Earth's Future

Key Points:
- We review the state of the art of approaches used to modeling the impacts of waterlogging on plants
- Most models use an aeration stress principle that effects root growth, few models account for phenology delays caused by waterlogging
- Next generation models should consider new genotypic traits and tolerance (e.g., aerenchyma, ion tolerance, and oxidative stress)

Supporting Information:
- Table S1

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The State of the Art in Modeling Waterlogging Impacts on Plants: What Do We Know and What Do We Need to Know

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Abstract Models are key tools in our quest to better understand the impacts of soil waterlogging on plant growth and crop production. Here, we reviewed the state of the art of modeling approaches and compared the conceptual design of these models with recent experimental findings. We show that many models adopt an aeration stress (AS) principle where surplus water reduces air-filled porosity, with implications for root growth. However, subsequent effects of AS within each model vary considerably. In some cases, AS inhibits biomass accumulation (e.g. AquaCrop), altering processes prior to biomass accumulation such as light interception (e.g. APSIM), or photosynthesis and carbohydrate accumulation (e.g. SWAGMAN Destiny). While many models account for stage-dependent waterlogging effects, few models account for experimentally observed delays in phenology caused by waterlogging. A model intercomparison specifically designed for long-term waterlogged conditions (APSIM-Oryza) with models developed for dryland conditions with transient waterlogging would advance our understanding of the current fitness for purpose of exsiting frameworks for simulating transient waterlogging in dryland cropping systems. Of the point-based dynamic models examined here, APSIM-Soybean and APSIM-Oryza simulations most closely matched with the observed data, while GLAM-WOFOST achieved the highest performance of the spatial-regional models examined. We conclude that future models should incorporate waterlogging effects on genetic tolerance parameters such as (1) phenology of stress onset, (2) aerenchyma, (3) root hydraulic conductance, (4) nutrient-use efficiency, and (5) plant ion (e.g. Fe/Mn) tolerance. Incorporating these traits/effects into models, together with a more systematic model intercomparison using consistent initialization data, will significantly improve our understanding of the relative importance of such factors in a systems context, including feedbacks between biological factors, emergent properties, and sensitive variables responsible for yield losses under waterlogging.

1. Introduction

Climate change is increasing the frequency and intensity of extreme events, including large rainfall events (Chang-Fung-Martel et al., 2017; Harrison, Cullen, & Rawnsley, 2016; Hirabayashi et al., 2013). Such events can lead to flash flooding, river surges, and rising ground water tables. Together, these factors increase the extent to which global food production and food security are impacted by crop waterlogging (Harrison, Tardieu, et al., 2014).

Flooding is an integral part of some agroecosystems. The Nile river floods, for instance, are well known for their importance in supplying nutrients and organic matter. Paddy rice systems have developed because they suppress weeds and provide thermal protection to the rice crop. However, soil flooding (or "waterlogging" in an agricultural context) is a serious problem for most dryland crops; it is dynamic, complex, and difficult to predict, resulting in complex, dynamic interactions within the soil-plant-atmosphere continuum. Waterlogging research is thus not straightforward due to poor reproducibility in field trials, high soil variability (clay content, layering structure, mineral content, etc.), and the unique nature of the waterlogging event.
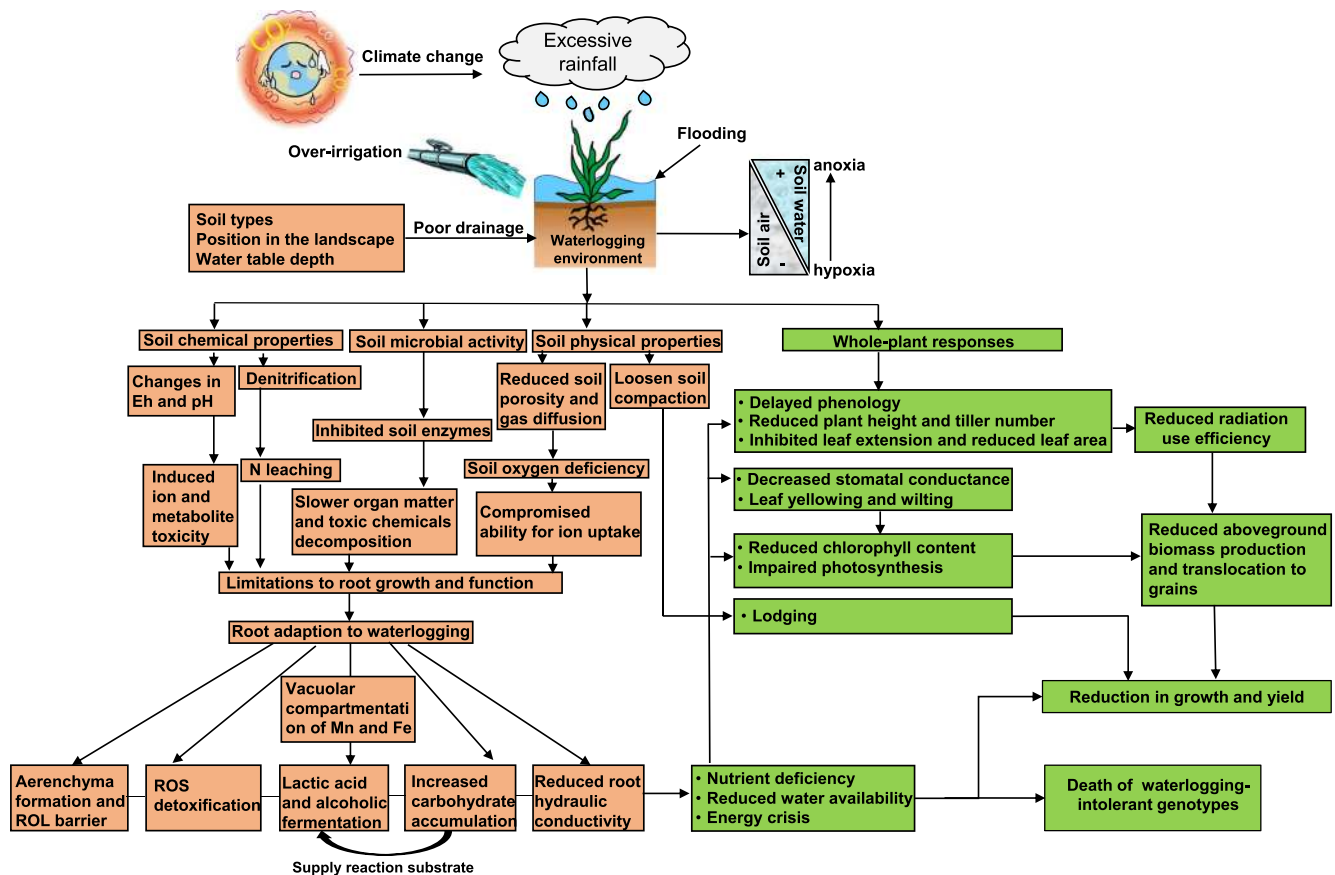
Figure 1. Physiological, morphological, physical, and chemical mechanisms implicated in plant growth responses to waterlogging.

Waterlogging may occur for many reasons, including geography, atmospheric conditions/climate, soil type, lateral ground water flows, and rising/perched watertables (Figure 1). In general, crops experience stress when water content is suboptimal or supraoptimal, depending on the type of waterlogging. In this review, we primarily focus on plant stress caused when soil water content is near saturation or when surface flooding occurs.

