic stress factors in agriculture, which negatively affect crop growth and development, and therefore, crop productivity (Fahad et al., 2017; Farooqi et al., 2020). Changes in root architecture and distribution are important mechanisms to cope with drought stress in crops (Dietz et al., 2021; Matsui and Singh, 2003; Siddiqui et al., 2021), as well as changes in root:shoot ratio (Seleiman et al., 2021). In a synthesis of global field trials synthesized data from 128 published studies, Zhou et al. (2018) showed that drought significantly decreased root length and root length density by 38 % and 11 %, respectively, but increased root diameter by 3.5 %.

In general, root:shoot ratio tends to increase under drought conditions, but the magnitude of increase depends on the crop as well as on timing and magnitude of the stress. Kou et al. (2022) reported, that under drought stress conditions, crops with fibrous root systems resulted in 22 % increase in root:shoot ratio, while in crops with tap root systems, the root:shoot ratio increased by 43 %. Zhou et al. (2018) reported that drought stress tends to increase the root:shoot ratio by 13.5 % (Table 1), with a wide range of variation depending on the crop and magnitude of drought stress. Additionally, root:shoot ratios responded negatively to drought at <25 % intensity (moderate drought stress), but increased at 25–50 % and > 50 % intensity (severe drought stress). Root:shoot ratio increased in wheat when drought stress was applied during the vegetative stage, which resulted in an increased crop growth rate due to the higher root water uptake and gas exchange (Bacher et al., 2022). Fang et al. (2017) reported different responses to moderate drought stress (rainfed vs. irrigated) in an old and a modern winter wheat cultivar grown under field conditions, where the root:shoot ratio increased in the old cultivar by 27 % and increased in the modern cultivar by 4 %. For legumes, a similar response of increasing root:shoot ratio under drought stress has been reported although some crop legume species, like cowpea, are more tolerant to drought stress (Du et al., 2020; Matsui and Singh, 2003; Pang et al., 2011). Root length density, root depth, and root dry matter can potentially be used for selection of drought tolerance cultivars (Matsui and Singh, 2003). However, selection for increased root:shoot ratio can be challenging. A study conducted with 99 wheat genotypes showed a negative correlation between root:shoot ratio and grain yield, high environmental variance and low heritability as limitations for breeding cultivars to have more root biomass and maintain grain yield under drought conditions (Mathew et al., 2018).

2.1.3. Nitrogen supply and soil nitrogen limitation

Plant root characteristics play a crucial role in acquisition of resources and plant performance, especially when the availability of nutrients in the soil is low. Several field studies on the effect of N deficiency report increased root:shoot ratio (Welbank and Williams, 1968; Myers, 1980; Anderson, 1988; Eghball and Maranville, 1993; Sharifi et al., 2005; Wang et al., 2005; Farrior et al., 2013; Xue et al., 2014; Hadir et al., 2021). In a meta-analysis of 50 field studies considering nitrogen (N), Lopez et al. (2023) found that the root:shoot ratio was often enhanced (mean of 44 %, based on 13 studies) under N-poor conditions. Two studies conducted by Anderson (1988) and Eghball and Maranville (1993) reported an increase in the root:shoot ratio of maize under nitrogen-deficient conditions, particularly in low N conditions.

Anderson (1988) observed a significantly higher root:shoot ratio in unfertilized trials compared to the high fertilization (application of 180 kg N per ha) across three years of evaluation. In winter wheat, Xue et al. (2014) also observed an increase in the root:shoot ratio with decreasing N supply. The data are similar to those provided by Wang et al. (2014), who found that no fertilization treatments significantly increased the root:shoot ratio in winter wheat. However, N applications were particularly beneficial for the shoots, leading to a decrease in the root:shoot ratio when N was applied (Welbank and Williams, 1968). While most studies have reported an increase in the root:shoot ratio under N deficiency, few studies have found variable effects on the ratio depending on other factors studied. Feng et al. (2016) reported that maize root:shoot ratio at silking was higher in the no fertilization treatment, except in the loamy clay soil in one out of the three years of the study. In sugarcane, N deficiency led to a decrease in the root:shoot ratio at the beginning of the production cycle at one out of two experimental sites, with similar ratios observed between treatments in later growth stages (Otto et al., 2014). In general, Lopez et al. (2023) reported that root:shoot ratio increased with decreasing N level by a mean of 44 % and 64 % for wheat (Table 1).

2.1.4. Air temperature

Air temperature is an important factor for phenological development and above and below plant growth (Gregory, 2006). Optimal temperature ranges, and thus, the effect of temperature on the root:shoot ratio, seem to differ strongly between crop species (Koevoets et al., 2016). For wheat, reported optimal air temperatures for root growth range around 16.3 ($\pm$3.7)°C, while optimal air temperatures for shoot growth range around 20.3 ($\pm$0.3)°C (Porter and Gawith, 1999). Under non-optimal root zone temperatures, root:shoot ratios increased compared with optimum temperature ranges (Koevoets et al., 2016). In a pot study with barley, Füllner et al. (2012) found a 21 % (from 0.39 to 0.31) mean decrease in root:shoot ratio when changing the root temperature from 10 °C to 20 °C. In another pot experiment where air temperatures were increased from 25/20 °C (day/night) to 36/28 °C Rehman et al. (2019) observed a root:shoot ratio decrease of 20 and 30 % in two wheat cultivars. These changes in root:shoot ratios might, however, not be directly related to temperature but adaptations to restrictions in water and nutrient uptake (Wilson, 1988; Equiza et al., 2001, de Lima et al., 2021).

