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**Plant x Environment interactions:
How is current knowledge reflected in crop models?**

Lena Gabutti

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Prof. Dr. Folkard Asch
Institute of Agricultural Sciences in the Tropics (Hans-Ruthenberg-Institute) (490)
University of Hohenheim

Prof. Dr. Simone Graeff-Hönninger
Cropping Systems and Modelling (340 AG)
University of Hohenheim

Abstract

Many crop models have been developed and used in the last 30 to 40 years in order to simulate crop development and growth in response to the environment, genotype, and management. It is crucial that the parametrization of phenology, which is one of the main differences between cultivars, is precisely assessed in crop modelling in order to obtain reliable predictions. This review aims to identify relevant crop simulation models regarding wheat, maize, and rice concerning plant x environment interactions, considering phenology and genotype x environment interaction (GxE) aspects, and to evaluate the potential that each selected model has on accurately reproducing plant responses. Another objective is to define the simulation parameters that must be considered, especially when introducing new varieties or new environments. Moreover, it investigates to which extent it is possible to define other varieties in response to environmental conditions compared to field trials and also determine if crop model outputs could help in selecting a variety that suits a new environment.

Literature for models belonging to the DSSAT family, i.e. CSM-CERES-Rice, CSM-CERES-Maize, CSM-CERES-Wheat, CSM-IXIM, and CSM-CROPSIM was searched. Other considered models are APSIM-Oryza, APSIM-Maize, APSIM-Wheat and its sub-model Nwheat. For rice, the ORYZA family was examined. Finally, the CropSyst model was chosen. Literature about varietal responses to the environment for rice, maize, and wheat was considered and compared to the simulation models. ORYZA(v3) resulted to be the more appropriate model for rice since it considers diverse ecosystems, while models belonging to the APSIM and CERES family were selected for maize and wheat. Phenology emerged to be the main process to simulate plant responses in GxE context. By improving the simulation of crop parameters such as leaf discolouration, increased degenerated spikelets, and increased grain shattering of rice and environmental factors such as influence of temperature during different processes and development phases of the crops, the simulation of phenology can be improved. For lowland rice, it is suggested to consider water temperature until the booting stage, thereafter air temperature. Additionally, it is recommended to monitor panicle temperature of lowland rice in order to predict heat-induced spikelet sterility. Crop duration of rice is an important element to monitor since it determines agronomic suitability and therefore it can help to define fitting cultivars for a distinct location. These aspects require a more detailed parameterization and a higher complexity of the models. Errors in field trials should be considered and not only errors in simulation outputs. It is recommended to follow a more mechanistic approach for all models. Moreover, the quality of the crop modelling papers needs to be improved by standardizing the terminology and by giving an explicit description of the functions of the models used. Enhancing the communication and information exchange among models and model users will upgrade the model's quality and progress.

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List of abbreviations

APSIM	<i>Agricultural Production System sIMulator</i>
AX	<i>One-side surface area of the largest leaf</i>
CERES	<i>Crop Environment Resource Synthesis</i>
CSIRO	<i>Commonwealth Scientific and Industrial Research Organisation</i>
CSM	<i>Cropping System Model</i>
CropSyst	<i>Cropping Systems Simulation Model</i>
DSSAT	<i>Decision Support System for Agrotechnology Transfer</i>
ET	<i>Evapotranspiration</i>
G1	<i>Kernel number per unit stem and spike weight at anthesis</i>
G2	<i>Maximum possible number of kernels per plant (maize)</i> <i>Kernel filling rate under optimum conditions (wheat)</i>
G3	<i>Kernel filling rate during the linear grain filling state (maize)</i> <i>Non-stressed dry weight of a single stem and spike when elongation ceases (wheat)</i>
GDD	<i>Growing Degree Days</i>
GxE	<i>Genotype - Environment Interaction</i>
IPAR	<i>Intercepted Photosynthetically Active Radiation</i>
IBSNAT	<i>International Benchmark Sites Network for Agrotechnology Transfer</i>
LAI	<i>Leaf Area Index</i>
LX	<i>Longevity of the most long-lived leaf in thermal time</i>
N	<i>Nitrogen</i>
P1	<i>Degree days from seedling emergence to the end of the juvenile phase</i>
P1D	<i>Percentage reduction in development rate in a photoperiod 10 h shorter than the optimum relative to the rate at the optimum photoperiod</i>
P1V	<i>Days at optimum vernalizing temperature required to complete vernalization</i>
P2	<i>Photoperiod sensitivity measured in days of tassel initiation delay per hour of photoperiod increase</i>
P5	<i>Degree days from beginning of grain filling to maturity</i>
PAR	<i>Photosynthetically Active Radiation</i>
PHINT	<i>Phyllochron interval: the interval in thermal time between successive leaf tip appearances</i>
RUE	<i>Radiation Use Efficiency</i>
TT	<i>Thermal time</i>

1 Introduction

The FAO estimates that the annual world demand for rice, wheat and maize will reach 3.3 billion tons by 2050, which corresponds to 800 million tons more than the combined harvest in 2014. Environmental degradation, climate change and stagnating yield endanger cereal production and food security (Reeves et al. 2016). Crop simulation models have a considerable potential in contributing to global food and nutrition security (Reynolds et al. 2018). Models are an abstract representation of reality (Holzworth et al. 2011). Crop simulation modelling is the quantitative utilization of crop-based models and is described mathematically or statistically (Ahmed et al. 2016; Ahmed et al. 2013), permitting to understand complex biophysical systems. Crop simulations started in the late 1970s and nowadays are relevant for the development of new and advanced crop management strategies (Ahmed et al. 2013). Crop simulations can be useful in decision making, for selecting suitable cultivars, forecasting crop growth and development; they can help find interaction effects (e.g. genotype x environment interactions, GxE), as well as reducing yield gaps (Asseng et al. 2014; Ahmed et al. 2013) due to their capacity of understanding complex crop-soil-weather systems. Compared to trial experiments, crop simulations produce a speedier and more comprehensive combination of outcomes influenced by management, environment, and variety. Comparisons between measured and simulated results are necessary to test models (Basso et al. 2016). These comparisons highlight any knowledge gap: further investigations can be designed to fill them (Bouman et al. 2001). It is relevant to prove model performance under various conditions since they are crop and site-specific, and do not apply for other places without being calibrated and validated beforehand (Ahmed et al. 2013; Kumara et al. 2015). Otherwise, model outputs would not represent the real field situation (Kumara et al. 2015).

Plant x environment interactions are expressed as the plant responses to the total ecosystem, influencing its growth and development (Wilkinson 2000). Plant productivity and adaptability to changing environmental conditions are regulated by genetic mechanisms leading to different plant responses (Duncan 2000). Genotype performance is usually evaluated through various environmental trials, encompassing numerous GxE (Jeuffroy et al. 2014). According to the definition of GxE, the genotype is referred to the genetic characteristics of a cultivar and not to the individual. The environment is related to climatic, soil and biotic (pests and diseases) conditions as well as management status in a distinctive trial zone in a specific location during one year if annual crops or during more years if perennials (Annicchiarico 2002). Nevertheless, GxE is not always considered for assessing cultivars and for evaluating adapted cultivar management plans even if crop models are ideal tools for analysing these interactions (Jeuffroy et al. 2014). Models have different complexity levels, and plant development and growth differ according to their input data and parametrization requirements. Therefore, it is essential to select which model is more suitable to accomplish the research objective (Soltani and Sinclair 2015). However, the parametrization of the phenology regarding new crop species is a serious challenge in crop modelling (Nisanka et al. 2015). Phenology is one of the main differences among cultivars: crop model outputs depend

on the accuracy of modelling this characteristic (van Oort et al. 2011). Hence, a precise assessment of phenology parameters is essential in crop modelling (Aggarwal and Mall 2002). On the other hand, according to Nissanka et al. (2015), conducting additional field trials would have almost no effect on uncertainty. Indeed, phenology parameters are often assessed by trial and error, which has disadvantages since it is time-consuming, has fewer possibilities to find the real best-fit parameters than an automated procedure, and does not give any information about uncertainty in estimating parameters (Nissanka et al. 2015). Additionally, phenological crop models often perform correctly in a given environment where they have been calibrated, but not necessarily in a new environment, hence generating a small-scale applicability problem (van Oort et al. 2015). There is a knowledge gap about phenological subroutines and parameter accuracy when tested in another environment, and local modelling efforts do not necessarily extend to general scientific interest (Sinclair and Seligman 2000).

This review aims to identify relevant crop simulation models regarding wheat, maize, and rice concerning plant x environment interactions, including GxE and its influence on phenology, and to evaluate the potential that each selected model has of accurately reproducing plant responses. In essence, it seeks to define the simulation parameters that must be considered when introducing new varieties or new environments. Moreover, it investigates to which extent it is possible to define other varieties in response to environmental conditions compared to field trials and to determine if crop model outputs could help in selecting a variety that suits a new environment.

2 Materials and methods

This review discusses plant x environment interactions, including genotype x environment interactions (GxE) and its influence on phenology, in selected maize, wheat and rice crop models. After research on the three crops and on possible GxE crop models, the models that appeared more relevant because of the number of publications about them were chosen. The search for literature used words or combinations of words like “genotype x environment”, “physiological crop models”, “crop models”, as well as the three crops of interest, on Google Scholar, CAB Abstract, Scopus and HohSearch (the portal of the University of Hohenheim). After studying the models that resulted from the search, their corresponding papers and their websites, the more relevant, up-to-date and most used crop simulation models were selected.

Some of the crop models contemplated in the review belong to the DSSAT family, i.e. CSM-CERES-Rice, CSM-CERES-Maize, CSM-CERES-Wheat, CSM-IXIM, and CSM-CROPSIM. Other considered models are APSIM-Oryza, APSIM-Maize, APSIM-Wheat and its sub-model Nwheat. For rice, the ORYZA family was examined and, more specifically, the ORYZA2000 version. Finally, the CropSyst model was chosen. The same search engines as for the previous literature probe were used and the selected crop models and crops were researched in more detail.

The topics regarding crop models discussed in the literature review concern aboveground plant x environment interactions. The main topics were photosynthesis, phenology, growth, and partitioning. Roots, water uptake, soil and nitrogen interactions were not analysed while, exceptionally, grain protein in wheat was considered. For each chapter, the order of the crops in the various sections was rice, maize, and wheat. Lastly, a chapter reviewed varietal responses to the environment for rice, wheat, and maize according to field observations. Even for this part, the same portals for the previous literature research were used.