Contemporary crop models account for waterlogging-induced changes in soil properties (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012; Gaydon, Probert, Buresh, Meinke, & Timsina, 2012; Jing et al., 2007, 2010) but few account for (1) the changes in plant traits under waterlogging stress, (2) incorporate genotypic variability within each species, or (3) account for the ability of crops to adapt and recover after waterlogging (Harrison et al., 2011; Pembleton et al., 2016). While several important mechanisms conferring waterlogging stress tolerance have been identified (Figure 1), only some of these have been incorporated in models (discussed below). Further, there is considerable genetic variability for the key traits conferring plant adaptive responses to low oxygen conditions within the same species (Cruz-Garcia et al., 2020). Understanding and implementing these physiological responses to changing environmental factors may benefit model-assisted design of climate change adaptation strategies (Peng et al., 2020; Pembleton et al., 2016). We posit that a better understanding of the biophysical dynamics that govern the complex feedback loops can be obtained by suitably constructed and appropriately parameterized models (Harrison et al., 2012, 2019; Harrison, Cullen, Tomkins et al., 2016; Liu, Harrison, Hunt, et al., 2020). Here, we selected models that are part of crop simulation frameworks and therefore capable of simulating stress responses and their impacts on biomass, yield, and resource pools. We excluded models that are either close derivatives of models of models studied here or that lacked ability to simulate systems dynamics.

In the following sections, we (1) analyze the physiological and biological aspects of waterlogging and how these affect crop yields, (2) contrast recent waterlogging experiments and conceptualizations used to

model waterlogging, and (3) critique past model validation, including an examination of model performance in waterlogged environments. We then compared recent experimental findings to highlight the limitations of current waterlogging research, concluding with opportunities for integrating recent experimental work with future modeling approaches.

2. Modeling Crop Waterlogging

Processes used to conceptualize waterlogging vary considerably. In line with our aims, the following section examines (1) the physiological and biochemical mechanisms used to model waterlogging, including the processes affecting yield, and (2) the extent to which such models have been validated with real data. The latter aim is designed to help in understanding how models were derived (whether theoretically or using real data) and demonstrates how well such models perform by comparing modeled responses to experimental data.

2.1. Waterlogging Stress Indices

Approaches for simulating stress indices shown below are based primarily on water table height and stress duration using empirical crop species factors.

2.1.1. Excess Water Table Duration Approach

A method for quantifying stress caused by fluctuating water tables developed by Sieben (1964) and Wesseling (1974) assumed that yield reduction caused by excessive soil water conditions could be related to the integral of water table height and time the water table remained in the root zone (assumed to be the top 30 cm of soil). The approach, SEW_{30} (computed as the summation of days times the height of the water table above 30 cm) was expressed as shown in Equation 1.

$$SEW_{30} = \sum_{i=1}^{N} (30 - X_i) \tag{1}$$

In Equation 1, X_i is the water table depth (0–30 cm) on day i and N is the number of days in the growing season. Units for SEW_{30} are cm days.

SEW_{30} integrates daily waterlogging over the growing season. Sieben (1964) calculated SEW_{30} for high water tables during the winter for several cereal crops from water table measurements at a point midway between subsurface drains, observing a correlation between SEW_{30} values and yields (Nibler & Brooks, 1975). Later research has shown reduced cereal yields with SEW_{30} values >1,000 (cm days) (Belford et al., 1992; McFarlane et al., 1989). Although such assessments of waterlogging intensity are convenient, they should be used cautiously in predicting effects on crop growth or yield. SEW_{30} values calculated in the field study by Setter et al. (1999) were highly variable even though the field was relatively flat (slope of <0.5%). As well, SEW_{30} does not account for depth of waterlogging (within or outside the arbitrary 30-cm datum), although many studies provide evidence that surface waterlogging causes more severe damage to crop growth and yield than subsurface waterlogging (Shen et al., 1999; Zhu et al., 2003). SEW_{30} also does not account for the timing of waterlogging relative to crop phenology which, as will be discussed below, can have large ramifications for crop growth.

2.1.2. Surface and Subsurface Excess Water

The Subsurface Excess Water ($SFEW$) model (Shen et al., 1999) includes both surface and subsurface water:

$$SFEW_{30} = \sum_{t=1}^{n} (30 - d_t) + \sum_{t=1}^{n} h_t \tag{2}$$

where n is number of waterlogging-stress days, h_t is average surface water depth on day t (cm, 0–30), and d_t is the average depth of the groundwater table on day t during waterlogging-stress periods. The value of 30 cm is the critical water table depth for yield losses, building on the SEW_{30} approach (Darzi-Naftchali et al., 2013; Hirekhan et al., 2007).

$SFEW_{30}$ was initially used to describe the relationship between cotton yield and the water table level (Shen et al., 1999; Zhu et al., 2003). Shen et al. (1999) and Zhu et al. (2003) found a linear relationship between $SFEW_{30}$ and relative yield in cotton ($R^2 > 0.90$). Despite the high correlation, SEW or $SFEW$ ignores both the physiological basis of crop damage from waterlogging and soil chemical factors that might be influenced by water tables that approach the soil surface. This method also does not discriminate between effects of surface water height (h_t) on crop growth.

2.1.3. Stress Day Index

The stress day index (*SDI*, Equation. 3) was developed to characterize effects of excessive/deficit water stress on crop yields. *SDI* provides a quantitative means for determining stress during a crop growing season and is applicable to irrigation and drainage requirements of crops (Hiler et al., 1974). *SDI* is calculated as the product of a stress day (*SD*) factor and a crop susceptibility (*CS*):

$$SDI = \sum_{i=1}^{n} CS_i \times SD_i \qquad (3)$$

where *n* represents the number of growing periods and *SD* is the stress on day *i* and is taken as the daily value of SEW_{30}. *CS* depends on the species and stage of development of a given crop calibrated using field and lysimeter experiments for corn and soybeans (Evans & Skaggs, 1984; Mukhtar et al., 1990). Values for *CS* according to Evans and Skaggs (1984) were 0.16 for crop establishment, 0.18 for early vegetative stages, 0.38 for late vegetative stages, 0.21 for flowering, and 0.06 for yield formation.

Using data from a large set of drainage experiments, the R^2 between *SDI* and relative corn yield was generally greater than 0.80 (Ahmad & Kanwar, 1989), indicating good correlation between *SDI* and yield penalty. This approach is more species specific compared with SEW_{30} and $SFEW_{30}$ though does have the limitation of calculating stress as a function of waterlogging duration. As for Equations 1 and 2, plant adaptation and recovery to transient waterlogging may not be fully captured by Equation 3.

2.2. Waterlogging Approaches in Crop Models

To varied degrees, systems models simulate abiotic stresses within the climate-soil-water-crop-animal continuum and allow dissection of genotype by management interactions under various environmental conditions (Harrison, Tardieu, et al., 2014; Ho et al., 2014; Ibrahim et al., 2019). In general, there are two algorithms used to mimic waterlogging in crop models. The first category incorporates stress day indices (e.g., *SDI* and DRAINMOD, Hardjoamidjojo & Skaggs, 1982; Hardjoamidjojo et al., 1982) or dynamic aeration stress factors that are independent of phenology (such as those employed in and CROPR; Qian et al., 2017), SWAGMAN (Shaw & Meyer, 2015), AquaCrop (Steduto et al., 2009), and CGMS-WOFOST (Li et al., 2016), while the second uses dynamic aeration stress factors computed as a function of phenology, such as APSIM-Soybean (Archontoulis et al., 2020; Ebrahimi-Mollabashi et al., 2019; Pasley et al., 2020), APSIM-Wheat (Asseng et al., 1997), APSIM-Oryza (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012; Gaydon, Probert, Buresh, Meinke, & Timsina, 2012), and APSIM-eucalypt (Paydar et al., 2005). In the following section, we describe processes used to simulate effects of waterlogging on crops; we also provide an overview (Table 1).

2.2.1. DRAINMOD

DRAINMOD is a field-scale, process-based, distributed simulation model, which has been applied at scales ranging from a point on the landscape to areas of several thousand hectares on hourly and daily time scales (Table 1). Hardjoamidjojo et al. (1982) incorporated the *SDI* concept into DRAINMOD; validation from data set from two sites on the Tidewater Research Station showed that relative yield (*YR*, the ratio of the measured yield to potential yield or maximum yield) was highly correlated (*YR* = 103-0.42*SDI*, R^2 = 0.74) with *SDI* (Table 1 and supporting information Table S1). Hardjoamidjojo and Skaggs (1982) then quantified the effects of excess and deficit soil water on corn yields in DRAINMOD. The model described only 63% of the variation in observed corn yields for the 12-year period. Hassanpour et al. (2011) also reported an overestimation of simulated canola yield in evaluating the performance of surface drainage and canola crop growth in DRAINMOD. The discrepancy between predicted and measured yields in this case may be attributed to the empirical factors in Equation 3. *CS* values for corn were assumed constant for each of the three growth stages (vegetative, silking, and tasseling to soft dough, after soft dough). Given that such *CS* are based on genotypes developed around 40 years ago, further work is required to derive *CS* values that are representative of current crop genotypes.