While the previously listed studies can give us a good understanding of physiological responses of roots and of the root:shoot ratio to changes in temperature, these experiments are also limited in transferability as they have been conducted under controlled conditions in pot experiments. One of the main differences between field trials and most pot experiments is the temperature gradient in natural soils, where temperature is not uniform but changes with depth. In a pot study with and without temperature gradients, Füllner et al. (2012) observed that barley roots exposed to a vertical gradient in soil temperature of 20–10 °C had a 161 % higher root:shoot ratio than plants grown under uniform soil temperature of 20 °C. Additionally, observations from most pot experiments are focussing on early developmental stages. Although, widely accepted methodologies to alter soil- and atmospheric temperatures under field conditions exist (Patil et al., 2013), field experimentation on root growth remains are rare. In a study where two maize varieties were grown in buried pots in three environments with mean air temperatures of 14.6, 16.9, and 18 °C respectively, Richner et al. (1996) observed highest root:shoot ratios under mean air temperatures of 14.6 °C at the four-leaf stage. Ordóñez et al. (2020) reported positive correlation between temperature and root:shoot ratios in a study with maize and soybean at 10 different sides in the U.S. State Iowa. Hou et al. (2018), applied infrared heaters 3 m aboveground for two years and an interaction between temperature and tillage on root biomass distribution of winter wheat was reported, with significantly higher root biomass in the upper 0–10 cm under no tillage and warming and significantly higher root biomass between 10 and 30 cm under tillage and warming, but no variation was observed in the root:shoot ratios

2.1.5. Soil tillage

Conventional tillage (CT) system with heavy machinery can result in subsoil compaction that limits water infiltration and restricts crop root growth, and therefore, affects biomass yield (Zhang et al., 2024; Horn, 2004; Horn and Smucker, 2005). The response of root:shoot ratio to tillage systems is complex and strongly depends on soil texture (Zhao et al., 2023; Schneider et al., 2017), soil bulk density (Oussible et al., 1992; Qin et al., 2004; Alvarez and Steinbach, 2009), weather and climate conditions (Álvaro-Fuentes et al., 2007; Muñoz-Romero et al., 2010), soil moisture and temperature (Liu et al., 2015; Guan et al., 2014; Hou et al., 2018), soil nutrient status (Oussible et al., 1992; Haugen-Kozyra et al., 1993; Schneider et al., 2017; Muñoz-Romero et al., 2010), and crop type (Álvaro-Fuentes et al., 2007; Andersen et al., 2013). Therefore, assigning a single root:shoot ratio for specific crops without considering the tillage effect could result in biased estimation of root-induced carbon to the soil, especially for modelling soil organic carbon storage and changes.

Generally, conservative and conventional tillage (CT) tends to increase root:shoot ratios for cereals by about 4 % (based on 19 studies with 45 root:shoot ratio data pairs, see supplement). In a 3-year study, Muñoz-Romero et al. (2010) studied the effects of root growth under CT and no tillage (NT) for spring wheat under rainfed conditions and the results showed higher root biomass in the top soil layer under CT, but no differences were observed in deeper soil layers. Additionally, the root:shoot ratio was lower in the NT vs. CT (0.13 vs. 0.18) due to increased shoot biomass. Rotary tillage before seeding increased the axile root:shoot ratio by 16 % in maize as reported by Bian et al. (2016). Despite that in most cases CT increases root:shoot ratios of cereals including maize, studies have also found the opposite or no response to tillage (based on 21 studies with 46 root:shoot ratio data pairs). Hou et al. (2018) found no significant differences in one of two years in irrigated winter wheat, whereas Wilhelm (1998) stated that NT increased the root:shoot ratio of winter wheat by 24 % compared to CT. Other studies reported no difference in root:shoot ratio of winter wheat under NT and CT under temperate climate (Ellis and Barnes, 1980; Qin et al., 2004). On average, soil tillage (conservation and conservative tillage) decreased root:shoot ratio only by 0.5 % as compared to no-tillage among several field crops under diverse environmental conditions (based on 29 studies with 68 root:shoot ratio data pairs). In case of legumes, tillage decreased root:shoot ratio by 13 % as compared to no-tillage (House et al., 1984; Muñoz-Romero et al., 2012; Das et al., 2021; Adamič and Leskovšek, 2021). Specifically for wheat, soil tillage increased root:shoot ratio by about 15 % as compared to no-tillage (9 studies with 18 root:shoot ratio data pairs). Considering only winter wheat, tillage increased root:shoot ratio by about 2.4 % as compared to no-tillage (Table 1).

