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Enabling modeling of waterlogging impact on wheat

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ABSTRACT

Most crop simulation models do not consider the effect of waterlogging despite its importance for crop performance. Here, we reviewed the impact of waterlogging during different wheat phenological stages on grain number per unit area, average grain size, and grain yield. Episodes of waterlogging from the onset of tillering to anthesis result in fewer, and during grain filling in lighter grains. To simulate such impacts, we implemented a new waterlogging module into the wheat crop simulation model DSSAT-NWheat, accounting for the effects of waterlogging on wheat root growth, biomass growth, and potential average grain size. The model incorporating the new waterlogging routine was tested using data from a controlled experiment, and it reasonably reproduced wheat yield responses to pre-anthesis waterlogging. A sensitivity analysis showed that the simulated impact of waterlogging on above ground biomass and roots, as well as leaf area index, grain number, and grain yield varied with phenological stages. The simulated crop was most sensitive to pre-anthesis waterlogging, consistent with experimental studies. The new waterlogging-enabled crop model is an initial attempt to consider the impact of excess rainfall and waterlogging on crop growth and final grain yield to reduce model uncertainties when projecting climate change impacts with increasing rainfall intensity.

1. Introduction

Waterlogging could be defined as the phenomenon in which prolonged saturation of a soil with water inhibits or entirely negates oxygen availability to plant roots (Liu et al., 2021a; Kim et al., 2024). All direct and indirect impacts of waterlogging together are a major cause of crop yield losses across the world, estimated to affect 15–20 % of the global wheat cropping area each year (Sayre et al., 1994; Kaur et al., 2020). Crop production in southern Asia, many parts of Europe, Russia, China and southern Brazil may be more sensitive to waterlogging than to

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drought (Zampieri et al., 2017; Liu et al., 2023). Waterlogging from high rainfall has damaged 33.9 million hectares (Mha) of India's arable area between 2015 and 2022 (Kulkarni et al., 2021). In Europe, excessive precipitation and waterlogging have been identified as major factors limiting wheat yield (Ceglar et al., 2020; Nóia Júnior et al., 2023a). In southern South America, prolonged waterlogging events have also caused severe yield losses, including a 40 % reduction in Brazil in 2017 and recurrent flooding across over 30 % of Argentina's Pampas Region in recent decades (Nóia Júnior et al., 2021; Kuppel et al., 2015). Despite the large worldwide damage of waterlogging on crops, studies on waterlogging impact on grain production are scarce.

The process of adapting agricultural crops to extreme weather events, such as waterlogging, demands sophisticated understanding of how crop genotypes respond to different weather conditions, at different phenological stages for different management options (Githui et al., 2022; Liu et al., 2020a). For this, it is necessary to have controlled experiments in greenhouse and field conditions, with physiological, morphological and growth measurements. These experiments may be repeated in different years and locations, making them costly and often unfeasible, particularly if a thorough insight into the solution space is sought (Liu et al., 2020b, 2023; Githui et al., 2022).

Crop models codify the gathered knowledge and understanding on crop growth processes and contribute to the understanding of the physiological mechanisms of plant response to abiotic stresses. They are widely applied for simulating crop growth and physiology in different environments, locations and years, as well as for climate change scenarios, assessing extreme weather impacts (Yan et al., 2022; Kassie et al., 2016). Indeed, many studies that project the impacts of climate change on agriculture used crop simulation models (Asseng et al., 2015, 2013; Liu et al., 2016; Zhao et al., 2017; Liu et al., 2019; Asseng et al., 2019). Yet, the majority of crop models do not consider the impact of waterlogging on crop growth (Liu et al., 2020b; Githui et al., 2022).

Waterlogging is frequently disregarded in crop models, with only one-third of wheat crop models accounting for its effects (Nóia Júnior et al., 2023b). Even when considered, these crop models usually only focus on how it affects carbohydrate accumulation, radiation use efficiency, transpiration, root activity, and leaf area index (LAI) (Liu et al., 2020c; Githui et al., 2022; Nóia Júnior et al., 2023b). In some crop models, the magnitude of simulated impact varies according to the phenological phase in which the waterlogging occurs (e.g., De San Celedonio et al., 2014). The wheat crop model in APSIM, for example, considers that the highest photosynthetic and roots activity reduction due to waterlogging occurs before wheat grain filling, with no impact during grain filling (Liu et al., 2021b). The EPIC model considers direct waterlogging effects only on photosynthesis and LAI (Githui et al., 2022), with indirect impacts on other growth mechanisms. In these crop models, wheat growth is penalized via lower photosynthesis due to its direct reduction or lower light capture from decreased leaf area with waterlogging. Simulated waterlogging may indirectly impact nitrogen uptake via reduced root growth, resulting in a simulated yield penalty. However, these models have only been tested in a few situations with waterlogged wheat, and it is not clear how waterlogging affects yield and its components, and by extension, yield. Some wheat crop models do not correctly simulate the relationship between number of grains per unit area and average grain size (or grain unit weight), resulting in overestimation of simulated yields, particularly in seasons with poor grain setting (causing low grain number per unit area) and grain filling (causing low average grain size) (Nóia Júnior et al., 2023c). The relationship between number of grains per unit area and average grain size is usually studied in controlled environments with few measured data (Calderini et al., 2001; Fischer, 1985; Asseng et al., 2017), making it difficult to improve wheat crop models.

The inability of most crop models to simulate waterlogged wheat growth potentially underestimates the projected impacts of climate change on agriculture (Van der Velde et al., 2020; Webber et al., 2020). To improve the representation of waterlogging in crop models, in this study we aimed to improve the waterlogging module in the wheat crop simulation model DSSAT-NWheat. For this, we reviewed published articles from 2008 to 2021 that studied the impacts of waterlogging during different wheat phenological stages on grain number per unit area, average grain size, and grain yield. Based on the general relationships of crop performance and waterlogging, a new waterlogging module was developed. This module was tested using data from a controlled waterlogging experiment in Lleida, Spain and from wheat field experiments in Loireauxence, France with side-by-side drained and undrained soils.

2. Material and methods

2.1. Review of waterlogging impacts on wheat grain number, average grain size and grain yield

We assessed 17 peer-reviewed articles published between 2008 and 2021 which quantified the impacts of waterlogging on wheat grain yield, grain number or grain size in controlled waterlogging treatments (Supplementary Table S1). Relevant articles were found by using keywords 'waterlogging', 'flooding' or 'excess of water' and 'wheat' in Web of Science and Google Scholar Databases. In the assessed articles, waterlogging affected different wheat phenological stages, from seedling emergence to onset of grain filling and with waterlogging duration varying from 2 to 58 days (Fig. 3d) with fully waterlogged soil (i.e., no variations in soil moisture along the soil profile depth). From the assessed articles, we collected the average grain yield, average grain size (or grain unit dry mass or thousand grain dry mass) and grain number per unit area per each waterlogging treatments and their control. With these values, we calculated the relative change of each treatment in relation to the control and averaged according to the wheat phenological stage. Experiments with waterlogging starting at seven different wheat phenological stages were collated, namely at wheat seedling emergence, onset of tillering, jointing, booting, heading, anthesis and onset grain filling. The experiments were conducted in seven countries from three continents (Fig. 1).

2.2. Modeling waterlogging on wheat with DSSAT-NWheat

The DSSAT-NWheat model has been evaluated and used to simulate wheat growth and development across many environments around the world, including different seasonal ranges of air temperatures, soil water, nitrogen and air CO_2 concentrations (Kassie et al., 2016). Here, we further-developed the waterlogging module of DSSAT-NWheat (Shelia et al., 2019), originally developed for APSIM Wheat (Asseng et al., 1997), by adding the soil waterlogging direct impact on carbohydrate accumulation and potential grain size in addition to the already existing impact on root growth. The latest versions of DSSAT (4.7 and 4.8) available for free download do not include the Shelia et al. (2019) waterlogging module, which is only available upon request from the authors of this paper. As a result, the default DSSAT-Nwheat available to users does not account for the impact of waterlogging on wheat growth. Here, we developed a new waterlogging module in DSSAT-Nwheat version 4.7, as presented here. Our new waterlogging module will be implemented in DSSAT-Nwheat version 4.8 and made freely available to the public. However, until that time, the module will also be available upon request from the authors.