2.2.2. CROPR

In CROPR, when the soil pressure head is below the anaerobic point (i.e., aeration stress is present), water supply is reduced and dry matter accumulation decreases. To enable simulation of waterlogging, Qian et al. (2017) incorporated the *SFEW* index and added an oxygen deficiency growth factor in CROPR. The revised model simulates dry matter accumulation as a function of a drainage index including surface and subsurface water. Performance of the revised model under waterlogging and submergence for a range of growth

Table 1
Waterlogging (WL) Processes Captured in DRAINMOD, CROPR, SWAGMAN Destiny, AquaCrop, SWAP-WOFOST, GLAM-WOFOST, and APSIM

Process	DRAINMOD	CROPR	SWAGMAN Destiny	AquaCrop	SWAP-WOFOST	GLAM-WOFOST	APSIM-soybean	APSIM-wheat	APSIM-Oryza
Temporal resolution	Hourly-daily	Daily	Daily	Daily	Daily	Daily	Daily	Daily	Daily
Spatial resolution	Point based	Point based	Point based	Point based	Point based	Regional	Point based	Point based	Point based
WT presence	X	X	X	X	X	X	X	X	X
WT depth below soil surface	X	X	X	X	X	X	X	X	X
WT duration					X	X	X	X	X
WL aeration factor		X	X	X	X	X	X	X	
Root depth		X	X	X	X	X	X	X	
Root exploration		X	X	X	X	X	X	X	
Soil water extraction		X	X	X	X	X	X	X	
Transpiration		X	X	X	X	X	X	X	
Leaf area growth		X	X	X	X	X	X	X	
Tillering								X	
N fixation	X		X	X			X	X	X
C and N cycling	X								X
Stage dependent effects of WL	X					X	X		
WL-induced phenology delays							X	X	
Plant adaptation and recovery after waterlogging		X							
Management interventions associated with waterlogging							X	X	X
Evidence of validation	R^2 between relative yield and SDI ranged from 63% to 74%	RMSE between simulated and observed cotton yield was 686 kg ha^{-1}	N/A	N/A	Mean bias error between simulated yield and observed yield ranged from 400–600 kg ha^{-1}	RMSE between simulated and observed wheat yield was 382 kg ha^{-1}	R^2 and RMSE of simulated root depth was 0.97 and 9 cm; R^2 between simulated and observed soybean yield was above 0.90	N/A	R^2 and RMSE of simulated N loss and observed N loss was 0.98 and 2.98 (% applied N). RMSE between simulated and observed yield was 453 kg ha^{-1}

Note. X represents with presence of a particular process. WT and WL represent watertable and waterlogging, respectively. N/A = not assessed.

Table 2
Summary of Key Concepts Used in Crop Models to Capture the Waterlogging Process

Model	Concepts used to model waterlogging	References
DRAINMOD	Waterlogging stress is computed using a drainage index (SDI, aeration stress) and a crop specific sensitivity factor (SDI).	Hardjoamidjojo et al. (1982), Hardjoamidjojo and Skaggs (1982), Hassanpour et al. (2011), Hiler et al. (1974), and Skaggs et al. (2012)
CROPR	Waterlogged dry matter growth is calculated by an aeration factor w_{AE} and the maximum efficiency of the aeration factor (A_{AE}, kg ha^{-1} m^{-1}).	Feddes (1978) and Qian et al. (2017)
SWAGMAN Destiny	Waterlogging stress is computed by the aeration stress factor that effects root growth, leaf growth, and photosynthesis, hence reducing biomass accumulation.	Timsina and Humphreys (2003) Meyer and Barrs (1991)
AquaCrop	Root respiration is reduced when water content in the root zone is above the critical value, hence reducing plant biomass and yield.	Mabhaudhi et al. (2014a, 2014a) and Vanuytrecht et al. (2014)
WOFOST	A transpiration rate reduction factor is used to reduce the transpiration rate due to waterlogging when the soil moisture content is greater than 0.3 (cm^3 cm^{-3}). During waterlogging periods, the aeration stress factor reduces daily photosynthesis and hence reducing photosynthate partitioning to grains.	de Wit et al. (2019)
APSIM	In APSIM-Wheat, maximum growth retardation due to waterlogging occurs after 3 days of aeration deficit in the root zone. The root aeration factor dictates leaf area growth and tillering and consequently yield.	Asseng et al. (1997)
	In APSIM-Soybean, a stage dependency aeration stress factor occurs when the difference between actual soil water and saturated volumetric water content is below 6.5%. The aeration factor delays phenology and reduces effective root length density, photosynthesis, water and N uptake, hence reducing biomass and yield.	Ebrahimi-Mollabashi et al. (2019)
	APSIM-Oryza captures the effect of the changes in nutrient dynamics on crop growth (e.g., leaf photosynthesis, leaf growth rate, and N translocation to organs) under aerobic and anaerobic soil conditions. It accounts for changes in N and C processes under flooded soil conditions; when organic residue is submerged in floodwater, decomposition rate slows, nitrification ceases, and CH_4 emissions are initiated, causing C loss.	Gaydon, Probert, Buresh, Meinke, Suriadi, et al. (2012), Gaydon, Probert, Buresh, Meinke, & Timsina (2012), Holzworth et al. (2018), Keating et al. (1999), Pasley et al. (2020), Gaydon, Probert, Buresh, Meinke, Suriadi, et al. (2012), and Gaydon, Probert, Buresh, Meinke, & Timsina (2012)

stages was further improved by introducing a factor related to the maximum efficiency of aeration (or crop waterlogging sensitivity). The revised CROPR model is thus able to simulate yield penalization caused by waterlogging at different growth stages through the maximum efficiency of aeration factor (A_{AE}, kg ha^{-1} m^{-1}, Table 2 and Table S1).

Crops may recover from waterlogging stress if waterlogging occurs during early growth stages. One or two weeks after waterlogging ceases, root growth rates recover to similar rates as in the control plants, but the negative effect of waterlogging on shoots may last longer (Malik et al., 2001; Pang et al., 2004). This indicates that crops are likely to suffer from stunted growth for a period before their growth returns to normal. The revised version of CROPR is one of the few models that considers such legacy effects of waterlogging stress on dry matter accumulation. When tested against independent data from five different waterlogging duration treatments (2d, 4d, 6d, 7d, and 8d), the RMSE of seed cotton yield was 686.22 kg ha^{-1}, with an NRMSE of 14.87% (Table 1).

2.2.3. SWAGMAN Destiny

SWAGMAN Destiny is a point scale, daily time step crop model that can be used to determine changes in water table and crop productivity, for a range of crops and pastures (Table 1). This model represents waterlogging through gas-filled soil pore volume, considering the root length density for each soil layer. Root growth within the waterlogged layer slows when water-filled pore space reaches 0.65 after 3 days (Meyer & Barrs, 1991; Timsina & Humphreys, 2003). Aeration stress in SWAGMAN Destiny affects new root growth and distribution and leaf area growth. Roots are preferentially grown in aerated soil layers (less root growth in soil layers with water content between the drained upper limit and saturation), and this effects leaf growth, photosynthesis, carbohydrate accumulate, and ultimately biomass accumulation and yield (Table 2 and Table S1).