2.2. Implementation of the effect of abiotic environmental stresses and tillage on root:shoot ratio in simulation models

2.2.1. Experimental data used for model calibration

The experimental data were taken from a field trial conducted at the agricultural research station Campus Klein-Altendorf of the University of Bonn, situated in the western Germany at 50°37′ N, 6°59′ E, and 176 m altitude. Winter wheat (*Triticum aestivum*) cultivar cv. Milaneco was sown on August 29th, 2020 harvested on August 8th, 2021.The shoot data used for the current study included leaf area index (LAI) collected four times, shoot biomass measured five times, and straw and grain yield at harvest. Root sampling was carried out on May 19th, 2021 using a root auger with an inner diameter of 9 cm and a length of 1 m, the root biomass and root length density were determined. Details on the experimental site, the trial and the data collection and post-processing can be found in the supplementary material.

2.2.2. Selected crop growth models

For the modelling exercise, the process-based soil-crop models STICS, SIMPLACE, AgroC, and MONICA were selected. They are process-based agroecosystem models (or soil-crop models) that represent main processes related to crop development and growth and the interactions with the environment. Typically, biomass production is a function of radiation and temperature. The growth may be further modulated by radiation use efficiency, temperature and CO_2 response curves, as well as water and nutrient stresses (Jamieson et al., 2008). Common main processes implemented in these 1D field-scale crop models are outlined in the supplementary material.

2.2.3. Model setup and calibration (baseline scenario)

Weather data, soil characteristics and initial volumetric soil water content from the experiment explained above were provided as input. The models were calibrated separately by adjusting the phenology parameters to match the observed dates for emergence, flowering, and physiological maturity. As for crop growth, intermediate and final above-ground biomass, root biomass, LAI and final grain yield were used for the model calibration. The calibrated models were then applied for the scenario runs.

2.2.4. Model scenarios

Five scenarios with respect to ambient CO_2 enhancement, changes in air temperature and precipitation, N availability, and tillage were generated. Only one input (e.g., air temperature) per scenario was changed and the others (e.g., CO_2 concentration) were kept constant. Model parameters (such as crop parameters) were held constant throughout the scenario runs in each of the models, allowing only the effect of the varying input to be studied. One exception was the temperature scenarios: The phenology parameters were adjusted so that the flowering and harvest dates were always the same in all scenarios, to allow better analysis and interpretation of the root:shoot ratios.

The baseline was considered as the simulation with the original input data (see Section 2.2.3). For the atmospheric CO_2 concentration 11 scenarios ranging from 424 to 570 ppm, with a 3 % (13–16 ppm) increase by scenario were created. For the precipitation scenarios (drought and excess water), the mean daily precipitation was reduced and increased by 10, 20, 30, 40, and 50 % from the baseline. In case of the temperature scenario, the mean daily temperatures were increased and reduced from the baseline by 1, 2, 3, 4 and 5 °C, respectively. For the N availability scenario, the initial soil N (0–90 cm) and the applied mineral fertilizer were set to (initial soil N/applied N fertilizer) 0/0, 25/0,50/0, 0/50, 25/50, 50/50, 0/100, 25/100, 50/100, 150/140 (baseline) and 200/200 kg N/ha. Finally, for the tillage scenario, the topsoil (0–27 cm) bulk density ranged between 1.14 and 2.06 g cm^{-3}, with continuous increments of 6 % by scenario. For the tillage scenario, the respective topsoil hydraulic properties were generated using the Hypres pedo-transfer functions (Wösten et al., 1999).

To allow for a better comparison with observations, we calculated the mean of the daily difference between the scenarios with the highest difference per model in a period where root observations in the field often take place, namely from end of tillering to end of flowering which relates to May 5th to June 24th 2021.