3 Crop models

3.1 ORYZA

ORYZA version 3 (ORYZAv3), or also just known as ORYZA, is an ecophysiological model released by IRRI (International Rice Research Institute), and the Wageningen University and Research Centre. This model can reproduce the growth and development of rice in lowland, upland, and aerobic rice ecosystems considering water, carbon and nitrogen balance as well (IRRI 2020). ORYZAv3 simulates conditions of limited water, nitrogen, and nitrogen-water interactions. Additionally, this model is available for 15 locations of Asia with 18 prominent rice varieties already calibrated and validated (IRRI 2020). ORYZA is assumed to be absent of diseases, pests, and weed influence (Bouman and van Laar 2006; Bouman et al. 2001). ORYZA evolved in time from its first version in 1994 called ORYZA1 for potential production (Kropff et al. 1994) to ORYZA_N for nitrogen-limited production (Drenth and Berge 1994) and ORYZA_W for water-limited production (Wopereis et al. 1991). ORYZA2000 (v1.0) is the integrated successor of the previous versions (Bouman et al. 2001) as well as the following adaptations (v.2.0, v2.12, v2.13) (IRRI 2020). These two last versions of ORYZA2000 are integrated into APSIM and DSSAT crop models respectively, called APSIM-ORYZA (2005) and DSSAT-ORYZA (2012). Compared to the versions 2.x, ORYZAv3 can simulate more outputs such as water-nitrogen interaction dynamics, climatic and abiotic stress, plant responses to drought and nitrogen deficiency, effects of combining irrigation water management options, and others (IRRI 2020). Furthermore, ORYZAv3 considers more ecosystems since ORYZA2000 is specific for irrigated lowland systems only (Li et al. 2017). In ORYZA2000 and ORYZAv3, the daily growth rate of the crop under favourable conditions is determined by phenological, morphological and physiological processes, which in turn are influenced by light, temperature, and varietal characteristics. The production of the dry matter rate regarding the organs and the phenological development rate are based on daily calculation scheme: their integration over time simulates dry matter production and development stages of the crop for a growing season (Bouman and van Laar 2006; Bouman et al. 2001; Kropff et al. 1994; Radanielson et al. 2018).

3.2 APSIM

The Agricultural Production System sIMulator 7.10 (APSIM 7.10) is an exhaustive model regarding agricultural systems which aims to reproduce biophysical processes. APSIM has been released by the CSIRO (Commonwealth Scientific and Industrial Research Organisation), the State of Queensland and the University of Queensland. APSIM is composed of modules regarding various crops, trees and pastures, soil processes (including nitrogen and phosphorus transformations, water balance, erosion, soil pH), climate and management controls. It also uses economic outcomes and ecological parameters related to management practices (APSIM 2020). APSIM was designed to be the beginning of a farming system simulator that combines estimations of yields under different management in order to predict how soil resources can be affected in time by various farming practices (Keating et al. 2003).

APSIM-Rice module is an implementation of ORYZA2000 (APSIM 2020; Holzworth et al. 2014). The rice-based cropping system of APSIM lacked appropriate descriptions regarding the effects of anaerobic conditions for an extended period of time on soil processes. The original soil and water elements belonging to ORYZA2000 were eliminated and only its crop growth routine was maintained, which was then integrated with the soil and water modules of APSIM (Gaydon et al. 2012a). Processes of chemical and biological origins occurring in inactive water bodies such as the production of algal biomass and nitrogen fixation were added to APSIM (Gaydon et al. 2012b). The new model is commonly referred as APSIM-Oryza (Holzworth et al. 2014). Physiological processes are reproduced by plant modules: they work on a daily time step using various inputs belonging to soil, weather, and crop management data (Keating et al. 2003).

APSIM-Maize reproduces the maize growth according to daily steps based on crops area and not on a sole plant. In APSIM-Maize, maize growth is affected by climate (rain, radiation, and temperature), soil nitrogen, and soil water supply. The module reports soil and water nitrogen uptake, crop cover and the related evaporation rate and runoff, root depth, maize stover and roots residues; it is able to predict leaf area development; stover, root, and grain nitrogen percentage and biomass, as well as grain yield and nitrogen percentage, and grain size and number over the day. The maize module takes origins on CERES-maize, but with the main difference that routines can kill the crop when severe water deficit are present during the beginning until the mid-vegetative stage (APSIM 2020).

APSIM-Wheat 7.5 R3008 simulates wheat growth and development according to daily steps based on crops area. In this module, the wheat crop responds to weather (temperature and radiation), soil nitrogen and water, as well as practices used in management. APSIM-Wheat can simulate leaf area growth expansion, phenological development, biomass and nitrogen concentration in various crop components such as leaf, stem, root and grains, and can predict grain size and number (Zheng et al. 2015). The most relevant sub-models for wheat-based cropping simulation systems are NWHEAT (wheat crop) SOILWAT (soil water), SOILN (soil nitrogen) and (RESIDUE (residue). NWHEAT, SOILWAT and SOILN were developed together with CERES crop (explained in chapter 0) (Asseng et al. 2002) and PERFECT model (Littleboy et al. 1992) but with some modification (Probert et al. 1998; Probert et al. 1995). NWHEAT illustrates growth and development, water uptake, crop nitrogen dynamics and uptake, the various stress responses and the content of grain protein content. The organisation of NWHEAT is strongly regulated according to CERES models (Asseng et al. 2002; Asseng et al. 1998). However, some adjustments are contained such as the concept based on the critical amount of water available in the soil instead of the original crop water deficit method. Additionally, the demand of water by the crop is related to the production of biomass through transpiration efficiency and is no longer a function of potential evaporation and leaf area index (LAI) like in the original CERES wheat; the addition of a leaf sheath biomass pool with consequent modifications regarding partitioning to the residual leaf blade and stem biomass pools. Other adjustments include the addition of a pool for the leaf sheath biomass with

consequent modifications regarding partitioning to the residual leaf blade and stem biomass pools; the addition of stress caused by high temperatures on leaf senescence (when temperatures are higher than 34°C); adjustment of the specific leaf area, root elongation rates, tillering, frost damage, carbohydrate partitioning, radiation use efficiency and the removal of the subroutines responsible for the respiration and root exudation. The body of the grain protein routine are the same as the one in CERES-Wheat (Asseng et al. 2002; Asseng et al. 1998; Keating et al. 2001).

3.3 DSSAT

The Decision Support System for Agrotechnology Transfer (DSSAT) is a decision support system which functions are to estimate resource use, production, and risks correlated with various agricultural practices (Jones et al. 1998). DSSAT has been developed by IBSNAT (International Benchmark Sites Network for Agrotechnology Transfer) to simplify the use of crop models in the agricultural sector (Jones et al. 2003). DSSAT principally support decision-making operations using different crop simulation models. Originally, crop models that currently belong to the DSSAT family were considered separately. One model provided by DSSAT for cereals is CERES (Crop Environment Resource Synthesis). The original single CERES crops that existed before being integrated into the DSSAT family are successively joined in a unique module able to reproduce wheat, millet, barley, sorghum, and maize. The rice module is kept individually due to its great differences in nitrogen balance routines and soil water as well as transplanting effects. CERES simulates growth on a daily time step considering phenological development (influenced by genotype, temperature and day-length), morphological development (extension growth of roots, leaves, and stems), soil water balance (transpiration, evaporation, percolation, runoff, infiltration for rainfed and irrigated fields and also water deficiency), biomass accumulation and partitioning, soil nitrogen transformations (such as mineralization/immobilization, ammonia volatilization, urea hydrolysis, de- and -nitrification, and N losses, uptake, use, and limitations) (Jones et al. 1998).

DSSAT version 4.7, which is the last version released in April 2019, simulates over 42 crops. DSSAT v4.7 contains changes and improvement such as application programs for spatial, seasonal, sequence and crop rotation analysis. It aims to estimate economic risks and environmental impacts related to irrigation, fertilizer, nutrient management, soil carbon sequestration, climate variability and change, and precision management (DSSAT 2020). The Cropping System Model (CSM), already implemented in the DSSAT v3.5, has a modular format and is composed of many elements that are divided according to scientific discipline lines and its interfaces allow for modules to be added and replaced (DSSAT 2020; Jones et al. 2003). Thus, all crops are incorporated in the CSM model in the form of modules and adopts a unique soil model, whereas previously each crop had its own soil model elements (Jones et al. 2003).

CERES-Rice follows the structure of the other CERES models, but it has some additional features compared to them. CERES-Rice considers the effect of transplanting on rice development and growth. Moreover, water balance is able to reproduce the use of water by the crop under flooded and upland conditions, and under intermitted dry and flooded soil systems. Eventually, the nitrogen submodel

needed more adaptations in order to reproduce nitrogen transformations under flooded and intermittent flooded and upland systems (Jones et al. 1998).

CERES-Maize, developed in 1986, is nowadays the most widely simulation model for maize (Lizaso et al. 2011). Thanks to modularizing the model structure, namely the CSM, it allowed facilitating information exchange between system components and the various model improvement (Jones et al. 2003). Another model proposed by DSSAT CSM-CERES version 4.5 for simulating maize is **CSM-IXIM** (here just called IXIM). CSM-CERES-Maize was modified in order to incorporate some improvements such as simulation of the carbon assimilation and partitioning, leaf area, kernel number, ear growth, plant nitrogen acquisition and distribution, and grain yield, and finally called CSM-IXIM model (Lizaso et al. 2011).

The origins of **CERES-Wheat** date back to the 1970s (DSSAT 2020). CERES-Wheat is a wheat model with the primary purpose to estimate yield (Ritchie and Otter 1985). The temperature and genetic information available in the CERES-Wheat model define the growth stages. The model simulates daily photosynthesis based on plant population, incoming solar radiation, canopy extinction coefficient, LAI, and radiation use efficiency (RUE). Assimilates are partitioned within different organs such as stems, roots, leaves, and grain according to various growth stages. Crop nitrogen demand and its availability in the soil define canopy nitrogen accumulation. Grain dry matter during the grain filling stage comes from photosynthesis and from the reallocation of dry matter pre-stored by the crop (Li et al. 2018). Nowadays, CERES-Wheat and **CROPSIM-Wheat** parameters, another model belonging to the DSSAT family, are as similar as possible (DSSAT 2020). CROPSIM-Wheat assumes that crops consist of uniform plants and computes growth and development of plants. The model uses a daily time step, reproduce crop and soil variables, and its main weather variables are daily precipitation, daily solar radiation, and maximum and minimum daily temperature. However, other environmental variables are considered, such as day length and soil temperature by layer (Hunt and Pararaiasingham 1995). CROPSIM-Wheat main input files address crop management, soil, weather as well as genotype. The latter is composed of two files. One is based on elements that normally change between cultivars, while the other is based on elements that are invariable between cultivars but react to the environment (Hunt and Pararaiasingham 1995). The CROPSIM model has been joined to DSSAT-CSM and is used not only for wheat but also for barley and cassava and later used as a template for a new model for cassava called YUCA (DSSAT 2020). CSM-CROPSIM-CERES-Wheat combines typical features of CROPSIM (Hunt and Pararaiasingham 1995) and CERES-Wheat (Ritchie 1991) and is used in some studies (White et al. 2008; Gbegbelegbe et al. 2017; Ottman et al. 2013). Due to a lack of information regarding the model, CSM-CROPSIM-CERES is not considered in this review.

3.4 CropSyst

Development of CropSyst (Cropping Systems Simulation Model) started in the 1990s and nowadays results to be one of the easiest models regarding plant growth processes representations (Stöckle et al.