2.2.1. Modeling soil waterlogging

The water flow module of DSSAT-NWheat was described in detail by Asseng et al. (1997) and was not further-modified in this study. The vertical water flow in a soil at or near to saturation (when soil water content is in between soil drained upper limit (or soil field capacity) and saturated soil water content) is controlled by soil saturated hydraulic conductivity (SSKS) and the soil saturated macro-flow water conductivity, which is defined as the saturated drainage rate (SLDR) in

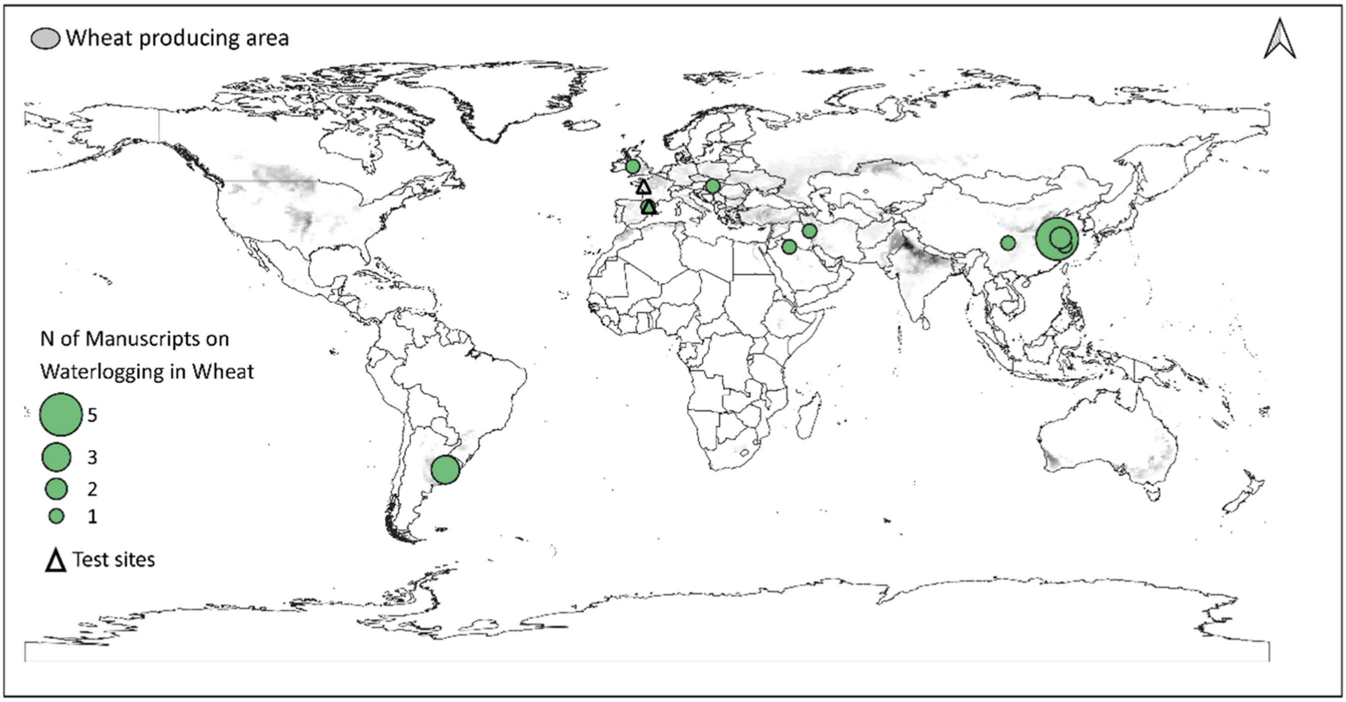


Fig. 1. Waterlogging experiments with wheat. Spatial distribution of reviewed experiments on waterlogging impact for wheat (green circles). A total of 17 published studies were used here to summarize how waterlogging affects wheat. A list of all studies is shown in Supplementary Table S1. The black triangles represent experiments that were used to test the new waterlogging module for DSSAT-NWheat with a waterlogging experiment in an outdoor controlled environment from Marti et al. (2015), and a field experiment with drainage and undrained fields in La Jaillière, Loireauxence, France.

DSSAT-SBuild (Supplementary Figure S4, DSSAT-SBuild is the software to build soil profile in DSSAT). SSKS (in cm h^{-1}) is a quantitative measure of a soil's ability to transmit water vertically between layers under saturated conditions, following a multi-layer cascading model driven by a hydraulic gradient. However, only a portion of the water, defined by the SLDR parameter (ranging from 0 to 1), can move downward each day. Therefore, the SSKS value is applied only to this SLDR-defined fraction, representing the rate at which saturated water flows from one soil layer to the next. The remaining water fills the current soil layer up to saturation (*e.g.* with SLDR = 0.95, only 5 % of the water above soil drained upper limit in a day remains in the current soil layer). In DSSAT-SBuild the SLDR is defined based on soil drainage classes, varying from soils with very excessive drainage (soil drainage = 0.95) to very poor drainage (0.01). The drainage classes and their respective SLDR value are shown in Supplementary Table S2.

Waterlogging is indicated with an aeration deficit factor (AF) which is calculated daily for each rooted soil layer. The aeration deficit factor is derived from experimental data and incorporated into crop models, which simulate its effects on root development and overall crop growth (Asseng et al., 1997; Lizaso, 1993). The AF is calculated as follows:

$$AF_i = \frac{SAT_i - SWC_i}{SAT_i - DUL_i} \tag{1}$$

Where, SAT_i is saturated soil water content, SWC is the soil water content and DUL is the soil drained upper limit (or soil field capacity), in a soil rooted layer *i*. AF_i is only calculated when soil layer is at or near to saturation, i.e., SWC > DUL.

2.2.2. Waterlogging impacts on roots

Waterlogging inhibits root growth and functioning (Colmer and Voesenek, 2009), which may lead to root death (Herzog et al., 2016). The module that accounts for the waterlogging impacts on roots, was previously implemented by Shelia et al. (2019). Our waterlogging modeling module was developed to consider the negative impacts of waterlogging on wheat growth at different soil depths (Malik et al., 2001). When AFi in a rooted soil layer falls below the default threshold of 0.6 for three consecutive days, the model reduces the effective rooting depth to 5 cm below the deepest non-saturated layer. All roots located in waterlogged layers below this point are considered 'dead', meaning they no longer contribute to water or nitrogen uptake. In DSSAT-NWheat, only 'active' roots are used to simulate these processes. The purpose of this module is to capture the loss of root function under prolonged saturated conditions, regardless of the depth of the affected soil layer. Therefore, it is recommended to set the soil layer thickness between 10 cm (more sensitive to waterlogging) and 15 cm (less sensitive to waterlogging) when creating a soil profile in DSSAT-SBuild. These depth thresholds are fixed in DSSAT-Nwheat and are not adjusted based on specific cultivars. Once waterlogging ends, dead roots remain non-functional and do not regain activity. However, the model allows for the regrowth of new active roots into soil layers that were previously affected by waterlogging.

2.2.3. Waterlogging impact on carbohydrate accumulation

Waterlogging causes stomata to close, reducing CO_2 within the leaves, which restricts photosynthesis and carbohydrate accumulation (Else et al., 2001; Jitsuyama, 2017). The waterlogging effect on carbohydrate accumulation is based on a wheat root aeration index (AF_{root}), calculated as follows:

$$AF_{root} = \left[\frac{\sum_{i=1}^{m} (AF_i)}{m}\right]^{P_{AF}} \tag{2}$$

Where, P_{AF} (Parameter of roots aeration index) is set to 3.0 (default), *m* is the deepest soil layer with roots, *i* is the rooted layer. The value of m is also dynamically affected by waterlogging impacts on roots, as described in Subsection 2.2.2.

Waterlogging affects daily carbohydrate accumulation in DSSAT-NWheat according to two new wheat cultivar parameters. First, the cultivar sensitivity to AF_{root}, considering the AF_{root} threshold value at which waterlogging impacts starts to affect carbohydrate accumulation (WLSI). Second, the maximum reduction of carbohydrate accumulation under waterlogging (WLMI). Both WLSI and WLMI vary from 0 to 1. A wheat cultivar has maximum sensitivity to waterlogging when WLSI is 1 and WLMI is 0, and maximum tolerance when WLSI is 0 and WLMI is 1 (Fig. 2). The default values of WLSI and WLMI in the DSSAT-NWheat ecotype parameters file are 0.2 and 0.1, respectively (Fig. 2), but they can be calibrated according to the waterlogging sensitivity of each cultivar.