3. Results and discussion

3.1. Scenario results

3.1.1. Simulated root:shoot ratios in the baseline scenario

In general, the shape of the simulated root:shoot ratio curves as well as the maximum absolute root:shoot ratio values varied widely among the models (Fig. 2). For the baseline from March 1st to harvest, the maximum absolute root:shoot ratio values were for AgroC = 0.3, STICS = 0.4., MONICA = 1.1, and SIMPLACE = 1.4. Strong differences in simulated root:shoot ratio over the entire growing season were observed
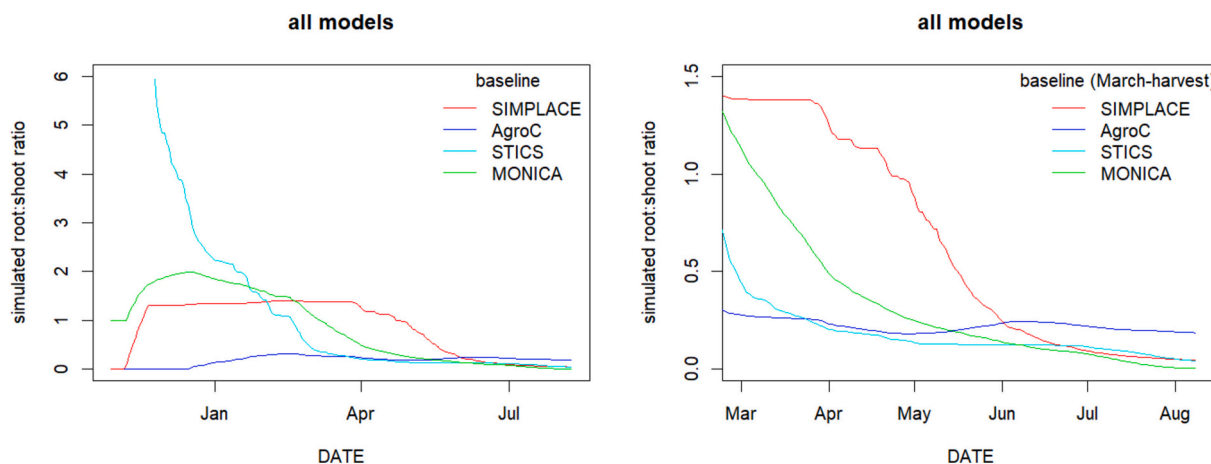
Fig. 2. Simulated daily root:shoot ratios for STICS, SIMPLACE, AgroC, and MONICA models for the baseline scenario from emergence to harvest in August (left) and from March 1st until harvest in August 2021 (right).

especially in early growing stages before March 1st. The mean winter wheat root:shoot ratio provided by the meta-analysis of Mathew et al. (2017) was 0.30. Bolinder et al. (1997) reported of winter wheat root: shoot ratios of 0.13–0.2 measured at or close to maturity in field studies and Hirte et al. (2021) of a root:shoot ratio of 0.09 at flowering of winter wheat (conventional farming). Thus, the simulated root:shoot ratios in the later growth stages were in the range of reported values.

3.1.2. Atmospheric CO_2 levels

The simulated root:shoot ratios for changes in atmospheric CO_2 levels only differed marginally from those simulated under the baseline scenario for all models (Fig. 3, and S1 to S4 in the supplement). The mean difference (mean of the highest difference of all eleven scenarios per day) was 1.5 % for MONICA, 3 % for STICS, 1 % for SIMPLACE with peaks at harvest of 3 % for MONICA, STICS, and SIMPLACE. AgroC did not consider feedbacks of changing atmospheric CO_2 concentrations on crop growth in the version used in this study. From end of tillering to end of flowering the root:shoot was affected by 0 % for STICS, 1 % for SIMPLACE, and 2 % for MONICA pointing again to the fact that changes in CO_2 concentration will not impact the root:shoot ratio substantially in the models. An absolute shoot biomass (Figs. S11–13) and root biomass

(Figs. S7–9) increment with increasing ambient CO_2 enhancement was simulated by STICS, SIMPLACE, and MONICA.

3.1.3. Water supply and drought

The root:shoot ratios simulated with SIMPLACE were very sensitive to changes in precipitation (Fig. 3). The maximum difference among scenarios was 53 % for the root:shoot ratio simulated in mid-May as the root biomass was low in the scenarios which received very little rainfall but shoot biomass was similar within all scenarios. At harvest, the shoot and root biomass were proportionally reduced in the scenarios with lower precipitation. Also, the STICS and AgroC model results showed a moderate to strong sensitivity of root:shoot ratios to drought stress. The mean difference of root:shoot ratios in the scenarios with changing precipitation was 12 % (season mean) with a maximum difference among scenarios at harvest with about 65 % for the STICS model. The mean difference of root:shoot ratios in the rainfall scenarios in AgroC was slightly lower with 11 % and the maximum difference among scenarios was ~50 % simulated after emergence, which decreased over time and increased again around DVS 1.5 up to 15 % at harvest (scenarios 3 vs. scenarios 8). MONICA showed the lowest response with 2 % mean difference of the root:shoot ratios for the precipitation scenarios.
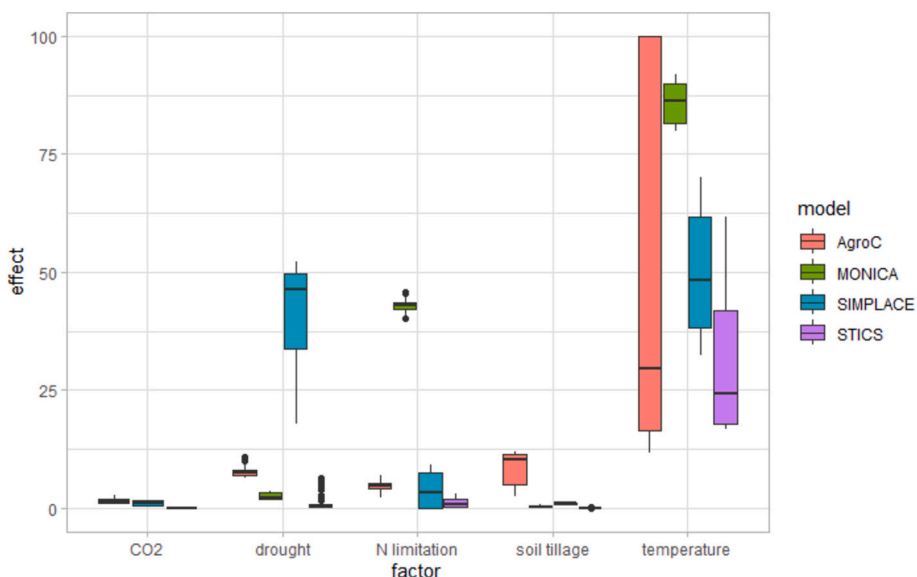