There are few studies that use SWAGMAN Destiny to assess effects of waterlogging on crop performance. One exception is the study by Shaw et al. (2013), who found that wheat yield reduction at 65% air filled pore space (AFPS) was 6% higher than that at 10% AFPS, although this study did not validate the model. Shaw et al. (2013) proposed three stages to model waterlogging. The first stage increases plant function with unlimited water and adequate soil oxygen concentrations for root respiration for up to 3 days, the second stage represents plant response to declining soil oxygen concentrations, and the third stage represents species-dependent plant adaptations used to model physiological response and adaptation to waterlogging. While the three-stage hypothesis is one of the few modeling approaches that accounts for plant adaptations under waterlogging, it may be further improved by accounting for tolerance difference between new crop genotypes (e.g., tolerant species exhibit similar or increased function compared to that before the waterlogging event, while sensitive species have decreased growth after waterlogging). Further tolerance mechanisms that could be included in are discussed in section 5.

2.2.4. AquaCrop

AquaCrop is point location based and simulates soil water balance and crop growth processes on a daily time step (Table 1). AquaCrop models waterlogging stress using an aeration stress factor, K_{saer} (Mabhaudhi et al., 2014a, 2014b; Vanuytrecht et al., 2014). Deficit aeration occurs when soil pore volume is below than 5%. To account for crop tolerance to short periods of waterlogging, the maximum effect of waterlogging occurs after a set number of days (default is 3 days). Root respiration is reduced when the water content in the root zone is above the critical value, reducing plant biomass and yield (Table 2 and Table S1). The majority of previous research using AquaCrop has generally been related to water-deficit stress (Araya et al., 2010; Nyathi et al., 2018) rather than waterlogging stress. The model was validated for several variables (canopy cover, soil water content, actual evapotranspiration, above ground biomass, and water productivity) under well-watered and severe drought conditions, although there is little information available on the performance of this model in simulating waterlogging effects on crop growth and yield.

2.2.5. World Food Studies

World Food Studies (WOFOST) is a point scale, daily time step crop model which can provide objective data for regional crop state monitoring and yield forecasting at regional and national scales on individual years (Table 1). When soil moisture content is greater than 0.3 (cm^3 cm^{-3}) in WOFOST (de Wit et al., 2019), a transpiration rate reduction factor indicating oxygen shortage is introduced. The maximum reduction in transpiration rate occurs after 4 days of anaerobic conditions. This factor inhibits daily gross assimilation growth rate and thus grain growth rate (Table 2 and Table S1). The transpiration rate reduction due to oxygen shortage is calculated as follows:

$$f_{max} = \frac{\theta_{sat} - \theta}{\theta_{sat} - K_{WL} \times \theta_{dul}} \tag{4}$$

$$f_{Trel} = 1 - \frac{d}{4}(1 - f_{max}), \, d \leq 4 \tag{5}$$

where f_{max} is maximum reduction value after 4-day oxygen stress and $K_{WL} \times \theta_{dul}$ is the lower limit of soil water content causing oxygen stress. f_{Trel} is water stress factor due to oxygen shortage. d is the number of successive days with oxygen stress.

Relatively few crop models apply waterlogging stress directly to transpiration (Tables 1 and 2). Although WOFOST has been widely studied, there are few studies that use WOFOST to assess crop yield reduction caused by waterlogging. This may be because the water module of WOFOST is simplified to suit crop simulations over large areas (de Wit et al., 2015). Most studies examining waterlogging stress were conducted when WOFOST was coupled with other models (e.g., SWAP, GLAM, and Noah LSM). Combinations of WOFOST with other models are now discussed.

2.2.5.1. SWAP-WOFOST

SWAP (Soil-Water-Atmosphere-Plant) simulates water flow in the unsaturated and saturated upper part of the soil profile, where the interaction between groundwater and surface water is important (van Dam et al., 2008). Potential transpiration rate in SWAP depends on atmospheric conditions, while potential root water extraction rate at a certain depth, $S_{P(z)}$ (day^{-1}) is proportional to root length density and potential transpiration rate (T_p):

$$S_{P(z)} = \frac{L_{root(z)}}{\int_{-D_{root}}^{0} L_{root(z)} dz} \times T_p \tag{6}$$

where $L_{root(z)}$ is the root length density (cm^{-2}) rate at a certain depth (z) and D_{root} is the root layer thickness (cm). Stresses due to dry or wet conditions and/or high salinity concentrations can reduce $S_{P(z)}$.

SWAP and WOFOST were coupled by Van Dam et al. (1997) to enable oxygen stress to occur when actual root respiration is lower than potential root respiration. Actual root water flux is achieved by multiplying potential root water uptake with stress factors for water and salinity stress:

$$S_a = \alpha_{rd} \alpha_{rw} \alpha_{rs} S_p \tag{7}$$

where S_a and S_p are the actual and potential root water uptake for both model compartments (d^{-1}) and α_{rd}, α_{rw}, and α_{rs} are the stress factors for the impact of drought, waterlogging, and salinity, respectively. α_{rw} and α_{rs} are calculated according to Feddes (1978) and Maas and Hoffman (1977). Integration of S_a over the root layer gives actual transpiration rate T_a(cm day^{-1}). Taking all environmental stresses into account, the daily gross assimilation growth rate (A_{gross}, in kg ha^{-1} day^{-1} dry matter) is determined as follows:

$$A_{gross} = f_{Trel} \times f_{CFET} \times f_{nut} \times f_{res} \times A_p \tag{8}$$

where f_{Trel} is a transpiration reduction factor determined by salinity, drought, and excessive water (Equation 8), f_{CFET} is a correction factor for potential transpiration introduced to account for changing atmospheric carbon dioxide levels that influence stomata and water vapor exchange, f_{nut} is the influence of nutrients, and f_{res} is the residual factor.

Validation of SWAP-WOFOST from three individual field experiments conducted at Ruurlo, Zegveld, and Cranendonck has shown good agreement between simulated and observed yields under different fertilizer levels and soil types (Kroes & Supit, 2011). Similarly, integration of WOFOST with Noah LSM (land surface model) resulted in satisfactory performance in simulating soil moisture. Although it was shown that the paired models were better than either individual model for studying effects of waterlogging, there are few studies that use SWAP-WOFOST to assess crop yield reduction caused by waterlogging.

2.2.5.2. GLAM-WOFOST

The General Large Area Model (GLAM) (Challinor et al., 2004) is a process-based, regional crop model (Table 1). To simulate crop loss due to heavy precipitation, WOFOST/CGMS can be modified by introducing a damage function that limits transpiration when soil moisture exceeds a critical soil moisture value. One function is the transpiration rate reduction factor due to oxygen shortage when the soil moisture content exceeds a critical soil moisture value in original WOFOST. However, this approach resulted in a poor correlation between simulated and observed wheat yield ($R^2 = 0.57$, RMSE = 382 kg ha^{-1}) under waterlogging conditions (Li et al., 2016).

Hu et al. (2004) developed another aeration stress factor for reducing transpiration rate defined by the WSF_{HU}, thereby decreasing simulated biomass and yield accumulation. This waterlogging stress factor is determined by crop species, soil water content, days of waterlogging, and the sensitivities of different growth stages. The waterlogging stress factor is calculated as follows:

$$WSF_{HU} \left\{ \begin{array}{ll} 1 - WSFC_0(1 - f(T_W))\left(\dfrac{\theta - K_{WL} \times \theta_{DUL}}{\theta_{SAT} - K_{WL} \times \theta_{DUL}}\right) & (K_{WL} \times \theta_{DUL}) \leq \theta < \theta_{SAT} \\ 1 - WSFC_0(1 - f(T_W)) & \theta > \theta_{SAT} \end{array} \right\} \tag{9}$$

$$f(T_W) = \left\{ \begin{array}{ll} \min\left(1, \max\left(0, -0.0000838 T_W^3 + 0.0032 T_W^2 - 0.048 T_W + 1.1255\right)\right) & i = 1 \\ \min\left(1, \max\left(0, -0.0000838 T_W^3 + 0.0032 T_W^2 - 0.048 T_W + 1.1255\right)\right) & i = 2 \\ \min\left(1, \max\left(0, -0.0000838 T_W^3 + 0.0032 T_W^2 - 0.048 T_W + 1.1255\right)\right) & i = 3 \\ \min\left(1, \max\left(0, 1 - \dfrac{1}{\min\left(1, \max\left(0, -0.0000838 T_W^3 + 0.0032 T_W^2 - 0.048 T_W + 1.1255\right)\right)}\right)\right) & i = 4 \\ \min\left(1, \max\left(0, 1 - \dfrac{1}{\min\left(1, \max\left(0, -0.0000838 T_W^3 + 0.0032 T_W^2 - 0.048 T_W + 1.1255\right)\right)}\right)\right) & i = 5 \end{array} \right.$$

$$\tag{10}$$

where WSF_{HU} is the water stress factor, $WSFC_0$ represents the sensitivity of different crops to waterlogging (0 to 1), f is a function that accounts for the effects of waterlogging days at different growth stages, and T_W is the number of waterlogging days. The growth stage i can be planting to terminal spikelet, terminal spikelet to flowering, flowering, grain filling, or maturity. This approach allows variation in the extent of waterlogging according to growth stage, but the model does not account for the delay in phenology caused by waterlogging in greenhouse experiments (Liu, Harrison, Ibrahim, et al., 2020).