2.2.4. Waterlogging impact on potential grain size

Waterlogging before and during anthesis affects potential grain size (Marti et al., 2015). In wheat, average grain size is most sensitive to biotic or abiotic stress between booting and the beginning of effective grain filling (Calderini et al., 2021a, 2001) (Supplementary Figure S5). DSSAT-NWheat, computes daily water deficit, nitrogen, heat and waterlogging stress factors, which impact potential growth, according to Eqs. 3 and 4. These equations are part of the original DSSAT-NWheat model. Our contribution consisted solely of incorporating the waterlogging stress term. Therefore, the placement and relative treatment of each stress component, including the separate multiplicative application of heat stress, follow the pre-existing model logic and are not the subject of methodological discussion in this study.

$$\text{Plant stress} = \min(\text{water deficit}_{stress},\ \text{nitrogen}_{stress},\ \text{ozone}_{stress},\ \text{waterlogging}_{stress})\ \times \text{heat}_{stress} \tag{3}$$

$$\text{Daily wheat accumulation of carbohydrate} = \text{Potential carbohydrate accumulationxplant stress} \tag{4}$$

Wheat grain number per unit area is closely related to growing conditions before and shortly after anthesis (Fischer, 1985), when the number of fertile florets is determined and when fertile florets set grains (Slafer et al., 2015). This is also the period when potential grain size is set (Calderini et al., 2021a; Acreche and Slafer, 2006). DSSAT-NWheat estimates grain number in the first day of grain filling (phenological stage 5 in DSSAT-NWheat), based on the stem (above-ground biomass not considering leaves) growth from start-of-stem-growth (phenological stage 2) to anthesis (phenological stage 4) (For further details on the simulation of wheat grain number per unit area by DSSAT-Nwheat, Asseng et al. (2017)). However, since daily stem growth depends on carbohydrate accumulation (and our newly introduced waterlogging stress factor now affects this process, as shown in Eqs. 3 and 4) waterlogging events occurring before or during these stages will indirectly influence the simulated grain number. Additionally, we introduced a waterlogging stress factor that directly affects potential grain size. In DSSAT-NWheat, the original potential average grain size was set to 55 mg of dry mass per grain (mg grain-1, this is a crop parameter named MXGWT in the wheat ecotype file of DSSAT-NWheat, with a default value of 55). In our new approach, the potential wheat grain size is now based on a weighted crop stress factor between phenological stage 2–4, as defined in Eqs. 5 and 6, after Calderini et al. (2001):

$$\text{Potential grain size}_{stress} = 0.25 \times \text{Plant stress}_{stage2} + 0.35 \times \text{Plant stress}_{stage3} + 0.40 \times \text{Plant stress}_{stage4} \tag{5}$$

$$\text{Potential grain size} = 55 \times \text{Potential grain size}_{stress} \tag{6}$$

Minimum potential grain size (MPGS) is as a default value within DSSAT-NWheat to 35 mg grain^{-1}, MXGWT and MPGS can be adjusted to different cultivars if supported by empirical evidence. In Eq. 5, plant stress corresponds to the average of the daily stress values calculated by DSSAT-NWheat during each phenological stage used in the equation.

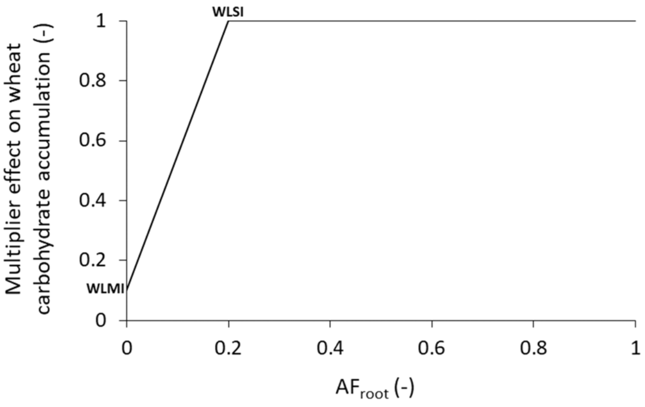


Fig. 2. Reduction of carbohydrate accumulation as a function of root aeration factor (AF_{root}) in DSSAT-NWheat. WLSI and WLMI are two new wheat cultivar parameters in DSSAT-NWheat, representing when waterlogging impacts starts to affect wheat carbohydrate accumulation (WLSI – *Water Logging Impact Start*), and the maximum reduction of carbohydrate accumulation under waterlogging (WLMI – *Water Logging Maximum Impact*). The values shown are the default in the code, but they may be parameterized according to wheat cultivar.

2.3. Evaluation of the adapted waterlogging module

The 17 peer-reviewed articles we considered primarily served to demonstrate the observed impacts of waterlogging on wheat grain number per unit area, average grain size, and overall grain yield. Due to the lack of openly available data, such as detailed soil information, weather conditions, and planting and harvesting dates—required as inputs for simulation with DSSAT-Nwheat—we tested the waterlogging module with data from only one experiment from these articles, conducted in Lleida, Spain. Additionally, we performed a further validation using a field experiment from Loirauxence, La Jaillière, in France. The experiments used to test our module are described below.

2.3.1. Outdoor controlled waterlogging experiment in Lleida, Spain

To test the performance of the new waterlogging module we simulated the waterlogging experimental setup of Marti et al. (2015) with DSSAT-NWheat. This experiment was conducted with wheat plants grown outdoors in the campus of University of Lleida, Spain (Latitude 41°37'47", Longitude 0°35'47") in columns (84 mm of diameter and 1.25 m deep) filled with a loamy sand soil with 81 % sand content. The soil was waterlogged through the blocking of the bottom of the columns, to prevent water drainage. Waterlogging condition was imposed by saturating the soil with water 1 cm above the soil surface. The waterlogging treatments were applied before anthesis, during 4–24 days (Supplementary Figure S1). The experiments were free from nutritional and water deficit stress and pests and diseases.

To simulate this experiment, we reproduced the sandy soil from Marti et al. (2015) with a depth of 1.25 m, divided into 11 layers with thicknesses ranging from 5 to 20 cm. To create the waterlogging condition of the experiment, we set SSKS of the bottom layer at 1 cm h^{-1}, which remains unchanged for the whole growing season. This resulted

Table 1
NWheat genetic coefficients for the winter wheat cultivars Soisson (Spain experiment) and Generic cultivar 1, cultivar 2 and cultivar 3 (France experiment).

Genetic Coef.	Definition	Soisson cv.	Generic cultivar 1	Generic cultivar 2	Generic cultivar 3
VSEN	Sensitivity to vernalization scale 1–4	4.43	4.43	3.70	3.70
PPSEN	Sensitivity to photoperiod	3.36	3.36	4.00	4.00
P1	Thermal time from seedling emergence to the end of the juvenile phase [°C d]	446	400	400	400
P5	Thermal time (base 0°C) from beginning of grain filling to maturity [°C d]	754	500	580	600
PHINT	Phyllochron interval	100	100	110	110
GRNO	Coefficient of kernel number per stem weight at the beginning of grain filling [kernels g^{-1} $stem^{-1}$]	32	29	22	28
MXFIL	Potential kernel growth rate [mg $kernel^{-1}$ d^{-1}]	3.20	1.60	1.60	1.60
WLSI	WLSI – Water Logging Impact Start	0.2	0.2	0.2	0.2
WLMI	WLMI – Water Logging Maximum Impact	0.1	0.3	0.3	0.3
MPGS	Minimum potential grain size	20	35	35	35

in undrained of excess water from the bottom of the soil and caused excess water to slowly return to top layers of soil surface. In the simulation setup, the water lost by evapotranspiration was added daily through irrigation, and in the phenological phase when waterlogging was applied (Supplementary Figure S1), excess irrigation was applied to saturate the entire soil profile. The wheat cultivar in this experiment was Soisson, and the parameters were calibrated to simulate the observed phenology and wheat yield in the control treatment without waterlogging (Table 1), using the automatic time-series calibration method for DSSAT wheat models (Röll et al., 2020).

2.3.2. *Field experiment from Loirauxence, La Jaillière in France*

ARVALIS data from field experiments (located in Loireauxence, research station of La Jaillière, France) with measured grain and seasonal accumulated water drainage and run-off (Supplementary Figure S2), with side-by-side drained and undrained soils from 1990 to 2014 were used to test the performance of the new waterlogging module implemented in DSSAT-NWheat.

The experiments were rainfed and sown between October and November with sowing dates provided by Arvalis. Each year of cultivation involved the use of a different cultivar, and the Arvalis experiments we simulated range from 1991 to 2014. In each year of the experiment, a single cultivar was sown across the entire area, encompassing both drained and undrained soils. To minimize the need for calibration specific to field, year, and cultivar, we categorized the cultivars into three groups based on the years they were grown, which we refer to as ’Generic Cultivars’ We calibrated Generic Cultivar 1 (predominantly derived from the wheat cultivar Soisson, representing 38 % of all data during this period) for the years 1991–2003. Generic Cultivar 2 (primarily derived from the wheat cultivar Altigo, representing 32 % of all data during this period) was calibrated for the years 2004–2012. Finally, Generic Cultivar 3 (mostly derived from the wheat cultivar Ascott, representing 50 % of all data during this period) was calibrated for the years 2013–2014. It is important to note that we did not test Generic Cultivar 3 for the non-drained fields with occurrences of waterlogging due to a lack of data.