Fig. 3. Maximum simulated winter wheat root:shoot difference in % for each factor across the scenarios (e.g. the 10 atm CO_2 elevation scenarios for four soil-crop models. Each boxplot represents the maximum difference among the 10 scenarios from 5th May to 24th June 2022 (daily values) per model.

The maximum difference among scenarios was about 7 % simulated for end of November with another peak of differences of 5 % at harvest by MONICA. From end of tillering to end of flowering the root:shoot ratio stayed relatively unaffected for STICS (1 %) and MONICA (1 %), whereas AgroC simulations showed a slightly larger difference (8 %), and largest was simulated by SIMPLACE with 40 %. A decline of the absolute root (Fig. S6–9) and shoot biomass (Figs. S10–13) with increasing dry conditions was simulated by all models. The only exception was MONICA with no decline of root biomass with increasing drought.

3.1.4. Nitrogen supply and soil nitrogen limitation

The MONICA model reacted most to N limitation (Fig. 3). The simulated root:shoot ratios differed by maximum ~50 % at harvest with a daily mean difference of 20 % for the MONICA modelling results. The root:shoot ratios in the N scenarios simulated by STICS differed by maximum ~30 % at harvest with a daily mean difference of 4 % only. Intermediate differences were calculated by the SIMPLACE model with maximum root:shoot differences of 20 % at harvest (scenarios 1 vs. 11). The root:shoot ratios simulated by SIMPLACE only started to differ after mid-May at DVS 0.5 as the shoot growth started to differ among the N scenarios (more shoot growth in scenarios with higher N availability), whereas the root biomass was similar for all scenarios. As for AgroC, the simulated root:shoot ratios differed maximum only by 11 % at harvest (scenario1 vs. scenario11). From end of tillering to end of flowering the root:shoot ratio was affected by 43 % for MONICA, which was much larger as those simulated for the other models with 1 % for STICS, 4 % for SIMPLACE, and 5 % for AgroC. A decrease in absolute root biomass with increasing N availability was simulated by all models (Figs. S6–S9). The only exception was SIMPLACE, which showed no decrease in root biomass with increasing N limitation.

3.1.5. Air temperature

The simulated root:shoot ratio was most sensitive to air temperature decrease and increase compared to all other environmental impacts analyzed (Figs. 3, S2–5 in SI). The impact of variations of air temperature on the root:shoot ratio already kicked in at or soon after emergence. Both, absolute root and shoot biomass, were affected. A linear decrease of root:shoot ratio from scenarios 1–5 (lower temperature than baseline) and an increase of root:shoot ratio from scenarios 7–11 (higher temperature than baseline) for AgroC and SIMPLACE. The difference of root:shoot ratio at harvest between scenario 6 (baseline) and the scenario with the highest temperature increase (scenario 11) was 50 % (SIMPLACE) and 13 % (AgroC). The decline of root:shoot ratio from end of tillering to end of flowering between scenario 6 (baseline) and the scenario with the highest temperature increase (scenario 11) was 50 % (SIMPLACE, AgroC). By contrast, in case of STICS and MONICA, increasing temperature (scenarios 1 to 11) lead to a linear decline of root:shoot ratio leading to multiple times lower values in case of high temperatures at harvest and a mean root:shoot difference from end of tillering to end of flowering of 86 % for MONICA and 30 % for STICS. A decrease in absolute root biomass in the later growth stages with increasing air temperature was simulated by all models. The only exception was SIMPLACE, which showed an increase in root biomass. An increase in absolute shoot biomass with increasing air temperature was simulated by all models but AgroC.

3.1.6. Soil tillage

The simulated root:shoot ratios for the tillage scenarios were only slightly sensitive in case of AgroC, SIMPLACE, STICS, and MONICA model outputs (Fig. 3). Tillage affected early root:shoot ratios in the AgroC and SIMPLACE outputs, and late root:shoot ratio in the STICS and MONICA model. The mean difference of root:shoot ratios in the tillage scenarios was 12 % (daily means comparing the scenarios with maximum differences of root:shoot ratios). The maximum difference of root:shoot ratio in the tillage scenarios was 6 % (scenario means of root:

shoot ratios) with a maximum span of 25 % (scenario 1 to 5 vs. scenario 11) shortly after emergence for the SIMPLACE simulation results. Much lower differences in the mean root:shoot ratios for the tillage scenarios with 1 % and a maximum span of 2 % at harvest was reported for the MONICA model. Similarly, the STICS model showed mean difference of the root:shoot ratio of 2 % (daily means comparing the scenarios with maximum differences of root:shoot ratios) but a much wider span with a maximum value of 22 % at harvest (scenario 1 vs. scenario 11). From end of tillering to end of flowering the root:shoot ratio was affected by 0.5 % for MONICA, 0 % for STICS, 1 % for SIMPLACE, and slightly larger with 8 % for AgroC.