2003; Stöckle et al. 1994). CropSyst is a daily time-step simulation model capable to reproduce multiple years and multiple crops. It simulates crop growth over one land area fragment with homogeneous management, soil, weather and crop rotation. The description of the crop growth regards the entire plant and its organs. The impact of cropping system management on the environment and on productivity are analysed by the model. Simulation of the crop canopy, soil water, soil-plant nitrogen budget, root growth, crop phenology, biomass production, dry matter production, yield, residue production and decomposition, pesticide fate, and erosion is done by the model. Among the management options, there are a cultivar selection, crop rotation including nitrogen fertilization, fallow, pesticide applications, irrigation, soil and irrigation water salinity, residue management, and tillage operations with over 80 alternatives. Cropping system management, together with weather, and soil and crop characteristics, influence crop growth and development simulation and are considered input factors in the model (Stöckle 2020; Stöckle et al. 2003).

4 Crop responses simulation

4.1 Photosynthesis

4.1.1 CO₂ assimilation

Daily total gross assimilation is estimated in ORYZA1 and ORYZA2000. Inputs of relevance are the latitude, the day of the year, the total green area index, the extinction coefficients for visible light in the canopy, and the total daily radiation. The efficiency of the initial use of the light regarding a sole leaf, the maximum rate of CO₂ assimilation of a single leaf, and leaf N content are also considered for the nitrogen distribution in the canopy (Bouman et al. 2001). Moreover, ORYZA1 and ORYZA2000 consider leaf rolling and the LAI of rolled leaves, contemplating so the reduced leaf area index (LAI) with consequently diminished surface able to intercept light and perform photosynthesis due to drought stress (Bouman et al. 2001; Wopereis et al. 1996; O'Toole and Cruz 1980). Additionally, ORYZA1 and ORYZA2000 take into account the stem CO₂ assimilation. Only half of the area belonging to the green stem, or sheath area, is joined to the "rolled" leaf area and LAI since stems absorb radiation but are less photosynthetically active than leaves. Thus, the assimilation subroutine can determine the total green area index. However, other reproductive organs such as panicle, which are able to absorb radiation, are not considered in the model (Bouman et al. 2001).

ORYZA1 and ORYZA2000 can lower the daily total gross assimilation based on the relative transpiration ratio in order to simulate reduced transpiration due to drought stress (Bouman et al. 2001). Under water-limited conditions, the crops close their stomata with the purpose of limiting the transpiration, engendering a higher resistance in the CO₂ exchange, and thus diminishing the photosynthetic rate (Tanner and Sinclair 1983). Under drought stress, however, there is a constant transpiration to gross photosynthesis ratio and this is assumed by both models (Tanner and Sinclair 1983; Bouman et al. 2001). Gross photosynthesis is specified as the ratio of plants under stressed transpiration to the ratio of plants under actual good water conditions (Bouman et al. 2001). If the LAI is reduced by drought stress, it means that the transpiration rate of plants under good water conditions will have higher values than that of plants under stress. This is primarily caused by radiation. So, the potential transpiration of the plants under good water conditions is necessary in order to obtain the potential transpiration of stressed plants (Wopereis et al. 1996). The actual transpiration rate per soil layer is obtained from the multiplication of potential transpiration rate by the relative transpiration ratio and by the depth of the roots in the soil layer. The extractable amount of water by the soil in every layer limits the total amount of transpired water (Bouman et al. 2001).

Many subroutines are necessary for calculating the daily canopy photosynthesis, in which solar constant, daily extra-terrestrial radiation, day-length, sine of the solar inclination and fluxes of scattered and direct radiation during a specific moment of the day, daily integral of the sine of the solar elevation over the day, instantaneous canopy CO₂ assimilation and instantaneous absorbed photosynthetically active radiation (PAR) are estimated. These last two parameters are incorporated over the day into the total gross

assimilation of the day and the rate of absorbed PAR during the day. The radiation is uniformly spread over the day based on the solar elevation; therefore, the rate of CO₂ assimilation and the amount of PAR absorbed are computed during the daytime. To obtain the total daily values is necessary to multiply the absorbed PAR by the daytime-length (Bouman et al. 2001).

ORYZA2000 differentiates between diffuse and direct radiation. Depending on the angle of incidence and the strength of the radiation flow, the radiation strikes with differing intensity of illumination the leaves in the shade, which receive only diffuse radiation, and the leaves in the sunlight, which receive both diffuse and direct radiation. The single leaves respond with a non-linear CO₂ assimilation/illumination ratio. Sun rays dispersed in the atmosphere by clouds, aerosol, and gases generate the diffuse radiation. Both radiations are used to estimate diffuse and direct PAR (Bouman et al. 2001). Moreover, the canopy does not absorb all the radiations, and some are reflected. Diffuse and direct radiations have varied light profiles in the canopy due to diverse extinction coefficient. For this reason, three distinct radiation fluxes are identified such as the diffuse and the total direct fluxes, and the component of direct radiation. In the end, it is possible to calculate the total absorbed radiation by shaded leaves as well as by leaves exposed to radiation (Bouman et al. 2001).

Using the leaf CO₂ assimilation rate and absorbed radiation rate of the green area index it is possible to obtain the instantaneous rates of CO₂ assimilation of the entire canopy and the instantaneous absorbed radiation. The instantaneous rate of CO₂ assimilation at a fixed canopy depth is obtained by calculating with a subroutine the absorbent flux of radiation for leaves under shade, the direct flux absorbed by leaves, the sunlight part reaching the leaf area in the canopy at a specific depth L , the maximal photosynthesis rate, and the initial RUE factor of one leaf. The assimilation rate at a distinct canopy height from the absorbed radiation at a certain depth L is computed in distinct ways for shaded and sunlit leaves (Bouman et al. 2001). The total canopy CO₂ assimilation rate of the day also depends on temperature, incoming radiation, and LAI. This daily rate is obtained by a set of subroutines in the model that combines instantaneous leaf CO₂ assimilation daily rates throughout the leaf layers in the canopy. This calculation considers the radiation course over the day and the exponential light profile of the canopy. The photosynthesis of every leaf is based on the concentration of nitrogen of the leaf, the concentration of the stomatal CO₂, the temperature, and the radiation intensity of both direct and diffuse radiation (Bouman et al. 2001; Bouman and van Laar 2006; Kropff et al. 1994). The photosynthesis (maximum leaf rate of CO₂ assimilation) is estimated by the maximal rate of assimilation under the environmental CO₂ concentration, the leaves' nitrogen content, and finally by a reduction factor that considers average temperature effects during the day. It is necessary to consider the nitrogen profile in the canopy since the nitrogen content results to be higher in the top leaves (Bouman et al. 2001).

Variety-specific photosynthesis parameters are the scattering coefficient of the leaves for PAR, the fraction of sunlight energy that is photosynthetically active, the ambient CO₂ concentration, and the reference level of atmospheric CO₂. The portion of N in leaves, the extinction coefficient of the N profile in

the canopy, and the light extinction coefficient for leaves are variety-specific parameters and are functions of the development stage. Moreover, the leaf light extinction coefficient as a table of light-use efficiency and the temperature effect on the maximum CO₂ assimilation rate of a single leaf are considered variety-specific parameters and are dependent on the temperature. The maintenance respiration coefficient is also a variety-specific parameter (Bouman et al. 2001).

CERES-Rice computes net photosynthesis as a function of RUE, LAI, extinction coefficient, and intercepted photosynthetically active radiation (IPAR) by the canopy. This differs from **ORYZA2000**, which computes gross photosynthesis and respiration separately. In **CERES-Rice**, the optimal temperature for photosynthesis is between 14 and 32°C. Otherwise, its effect is reduced. Hence, photosynthesis sensitivity results to be higher in **CERES** than in **ORYZA**. This is probably because in **ORYZA** maintenance respiration and gross photosynthesis are two distinct processes. In **CERES-Rice**, the CO₂ effect on net assimilation is obtained through the multiplication of the net rate by a factor considering CO₂ effects on C3 and C4 plants. Water, temperature, and nitrogen stress effects on net photosynthesis in environments with raised CO₂ are regulated by their influence on the growth of leaves and consequently on the absorption of the radiation (Wikarmpapraharn and Kositsakulchai 2010). In **ORYZA2000**, the total canopy CO₂ assimilation rate over the day is computed from the LAI, daily incoming radiation, and temperature. The rate of assimilation for the day is calculated by the integration of daily instantaneous leaf CO₂ assimilation rates and all the canopy leaf layers. The photosynthesis of an individual leaf is regulated by the content of nitrogen in the leaf, the radiation intensity (diffuse and direct), the concentration of the stomatal CO₂, and the temperature. In order to attain the net daily growth, the requirements for maintaining the respiration are deducted from the rate of the gross assimilation (Bouman and van Laar 2006).

4.1.2 Evapotranspiration

In **ORYZA2000**, potential evapotranspiration (ET) is calculated based on the main field, meaning that evaporation calculation before transplanting does not consider seedbed but only bare field for transplanted rice. Seedbed is believed to always being optimally supplied by water. For calculating the ET, three ways are available (Wikarmpapraharn and Kositsakulchai 2010): Penman (Monteith 1965), Priestley-Taylor (Priestley and Taylor 1972), and Makkink (Bruin and Lablans 1998) equations. Penman is considered the best option, but requires many input parameters (Wikarmpapraharn and Kositsakulchai 2010) such as wind speed, daily maximum and minimum temperature, maximum and minimum relative humidity or dew-point temperature, and solar radiation (Stöckle et al. 2003). The method used by **ORYZA** for determining the ET is user-defined according to the availability of meteorological data. Water limitation is considered for crop growth and development and causes accelerated leaf death, expansive growth, delayed flowering, leaf rolling, assimilate partitioning, and spikelet sterility. For every event course mentioned, stress factors are determined according to the tension of water in the rooting part of the soil (Wikarmpapraharn and Kositsakulchai 2010; Bouman et al. 2001).

Daily potential ET options in **CERES-Maize** version 4.0 are based on two equations: Penman-Monteith (Monteith 1965) and Priestley-Taylor (Priestley and Taylor 1972). The first equation requires fewer inputs (daily solar radiation and minimal and maximal temperature), while the second equation needs other weather data as mentioned for ORYZA2000 (Stöckle et al. 2003; López-Cedrón et al. 2008). Potential ET is partitioned into potential evaporation and transpiration considering the fraction of solar radiation that arrive at the soil. So, it can be used as latent energy for evaporating water from the soil surface since it is assumed that the soil is wet. How much solar radiation arrives at the soil depends on the LAI. Therefore, actual soil evaporation and plant transpiration are a result of the water available in order to obtain the required potential rates. The extinction coefficient for potential evaporation and transpiration is set as the same value and it differs from previous CERES models (López-Cedrón et al. 2008).