We calibrated the three generic cultivars using the same waterlogging parameters, as the available data were insufficient to assess cultivar-specific sensitivities to waterlogging. Although Generic Cultivar 1 is primarily represented by Soisson (32 % of the group’s data, and also used in the controlled experiment described in subsection 2.3.1, where it was calibrated with different crop parameters within the model), other cultivars with varying waterlogging sensitivities were also included. The goal of this study was to test the new waterlogging module in the DSSAT-NWheat model using field data from both drained and undrained soils, rather than to determine the waterlogging sensitivity of individual cultivars. Identifying cultivar-specific responses would require a larger dataset with multiple cultivars tested under identical conditions within the same year. However, since only one cultivar was tested per year in this experiment, such comparisons were not possible. Therefore, our analysis did not focus on determining waterlogging sensitivity among cultivars from Loirauxence and La Jaillière, France. Also for this reason, we used the term ’generic cultivars’.

The crop protection programs were similar to local farm practices and included fungicide, herbicide, and insecticide applications to prevent any damage to the crop. Phosphorous and potassium fertilizers were applied during autumn if needed to prevent late-season shortage of these nutrients affecting nitrogen uptake, yield and grain quality. The calibrated cultivar parameters used in this experiment are given in Table 1. For the cultivar Soisson, we adjusted the crop parameters MXFIL (potential kernel growth rate) and MPGS (minimum potential grain size) based on observed data (Fig. 4). For the other three generic cultivars, no observed data on grain size or grain number were available; thus, we used generic parameters with default values from DSSAT-NWheat and applied them uniformly across genotypes. We followed the same approach for other crop parameters. Since more detailed observed data were available for the Soisson cultivar, its calibration was more specific. For the remaining cultivars, in the absence of detailed information, we kept the recommended default values.

Soil attributes used in the simulations are given in Supplementary Table S3. Daily weather data with maximum and minimum temperature (°C), rainfall (mm) and solar radiation (MJ m^{-2} d^{-1}) were from a weather station located on the experimental site. Arvalis also provided observed input nitrogen data applied over each season for each cultivar.

2.3.3. *Sensitivity analysis*

To determine the potential impact of waterlogging on simulated wheat growth with the waterlogging module in DSSAT-NWheat, we conducted a sensitivity analysis. The sensitivity analysis was carried out by simulating waterlogging starting in different phenological stages and with six different waterlogging durations, from 4 to 24 days. This analysis was carried out under the same soil and climate and management conditions as the outdoor controlled waterlogging experiment in Lleida, Spain described in the subsection 2.3.1. The waterlogging conditions were created by setting SSKS of the bottom soil layer at 1 cm h^{-1}, which prevents water from draining from the soil and causes excess water to return to topsoil layers in the surface. Surface runoff may occur depending on soil conditions, following the default soil water balance structure implemented in DSSAT, which includes a runoff routine based on the Soil Conservation Service curve number method (Porter et al., 1999). In the simulation setup, water lost by evapotranspiration was replenished daily through irrigation. During the phenological phase when waterlogging was applied, additional irrigation was used to saturate the entire soil profile, ensuring waterlogging across all soil layers. Simulated waterlogging was applied during the following phenological stages: seedling emergence, 2-leaves, 3-leaves, onset of tillering, onset of stem elongation, anthesis, and onset of grain filling.

Table 2
Statistical indexes and errors used for evaluating the DSSAT-NWheat performance.

Statistical indexes and errors	Formula*
Willmott agreement index (*d*)	$d = 1 - \frac{\sum_{i=1}^{n} (Sim_i - Obs_i)}{\sum_{i=1}^{n} (\lvert Sim_i - \overline{Obs}\rvert + \lvert Sim_i - \overline{Obs}\rvert)^2}$
Relative root mean squared error (rRMSE)	$rRMSE = \sqrt{\frac{1}{n} \times \sum_{i=1}^{n} (Sim_i - Obs_i)2/\overline{Obs}} \times 100$

* Sim_i and Obs_i are the simulated and observed wheat yield; *n* is the number of observations; and $\overline{Obs}$ and $\overline{Est}$ are the average of Obs_i and Sim_i, respectively.

2.4. Data analysis

Data and statistical analyses were conducted using the statistical software program R (R Core Team, 2017). To evaluate the predictive performance of the waterlogging module in DSSAT-NWheat we computed the relative root mean squared error (rRMSE), the coefficient of determination (r^2) and the Willmott agreement index (*d*) (Willmott et al., 1985), based on the estimated wheat yield at the tested location together with the corresponding observed yield. The equations for the indices used to evaluate the model performance are presented in Table 2.

3. Results

3.1. Review of waterlogging impacts on wheat yield components

Waterlogging from the onset of tillering to anthesis results in a 25 ± 10 % decrease in grain number per unit area in the 17 reviewed articles reporting wheat waterlogging experiments (Fig. 3). The highest variation in waterlogging impacts on wheat grain number per unit area (i.e., highest s.d. shown in Fig. 3a) are shown when waterlogging occurred at the onset of tillering and heading (Fig. 3a). Grain number was less affected when waterlogging occurred at the onset of grain filling, with a 5 ± 5 % decrease.

Episodes of waterlogging resulted in lower average grain size compared with the control treatments with no waterlogging (Fig. 3b). Differently from the wheat grain number, the average grain size was more sensitive to waterlogging when it occurred during the onset of grain filling, with a 30 ± 5 % decrease. Waterlogging during seedling emergence had almost no impact on average grain size. With the combined effect of waterlogging on average grain number and grain size per unit area, grain yield was more sensitive to waterlogging when it occurred during the onset of tillering, anthesis and the onset of grain filling, with on average 37 ± 10 %. Waterlogging impacts on grain yield were lower during seedling emergence.

3.2. DSSAT-NWheat performance to simulate the impacts of pre-anthesis waterlogging on wheat yield components

We tested the improved DSSAT-NWheat to simulate the impacts of waterlogging on yield and yield components, with an outdoor controlled waterlogging experiment in Lleida, Spain (described in subsection 2.3.1). First, the simulations were done with the default DSSAT-NWheat without any improvements to simulate waterlogging impacts. As part of this, the simulated wheat yield was 9.3 t ha^{-1}, regardless of the duration of pre-anthesis waterlogging (Fig. 4). Second, the simulations were performed with DSSAT-NWheat with added modules for simulating the impacts of waterlogging on wheat roots (R) and carbohydrate accumulation (CA). In this case, the simulated wheat yield shows a decline due to pre-anthesis waterlogging, of almost 3 t ha^{-1} with 24 days long waterlogging period (Fig. 4a). This yield decline is mainly due to the decreased simulated grain number (Fig. 4b), with increased grain size compensating for it (Fig. 4c). The simulated grain size increased up to 57 % compared to the simulations with DSSAT-Wheat without any improvements to simulate waterlogging impacts. To better simulate the impacts of waterlogging on yield components, we added an impact of waterlogging on potential grain size (GS). Potential grain size responses to stress are known (Calderini et al., 2021b, Reynolds et al., 2022) but are often not represented in crop models, which typically simulate a compensatory effect—larger grain size when grain number is low, and vice versa (Fig. 4c). However, this compensation may occur for potential grain yield but is not always observed, especially when both grain number and potential grain size are simultaneously affected (Supplementary Material Figure S7). Simulated potential grain size in DSSAT-Nwheat is therefore now affected by stress around anthesis.

Considering decreased rooting depth, carbohydrate accumulation and potential grain size under waterlogging conditions, the new improved DSSAT-NWheat satisfactorily simulated wheat yield loss due to waterlogging, with lower grain number and grain size (Fig. 4).