As AgroC solves the Richards equation for soil water dynamic calculations, it may be more sensitive to changes in the soil hydraulic characteristics induced by bulk density changes compared to the bucket-based models.

3.2. Simulated maximum absolute root biomass responses to abiotic stresses and tillage

The simulated maximum absolute root dry matter biomass in the season (potential root-C input into soil excluding exudates and secretes) plays an important role in simulating SOC dynamics and carbon sequestration. As the root:shoot ratio is affected by both, root and shoot biomass, we explored if the effects were rather on simulated absolute root or shoot biomass.

On average, the total C input in the soil by winter wheat roots (6 t ha^{-1} grain yield) is about 1200 kg ha^{-1} within one growing season (Kuzyakov and Domanski, 2000). The simulated maximum root dry matter biomasses in the baseline scenarios were 1.3 (MONICA), 1.7 (STICS), 1.9 (SIMPLACE) 3.9 t ha^{-1} (AgroC) (Fig. S5). Assuming a 40 % C content in the dry matter of the roots, (Kuzyakov and Domanski, 2000), this is equal to about 520 (MONICA), 680 (STICS), 750 (SIMPLACE) 1560 kg C ha^{-1} (AgroC). Of the four models, only AgroC simulates root exudates. The total C amounts translocated in the soil by winter wheat (6 t ha^{-1} grain yield) including exudates, rhizodeposits, and root and rhizomicrobial respiration is about 1500 kg ha^{-1} (Kuzyakov and Domanski, 2000). In AgroC, the total amount of root exudates transferred to the soil is a function of glucose assimilated and is defined as 5.3 % of the total glucose assimilated. Thus, additional 525 kg ha^{-1} of C (baseline) are translocated to the soil via the exudates during the winter wheat season in AgroC.

In the case of air temperature, simulated absolute root biomass was highly affected (Fig. S5-S10). Although the simulated shoot dynamics and absolute values, including yield, where similar among the models (baseline), the simulated absolute root biomass values over time differed widely among the models (Fig. S5). In general, dry conditions decreased absolute root biomass in SIMPLACE, STICS, and AgroC but not in MONICA. On the other hand, low N conditions decreased absolute root biomass simulated by STICS, MONICA, and AgroC but not in SIMPLACE. The simulated absolute maximum root dry matter biomass was strongly negatively affected by drought and N limitation in most models. Drought decreased the absolute maximum root biomass by up to 70 % in AgroC, 60 % in SIMPLACE and STICS, and 1 % by MONICA considering all drought scenarios (scenarios with reduced precipitation). Also the N deficiency affected maximum root biomass negatively (decline of up to 55 % in STICS, 53 % in MONICA, 50 % in AgroC, and 2 % in SIMPLACE). Soil tillage (here reflected by decreasing of soil bulk density and respective changes in the soil hydraulic characteristics) fostered a slight increase of absolute maximum root biomass of up to 11 % for AgroC, 9 % for STICS, and 2 % for SIMPLACE, but no change was detectable for the MONICA simulation results. Elevated atmospheric CO_2 increased simulated absolute maximum root biomass by up to 13 % for SIMPLACE, 10 % for MONICA, and 7 % for STICS considering all scenarios. An increase of air temperature led to an increase of absolute maximum root biomass up to about 300 % for SIMPLACE, 600 % for AgroC, 47 % for STICS, and 35 % for MONICA.

3.3. Comparison of observed and simulated responses to changing environments

According to our literature research, Table 1 summarizes the observed and simulated effects of abiotic factors in common crops and in particular, for winter wheat. Results show that, in general, root:shoot ratio increases under elevated CO_2, drought and N deficiency, while it tends to decrease with temperature above the optimum. Tillage resulted in a minimum effect on root:shoot biomass ratio.

According to the model scenario results, the effects of abiotic factors and tillage on simulated winter wheat root:shoot ratios (mean values from end of tillering to end of flowering) were as follows: The root:shoot ratio i) increased slightly by up to 2 % in case of elevated atmospheric CO_2 concentrations, ii) increased slightly to moderately (1 to up to about 40 %) in case on increasing drought and N limitation, iii) decreased moderately to strongly in case of increased air temperatures, and iv) increased slightly to moderately (mean change of 0 to 8 %) in case of tillage. Thus, the wheat root:shoot biomass responses seem to be adequately simulated in case of atmospheric CO_2 increase and tillage, moderately in case of drought (depending on the model being used), and rather underestimated in case of N limitation with also a high variation in simulated results among the models. For air temperature increase (above the average), the models reproduced the negative effects on root: shoot ratio but the observations and the model simulations varied widely (Table 1 and Fig. 3). Observations, though scarce, suggest a decrease of root:shoot ratio of 20 to 30 % in wheat under warmer conditions.