Li et al. (2016) compared both methods in GLAM-WOFOST then revised the runoff, surface storage, and infiltration scheme in GLAM, resulting in an improvement in model validation (data set from wheat production data from 1985 to 2000 of Jiangsu, Anhui, and Zhejiang provinces in China), with RMSE and R^2 values of 307 kg ha^{-1} and 0.78 in using WSF_{HU} (Hu et al., 2004) and RMSE and R^2 values of 307 kg ha^{-1} and 0.71 in using WSF_{HU}. The improvement performance was mainly because the scheme proposed by Hu et al. (2004) included a growth stage specification, rather than aeration factor in WOFOST that ignores the sensitivity of each growth stage to waterlogging. This indicates that stage-specific waterlogging effects are important in accurately simulating waterlogging.

2.2.6. Agricultural Production Systems Simulator

Agricultural Production Systems Simulator (APSIM) is a dynamic, point scale, daily time step model that combines biophysical and management modules within a central engine to simulate cropping systems (Table 1) (Holzworth et al., 2018). APSIM enables simulation of diverse farming systems including the transition between anaerobic and aerobic soil conditions (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012; Gaydon, Probert, Buresh, Meinke, & Timsina, 2012). Waterlogging effects in APSIM are primarily determined by a stress factor that reduces photosynthesis (Keating et al., 1999) and root distribution as soil moisture approaches saturation (Asseng et al., 1997; Ebrahimi-Mollabashi et al., 2019; Pasley et al., 2020). Different waterlogging mechanisms are modeled in each APSIM module.
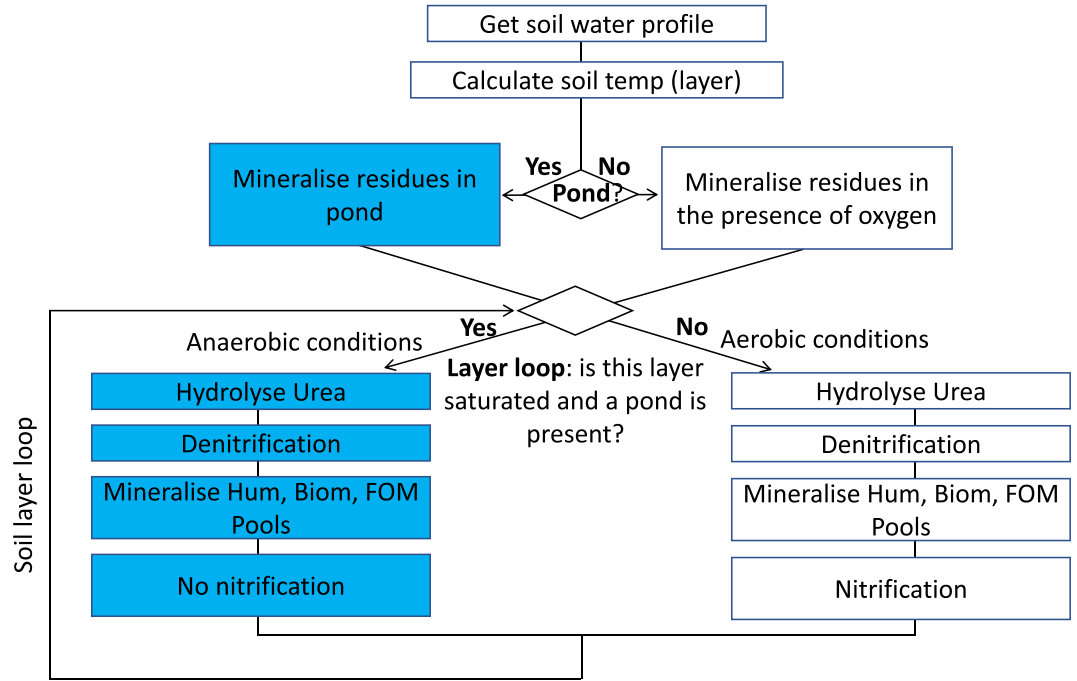
2.2.6.1. APSIM-Oryza

Prior to APSIM-Oryza, APSIM was unable to simulate processes associated with saturated soil conditions encountered in rice-based systems, due to the model's heritage in dryland cropping. To address this, Gaydon, Probert, Buresh, Meinke, Suriadi, et al. (2012) incorporated photosynthetic aquatic biomass (PAB—algae and other floodwater flora) into APSIM-Pond and modified soil carbon and nitrogen cycling to account for anaerobic conditions. The improved APSIM model performed well (RMSE = 1,061 kg ha^{-1} [cf. SD of measured data = 2,160 kg ha^{-1}]) in simulating rice grain yield during multiseason crop sequences. The calibrated APSIM-Oryza was subsequently validated against a 2-year field experiment at Muñoz, Philippines. R^2 between simulated and observed N loss percentages across nitrogen treatments was 0.98, with an RMSE of 2.98 (% applied N), compared with the average measured standard deviation within treatments of 3.65 (% applied N).

The APSIM-Pond module is a transient module, activated when there is ponding on the soil surface (i.e., waterlogging). The logic for switching between aerobic and anaerobic soil conditions is shown in Figure 3. If at any of the decision points in Figure 2 the answer is "no," aerobic conditions prevail, as for any nonflooded crop. If floodwater rises and a subsequent soil layer is saturated, daily organic matter cycling within that soil layer is governed by anaerobic rate constants (Jing et al., 2007, 2010; Kirk & Olk, 2000). If the floodwater disappears (dries or is drained), the system can move back to aerobic organic matter cycling. In this way, APSIM-Oryza captures the effect of the changes in nutrient dynamics in soils and on crop growth (e.g., leaf photosynthesis, leaf growth rate, and N translocation to organs) under aerobic and anaerobic soil conditions. Although the model does not account for stage-dependent waterlogging effects on growth, it accounts for changes in N and C processes under flooded soil conditions (Table 1). For example, when organic residue is submerged in floodwater, decomposition rate slows, nitrification ceases, and CH_4 emissions are initiated, causing C loss. PAB is assumed a significant source of organic C in rice-based cropping systems. APSIM-Oryza was able to simulate the dynamics of C and N under waterlogged environments (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012), and the model adequately simulated long-term average rice yields in a zero-N treatment (Gaydon, Probert, Buresh, Meinke, & Timsina, 2012).