CERES-Wheat considers the water balance in the soil and also the possible yield reduction due to water deficiencies. One of the factors comprised in water balance is the evapotranspiration. ET is computed by separating crop transpiration and soil evaporation for plants under conditions of no soil water shortage. ET is then obtained from an equation in which daytime net radiation and equilibrium evaporation are estimated. It is assumed that during night stomata are closed and no ET takes place. Potential ET is computed as equilibrium evaporation multiplied by a constant that takes into consideration unsaturated air (Ritchie and Otter 1985). CERES-Wheat can use either the Priestley-Taylor (Priestley and Taylor 1972) or the Penman (Monteith 1965) equations to define the potential ET. With the Priestley-Taylor equation, the albedo is obtained from the stage of growth and from the values of the LAI. Moreover, it uses constants which are dependent on temperature in order to consider advection on potential ET, radiation effects, and unsaturated air (Kang et al. 2009).

In **CROPSIM-Wheat**, water balance elements are computed for a multi-layer soil. Potential ET is simulated using a modification of the Priestley-Taylor (Priestley and Taylor 1972) equation which is analogous to the equation in CERES. The procedure is based on the absorbed fraction of solar radiation, which is determined by the average daily temperature. The latter gives more importance to the maximum temperature than to the minimum. Absorbed solar radiation depends on incoming solar radiation utilizing the albedo. The albedo changes according to soil input values if there is no crop or if there are complete or even mature and complete crop covers. The crop cover is defined by the extinction coefficient of the canopy for radiation with short waves. Potential transpiration is obtained by the multiplication of potential ET by the intercepted solar radiation. The actual transpiration corresponds to potential transpiration if enough water is available. To estimate how much water is available, the water accessible around the roots is summed. The evaporation of the soil is defined by adopting the model described by Ritchie (1972). The evaporation is examined separately according to constant and falling rate phases. The constant rate is described by enough wet soil so that water can be transported to or lost from the surface. This rate corresponds to the potential evaporation of the soil. The falling rate phase is characterized by the dependency of the evaporation which is determined by the flux of water through the upper

soil layer to the soil surface since the availability of water on the soil surface is lower than the threshold value (Hunt and Pararaiasingham 1995).

In **APSIM-Nwheat**, the potential ET is obtained like in the CERES model, namely as a function of air temperature, solar radiation as well as soil and crop albedo (Asseng et al. 2011). This approach is described by Priestley and Taylor (1972). Like in the CERES model, the soil evaporation is calculated in two stages (Asseng et al. 2011; Ritchie 1972). In the first stage, energy is limited and depends on LAI and radiation. The water flow from the soil to the surface affects the second stage. The top layer can evaporate and can be re-provided with an unsaturated upward flow from below. In APSIM-Nwheat, the biomass production is linked to transpiration and the demand of the water uptake by the coefficient of the transpiration efficiency and the vapour pressure deficit, while in CERES model the demand of water uptake depends on LAI and radiation. Therefore, in APSIM-Nwheat the actual water uptake depends on the distribution of the density regarding the rooting length, the potential uptake demand, and the water available in the soil among the different soil layers (Asseng et al. 2011).

For computing ET with **CropSyst**, two alternatives are possible like in most of the other models. One is the Penman-Monteith (Monteith 1965), while the other is the Priestley-Taylor equation (Priestley and Taylor 1972) (Stöckle et al. 2003).

4.1.3 Biomass and dry matter production

In **ORYZA2000**, the dry matter accumulation over the day is achieved after deducting maintenance and respiration requirements from the rate of the canopy assimilation over the day. The latter is obtained by combining the rate of the instantaneous leaf photosynthesis over the day and over the canopy height (Wikarmpapraharn and Kositsakulchai 2010).

The **CERES model**, which include the three crops, computes the PAR assuming to be half of the solar radiation that comes over the day (Ritchie et al. 1998; Monteith 1977). In DSSAT v3 CERES, the potential biomass is determined by multiplying IPAR with RUE. The biomass production considers the potential biomass production and the minimum values of water deficiency, nitrogen deficiency, and temperature reduction factor. CERES considers that all the crops are the same and have the same distance within rows (Ritchie et al. 1998).

Indeed, regarding light interception and photosynthesis, the original **CERES-Maize** takes for granted that half of the total incident radiation corresponds to PAR. Consequently, the production of the dry matter is calculated by multiplying PAR by RUE. Originally, the RUE was set to 5 g MJ⁻¹, but then lowered to 4.33 g MJ⁻¹. By using RUE for converting PAR into dry matter production means that CERES-Maize does not consider growth or maintenance respiration (Yang et al. 2004). Hence, CERES-Maize computes the daily rates of crop growth as suggested by Monteith (1977) (Lizaso et al. 2005a). This approach predicts yield and crop growth under both favourable and stress situations where growth is affected, and RUE is lowered. However, this method is restricted by different responses to

environmental conditions of photosynthesis and respiration, which are the predominant processes defining crop growth (Lizaso et al. 2005a). For example, the temperature rises the photosynthetic rate in maize until reaching 35°C, then it drops with further rise in temperature. Nevertheless, the dark respiration rate increases with temperature. However, photosynthesis interacts with numerous environmental factors such as temperature, light, leaf water and nitrogen status as well as CO₂. The temperature optimum for photosynthesis is lower when light intensity is low compared to saturated light intensity (Oberhuber and Edwards 1993). Therefore, Lizaso et al. (2005a) create two new sub-models for photosynthesis and respiration respectively to link with CERES-Maize in order to substitute the Monteith equation and calculate the daily rates of crop growth as the net result of the respiration rate and gross assimilation rate over the day. Photosynthesis simulation is however limited by the restricted daily model inputs related to the weather (maximum and minimum temperature, rainfall, and solar radiation). The water in the soil and nitrogen are not considered limiting factors. This new model is called CERES-PR and is integrated into the version 3.7 (Lizaso et al. 2005a). Moreover, it considers the leaf area model CERES-LA (see subchapter 4.3.2) (Lizaso et al. 2005a; Lizaso et al. 2003a). CERES-PR reproduces the absorption of the light, the daily respiration of the canopy, and the instantaneous leaf gross assimilation. The instantaneous leaf assimilation is computed in hourly steps for every leaf and then incorporated for the entire canopy and the hours of light during the day. To compute leaf assimilation, the intensity of the light, the temperature of the air, and the age of the leaves are used. Eventually, the potential daily gross rate is obtained by simulating daily maintenance of the canopy and growth respiration and then subtracting them from the daily gross assimilation. CERES-PR can reproduce single values of leaf assimilation for each leaf, leaf surface area, and the age of the leaf, making its leaf photosynthesis simulation unique (Lizaso et al. 2005a). Lizaso et al. (2005b) showed that the model CERES-PR predicts crop processes more realistically under stress situations. However, leaf-level fluxes regarding water and CO₂ are not computed (Lizaso et al. 2005b).

Additionally, López-Cedrón et al. (2005) compared CERES-4.0 with CERES-Maize-2003 and CERES-3.5. The main dissimilarities between the three models are the photosynthetic reduction factor, the RUE, the extinction coefficient for PAR (discussed here in subchapter 4.1.3), the relative rate of grain fill, the grains per plant computation, the efficiency of conversion of mobilized vegetative dry matter to grain, and the LAI computation (discussed in subchapter 4.4.2). The photosynthetic reduction factor affects the RUE and is a daily computed temperature function. In the two previous model versions, minimum and maximum temperature are used for representing daytime average temperature. In CERES-4.0, four temperature functions are used to determine the reduction factor. The cardinal temperatures for the average temperature during daylight hours are 6.2°C, 16.5°C, 33°C and 44°C for base, optimum, second optimum and maximum temperature respectively. The RUE in CERES-2003 decreases with vapour pressure shortage. The latter is calculated by using an equation that does not involve dew point temperature, compared to CERES-3.5 and CERES-4.0. In these two models, RUE has a value of 4.2 g/MJ (PAR) and is constant. In CERES-2003, The PAR extinction coefficient is equivalent to 0.65, while in

the other two models it depends on the distance among rows and plant density (López-Cedrón et al. 2005).

Dry matter growth and partitioning in **IXIM** is totally different from the original CERES. Instead of using PAR use efficiency like in CERES, new modules are introduced calculating gross assimilation of the canopy over the day, light absorption of one leaf, instantaneous leaf CO₂ assimilation, and canopy respiration (Lizaso et al. 2011).

APSIM-Maize does two estimations every day of the biomass that is produced over one day. Biomass accumulation is founded on resource capture and resource use efficiency. Limitations are due to the water transpiration and radiant energy. The actual daily biomass production is the minimum of these estimates (APSIM 2020; Soufizadeh et al. 2018). When drought stress is present, biomass production depends on IPAR and canopy RUE. In turn, IPAR depends on LAI and the canopy extinction factor. Nitrogen stress is considered by the model influencing leaf expansion, and also LAI and IPAR. Even influences on nitrogen content per unit leaf area on RUE are considered. Differently, when water is limited, biomass accumulation is determined by transpiration and its efficiency. Transpiration is regulated by the extraction of the water by the roots. Therefore, it depends on soil water content, roots soil exploration, and roots water uptake rate. The simulation of roots biomass depends on aboveground biomass accumulation since RUE and transpiration efficiency are related to aboveground biomass only (Soufizadeh et al. 2018).

The biomass production rate is computed by **CERES-Wheat** from radiation through the RUE coefficient, as described by Ritchie et al. (1998). **CropSyst** uses RUE as well but also combines it with water availability through the coefficient describing the use efficiency of the water transpired. Potential daily biomass production in CERES-Wheat is obtained from IPAR, which is in turn calculated from LAI, a light extinction coefficient, PAR, and RUE (Castañeda-Vera et al. 2015). The production of the actual dry matter is less than the potential due to water stress or inadequate temperature (Ritchie and Otter 1985). In CropSyst, this calculation considers the minimum value of the biomass growth which is dependent on radiation (which depends on IPAR), and the minimum of the biomass growth dependent on transpiration. Moreover, CropSyst differentiates LAI from green area index. The latter involves the green photosynthetically active fraction on the canopy only (Castañeda-Vera et al. 2015).

In **CROPSIM-Wheat**, potential dry matter accumulation is defined by crop growth rate and the PAR conveyed as the RUE. The RUE is supposed to be a function of the PAR. The rate of the potential dry matter accumulation for a specific canopy area index (consisting in lamina plus stem and spike area) is determined by the multiplication of the RUE with the PAR intercepted. The IPAR is obtained by the canopy area index, the daily receipt of the PAR, and the extinction coefficient describing the PAR. This factor is set to be 0.65 but it can be changed since it is an input factor (Hunt and Pararaiasingham 1995).