Mathew et al. (2017) revealed a significant negative correlation of root:shoot ratios with mean annual precipitation and SOC, but a significant positive correlation with soil pH, and mean annual temperature. We report an root:shoot ratio increase by a mean of 14 % under drought conditions versus well-water conditions in line with Mathew et al. (2017) who suggest an increase of root:shoot ratio with decreasing mean annual precipitation. Similar to the results in our study, the root:shoot ratios were often strongly increased under N deficiency (Lopez et al., 2023). An increase in the root:shoot ratio due to stress (drought, N deficiency) may be a result of increased C allocation to the roots leading to an increase in root biomass. According to the 'functional equilibrium' theory, plants increase the allocation of resources to maintain the development of the organ under stress as a way of counteracting the effects of stress (Poorter and Nagel, 2000).

According to our literature research, the effects of increasing air temperature on root:shoot ratio vary widely and also in different direction (−20 % to +26 %). Mathew et al. (2017) reported a significant positive correlation of root:shoot ratio with mean annual temperature. We need to have in mind that trials were conducted in temperate and (sub)tropical climates, whereas in our study we considered studies with treatment pairs of low and high temperature. In our review, root:shoot ratio decreased only by 0.5 % in case of conventional tillage vs. no-tillage, which is in line with Mathew et al. (2017) who reported a non-significant positive correlation of root:shoot ratio with soil bulk density.

3.4. Model evaluation

RUE correction factors for atmospheric CO_2 enhancement are implemented in SIMPLACE, STICS, and MONICA. This approach (or the applied model parameters) seems to underestimate the effect of atmospheric CO_2 enhancement on root:shoot ratio, especially, the absolute increase in root biomass. AgroC does not consider elevated CO_2 effects on crop growth.

The simulated effects of drought stress on the root:shoot ratio were moderate and in a similar range than the observations. SIMPLACE explicitly considers the effect of drought stress on root:shoot ratio via a root factor that leads to a higher C allocation to the roots (Fig. 3). This leads to strong effects on root:shoot ratio of up to 40 % in the driest scenario. In AgroC, the root:shoot ratio is predefined and drought effects are not explicitly considered. The simulation results indicate no or only a very minor effect of drought stress on root:shoot ratio but a clear effect on absolute root biomass. In MONICA, a drought stress factor, which varies by developmental stages and organs, influences assimilation, but drought stress effects are not explicitly considered. Thus, despite that the models MONICA and SIMPLACE are able to capture directly the drought effects on C allocation into the roots, the simulated responses widely vary.

The observed N limitation effects on root:shoot ratio were moderately to high (mean of 44 % for all crops and 64 % for wheat), whereas the simulated ones ranged from 1 to 43 %. In SIMPLACE, the fraction of biomass transferred to the leaves is reduced by a factor in case of low N conditions. However, this led to a minor effect on root:shoot ratio (4 % from end of tillering to end of flowering). For AgroC and STICS, no explicit approach is implemented and the assumed N deficiency affected root:shoot ratio by 5 and 1 %, respectively. MONICA was the only model were N deficiency led to a clear effect on root:shoot ratio. MONICA uses a crop reduction factor for nitrogen stress that also reduces root growth when tissue N concentration falls below a defined threshold (Eq. S13). This apparently favorable approach leads to a proportionally stronger decline in shoot than in root biomass (Figs. S7 and S11).

Simulated soil tillage barely affected root:shoot ratio, which was similar to the observations for winter wheat (~2.4 % increase) (Table 1). Decreasing soil bulk density (soil tillage scenarios, soil hydraulic parameters were also affected), did not or only slightly increase simulated root:shoot ratios for STICS, AgroC, and MONICA. With regards to SIMPLACE, which accounts for soil strength, the root:shoot ratio was mostly affected in the early development stages before shoot stem elongation. We therefore assume that, for winter wheat, the model equations applied can reproduce the effects of soil tillage well.

Increasing and decreasing air temperatures (from the average baseline value) decreased observed root:shoot ratio by 20–30 %. Air temperature affects the simulation of crop growth in various ways, e.g. via the temperature driven crop development, or RUE correction factors for temperature to account for heat stress, but also via effects on soil N mineralisation. Air temperature decrease from 0° to −5 °C led to a stepwise decrease of root:shoot ratio in all models. While the daily increase from 1 to 5 °C led to an increase of root:shoot ratio for AgroC and SIMPLACE with maximum differences of root:shoot ratios at harvest of 50 % (SIMPLACE) and 13 % (AgroC). In case of STICS and MONICA, increasing temperature led to a linear decline of root:shoot ratio when comparing all eleven scenarios (Figs. S3 and S4).