2.2.6.2. APSIM-Wheat/Barley

Waterlogging algorithms in APSIM-Wheat/Barley differ from those in APSIM-Oryza. In the former model, aeration deficit assumptions are based on experiments outlined by Asseng et al. (1998), where

Figure 2. Logic of daily process simulation in APSIM-Oryza (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012). Blue filled frames represent simulations under anaerobic conditions. If there is no surface ponding, the anaerobic condition is identical to the aerobic conditions path. FOM: soil fresh organic matter pool; Biom: microbial biomass; HUM: humus.

after 3 days of oxygen deficit in the root zone, an aeration stress is calculated using Equation 11 (Table 2 and Table S1).

$$AF_i = \frac{SAT_i - SW_i}{SAT_i - DUL_i} \tag{11}$$

where SAT_i as the saturated soil water content in a soil layer i. SW_i as the soil water content and DUL_i as the drained upper limit. If a soil layer i containing roots is filled with water below an effective threshold ($P2_{AF}$, 0.6) for 3 days ($P4_{AF}$), root depth (R_{depth}) will be reduced. A root depth of $P3_{AF}$ can survive in a saturated soil layer which is close to a nonsaturated layer above:

$$\text{If } AF_i < P2_{AF} \text{ for more than } P4_{AF}, \text{ then}$$
$$R_{depth} = Dlayer_i - thick_i + P3_{AF} \qquad RLD_i \text{ to } RLD_m = 0.0$$

where $Dlayer_i$ is the bottom depth of the layer i in the profile, $thick_i$ is the layer thickness, and m is the soil layer with the deepest roots. The root length density will then be set to zero in the saturated layers. Waterlogging effects on crop growth are calculated using an aeration deficit factor $AF1$ (range of [0,1]):

$$AF1 = \left[\frac{\left(\sum_{i=1}^{m} AF_i \right)}{m} \right]^{P5_{AF}} \tag{12}$$

with the parameter $P5_{AF}$ having a default of 3.0. An aeration deficit factor $AF2$ is then calculated as the maximum of $AF1$ and the crop sensitivity to aeration deficit AFS with a range of (0,1):

$$AF2 = \max(AF1, AFS) \tag{13}$$

where aeration deficit impacts on crop growth through AFS range from maximum sensitivity at emergence to no sensitivity during grain filling.

However, waterlogging impacts on plant processes depend on crop genetic tolerance, suggesting that traits imbuing tolerance (discussed in the following sections) could be better accounted for in the model. Past work has shown that APSIM-Barley grown on vertical texture contrast soils overestimated yields of barley crops

subjected to saturated conditions during vegetative growth stages (Matuszek, 2017). The same authors also suggested that modeled outputs might be improved by parameterizing the root exploration and root water extraction coefficients using more experimental data.

2.2.6.3. APSIM-Soybean

Ebrahimi-Mollabashi et al. (2019) used comprehensive experimental data sets to refine the aeration stress factor for modifying root growth in APSIM-Soybean. All APSIM modules simulate root increments as a function of a potential root front velocity (RFV, cm day^{-1}), soil hospitality (XF_i; 0–1, accounts for soil physical and chemical limitations, i denotes layer number), temperature, and excessive water conditions:

$$\text{dlt root depth} = \text{RFV} \times XF_I \times temp_{factor} \times WF_i \tag{14}$$

where RFV varies with crop stage, XF_i reflects soil physical and/or chemical constraints in the soil profile, $temp_{factor}$ is the effect of soil temperature on the rate of root growth, and WF_i is the factor that accounts for excess water that is activated when AFPS values fall below than 0.03 mm/mm. WF_i inhibits downward root growth as soil moisture tends toward saturation using a formulation similar to that proposed by Paydar et al. (2005).

The critical AFPS value was added to APSIM-Soybean such that root growth is inhibited when volumetric soil moisture approaches 3% below saturation (Ebrahimi-Mollabashi et al., 2019). After incorporating this factor into APSIM-Soybean, the model explained 77% of the variability in soybean yields with a RMSE of 8.5 g per plant (70 g per plant). In subsequent scenario analysis, the same authors showed that water tables near the ground surface increased runoff, soil water evaporation, aeration stress, and denitrification but decreased root depth, drainage, and N leaching compared to deep water tables. Pasley et al. (2020) implemented new stage-dependent surplus water functions for phenology (oxdef pheno), photosynthesis (oxdef photo), and N-fixation (oxdef fix) in APSIM-Soybean. Three years of field data from central Iowa, USA, was used to test the model accuracy in APSIM-Soybean; the relative root mean square error (RRMSE) for simulated yield improved by 26% and the RRMSE simulated biomass improved by 40%.

3. Synthesis: Pathways Used to Model Waterlogging

In past work, waterlogging has been modelled using many concepts (Tables 1 and 2). These include the use of water tables in the top 30 cm of soil, gas, or oxygen filled soil pore volume; volumetric soil moisture above a threshold; or relative to soil water saturation. The majority of models adopt a principle of aeration stress in which surplus water reduces air-filled soil pore spaces, and most studies account for effects of surplus water on root growth or root length density. However, the way in which aeration stress is then used varies considerably. In some cases, aeration stress depends on crop stage or species (e.g., DRAINMOD and APSIM-Wheat) and may then either directly affect biomass accumulation (e.g., AquaCrop) or impact on the processes leading up to biomass accumulation such as photosynthesis, carbohydrate accumulation (e.g. SWAGMAN Destiny), and light interception through effects on leaf area (e.g. APSIM). While many models account for stage-dependent effects of waterlogging through empirical or mechanistic approaches with, for example, variable factors for aeration stress, few models account for experimentally observed effects of waterlogging delaying phenology. APSIM-Soybean and APSIM-Wheat are two of the few approaches that account for waterlogging effects on phenology based on the fraction of roots submerged.

We showed that many models (e.g., AquaCrop, WOFOST, CROPR, and SWAGMAN Destiny) have been developed for dryland/irrigated agricultural soils without a water table (Wang & Smith, 2004) or capacity for surface ponding. Consequently, these models are able to simulate water limitations on crop processes but have limited capacity to simulate excessive water impacts over the long-term (Shaw & Meyer, 2015; Warren et al., 2015). In contrast, models designed to simulate long-term waterlogged scenarios (e.g., APSIM-Oryza) tend to be equipped with soil and water modules that can adequately simulate the dynamics of C and N in alternately flooded and nonflooded soil environments under diverse cropping systems (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012; Gaydon, Probert, Buresh, Meinke, & Timsina, 2012). As such, APSIM-Oryza is one of few models that can simulate both shallow water table dynamics and dryland cropping environments accounting for appropriate mechanisms (e.g., photosynthesis, nitrogen leaching, denitrification, and an aeration stress determined by the sensitivities of the different growth stages, Tables 1 and 2).

These results suggest that at the point/field scale, APSIM-Oryza (Gaydon, Probert, Buresh, Meinke, Suriadi, et al., 2012; Gaydon, Probert, Buresh, Meinke, & Timsina, 2012) and APSIM-Soybean (Ebrahimi-Mollabashi et al., 2019; Pasley et al., 2020) are two of the most suitable models to simulate physiological effects of waterlogging, while at the regional scale, GLAM-WOFOST may be one of the most reliable models to examine waterlogging on larger scales. APSIM-Oryza accounts for anaerobic effects caused by waterlogging on soil C and N dynamics (e.g., inhibition of nitrification and decomposition of soil organic matter), while APSIM-Soybean is one of the most appropriate modeling frameworks for simulating waterlogging stress, due to both mathematical-physiological completeness (e.g., stage dependence to reduce photosynthesis and N fixation and delay phenology) and good validation performance.

In future, we suggest that the crop modeling community should contrast the performance of a model specifically designed for long-term waterlogged conditions (i.e., APSIM-Oryza) with waterlogging algorithms proposed in existing crop models developed for dryland conditions with only transient waterlogging.

The current study has also revealed that relatively few studies report validation of waterlogging models; of those that did, DRAINMOD (Evans et al., 1991; Hardjoamidjojo & Skaggs, 1982; Hassanpour et al., 2011), APSIM-Oryza, and GLAM-WOFOST (Li et al., 2016) were adequate (RMSE between simulated and observed yield was 382 and 453 kg ha^{-1}, respectively); APSIM-Soybean and APSIM-Oryza fit the data well.

Integrating the algorithms from APSIM-Soybean or APSIM-Oryza into other crop types in the APSIM framework may improve the ability of the model to simulate waterlogging under varied cropping environments. These results also suggest that future waterlogging models should be more thoroughly validated. However, we acknowledge that cross comparison of models is difficult because each model is often developed for different purposes, many of which are specific (e.g. see Harrison, Jackson, et al., 2014; Harrison, Christie, et al., 2014).