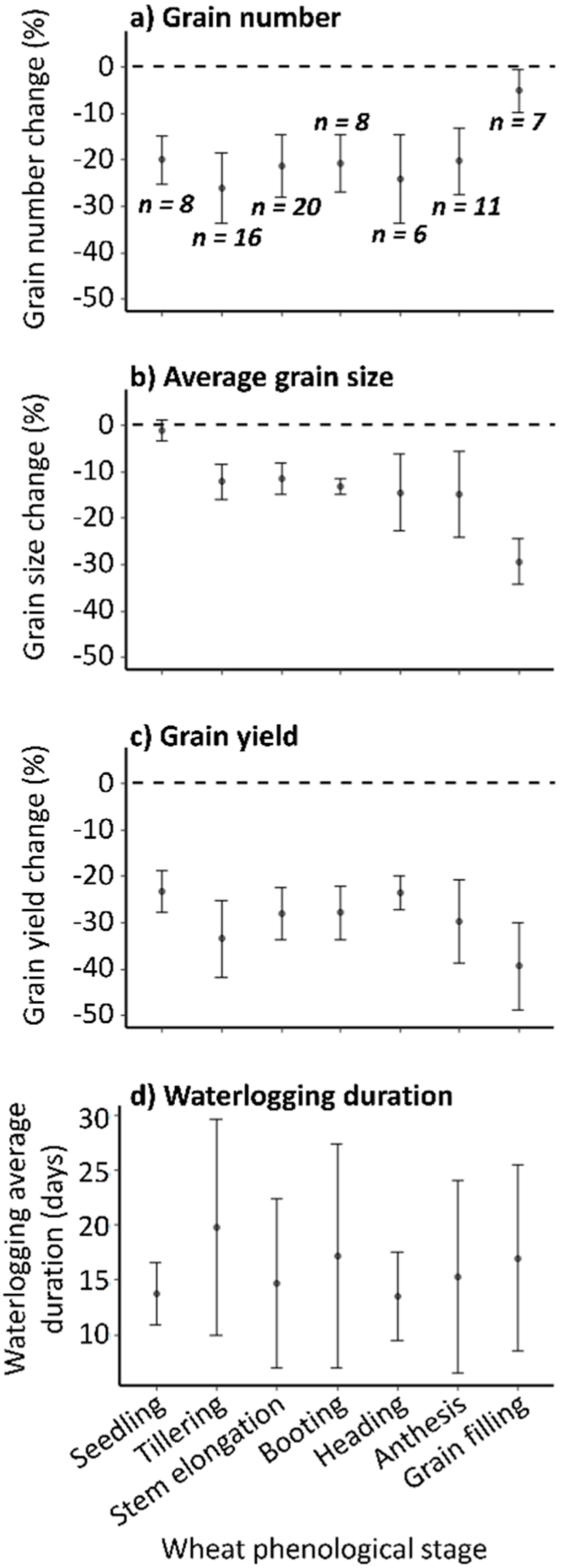
With the new improved DSSAT-NWheat the rRMSE between simulated and observed waterlogged grain yield, grain number per unit area and grain size was 18 % (Table 3). For grain yield and grain number r^2 was 0.68, and for average grain size r^2 was 0.30. The accuracy of the model, represented by the index *d*, was 0.86 for grain yield, 0.79 for grain number per unit area and 0.38 for average grain size. Even with these improvements, the DSSAT-NWheat tends to underestimate the average grain number and to overestimate the average grain size, particularly when waterlogging occurred from 4 to 12 days (Fig. 4b and c).

The improved DSSAT-NWheat model have demonstrated increased sensitivity in simulating the impacts of waterlogging on wheat yield, particularly during the anthesis and grain filling stages (Fig. 5b and c). Notably, there has been an escalation in loss estimates when the duration of waterlogging exceeded 4 days, compared to the previous version of DSSAT-NWheat, which included the waterlogging module developed by Shelia et al. (2019) (Fig. 5).

We further evaluated the new improved DSSAT-NWheat waterlogging model for the field experiment with side-by-side drained and undrained soils conducted from 1990 to 2014 in Loireauxence, La Jaillière (44), France (Fig. 6). The DSSAT-NWheat simulated drained water with r^2 of 0.72, rRMSE of 44 % and *d* of 0.64. Runoff water was simulated with r^2 of 0.9, rRMSE of 107 % and *d* of 0.78. The simulations of grain yield showed a similar performance with r^2 slightly increasing from 0.05 to 0. 11 when comparing grain yield simulated with DSSAT-NWheat with no waterlogging module (Fig. 6c) to with DSSAT-NWheat with waterlogging module (Sim. NWheat improved R + CA + GS) (Fig. 6d), respectively. In addition, the rRMSE slightly increased from 19 % to 20 %, and the d-index from 0.41 to 0.43 when comparing grain yield simulated with DSSAT-NWheat with no waterlogging module (without simulations of the impact of waterlogging on wheat growth) (Fig. 6c) to with DSSAT-NWheat with waterlogging module (with simulations of the impact of waterlogging on wheat growth) (Fig. 6d).

3.3. Sensitivity analysis

The capacity of the model to simulate the impacts of waterlogging on wheat growth variables and yield components is shown through the sensitivity analysis, with waterlogging occurring at different phenological stages and with different durations (Fig. 7). For winter wheat (cultivar Soisson), simulated waterlogging starts to impact yield components during the onset of tillering, except for root biomass. Simulated root biomass is less impacted by waterlogging when it occurred in the early phenological stages (Fig. 7b). The highest impacts on root biomass occur during the onset of grain filling, with a reduction of up to 60 % after 24 days of waterlogging compared to control treatment with no waterlogging. The biomass at maturity and the grain number per unit area are affected from the onset of tillering to the onset of grain filling,



(caption on next column)

Fig. 3. Observed waterlogging impact on wheat grain number, average grain size, and grain yield. The observed impacts of waterlogging applied in different phenological stages on (**a**) grain number per unit area, (**b**) average grain size, and (**c**) grain yield. (**d**) Observed waterlogging average duration in each phenological phase. The 17 peer-reviewed articles are shown in Supplementary Table 1. The number of experiments (*n*) per for each phenological stage is shown in (**a**). Points are means and the vertical bars represent ± 1 s.d. the black dashed lines represent the control treatments in (a-**c**), and the results are presented as a percentage difference from the control.

with the highest impact occurring at the onset of stem elongation (Fig. 7a and d). At this stage, both biomass at maturity and grain number per unit area decrease by 50 % with 24 days of waterlogging.

Leaf area index is impacted by waterlogging from 3-leave-stage to the onset of stem elongation, with the highest sensitivity at the onset of tillering. The average grain size decreased with waterlogging from the onset of stem elongation to the onset of grain filling, and it declines more than 50 % with 24 days of waterlogging in the onset of grain filling. As a result of the decline of all wheat yield components under waterlogging conditions, grain yield can decrease by up to 65 % compared to the control (with no waterlogging), with waterlogging occurring from the onset of stem elongation to the onset of grain filling.

4. Discussion

4.1. Modeling performance of the new waterlogging module in DSSAT-NWheat

Oxygen availability is restricted in waterlogged soils, suppressing root respiration and causing decreased root activity (Van Veen et al., 2014). Plants can temporarily maintain energy production during waterlogging via glycolysis and ethanol fermentation, but prolonged waterlogging leads to the accumulation of toxic metabolites and increased reactive oxygen species, resulting in root cell death (Pan et al., 2021). This inhibits root growth and nutrient transport to shoots, and can lead to nutrient deficit stress (Herzog et al., 2016). Reduced root function and increased nutrient leaching from excessive soil water due to waterlogging may lead to nutrient deficit stress (Salazar et al., 2014; Kaur et al., 2020). Even in the absence of nutrient deficiencies, waterlogging limits root water conductivity, causing stomatal closure and reduced crop growth (Else et al., 2001; Jitsuyama, 2017).

Crop models consolidate scientific knowledge of crop growth processes and enhance understanding of plant responses to abiotic stresses, such as waterlogging. However, they often simplify these processes and omit detailed physiological and biochemical responses (boote et al., 2013; Nóia-Júnior et al., 2025a). For example, the current models, including the waterlogging module introduced in this study, do not account for the plant's ability to cope with toxins (both elemental, such as excessive Fe or Mn, and organic compounds, such as phenolics and carboxylic acids) produced during hypoxic conditions (Yemelyanov et al., 2023). Additionally, reduced nutrient availability due to limited mitochondrial energy production for active nutrient uptake, and oxidative stress induced by waterlogging (León et al., 2021), are also factors that have not been integrated into the model. This level of complexity is often omitted because the inclusion of more physiological processes increases the need for additional crop parameters and inputs, which require new field experiments for calibration. Beyond a certain point, adding such complexity can increase model prediction error (Reynolds and Acock, 1985). In this study, we implemented a new waterlogging module into the wheat crop simulation model DSSAT-NWheat, accounting primarily for the effects of waterlogging on wheat root growth, carbohydrate accumulation, and potential average grain size. Many of the physiological and biochemical factors mentioned above were not considered in the module, in line with common simplifications in crop models.