3.5. Suggestions for model improvement

The high variability and uncertainty of the modelling results (Fig. 3), especially for temperature, drought and N limitations scenarios, indicate a clear need to fill research gaps with regards to the impacts of abiotic stress, particularly in below ground dynamics for root:shoot ratio and absolute root biomass growth, and consequently, the need for model improvement. Our results are in line with previous model intercomparison showing large differences among models when simulating root: shoot ratio and crop to soil feedback (Couëdel et al., 2024). We call for more systematic field experiments, particularly on the effects of single abiotic stress and their interactions considering the effects of shoot and root growth, as well as their influence in biomass partition over different developmental stages (Wang et al., 2024). Such experiments are critically required to develop and improve mechanistic models that account for the effect of abiotic stress under a wide range of environments (precipitation and soil). For example, the simulated root biomass could not be validated, because, while there is extensive research in aboveground effects, time series data on below ground root growth processes remains scarce. Besides, the partitioning of assimilated carbon to different above and below-ground components vary during growth stages and also under different stress factors. This will also impact

parameterization of different models. This is further complicated by the complexity of an accurate estimate of the below-ground biomass (Rogers et al., 1995; Madhu and Hatfield, 2013). However, emerging root phenotyping technologies can facilitate the study of below ground processes (root growth and exudate quantification) in the coming years (Tracy et al., 2020).

Model improvement can be complex and challenging, especially if no general approaches (i.e. mathematical equations of the relationships of interest) are available. In general, there are two approaches for model improvement: (i) General approaches (e.g. the relation between biomass production and the amount of radiation absorbed by photosynthetically active tissues, see Sadras et al., 2016) are available and can be implemented as equations into the model structure; (ii) The use of experimental data that meet modelers requirements (Kersebaum et al., 2015), which can serve for model improvement. In recent years, the Agricultural Model Intercomparison and Improvement Project (https://agmip. org/) consortium was created, which brings together the crop modelling community and has allowed for modelling improvement. One example is the improvement of heat stress routines in wheat crop models, which helped to reduce model uncertainty (Maiorano et al., 2017). In another example, a literature review was conducted with the aim to improve the ability of crop models to simulate heat stress impacts on wheat based on the extensive data set of the "Hot Serial Cereal experiment" (Rezaei et al., 2015; Webber et al., 2017).

In a similar way, to improve the overall model simulation capabilities of root:shoot biomass ratios under varying conditions, we suggest to prioritize research on the responses of root:shoot ratio to air temperature changes and N and drought stress. This will allow for a more comprehensive understanding of root:shoot ratio as affected by these factors, which can then be implemented into models. As for temperature, there are only very few and contradictory field studies on air temperature increase with respect to root responses. Moreover, drought and especially N stress have strong effects on the root:shoot biomass ratios. Despite that the two later factors are considered in the evaluated models, the responses were inconsistent. For the current study, we focused in evaluation wheat models, due to its importance as a staple crop. However, further basic research would be also needed for under-represented crops, as our review showed the root:shoot responses to environmental stress can vary by crops. Lastly, as the effects of CO_2 enrichment, and especially of tillage, on the mean root:shoot ratio was rather small in the case of wheat, and the simulation capabilities of the models were generally good, we consider model improvements with respect to these two factors to be less critical.

4. Conclusions and outlook

Process-based soil-crop models are becoming increasingly important for estimating the effects of agricultural management practices and climate change on SOC stocks. However, there is a large uncertainty in the calculation of C inputs from roots, especially under changing environmental or management conditions. Our model intercomparison study is one of the first to address root biomass simulation and root: shoot ratio. It is a first step towards identifying weaknesses for model improvement and improved understanding of effects of environmental factors on root:shoot ratio, root biomass-derived C input, and thus, simulations of SOC dynamics and carbon sequestration. We conclude that there is a lack of time series of field experimental data on below ground processes on effects of major abiotic environmental stresses and tillage systems on root:shoot ratio. This is especially the case for changes in CO_2, air temperature and drought stress. This lack of field data makes it difficult to implement general approaches that can be translated into field-scale models and proof of concepts and demands for model improvements.

CRediT authorship contribution statement

S.J. Seidel: Writing – original draft, Visualization, Software, Funding acquisition, Data curation, Conceptualization. **S.H. Ahmadi:** Writing – review & editing, Data curation, Conceptualization. **L. Weihermüller:** Writing – review & editing, Software. **A. Couëdel:** Writing – review & editing, Software. **G. Lopez:** Writing – review & editing, Software, Data curation. **D. Behrend:** Writing – review & editing, Data curation. **B. Kamali:** Writing – review & editing, Software. **T. Gaiser:** Writing – review & editing, Methodology. **I.M. Hernández-Ochoa:** Writing – review & editing, Software, Data curation, Conceptualization.

Declaration of competing interest

We confirm that neither the manuscript nor any parts of its content are currently under consideration or published in another journal.

We disclose any financial and personal relationships with other people or organizations that could inappropriately influence (bias) their work.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2024.176738.

Data availability

Data will be made available on request.

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