In **APSIM-Wheat**, the daily biomass accumulation (photosynthesis) coincides with the dry-matter aboveground biomass. Its calculation is based on the potential biomass accumulation consequent to the radiation interception. The potential biomass accumulation can be restricted by water deficiencies in the soil. The intercepted radiation, the RUE, as well as the diffuse, stress and carbon dioxide factors are used to compute the radiation-limited dry biomass accumulation. In APSIM-Wheat, only the leaves produce photosynthate (Zheng et al. 2015). The radiation interception is computed by the LAI and the extinction coefficient (Zheng et al. 2015; Monsi and Saeki 2005). The RUE is a function of growth stages. From emergence to the grain filling its value is constant and does not change according to the daily incident radiation as in APSIM-Nwheat. Stress factors such as temperature, nitrogen, phosphorus and oxygen can reduce the actual daily radiation-limited biomass accumulation. However, in APSIM 7.5 R3008 no phosphorus and oxygen stress are considered. The temperature factor depends on the daily mean temperature and temperature stress is possible from sowing until harvesting. The nitrogen factor is calculated by subtracting the leaf minimum and critical nitrogen concentration from the leaf nitrogen concentration. The CO₂ factor is established by environmental CO₂ concentration and daily mean temperature (for C3 plants like wheat). The actual daily biomass accumulation comes from the water restriction used on the potential biomass accumulation determined principally by radiation. The water-limited biomass depends on the daily water uptake and demand. The radiation limits the accumulation of the biomass when the water available in the soil is not restricted. Inversely, the water limits the accumulation of biomass when water available in the soil is limited (Zheng et al. 2015).

APSIM-Nwheat is able to calculate the potential daily biomass production according to light interception and RUE. The potential growth can be lowered by temperatures that are not ideal, and by water- and nitrogen-deficiencies (Asseng et al. 2011). APSIM-Nwheat adapted the coefficients for the RUE and transpiration efficiency as an independent RUE-CO₂-temperature function and independent CO₂-transpiration efficiency function for the purpose of catching the reaction of a high CO₂ concentration on crop growth (Asseng et al. 2004).

In **CropSyst**, biomass growth is basically determined by crop potential transpiration and crop IPAR (Stöckle et al. 2003). The potential growth is affected by nitrogen and water limitations, but also by temperature and light (Stöckle et al. 2003; Stöckle 2020). Crop potential transpiration dependent biomass production is obtained through the multiplication of the crop potential transpiration by the biomass-transpiration coefficient and the whole divided by the daytime mean atmospheric vapour pressure deficit. However, when the latter is low it becomes unstable. Therefore, unstressed biomass production is computed. Here, IPAR-dependent biomass production is obtained by multiplying RUE by IPAR. The daily potential biomass production is the minimum of the crop potential transpiration dependent biomass production and IPAR-dependent biomass production. This is used for obtaining the actual daily biomass production by considering water and nitrogen limitations. In order to estimate water limitation, it is indispensable to define the impact of N deficiencies on the transpiration of the crop. This is taken into

account by enhancing canopy resistance. The actual crop transpiration or water-limited is based on the performance of crops to take up soil water in order to satisfy N-limited crop transpiration requirements (Stöckle et al. 2003).

4.2 Phenology

In **ORYZA2000**, temperature is the principal influencing factor in phenological development (Bouman et al. 2001; Penning de Vries, F. W. T and van Laar 1982). In varieties sensitive to photoperiod, however, day-length can have some influences such as the induction of flowering. This is defined by various subroutines calculating the effective heat units over the day for the development, and the development rate as a function of the day-length, development stage, and heat units. When temperature is too low and rice cannot growth, the cold days number is calculated. The crop dies and the model stops working when a specific number of too cold subsequent days has passed. The development stage is expressed as thermal time (TT) in growing degree days (GDD) (Bouman et al. 2001). Thermal time, which determines the length of each phase, is defined as the mean air temperature daily accumulation between a base and a cut-off temperature allowing to differentiate growth stages. The TT is adjusted by factors dependent on genetics and environment. Water stress can accelerate TT. For some crops or cultivars, TT is not enough and vernalization and photoperiod must be considered since they modify the time necessary for all the phases between emergence and the initiation of flowering to be completed. Soil water, nitrogen stress, and phosphorous stress are other environmental factors influencing all phases with exception of the sowing to emergence phase (Stöckle et al. 2003; Soltani and Sinclair 2015). There is a linear relationship between the development rate of the rice and the mean temperature of the day between a base temperate of 8°C and an optimum temperature of 30°C. Temperatures over the optimum lead to a decrease of the rate until the maximum temperature of 42°C is reached. The rate of development is equal to zero when the temperature is lower than the base temperature or above the maximum temperature. When the average temperature is lower than 12°C for more than 3 days the rice dies. Therefore, the phenological development rate depends on the development rate for various phenological stages, the daily increment in heat unit and the photoperiod (Bouman et al. 2001). Rice crop life cycle in **ORYZA2000** is based on four phenological phases. The first phase is called basic vegetative phase (or juvenile phase) defined from emergence of the seedling to the start of the photoperiod-sensitive phase. The second is the photoperiod-sensitive phase which is from the end of the previous phase until the initiation of the panicle is reached. The third is the panicle formation phase continuing up to 50% flowering is obtained. The last is the grain filling phase, which ends once reaching physiological maturity (Bouman et al. 2001; Wikarmpapraharn and Kositsakulchai 2010). Differently from **ORYZA2000**, **CERES-Rice** counts nine phenological phases, of which five are aboveground phases. Similarly to **ORYZA2000**, TT defines the duration of each stage with a base, optimal and maximum temperature of 9°C, 33°C, and 42°C respectively. If the temperature reaches values outside this range, TT is computed differently, namely through the division of the day into 3h-sections and then considering a temperature adjustment for every portion (Wikarmpapraharn and Kositsakulchai 2010). In **ORYZA2000**, every

phase has a constant for the variety-specific development rate, determined by photoperiod and temperature. Discrepancies in total crop duration according to varieties normally depend on the basic vegetative phase, which can have different durations. The factor PPSE quantifies the photoperiod sensitivity of a variety. Phenological development parameters such as the base temperature for the growth of the juvenile leaf area and development, the maximal and optimal temperature for development, the development rate for the four phases, the maximum optimum photoperiod, the photoperiod sensitivity, and the relation between the delay in phenological development and the age of the seedling are variety-specific. Phenological development can be affected by various events. For instance, transplanting shock in transplanted rice is considered and it leads to a delay in the development. The age of the seedling in the model defines transplanting shock. Drought is another example of an event affecting phenological development. It affects growth and development of the crop and in ORYZA1 leaf rolling, incremented root depth, limited expansion rate of the leaf, incremented leaf senescence, altered assimilate partitioning, spikelet sterility, delayed vegetative development, and reduced rate of photosynthesis (due to lowered transpiration rate) are considered as consequences of water-limited production. Drought during the vegetative stage leads to a delay in flowering; moreover, a reduction factor is used regarding the leaf expansion to replicate drought consequences (Bouman et al. 2001).

In the **CERES model**, which is valid for the three crops, the phasic development is based on nine growth stages for quantifying the physiological age of the crops. The model can simulate all the growth stages leaving out the fallow duration because it is user-specific (Ritchie et al. 1998). Cereal crops time scale is connected to the crop growing parts temperature. Therefore, Ritchie et al. (1998) consider relevant to simulate how temperature influences some development features without considering photoperiod or other environmental pressures. Like in ORYZA, the TT describes how long crop development will last (Ritchie et al. 1998; Ritchie and NeSmith 1991). The time between diverse developmental stages is quantified and then stated as the equivalent development rate. So, it is possible to see the temperature response function of cereal development processes. Variations in the duration of the vegetative phase length can occur due to different cultivars with various photoperiod sensitivities. The rate at which crops change from vegetative to reproductive phase can be affected by the daytime and night-time length. For instance, differences in photoperiod reactions are shown under different photoperiods as the number of leaves developed on crops grown. Maize and rice are short-day crops due to the low vegetative development achieved in long days conditions. On the other hand, wheat belongs to the long-day crops and when the length of the days is short, its development is reduced. The optimum photoperiod for maize is about 12.5h, while for rice between 11-15h. Maize and rice have a different juvenile phase which changes among cultivars. The juvenile phase, or basic vegetative phase, consists of the stage when the crop is not influenced by photoperiod modifications. The fluctuation of the length of the juvenile phase for each cultivar gives information about the crop maturity type. This latter concept is qualitative only, and it depends on the regions. One cultivar can be long or short season depending on the places if the photoperiods are diverse. The juvenile phase can be simulated only if the variation between cultivars

are known. Temperature controls almost the entire duration of the juvenile phase. Leaf primordia are developed between juvenile and floral induction. Once floral induction finishes, leaf initiation stops, and the leaf number is established. The appearance rate of the last differentiated leaves, which are not yet emerged, is commanded by temperature. Thus, the TT needed for the vegetative stage to conclude is the result of what has occurred during the juvenile and the induction of flowering phases. Winter wheat varieties need low temperature to commence the formation of the spikelet. Vernalization is the low temperature needed by winter wheat to flower and it starts at germination. Temperature ranging between 0 and 8°C are needed for vernalization to take place (Ahrens and Loomis 1963), while the optimum is between 0 and 7°C. In CERES, the daily vernalization factor is determined by measuring the minimum and maximum daily temperature. A 50 vernalization days threshold is considered to be enough in order to achieve the vernalization of all cultivars, which have different sensitivities to it. Spring wheat varieties, which are mostly insensitive to vernalization, are regulated in the model like winter wheat but with lower values for the cultivar coefficient. Devernalization happens when the young seedling are under high-temperature conditions (Ritchie et al. 1998).

As reported for the CERES model (Ritchie et al. 1998), in **CERES-Maize** nine phenological phases are recognized. The first is from the emergence of the seedling to the end of the juvenile phase, followed by a second phase which runs until tassel initiation (photoperiod-sensitive phase); a third phase, from the initiation of the tassel up to silking; a fourth phase, from the end of the third phase to the beginning of the effective filling period of grain which is commonly called lag phase, then followed by the fifth phase, the effective filling period of grain. The sixth phase, from the end of the fifth phase until reaching the physiological maturity (black layer), followed by the seventh phase prior to sowing or fallow. The second to last phase is defined from sowing to germination, and the last, or ninth phase, is germination to seedling emergence (Kiniry 1991; Yang et al. 2004). CERES-Maize uses cultivar-specific input parameters for the purpose of predicting the GDD from emergence until the conclusion of the juvenile phase (P1), as well as photoperiod sensitivity (P2). The duration from the initiation of the tassel until silking is considered as a proportional function regarding the GDD collected during the two previous stages; while from silking until the grain starts to be effectively filled the GDD-value is settled at 170. From silking to maturity, another hybrid-specific input parameter P5 defines the duration of the last stage in GDD. Thus, P1 and P2 determine silking (or tassel initiation), which have a relevant role in simulating grain yield. P1, P2, and P5 are essential for simulating aboveground phenological development of maize (Kiniry 1991; Yang et al. 2004; Román-Paoli et al. 2000). Other cultivar coefficients relevant for CERES-Maize are the maximum number of kernels per plant that can be obtained (G2), the rate of filling the kernel when the state of grain filling is linear and under optimum conditions (G3), and the phyllochron interval (PHINT, the interval in TT among successive leaf tip appearances) (Bao et al. 2017). Temperature is the principal factor leading to organ growth, while absorbed solar radiation from a fixed value of RUE generates dry matter. The RUE is dynamic and variable and consequently is susceptible to temperature and to the intensity of the light (Yang et al. 2004). In CERES-Maize, the base temperature