We evaluated the new waterlogging module in DSSAT-NWheat based

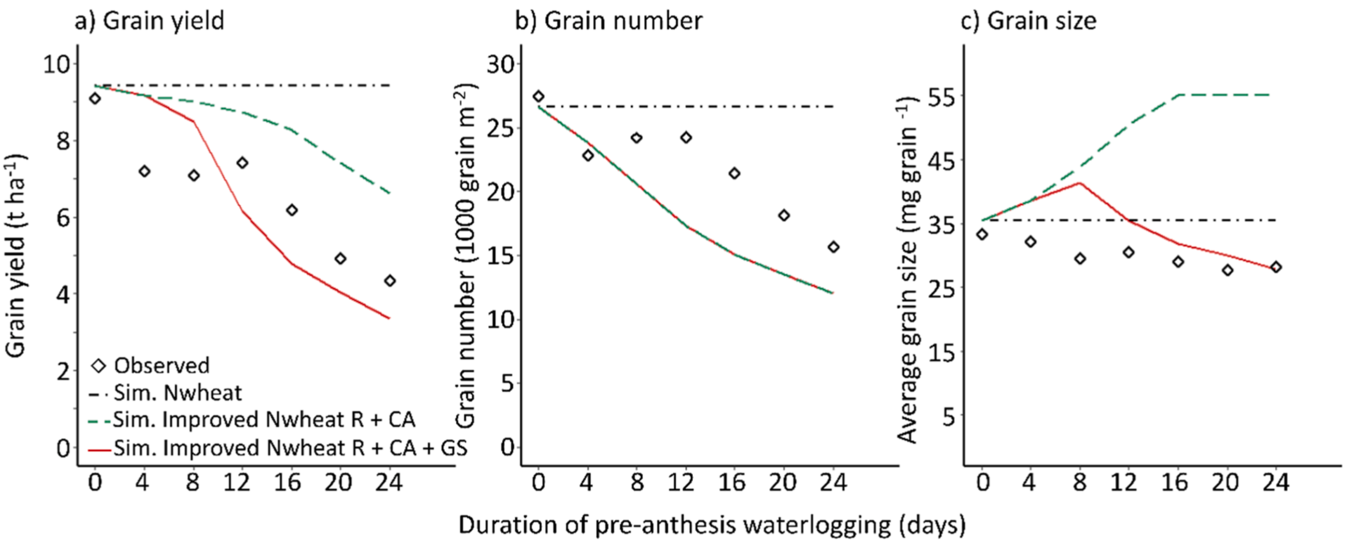


Fig. 4. Performance of the improved DSSAT-NWheat in simulating pre-anthesis waterlogging impacts on wheat. Performance of DSSAT-NWheat in simulating pre-anthesis waterlogging impacts on wheat (**a**) grain yield (**b**) grain number and (**c**) grain size. Data (points) are from an outdoor controlled experiment where wheat plants where waterlogged for 0–24 days before anthesis (Marti et al., 2015). Simulations (lines) were done with DSSAT-NWheat with no waterlogging module (Sim. NWheat), with the waterlogging module accounting only for the impacts of waterlogging on wheat roots and carbohydrate accumulation (Sim. NWheat improved R + CA) and with the waterlogging module accounting for the impacts of waterlogging on wheat roots, carbohydrate accumulation and potential grain size (Sim. NWheat improved R + CA + GS). The acronyms R represents the waterlogging module with impacts on wheat roots, CA in carbohydrate accumulation and GS in potential grain size.

Table 3
Performance of the improved DSSAT-NWheat in simulating pre-anthesis waterlogging impacts on wheat. Data are from an outdoor controlled experiment where wheat plants where waterlogged for 0–24 days before anthesis (Marti et al., 2015) with the DSSAT model with a waterlogging module affecting wheat roots, carbohydrate accumulation potential grain size. Statistical indices are the relative root mean square error (rRMSE), the coefficient of determination (r^2) and the Willmott agreement index (d) (Willmott et al. 1985).

Wheat yield components	rRMSE (%)	r^2	d
Grain yield	18	0.69	0.86
Grain number	18	0.68	0.79
Grain size	18	0.30	0.38

on its ability to simulate yield under waterlogged conditions, using data from an outdoor controlled experiment with measured pre-anthesis waterlogging impacts and from an undrained wheat field.

In the first test set, conducted in an outdoor controlled experiment in Lleida, Spain, the improved DSSAT-NWheat model demonstrated good performance in simulating the impacts of pre-anthesis waterlogging on wheat yield and yield components. The model was tested under pre-anthesis waterlogging conditions, and the simulations showed a decline in yield due to longer waterlogging periods. For example, with a 24-day pre-anthesis waterlogging period, yield declined by about 3 t ha-1, primarily reduced growth resulting in a reduction in grain number. The rRMSE for grain yield was 18 %, with an r^2 of 0.69. In comparison, an experiment using APSIM achieved enhanced simulation accuracy for waterlogging effects on wheat carbohydrate accumulation, with an r^2 of 0.70 and an rRMSE of 11 % (Liu et al., 2023). While the model performed reasonably well, it tended to underestimate grain number and overestimate grain size, particularly when waterlogging occurred for 4–12 days. Despite these issues, the improved DSSAT-NWheat model showed an increased sensitivity in simulating the impacts of pre-anthesis waterlogging on yield.

In contrast, the second test set, conducted in Loireauxence, France, presented additional challenges. The lack of data on key variables, such as soil moisture and water table depth limited the crop model's ability in simulating these conditions. For this field, we only had information indicating that one plot was drained while the other was not, restricting the setting of parameters for this location. Additionally, expected field-scale factors, such as plant diseases, soil variability, and microclimatic variations within the field—which could further impact observed and simulated responses—were not reported. We also used generic cultivar parameters when simulating this experiment, which ignores potential genotypic differences in adaptive traits for waterlogging tolerance, such as root porosity, radial oxygen loss, and root architecture (Pedersen et al., 2021). These factors led to limited model performance in this second test, although the new waterlogging module demonstrated its capability to improve grain yield simulations for this field. This is particularly relevant for regions such as northern France—where the test site is located—where excess water is often the main constraint to wheat productivity (Nóia-Júnior et al., 2025b). In such environments, yield losses caused by heavy rainfall are common but are typically not captured by crop models (Nóia-Júnior et al., 2025a), making simulations more challenging. Despite these limitations, our new routine still led to a slight improvement in simulations, indicating that yield was penalized in undrained fields due to waterlogging.

While the waterlogging module provides useful insights, several model deficiencies became apparent, particularly the need for more detailed calibration data and an understanding of key environmental and genetic factors that influence plant responses to waterlogging. A full exploration of these drivers of model error is needed. Future studies should focus on improving parameterization for different soil types, incorporating genotypic variation, and including additional physiological processes, such as nutrient uptake limitations under anaerobic conditions. The model's simplification of waterlogging effects may also overlook important physiological responses, such as the production of toxic metabolites in hypoxic environments and oxidative stress. In our new module, we considered only the direct impacts of waterlogging on selected aspects of wheat growth, including root function, potential grain size, and carbohydrate accumulation. Other processes possibly to be affected by waterlogging, such as biomass partitioning and phenology (Nóia Júnior et al., 2023a; Garcia-Vila et al., 2025), were not included. Likewise, indirect effects such as reduced nitrogen availability due to increased leaching or limited However, indirect effects such as reduced nitrogen availability due to increased leaching or limited root