A clear research gap is a comparison of the performance of several waterlogging crop models within the same experimental context, that is, with the same waterlogging treatments. Filling this gap would generate new insights into the relative appropriateness of the conceptual design of each model and provide guidance as to the level of process detail and/or parameterization necessary to appropriately simulate impacts of waterlogging at field scale. Indeed, in many cases, more granular approaches might obviate the need for finer-level processes (e.g., effects of aeration stress on dry matter production rather than effects on photosynthesis or carbohydrate accumulation), but this conclusion cannot be drawn until models are compared using the same experimental data, initialization, and parameterization conditions (Meinke et al., 1998).

Variable impacts of waterlogging on phenology could be better simulated via improved linkage between physiological and abiotic processes that occur dynamically during and after waterlogging: we believe that the period of plant recovery and adaptation after waterlogging deserves further attention. For example, in APSIM-Wheat and APSIM-Barley, aeration deficit impacts on crop growth range from maximum sensitivity at emergence to no sensitivity during grain filling, while the crop sensitivity factor in Equation 3 was 0.16 for crop establishment, 0.18 for early vegetative stages, 0.38 for late vegetative stages, 0.21 for flowering, and 0.06 for yield formation. These values contrast with experimental work by Liu, Harrison, Ibrahim, et al. (2020), who showed that barley was least sensitive to early waterlogging and most sensitive to waterlogging near anthesis. Instead of arbitrary, crop-specific empirical factors related to waterlogging stress at various phenological stages, we suggest that models be based on crop physiological principles, which could then form the basis for simplified but well-informed phenomenological descriptions of such processes (Meinke et al., 1998). For example, for cereals waterlogging during vegetative stages could be linked with tiller number and kernels per spike, with greater aeration stress over longer periods reducing tiller number and kernels per spike (Masoni et al., 2016). During reproductive stages, waterlogging could be linked with spikelet fertility and/or grain weight (de San Celedonio et al., 2014; Liu, Harrison, Ibrahim, et al., 2020).

Higher degrees of waterlogging (greater saturation) for longer durations would then have greater detrimental effects on these physiological variables. Relief of waterlogging would then allow the crop to grow and potentially recover depending on the stage of phenology and soil water conditions; the realization of growth recovery and yield would then be an emergent property modeled through physiological concepts. Harrison et al. (2011) and Bell et al. (2015) discuss similar concepts in modeling the recovery of wheat after defoliation. However, any model development needs to incorporate the appropriate balance parsimony (simplicity) and

complexity (having an excessive amount of coefficients needing parameterization), depending on the model's primary purpose.

4. Effects of Waterlogging on Growth Vary With Phenology and Crop Type

In rainfed and irrigated environments, waterlogging may occur at any stage of crop development (except for some irrigated paddy rice systems, which need to be continuously flooded up to 7–10 days before harvest). In dryland systems, little work has been done on the impact of waterlogging at different phenological stages on subsequent growth, development, recovery, and yield. Nonetheless, many models do account for stage-dependent effects of waterlogging on crop growth as discussed above (e.g., DRAINMOD, CROPR, and APSIM-Barley/Wheat/Soybean). By way of example, experiments on the susceptibility of barley to waterlogging have ranked stage dependency in Figure 3 (de San Celedonio et al., 2014; Leyshon & Sheard, 1974; Masoni et al., 2016). This ranking is partially supported by data of Watson et al. (1976), who found barley yield losses of 56% when waterlogging was applied 2 weeks after sowing, 43% at anthesis (ZS60-69), and 35% at tillering (ZS20-29). Ploschuk et al. (2020) observed that wheat was the more tolerant with early (ZS15) and late (ZS25) waterlogging, related to fewer grains per spike.

Ploschuk et al. (2020) observed that barley and canola tolerated vegetative waterlogging more so (yields 85% and 79% of controls) than reproductive waterlogging (32% and 26% of controls), mainly due to fewer spikes per plant (barley) or reduction in seeds per silique (canola). Field pea was greatly affected by waterlogging at both timings, attaining a yield of only 6% of controls on average due to much fewer pods and fewer seeds per pod. Overall, this shows that yield penalties vary depending on the timing (relative to crop phenology), crop type and duration of waterlogging stress. The way in which such effects are captured differs between models. For example, DRAINMOD used the crop susceptibility factor (Table 2 and Table S1) to account for yield penalization caused by waterlogging at different growth stages. Similar approaches were used in CROPR using an aeration factor and in APSIM using an oxygen deficiency factor to reduce potential dry matter production and translocation to grains. Generally, these stage factors are defined agronomically (i.e., the extent to which biomass and yield are reduced by waterlogging) through the plant's response to waterlogging stress at different growth stages.

5. Plant Physiological Processes That Should Inform Future Model Development

In the following section, we briefly outline recent experimental results that may have implications for future model development. The extent to which these processes influence model validity depends on the context as well as site-specific conditions. Given the importance attributed to such processes in the literature, it is worth briefly outlining these processes here.

5.1. Accounting for Soil Oxygen Content

Ethylene production is accelerated under waterlogging, which in turn stimulates aerenchyma formation in adventitious roots (Shiono et al., 2019; Yamauchi et al., 2020). Aerenchyma is tissue with air spaces that provide an internal pathway for oxygen diffusion in organs under waterlogged conditions (Yamauchi et al., 2013) and is usually formed within 5–7 days of the onset of hypoxia in wheat (Li et al., 2019), barley (Shiono et al., 2019; Zhang et al., 2016), rice (Gao et al., 2020), maize (Gong et al., 2019), and soybean (Takahashi et al., 2018). A significant part of accumulated oxygen in aerenchyma can be lost to the rhizosphere via radial diffusion from the root, prior to being used for metabolic purposes. The flux of oxygen from roots to rhizosphere is termed as radial oxygen loss (ROL). To minimize the loss of oxygen into the surrounding environment, some plants develop a complete or partial barrier to ROL in their epidermis. In light of this, future models may benefit from the integration of both aerenchyma and root porosity accounting for genotypic differences that may occur with varying environmental conditions.

5.2. Accounting for Changes in Soil Chemical Properties

Soil aeration has significant consequences for nutrient dynamics and availability to plants. As discussed for APSIM-Oryza, crop models adapted for waterlogging should have the ability to switch between anaerobic and anaerobic soil conditions to simulate on the different N and C dynamics (Gaydon, et al., 2012). Anaerobic soil conditions have lower soil redox potential, resulting in significant changes to the soil
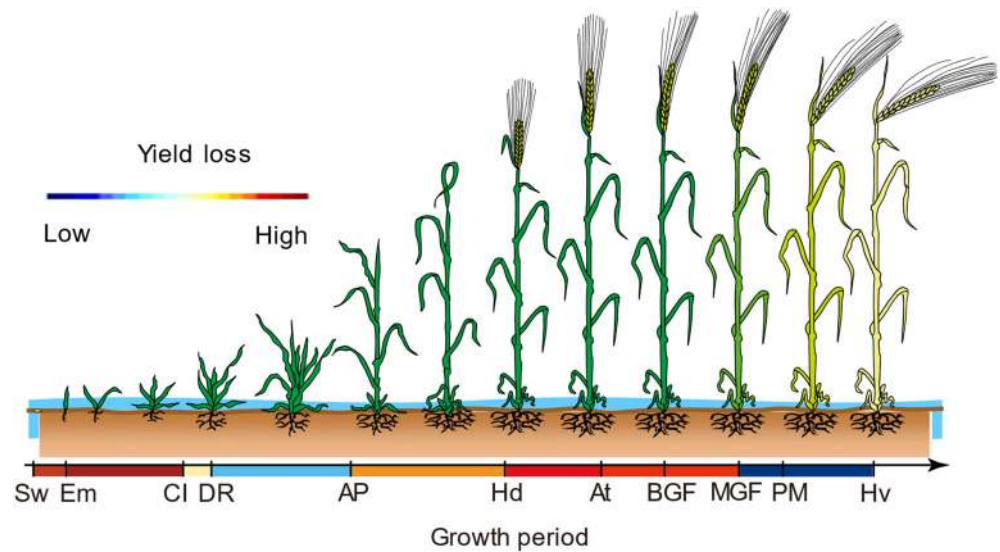
Figure 3. Effects of the timing of waterlogging relative to phenology on crop yield reduction. Example is shown for cereals. Color chart indicates the degree of yield loss. Abbreviations: AP, awn primordium; At, anthesis; BGF, begin grain filling; CI, collar initiation; DR, double ridge; Em, seedling emergence; GS, growth stage; Hd, heading time; Hv, harvest; PM, physiological maturity; Sw, sowing.

elemental profile (Khabaz-Saberi & Rengel, 2010; Shabala & Mackay, 2011). A lowered redox potential and pH variation can result in toxic element accumulation for roots, such as higher concentrations of Fe^{2+}, Mn^{2+}, ethylene, carbon dioxide, and organic acids within the rhizosphere (Figure 1).