of development is of 8°C and it is valid for all the phenological phases with the exception of the seedling emergence. When the temperature passes 34°C, the daily TT decreases until it is zero at 44°C. From germination to seedling emergence, the daily TT needs 10°C as base temperature, and germination requires one day. Thereafter, 45 daily thermal times with 10°C as fixed base temperature are needed for coleoptile elongation guaranteeing enough soil moisture for germination during planting. Three systems are involved from seedling emergence to silking. The first is the final number of leaves. This number is defined from the number of leaf primordia that are grown from the emergence of the seedling until the tassel initiates. The other system is the date when the tassel initiates and is defined by using daily TT and photoperiod. The last one is silking, which is characterized by the conclusion of the leaf growth and is defined from the rate of the leaf-tip appearance and the total number of leaves. In the model, the tassel and leaf initiation, as well as the leaf-tip appearance, are processes that developed individually. The initiation of leaf primordia and the appearance of leaf-tip use a daily TT of 8°C described before. For the tassel, which is the phase when leaf primordia finished and branches of the tassel commence to growth, it is first necessary to determine the total number of leaves. The crop development rate is independent of photoperiod and dependent on temperature during the juvenile phase. The development of the apical crops is not influenced by the temperature once the genotype-specific sum of 8°C daily TT is reached. Nevertheless, high temperature before tassel initiation can influence the final number of leaves. In the model, only the photoperiod defines the duration of the inductive phase. The temperature however establishes when leaf primordia initiate. Here, the elevated temperature increases the leaf initiation rate but not the apex development rate. Consequently, the total leaf number is higher and delays silking. Similarly, the temperature characterizes when the leaf initiates and how long the juvenile phase lasts. The elevated temperature raises the development rate with no changes in the final number of leaves. In the model, silking as well as the conclusion of leaf growth happen on the same day. Grain development takes place during silking until reaching the physiological maturity. Three phases are determined: the lag phase, the effective fill period (almost linear grain filling), and the successive phase namely the achievement of the physiological maturity. The daily thermal temperature of the lag phase does not change significantly among genotypes and is defined at 170 daily TT. When the lag phase is about to conclude, the effective fill period starts and finishes when 95% of the daily thermal temperature from silking to physiological maturity is reached. The remaining 5% are used for reaching the physiological maturity. To avoid delayed maturity due to cool temperatures during the last period, maturity takes place when the daily TT time is lower or equal to 2.0 on a day during this phase (Kiniry 1991).

APSIM-Maize has 11 crop stages. Each of them is defined according to the accumulation of TT with exception of the sowing until germination phase, which depends on soil moisture. The phenology routine computes the TT daily from air temperature in degree days every three hours. The sum of these values allows estimating the time necessary to compute every phase. Between the stage when the crop emerges and flowers, the TT obtained over the day is lowered. This is due to water or nitrogen stress which

postpones the phenology. When the crop is sown and germinates, the TT depends on the soil water level; while between germination and emergence the TT to reach is influenced by the sowing depth. Depending on temperature, the final number of leaves that a crop plant can have and the leaf appearance rate define the time necessary to compute the phase between emergence and flag leaf appearance. Until floral initiation, the final leaf number is equal to the number of seeds at germination added to the number of leaves that are initiated later, following a rate of 21 degree days per leaf. Therefore, the final leaf number, the timing of flag leaf and flowering appearance are determined by the timing of floral initiation. Similarly to the other models mentioned before, between the emergence and floral initiation phases a fixed TT, dependent on cultivar specific period, characterizes them. Cultivar-specific fixed TT durations are present between various phases: when the crop flowers and starts to fill the grain, when the grain is filled, when the grain is filled and almost mature, and when maturity and harvest ripeness are reached (APSIM 2020; Soufizadeh et al. 2018).

Phasic development depends on the growing stage duration (Ritchie and Otter 1985). Nine growing stages are considered in **CERES-Wheat** v2.1 and in **APSIM-Nwheat**. The first five phases are above-ground and the other four describe relevant events during the crop course. The first phase is from emergence to terminal spikelet initiation (juvenile phase), followed by a second phase lasting from terminal spikelet until the conclusion of the leaf growth (vegetative growth). The third phase stretches from the end of the second phase until the conclusion of the pre-anthesis ear growth, followed by phase four, the filling of the grain. Phase five corresponds to the achievement of maturity. Phase six is the consequent harvest, followed by phase seven, of fallow or pre-sowing. The successive sowing and germination of the crop correspond to phase eight, finally followed by phase nine, the initiation of the terminal spikelet (Ritchie and Otter 1985; Keating et al. 2001). In **APSIM-Nwheat**, sowing to germination depends on soil moisture, otherwise the TT defines the commencement of each stage modified according to photoperiod and the vernalization effect (Keating et al. 2001). The phasic development in **CERES-Wheat** is influenced by GxE. Temperature is the most significant variable affecting the development rate. The latter is hypothesized to be directly proportional to temperature from 0°C to 30°C. Vernalization starts at germination and its optimum temperature is between 0 and 7°C, while its effect decreases from 7 to 15°C. Vernalization is considered in the model by the vernalization coefficient (Ritchie and Otter 1985). Indeed, CERES-Wheat uses six variety-specific parameters, of which three control phenological development. They are P1V (sensitivity to vernalization from emergence to terminal spikelet), P1D (sensitivity to photoperiod), and P5 (duration of the grain-filling period). Two other parameters are G1, that controls grains number settled by each plant, and G2, the maximum grain-filling rate. G3 represents the dry mass of a single stem and its leaves at anthesis. G3 is also used for determining ears number (Porter et al. 1993). Moreover, Rinaldi (2004) mentions other cultivar-specific genetic parameters such as P2D for photoperiod (relative decrease in the rate of development when plants are grown under a photoperiod 1 hour shorter than the optimum) and PHINT, the phyllochron interval. Photoperiod, vernalization days and phyllochron modify the TT necessary from emergence to terminal spikelet development (Ritchie

1991). Devernalization can happen if the young seeds are subjected to high temperature. The model reduces the vernalization days proportion if the temperature is higher than 30°C and the vernalization days lower than 10. Day-lengths shorter than 20 hours can lead to a delay in development. The delay depends on genetic-specific characteristics. As in the other models, both vernalization and photoperiod modify the TT accumulation in the first stage (emergence to terminal spikelet initiation) (Ritchie and Otter 1985).

If there is no water stress and the temperature is optimal, seed germination occurs in **CROPSIM-Wheat**. This model considers air temperature instead of soil temperature, and the time of emergence depends on sowing depth. The rate of elongation can decline if water content decreases and when no extractable water is available, no elongation will occur. The phases of reproductive development in CROPSIM-Wheat are eight. The first phase is from germination until reaching double ridges, followed by phase two until terminal spikelet, then phase three until the expansion of the last leaf. Phase four consists on the emergence of the spike, and phase five takes place until anthesis starts. Phase six continues until the conclusion of anthesis, followed by the initiation of grain filling in phase seven, and concluding in phase eight with the grain filled. The various phases last according to biological and chronological days at optimum temperature and photoperiod without accounting for any stresses related to drought or nutrients. The development of the crop age depends on daily minimum and maximum temperature and, if applicable, photoperiod and vernalization. Water effect on progression rate is not taken into consideration. Once the characteristic day number of a specific phase is reached, the following phase starts. From germination until reaching the anthesis, the base temperature is set to 0°C, while for reaching the filled grain it is set to 8°C. The day-length effect uses a curvilinear function like in CERES. Photoperiod and vernalization factors can lower the development rate of the crop on any specific day. Photoperiod sensitivity is accounted until reaching the expansion of the last leaf and is characterized by different sensitivities depending on the stage; vernalization sensitivity is also accounted until reaching the last leaf, but the factor does not change after the terminal spikelet has developed. The vernalization factor depends on vernalization days. Vernalization happens between -1 and 12°C with a higher effect between 0 and 8°C. Once the temperature is higher than 30°C, the vernalization stops. At terminal spikelet, the vernalization process stops. However, the crop is supposed to react to the vernalization effect until achieving the anthesis phase. Therefore, the value of the factor which is obtained during the terminal spikelet development is preserved until the beginning of the anthesis (Hunt and Pararaiasingham 1995). Similarly to CERES-Wheat, CROPSIM-Wheat cultivar-specific genetic parameters are P1D, P1V, P5, G1, G2, G3, and PHINT (Gbegbelegbe et al. 2017).

In **APSIM-Wheat**, 11 phenological phases are recognised. The first phase is sowing, followed by germination, the successive emergence, the conclusion of the juvenile phase, the successive initiation of flowering, followed by flowering, the consequent start in filling the grain, the accomplishment of grain filling, followed by a maturity phase, the successive harvest ripening and, lastly, when the crop ends.

With the exception of sowing and germination that also depend on how deep it has been sown, each phase is established by the TT accumulation regulated according to additional factors. The crown temperature follows the original routine belonging to CERES-Wheat, which corresponds to air temperatures equal or above zero degrees. Thermal time, vernalization and photoperiod are defined like in the other models. Therefore, through adjustments of the TT according to the specific stage in order to obtain the target TT, the successive phenological stage can occur. In APSIM 7.5 R3008, soil water, nitrogen, and phosphorus stresses do not influence phenological development. From sowing to germination, soil water availability in the seeded layer defines seed germination. If germination does not happen within a definite period, the crop dies. How deep it has been sown influences the TT target in particularly between the germination and the emergence phase like for the other models. Photoperiod, which is obtained by day of year and latitude, has an effect on phenology during emergence and floral initiation. Between emergence and floral initiation, vernalization affects phenology. The CERES approach is followed by APSIM-Wheat to simulate vernalization, which depends on daily average crown temperature, and daily minimal and maximal temperature. If the daily maximal temperature is above 30°C, then devernalization can occur. The vernalization factor is composed of a sensitive component to vernalization that is cultivar-specific (Zheng et al. 2015). Similarly to CERES, APSIM-Wheat and APSIM-Nwheat cultivar coefficients are vernalization sensitivity (p1v), photoperiod sensitivity (p1d), TT from the beginning of grain filling to maturity (p5), coefficient of kernel number per stem weight at the beginning of grain filling (Grno), potential kernel growth rate (Fillrate), potential final dry weight of a single stem excluding grain (stwt), and phyllochron interval (phint) (Asseng and van Herwaarden 2003; Asseng et al. 1998; Asseng et al. 2004; Keating et al. 2001). According to Soltani and Sinclair (2015), APSIM version 7 has about 25 parameters that can be adapted depending on the cultivar, while CERES has only 7 cultivar parameters based on yield and phenology. However, CERES has 32 “ecotype” parameters, which are constants for cultivar groups (Soltani and Sinclair 2015).