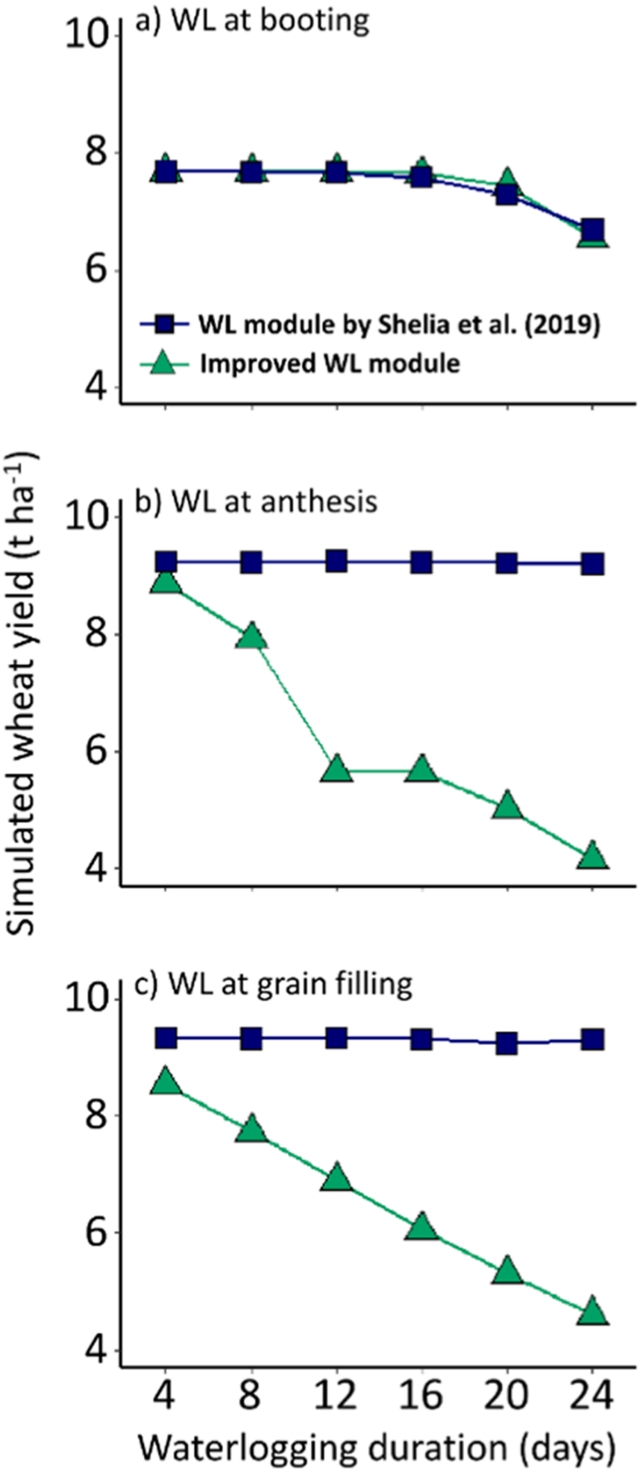


Fig. 5. Simulated waterlogging impacts on wheat with different waterlogging modules approaches. Simulated impacts of waterlogging applied during (**a**) booting (**b**) anthesis and (**c**) grain filling on grain yield simulated using a waterlogging module implemented by Shelia et al. (2019) in DSSAT-Nwheat and the improved waterlogging module for DSSAT-Nwheat proposed in this study.

uptake—caused by shallower rooting under waterlogged conditions are included, but were not evaluated due to lack of data. These limitations should be acknowledged, and further data from field experiments are essential to reduce model uncertainty and improve performance in diverse conditions. In addition, our new waterlogging module would benefit from further validation using controlled experiments in which waterlogging is the only isolated factor affecting yield at phenological stages beyond pre-anthesis, as was the case in the present study. Such experiments are rare, and when they do exist, they are often not available in open data repositories, limiting their use for modeling (Nóia Júnior et al., 2023a). Although the module is designed to affect crop growth at any stage, it was validated using controlled experiments only for pre-anthesis waterlogging impacts. Nevertheless, the sensitivity analysis results shown in Fig. 7 are consistent with the findings from a literature review of multiple studies, as summarized in Fig. 3.

Despite the challenges and limited data for traditional model evaluation, the model utility remains significant for simulating waterlogging impacts on wheat growth. However, its current limitations restrict prediction accuracy across different contexts, as is typical with any crop simulation model, with or without a waterlogging module implemented (Rötter et al., 2018, 2011).

4.2. *Simulated impacts of waterlogging on wheat yield components*

The DSSAT-NWheat model uses the stem weight at the beginning of grain filling to simulate grain number per unit area. Once grain number per unit area is determined, DSSAT-NWheat simulates carbohydrate accumulation in grains, with the maximum grain size limited by the MXGWT parameter. With few grains, all the simulated carbohydrate assimilated during grain filling plus the carbohydrate remobilized from the shoot is distributed to the few grains, causing the simulation of heavy grains (*i.e.* high average grain size). Although this is the physiological concept within the DSSAT-NWheat, high average grain size may also be caused due to the non-development and growth of potential grains close to the labile florets, positioned more distally and with constitutively low grain size, which usually occur during limited grain set situations. In this case, these potential grains with low grain size would not succeed (would not grow and become grains), resulting in an increase in the average grain size of harvested grains (because only the bigger grains would be harvested) (Beral et al., 2022). Waterlogging accelerates flag leaf senescence (Li et al., 2012), affecting post-anthesis biomass production and translocation to grains, further impairing the filling of small grains. However, the current waterlogging module in DSSAT-NWheat does not directly simulate these effects, such as the non-development of small grains and accelerated flag leaf senescence. This relation between grain number per unit area and grain size was here demonstrated for waterlogging simulations before wheat anthesis, which resulted in few but heavier grains on average. To minimize the overestimation of grain size, we implemented an equation to limit the potential grain (Eqs. 5 and 6) size when abiotic stress occurs before anthesis similar to observations made experimentally (Liu et al., 2020a). This also improved the simulation of waterlogging impact on grain size.

Grain volume enlargement involves the coordinated expansion of the pericarp of maternal origin and the endosperm of the seed, and is almost complete when grain filling begins (Calderini et al., 2021a; Reynolds et al., 2022). The expansion of these tissues determines the potential grain size and proteins storage capacity (Herrera and Calderini, 2020). The growing conditions around anthesis are therefore critical for potential grain size determination, a time when simultaneously also grain number per unit area is set (Acreche and Slafer, 2006; Calderini et al., 2021a; Slafer et al., 2023). In addition to the impacts of waterlogging on the potential grain size, grain size may also be affected by any other abiotic constraints at this developmental stage, like heat, drought, ozone and nitrogen deficit, all factors considered in DSSAT-NWheat. The combined impact of these factors on grain size determination still needs to be tested with field data.