The decomposition of organic matter in waterlogged soils produces compounds such as ethanol, ethylene, acetaldehyde, and various short-chain fatty acids and phenolics, defined as soil phytotoxins. These can damage plant tissues and reduce soil quality (Setter et al., 2009; Shabala, 2011). While APSIM-Oryza accounts for decomposition of organic matter, it does so at a higher level without considering production of these types of chain fatty acids. Crop genotypes tolerant to the background constraints (element toxicities or pH extremes) in specific soils have a greater capacity to tolerate waterlogging stress (Yaduvanshi et al., 2012). A deficit of many models is the effects of waterlogging on elemental ion concentrations and consequences for root growth arrest. These processes need not be modeled at the biochemical level but could be adequately modeled using a phenomenological approach that adequately describes the impact of elemental toxicities for plants or for decomposing organ matter (see section 3).

5.3. Accounting for Reduced Nutrient and Water Availability
5.3.1. Root Hydraulic Conductance
Waterlogging-induced reduction of stomatal conductance is often associated with diminished root hydraulic conductance (Bramley et al., 2010; Jitsuyama, 2017). The phenomenon is more pronounced in the waterlogging-sensitive plants, possibly due to a higher degree of damage of their root system (e.g., lower biomass). Water absorption by roots is at least partially (~50%) governed by root water channels (aquaporins) of the plasma membrane intrinsic protein (PIP) family (McElrone et al., 2007; Tournaire-Roux et al., 2003). The production of PIPs aquaporin-like proteins differs between anaerobic and aerobic conditions among several soybean cultivars with varying degrees of waterlogging tolerance (Jitsuyama, 2017; Tan & Zwiazek, 2019). Incorporating this trait into crop models may help to account for genetic diversity for waterlogging tolerance under waterlogging conditions.

5.3.2. Net CO_2 Assimilation and Stomatal Conductance
Net CO_2 assimilation and stomatal conductance decrease during periods of waterlogging stress (Kreuzwieser et al., 2002; Yang et al., 2020; Yordanova & Popova, 2007). Such effects have been incorporated in many past crop models (Tables 1 and 2). However, the reduction in photosynthesis depends on genotypic tolerance to waterlogging. For example, Oosterhuis et al. (1990) found a 16–33% reduction in net photosynthesis after 48 hr of flooding at V4 stage and a 22–32% reduction at R2 stage. Mutava et al. (2015) found a 28–39%

Table 3

Waterlogging (WL) Processes That Have Been Experimentally Identified as Important (With Respect to Growth) and Their Inclusion in Crop Models

Process	Models
Aeration factor	7
Depth of watertable	9
Oxidative stress damage	0
Soil N deficiency	2
Aerenchyma formation	0
Crop lodging	0
Cumulative WL effect on biomass/RUE	6
Energy crisis	0
Posteffect of WL on growth	1
Recovery from WL	1
Reduction in transpiration	7
Soil salinity	0
Reduced leaf area	7
Reduced photosynthesis	7
Reduced tillering	1
Slowing phenology	1
Reduced root growth/depth/length density	7

Note. Soil processes are shaded brown, and plant processes are shaded green.

reduction after 15 days of flooding initiated around V6 (sixth leaf). These results revealed that waterlogging can impact plant processes differently depending on when the stress occurred. Thus, we call for a stage-dependent aeration factor on photosynthesis to be included in models.

5.3.3. Accounting of Oxidative Stress Damage and Tolerance

Another pathway through which contemporary models could account for effects of waterlogging is oxidative stress damage. This is because exposure of plants to hypoxia or anoxia conditions causes oxidative stress, which affects plant growth due to the production of superoxide radicals, hydroxyl radicals, and hydrogen peroxide (Gill et al., 2019; Mittler et al., 2004). ROS accumulation also results in a significant disturbance to plant ionic homeostasis, directly affecting activity of various cation (Gill et al., 2019; Shabala et al., 2014) and anion channels (Pottosin et al., 2018). To cope with oxidative stress, plants use both enzymatic and nonenzymatic sources to counter overproduced ROS. Depending on the level of detail being modeled (cell, organ, plant, or crop), ROS may be a useful proxy for gauging effects of waterlogging on growth at a finer scale.

6. The State of the Art and Future Opportunities in Modeling the Impacts of Soil Waterlogging on Plants

Although many models account for surplus water via air-filled soil pore spaces, the way in which such aeration stress affects crop growth varies considerably, from stage dependence impacts on biomass accumulation to waterlogging influence on photosynthesis, carbohydrate accumulation, and light interception. While many models account for stage-dependent effects of waterlogging through empirical or mechanistic approaches (e.g., variable factors for aeration stress), few models account for experimentally observed effects of waterlogging delaying phenology (APSIM-Soybean is an exception to this). APSIM-Soybean and APSIM-Oryza had the highest accuracy across point-based models, while GLAM-WOFOST was most reliable of the regional models examined.

We also documented the physical, chemical, and biological mechanisms with which waterlogging can affect plant growth and yield. This includes elemental toxicities caused by changes in the soil redox potential, phytotoxicities arising from anaerobic decomposition of organic material in the soil (Table 3), and alteration to plant metabolism and energy availability (with a consequence to nutrient and water uptake) caused by low-oxygen environment in the rhizosphere (Table 3). Different genotypes have shown a great range of diversity dealing with these constrains; however, to the best of our knowledge, no waterlogging crop model accounts for this. Such approaches could be modeled phenomenologically, by (for example) accounting for the reduction in aeration stress caused by aerenchyma, by soil elemental toxicities on root growth, or by decomposing soil organic matter and anaerobic conditions on soil N availability.

As scientific understanding of plant physiological and soil biophysical progresses, process-based representations within the models can be improved. Depending on the purpose of the models, such detailed process descriptions could then be replaced by simpler but well-informed phenomenological descriptions of these processes. For this to occur, caution is needed to ensure that the level of process details contain within a model is commensurate with its purpose and that the parsimony principle is adhered to Meinke and Stone (2005).

In terms of validation of the theory, there are very few comparisons of multiple waterlogging models on the one data set. Such comparisons would facilitate understanding of why some models simulate waterlogging better than others. This would also provide insight into the different levels of mathematical complexity needed to simulate waterlogging effects at the plant, field, farm, region, and global levels.

We suggest that priority areas for research on modeling waterlogging should include (1) incorporating plant-based parameters (e.g., aerenchyma formation, root hydraulic conductance, nutrient use efficiency, photosynthesis, oxidative stress damage, and tolerance) into current models, (2) accounting for the ability to

recover through realistic plant adaptation and development following transient waterlogging, and (3) comparing models specifically adapted to long-term waterlogging (e.g., rice crop models) with those designed for dryland conditions.

Using models with representations of the major physiological processes and the environmental drivers (radiant energy, temperature, and water, nutrients), it may then become possible to diagnose the effects of various stresses in a retrospective way and, importantly, to identify areas and conditions that will likely lead to yield reduction. With this understanding, improved management for optimized yield outcomes should be possible, giving practitioners the necessary tools to make informed decisions concerning cropping in waterlogged areas.

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