In **CropSyst**, the thermal time describes the performance of the crop development similar to the other models (Stöckle et al. 2003). CropSyst does not have a classification of the parameters (Soltani and Sinclair 2015). Soltani and Sinclair (2015) modified some specific parameters for the purpose of reproducing different cultivars growth, development and yield. These parameters are the days required to start and complete vernalization, minimum factor for vernalization, stem/leaf partition, leaf duration, day-length for insensitivity and to inhibit flowering, specific leaf area, degree day to peak LAI, unstressed harvest index, degree day to beginning of flowering as well as to the beginning of grain filling to the beginning of maturity (Soltani and Sinclair 2015).

4.3 Growth

CERES modules have some basic principles that distinguish between growth and development. Since a good differentiation of these concepts is pertinent and valid for other models, their definitions are described in this section. **Growth** considers mass accumulation and expansion. Mass accumulation is

concerned with the absorption of PAR for plant biomass assimilation. Hence, the principal environmental factors on which the mass growth depends are the amount of PAR of the sun and the number of leaf surfaces that are available in order to absorb the PAR. Only a small part of the carbon fixed through photosynthesis is present in the final dry matter of the harvest due to losses during respiration. Growth has another factor, namely area or volume expansion of crop components, which is not regulated by the net amount of carbon fixed. Temperature, as well as water- and nitrogen stresses, affect the cell expansion. This is due to the fact that crops which grow vegetatively at diverse temperatures and at similar radiation levels later achieve diverse size and mass. Mass and expansion are therefore different and imply that crop partitioning is modified for the purpose of adjusting the dissimilarities in the size of the crop. This happens when the rate of the net assimilation is similar, and it is tuned to the leaves area incorporating the PAR. The **development** has two components, the phasic and the morphological development. Phasic development includes transformations in various phases of growth and is mainly correlated with important modifications in the partitioning of the biomass. Phasic development has a high degree of variation among cultivars which allows a location-specific selection of cultivars based on the time necessary for the growing season coordinated with the water supply or the warm season length. This aspect is relevant once it is decided to assess a risk analysis of the crop production. Morphological development is the start and end of the development of numerous plant organs within the crop's life cycle. It determines the number of tillers, leaves, and grains that are generated by a crop. Phasic and morphological development rates are especially influenced by temperature. However, their response to temperature can be dissimilar. Photoperiod, to which each species responds differently, is relevant for the determination of the growth duration added to temperature effect. Thus, due to the differences among sensitivities to stresses, it is important to separate growth from development processes (Ritchie et al. 1998).

4.3.1 Crop growth rate

In **ORYZA2000**, the gross daily growth rate depends on the gross CO₂ assimilation rate over the day, the maintenance respiration costs, the number of available stem reserves for the growth and the assimilate requirement to produce dry matter. For obtaining the rate of the net growth over the day is necessary to subtract the relocated amount of stem reserves from the gross value. The carbohydrate requirement for producing dry matter of leaves, stems, storage organs (panicles), roots, and stem reserves, as well as the fraction that is necessary in order to allocate the reserves available in the stem and that are accessible for growth, is a variety-specific parameter (Bouman et al. 2001).

IXIM totally replaced the code used for simulating dry matter growth in **CSM-CERES**. CSM-CERES computes daily growth rate based on the PAR use efficacy and defines so the intersection between the canopy leaf area and PAR. IXIM expresses the instantaneous leaf CO₂ assimilation, the area of one leaf, the light capture, and the canopy respiration instead of following the CSM-CERES method (Lizaso et

al. 2011; Yakoub et al. 2017). Light capture, photosynthesis, and respiration follow the processes mentioned by Lizaso et al. (2005a) and Lizaso et al. (2005b) as described in chapter 4.1.3.

In **CropSyst**, the crop growth is dependent on three main influencing factors: nitrogen uptake (nitrogen-limited), transpiration (water-limited), and carbon fixation (radiation-limited). The water-limited growth is influenced by the aboveground biomass/water transpired ratio, by the actual transpiration, and lastly by the daytime mean vapour pressure deficit. The radiation-limited growth is affected by the radiation conversion to aboveground biomass, the total irradiance over the canopy, the fraction of incident radiation arrested by the canopy, and the temperature limitation factor following the calculation of Monteith (1977). Water- and radiation-limited growth values are compared. Then, the smaller of the two values is adopted to define the potential of the new growth and of the N dependent growth. The latter is determined by the concentration of crop nitrogen expected after the new growth, the critical nitrogen concentration necessary for the crop to grow at the potential rate, and the crop minimum nitrogen concentration that stops the crop growth. After the new growth, the concentration of the crop nitrogen is equal to the accumulated N uptake to total crop biomass ratio, which comprises the new growth (Stöckle et al. 1994).

4.3.2 Leaf-related variables: leaf area, leaf number, leaf senescence, and leaf area index

In **ORYZA2000**, the leaf area increase is founded on an average temperature over the day when the canopy is not closed so that the production of carbohydrates does not restrict the leaf to expand. When the canopy is closed, then the increment in the area related to the leaves is calculated by considering the increment of its weight. The increment of the dry weight over the growing season is obtained through the integration of the rates representing organs growth over the day and the area of the leaves (Bouman et al. 2001; Kropff et al. 1994). The green leaf area, together with the green stem area, establish the amount of absorbed light and, consequently, the CO₂ assimilation. The daily growth rate of LAI considers transplanted rice as well as direct-seeded rice and these have separate rate calculations (Bouman et al. 2001). When the growth phase of transplanted rice grown in the seedbed just started, the leaves do not shade each other. Therefore, it is not only the amount of available assimilates that limits the leaf area expansion, but also the temperature (Horie et al. 1979). So, when the canopy is not closed, the temperature regulates the exponential growth of the plants. During the growth, even nitrogen limitation is considered (Bouman et al. 2001). Once completed the exponential growth phase, only the carbohydrates that are available for the leaf growth influence the leaf area (Penning de Vries, F. W. T. et al. 1989). In the following phase, called linear phase, the relationship between green leaf weight and green LAI is fixed and is known as specific leaf area. **ORYZA2000** can gradually transit between the two phases of growth (Bouman et al. 2001). During transplanting, transplanting shock according to the age of the seedlings is calculated. After transplanting and after the shock period, the growth continues exponentially. Here, drought effects are considered and affect both phases. In transplanted rice is assumed that the seedbed has always enough water for its growth, but it is not always so in the fields (Bouman et al.

2001). Stressed plants during the vegetative phase have reduced leaf expansion rate (Tanguilig et al. 1987). For direct-seeded rice, ORYZA2000 works exactly like for transplanted rice after transplanting. The senescence and the death rate of leaves are accelerated by drought (Lilley and Fukai 1994). Once the soil-water tension is about 300 kPa, leaves start dying and at 700 kPa all the leaves are completely dead. ORYZA2000 considers this if the simulation requires water-limited conditions. As long as drought is present (called drought-induced death leaf factor), the amount of green leaf biomass does not increase. When drought stress is present, leaves roll. This consequently affects photosynthesis because of the reduced amount of intercepted solar radiation. Leaf rolling is considered in ORYZA2000 through a rolling factor and it is linearly related to the soil-water tension. With about 200-300 kPa water tension, leaf rolling starts and reach the maximum with 400-1000 kPa water tension. The leaf-rolling factor of each soil layer is considered by linear interpolation from the previous water tension of the soil. By summing each rolling factor obtained for every layer it is possible to calculate the average leaf-rolling score. Moreover, this factor is used in order to simulate the repercussions on spikelet sterility due to drought stress (Bouman et al. 2001). During the vegetative phase, the leaf expansion rate of stressed plants decreases (Tanguilig et al. 1987) until it stops if the plants are young (Bouman et al. 2001). Flowering can be delayed if drought appears during the vegetative phase (Yoshida 1981). If the soil is excessively dry, then it cannot generate new foliage and the rate of the crop development is halted. For this reason, a factor for the leaf expansion is utilized in ORYZA2000 to simulate the drought effect on delayed flowering. This factor is used even for the drought effect on the assimilates partitioning in shoot, root and rooting depth (Bouman et al. 2001). Under drought stress, leaves stop expanding but the photosynthesis continues and the carbohydrate reserves raise making them more available for roots than for shoot (van Keulen and Seligman 1987; O'Toole and Moya 1981). A source-sink limited phase is present during the growth of the leaf area. When leaves are still small, they do not shade each other and therefore the available assimilates do not limit the leaf area growth. Here, the exponential increment of the area is due to the sum of the temperature multiplied by the relative leaf growth rate. When the LAI reaches a value larger than 1, it means that the amount of the carbohydrates limits the growth. This growth phase is linear, and the growth of the leaf area is obtained through the multiplication of the increment of the leaf weight by the specific leaf area that the development stage defines. The transition between the two growth phases may be determined by the quantification of the leaf area growth in both the exponential and the linear equations. Moreover, starting from flowering leaf loss is considered. Leaf loss is represented by the loss rate factor. The latter depends on the development stage and is multiplied by the residual green leaf biomass. Furthermore, the rate of leaf loss expresses the consequences of nitrogen limitations (Bouman and van Laar 2006). A variety-specific leaf growth parameter is the specific leaf area: it is possible to establish it from field experiments and varies within development stages (Bouman et al. 2001).

The **CERES model**, including all the three crops, evaluates the sink capacity of the aboveground biomass every day in order to understand if the crop has a sink- or source limitation. Ritchie et al. (1998)

mentioned the difficulties in estimating sink-limitations of the crop growth when one of the early vegetative stage is taking place, particularly with the aim of collecting LAI values. Together with leaf appearance, the leaf expansion rate of emerged leaves needs to be determined to estimate the LAI. The entire expansion of the leaf depends on its growth on the principal stem and its tillers. The latter are not easy to simulate properly due to the substantial irregularity of number and area that tillers show in the field. CERES does not have a standard procedure for computing the expansion growth of the leaf area in the main stem among the different modules. Leaf senescence is considered in all CERES models as linked to crop leaf development. Apart from wheat (as explained later under CERES-Wheat), the other CERES models try to simulate the natural senescence due to crop development, which is hastened when the crop density and the LAI values are high. Consequently, the leaves that are not on the surface are shaded leading to senescence. Additionally, water and nitrogen deficiencies accelerate the process. Then, the LAI can be established by subtracting the senescent leaves from the total leaf area (Ritchie et al. 1998).

In **CERES-Maize**, temperature is the principal cause for the expansion of the leaves and for the growth of the leaf biomass. The expansion of the leaf area stops at the silking point since here the maximal LAI values are reached. The leaf senescence continues, then, in two distinct phases. The first phase is defined from the beginning of silking until the grain starts to be filled and lasts for a total of 170 GDD. The second phase starts from the end of the first one and lasts until reaching the maturity. Eventually, the two phases are compared with the total leaf senescence that could take place when light intensity and temperature are low. The actual leaf senescence is the smaller of the two estimates. The disadvantage of this procedure is the sudden decline in LAI once silking starts and also the shift from a linear (first phase) to an accelerated leaf senescence (second phase) (Yang et al. 2004).