4.3. *Factors that affect the intensity of waterlogging impacts on wheat growth*

The impacts of waterlogging on wheat growth varies particularly

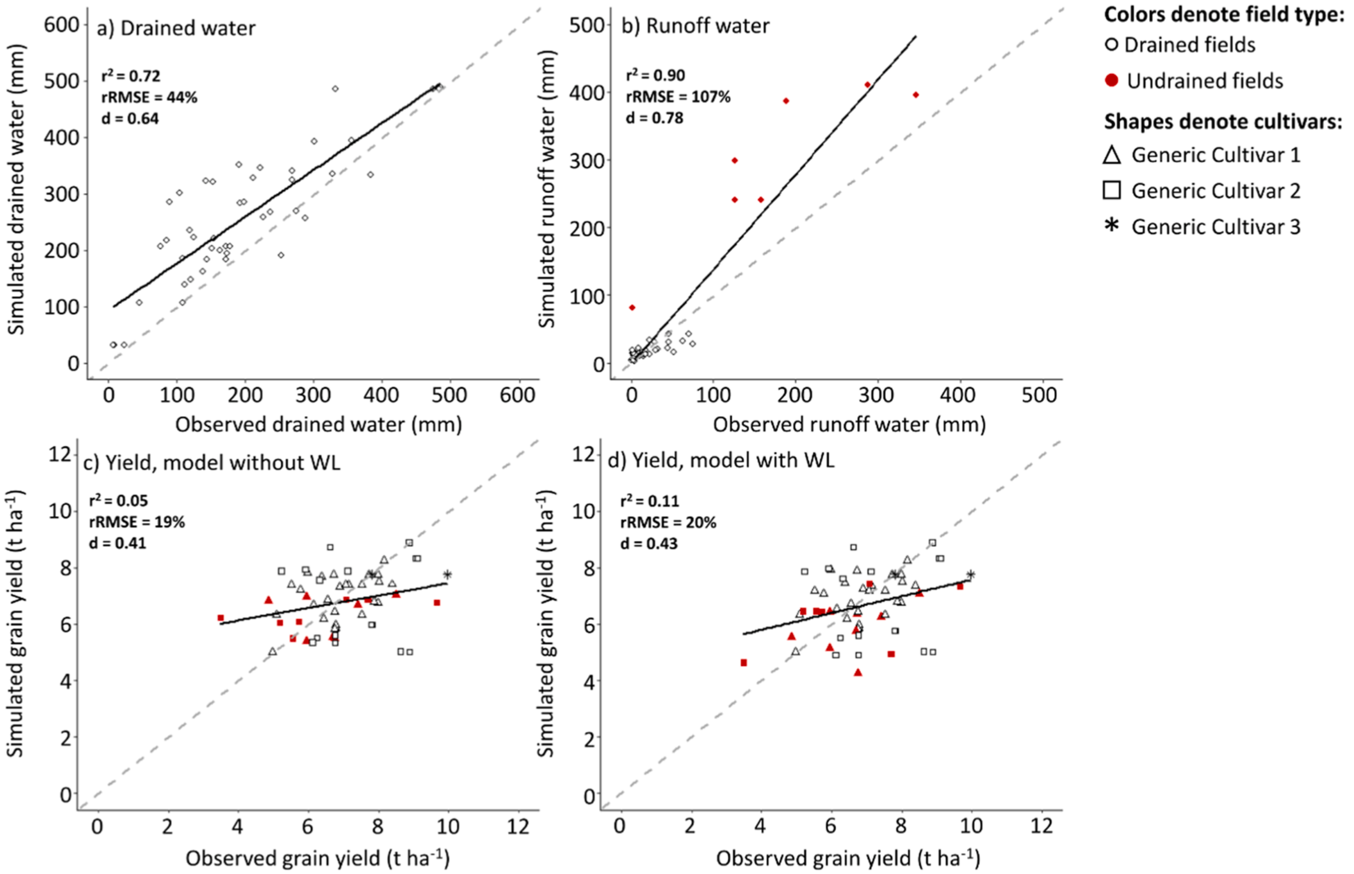


Fig. 6. Simulated versus observed drained water, runoff, and grain yield. Performance of the improved DSSAT-NWheat to simulate seasonal accumulated (**a**) drained and (**b**) runoff water and grain yield (**c**) before and (**d**) after the implementation of the waterlogging module (impact of waterlogging on R+CA+GS) in DSSAT-Nwheat. Data are from 1990 to 2012 in drained (open black symbols) and undrained field (closed red symbols) in Loireauxence, La Jaillière, France. Drained water in undrained fields were not measured. The acronym WL refers to waterlogging in (**c**) and (**d**). Different colors denote drained (open black symbols) and undrained (closed red symbols) fields in all plots, and different shapes denote cultivars in (**c**) and (**d**).

according to its duration and crop phenological stage. We showed that wheat may be less affected by waterlogging during the seedling emergence stage, and can drop drastically during anthesis and grain filling, either due to lower grain numbers or grain size (Fig. 3), which was also simulated with the DSSAT-NWheat (Fig. 7). In addition, waterlogging impacts on wheat and on any crop also vary according to the soil waterlogged depth, air temperature, soil type, mineral nutrition management and genotype, which includes adaptive traits like root porosity, radial oxygen loss, and root architecture that allow some genotypes to better tolerate waterlogging (Herzog et al., 2016). Some of these factors can be indirectly considered via parameters, like a parameter on root survival length under waterlogging, if genetic variation is available for this. Other possible interactions are not included, like a low air temperature leading to slower soil oxygen depletion which could make the impacts of waterlogging on crop growth less severe (Trought and Drew, 1982). However, more field experimental data are need to evaluate how critical these factors are under field conditions to be eventually included into a crop model.

The DSSAT-NWheat model, enhanced with a waterlogging module, represents a substantial advancement in simulating high-intensity rainfall impact on wheat growth and yields. Model simulated outputs correspond reasonably with established crop response curves, depicting reductions in grain number per unit area and grain size under waterlogged conditions. However, the limited availability of comprehensive datasets for validating such model routines underscores a critical need for further detailed research on waterlogging impacts on wheat under field conditions, as previously noted (Rötter et al., 2011; Boote et al., 2013).

Author contributions

All co-authors conceptualized the study. JCD, JPC, PM and SA supervised the study. VSt and VSh implemented the waterlogging module in DSSAT-NWheat. GS made available the data from the outdoor controlled waterlogging experiment in Lleida in Spain, and BP and AD the wheat data from field experiments with side-by-side drained and undrained soils in France. The grain number per unit area and average grain size data in France, was made available by JCD and JPC. RSNJ and Vst performed the formal analysis. RSNJ wrote initial draft, all co-authors assisted with writing and reviewed the manuscript.

CRediT authorship contribution statement

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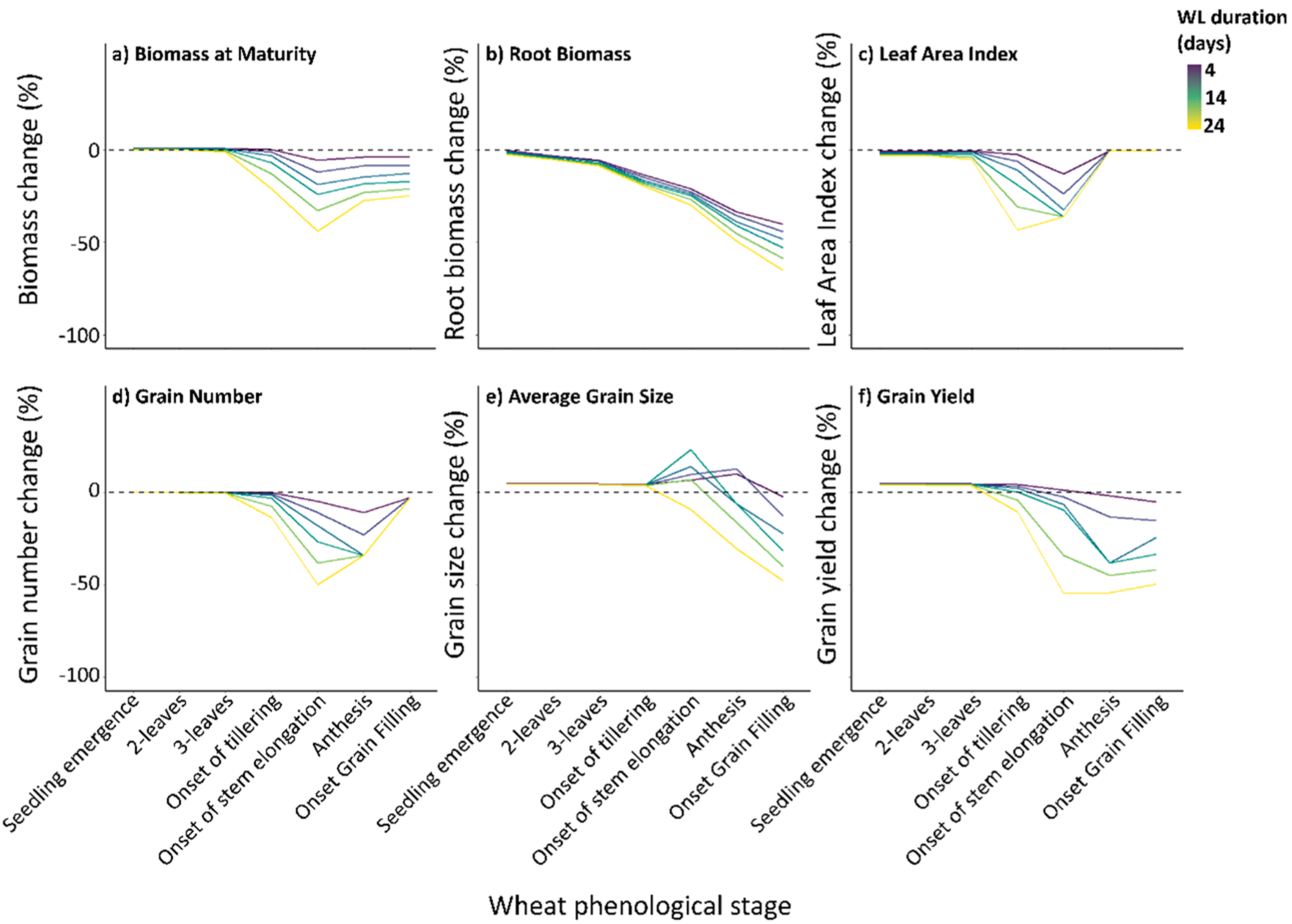

Fig. 7. Sensitivity analysis of the impacts of waterlogging on winter wheat growth simulated by DSSAT-NWheat. Impacts of simulated waterlogging on wheat (**a**) biomass at maturity, (**b**) root biomass, (**c**) leaf area index, (**d**) grain number per unit area, (**e**) average grain size and (**f**) grain yield. The sensitivity analysis was carried out by simulating waterlogging starting in different phenological stages, from wheat seedling emergence to the onset of grain filling, with six different durations varying from 4 to 24 days as schematically shown in Supplementary Fig. S1. Sensitivity analysis of the impacts of waterlogging on spring wheat are shown in Supplementary Fig. S6.

Ewert: Writing – review & editing, Conceptualization, Methodology. **Pierre Martre:** Supervision, Writing – review & editing, Conceptualization. **Heidi Webber:** Methodology, Writing – review & editing, Conceptualization. **Valentina Stocca:** Writing – review & editing, Methodology, Conceptualization, Software, Formal analysis. **Yean-Uk Kim:** Writing – review & editing, Conceptualization, Methodology. **Rogério de S. Nóia Júnior:** Writing – original draft, Methodology, Data curation, Writing – review & editing, Visualization, Formal analysis, Conceptualization. **Van der Velde Marijn:** Methodology, Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2025.110090.

Data availability

Data will be made available on request.

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