The amount of incident PAR caught by the canopy and the capacity to transform PAR into dry matter define the amount of biomass accumulated. The amount of incident radiation that the crop intercepts is defined by the green leaf area and its expansion and duration. Therefore, leaf blades furnish the main way for transportation and for carbon harvesting. Moreover, in maize and wheat kernel initiation is related to the radiation that can be intercepted around the anthesis phase (Fischer 1985; Andrade et al. 2000; Otegui and Andrade 2000). Since this relationship has been used for improvements of kernel number prediction in simulation models, an accurate reproduction of the green leaf area development is essential for simulating the crop growth. Many approaches have been adopted to predict the green leaf area (Lizaso et al. 2003a). Furthermore, the duration of the green leaf area varies considerably among genotypes (Elings 2000). Simulation of leaf area has been reported to be a limiting factor in CERES-Maize for obtaining an accurate prediction. CERES-Maize uses four functions of leaf tip number for reproducing the growth of canopy leaf area. Senescence depends on the TT and is hastened by numerous stresses. Expansion and senescence are affected by these stresses, but their effects on leaves are not simulated by the model. Therefore, genetic differences in leaf development are not considered. The

expansion and senescence of single leaves can be adjusted so that it is possible to accurately simulate variety-specific responses to water stress, temperature, and inter-plant competition (Lizaso et al. 2003a). So, Lizaso et al. (2003a) developed a new model for reproducing leaf growth and development taking into account the leaf expansion of specific cultivars and single leaf senescence according to phenology. Since the leaf area model depends on the TT, its components were modified and then compared to CERES-Maize v3.1. The components mentioned are leaf expansion, leaf longevity, and leaf senescence. By doing this, three new cultivar-specific inputs were added to the proposed new leaf area model called CERES-LA, which allows simulating separately leaf expansion and leaf senescence: longevity of the most longevous leaf (LL_x), final number of leaves (LT), and area of the largest leaf blade (Ae_x). The model CERES-LA, defined as the new leaf area model able to reproduce the variety-specific growth of single maize leaf, obtained better prediction than the original CERES-Maize model (Lizaso et al. 2003a).

In **IXIM**, expansion and senescence per-leaf foliar surface are reproduced according to the description of Lizaso et al. (2003a). Some other adjustments to the model were reported. For instance, the leaf number is predicted early in the season taking advantage of information contained in genetic coefficients. The leaf number is calculated again later, once the differentiation of the leaves finishes and also after the photoperiod-sensitive induction to flower is realized. Its equation is adjusted so that cultivars belonging to very short and long seasons are appraised since it is often considered that only 25% of the duration of the TT regarding the vegetative stage is used by the juvenile phase and 10% by the flowering induction phase. Moreover, the leaf area simulation is affected by temperature and stress, which are considered by further changes to the model. The most limiting stress factors are the lack of water in the soil, aeration, nitrogen and phosphorus. When the crop is under conditions of water stress, the leaf rolling effect decreases the efficiency of the canopy to capture light. The consequence of the leaf rolling effect on the PAR absorption is evaluated by calculating how much light is effectively captured by the leaf area. IXIM was developed with minimum weather data inputs, so atmospheric demand is not simulated. Only some similar variables are used. One of them is the part of the radiation that is transmitted through the atmosphere and is computed every hour from the solar radiation that reach the canopy and from the extra-terrestrial solar radiation. IXIM needs two additional coefficients compared to CERES for the purpose of reproducing the cultivar-specific leaf area. The two new inputs are the one-side surface of the largest leaf (AX) and the longevity of the most long-lived leaf (LX), which is described as the TT passed among half of the leaf expansion and half of the senescence (Lizaso et al. 2011). Therefore, it is possible to reproduce the seasonal leaf area with IXIM (Yakoub et al. 2017).

In **APSIM-Maize**, the potential LAI comes from the number and from the size of the leaves, the number of plants that are settled per m^2 and the factor for the water stress influencing the leaf expansion. The size of the leaf is obtained from the final number of the leaves supposing that it adopts what Keating and Wafula (1992) support, namely a bell-shaped distribution in which leaves grow along the stalk. Before the floral initiation starts and consequently the final number of the leaves is known, the

provisional final number of the leaves is obtained by estimating the date of floral initiation, making it possible to simulate the size of the leaf. The actual LAI is lower than the potential LAI when the biomass partitioned to the leaf that day is not enough. The maximal specific leaf area determines the maximal leaf area which can be enlarged per gram biomass. The larger the LAI, the smaller the specific leaf area, namely that younger and smaller crops have thinner and larger leaves. Factors like the age of the leaves, the competition for the light, water stress and frost lead to senescence. The senescence routine in APSIM maize computes a senesced LAI every day for every stress type and considers the maximal values of the four stresses contemplating them as the total senescence of the day. After flowering, some of the oldest green leaves die daily. This process is caused by the age of the leaf. The number of dead leaves that is obtained is finally converted into senesced LAI. When the LAI is greater than 4, light competition reduces the leaf area. Therefore, the LAI senesces (APSIM 2020).

In **CERES-Wheat**, light interception and dry matter production are strongly affected by plant leaf area (Ritchie and Otter 1985). As mentioned for the CERES-model in CERES-Wheat, the leaf area is based on two rates: the leaf appearance and the expansion of growing leaves (Castañeda-Vera et al. 2015; Ritchie et al. 1998). The leaf area expansion rate is responsive to environmental stresses. Cool temperature or moderate drought stress lower the expansion growth more significantly than when photosynthesis is diminished. This leads to an increment in the specific leaf weight and assimilates proportion partitioned to the roots. CERES-Wheat computes the repercussion of water deficit and temperature on photosynthesis and on the leaf growth. The daily plant leaf area growth is founded on the total width of the leaves that are expanding on the plant, the maximum daily rate of length extension growth of a leaf, the reduction factor in case of non-optimal temperature, and the reduction factor for water deficit. The total width of expanding leaves depends on the growing leaves number on a plant including tillers. The leaf expansion growth optimum temperature is 21°C. Nevertheless, soil water availability can restrict leaf growth before transpiration is decreased. The rate of leaf extension diminishes even if the daily maximum possible water assimilation of the roots is less than 1.5 times the potential transpiration (Ritchie and Otter 1985). CERES-Wheat supposes that only four green leaves can be supported by the tiller. Once the fourth leaf developed, senescence starts in the oldest leaf (Castañeda-Vera et al. 2015; Ritchie et al. 1998). In CERES-Wheat, leaf senescence is related to crop phasic development. While the plant reaches physiological maturity, the plant increases its senescence rate. Moreover, low temperature and water deficiencies can hasten it as well as light competition between densely packed plants. Regarding cool temperature stress, the senescence degree is influenced by the hardening degree due to past exposure to cold. Leaves that are still unhardened are more vulnerable to senescence (Ritchie and Otter 1985). Li et al. (2018) mentioned relevant genotype parameters regarding leaf area, namely the first leaf area of a standard leaf (LAIS), the increment in potential leaf area during the vegetative phase (LAFV), the increase in potential leaf area during the reproductive phase (LAFR), the specific leaf area of the standard first leaf (SLAS), the beginning of final leaf senescence (LSPHS), the end of final leaf senescence (LSPHE), and PHINT.

In **CROPSIM-Wheat**, leaf expansion on the principal stem is obtained by the potential individual leaves area and the leaf appearance rate. The potential area is related to the area of the antecedent leaf on the culm. Cultivar characteristics define the potential increment from one leaf to another. Leaf area potential increment is calculated everyday based on the phyllochron time over the day, its interval, and the potential size of leaf expansion. Water and nitrogen stresses can influence the final leaf size. The potential rate of leaf expansion together with the specific leaf area determine the potential accumulation of the leaf dry matter. Leaf longevity occurs at 4 phyllochron preceding the last leaf phase. In general, leaf longevity is affected by environmental factors such as extreme shading, which diminishes the longevity by accelerating the aging process, or low temperature, that can lead to premature leaf death. After the last stage of the leaf, senescence is reproduced according to a linear interpolation. Leaf dry matter redistribution takes place when leaves die and when nitrogen is transported from the leaf into the grain. In the first case, a portion of carbohydrate and nitrogen go back to the main body to be used elsewhere. It is hypothesized that nitrogen is remobilized as an organic compound and therefore it is directly related to dry matter redistribution. The number of the leaves is based on the reproductive development rate, which is dependent on the photoperiodic sensitivity and the time needed to accomplish the terminal spikelet phase to reach the last phase of the leaves development. As a consequence, once the terminal spikelet is concluded, the leaf number could be potentially influenced by photoperiod (Hunt and Pararaiasingham 1995).

In **APSIM-Wheat 7.5 R3008**, the plants are supposed to have only one stem. Consequently, the production of tillers is not reproduced. During the emergence, the number of nodes at the beginning is identical to the number of leaves at the start of development. While tillers are forming, nodes develop during the TT interval that is influenced by how many nodes of the principal stem are available after sowing. In APSIM-Wheat, the node phyllocron is constant and does not take into account any stress from water and nitrogen on leaf appearance. The potential daily increment of the number of the nodes in the stem happens during the formation of the tillers and is computed by the TT over the day and the node phyllocron. Since in APSIM-Wheat only one stem is considered, all the leaves come from it. The potential number of the leaves that belong to one node is determined by a function counting the number of nodes over the day. Regarding the entire plant, the potential increase of the leaf number over the day depends on the potential increase in one node and in the number of the nodes. Environmental stresses that affect the expansion of the canopy such as nitrogen, phosphorus and soil water are taken into consideration. The increase of the actual number of the leaves is computed according to the relationship among actual and stressed increase of the LAI. At emergence, every plant has its specific initial leaf area. When tillering is taking place, the daily increase in LAI is defined as the minimum between the stressed LAI and the carbon-limited LAI. While tillering, the “stressed” increment of the leaf area over the day is measured: the potential increment of the LAI is diminished by the previous mentioned environmental factors. The potential increment of the leaf area over the day is consequently determined by the potential increase of the number over the day as well as of the size of the leaves. The increase of the

leaf dry weight and the maximal area of the leaves define the leaf area founded on the carbon production. The maximal specific leaf area is connected with the LAI. The leaf senescence phase starts when it reaches 40% between the initiation of flowering and the conclusion of the juvenile phase and ends with the harvest ripening. During this last phase, all green leaves are already dead, and the number of senescent leaves is measured by the TT over the day. Age, water stress, light intensity, frost and heat are the five causes of leaf senescence. The day's total LAI senescence is described as the maximum value of the five causes listed. The total plant leaf area must be higher than the minimal plant area. Regarding nitrogen, only a minimal part is kept on in the senesced leaves, while the remaining nitrogen is retranslocated, even to the stem. The senescence of the leaf biomass is defined as the ratio between the senescence of the leaf area and the total green LAI according to the time-span treated (Zheng et al. 2015).

In **CropSyst**, the LAI depends on the biomass accumulation. The LAI is obtained through the multiplication of the specific leaf area with the accumulated aboveground biomass and dividing all by the partition coefficient which control the part of biomass allocated to the leaves multiplied by the accumulated aboveground biomass. The LAI changes with changing biomass production per day. The LAI production finishes with the end of the vegetative period. Once a given daily LAI part concludes its period, which is given in TT, then it is eliminated from the actual LAI by simulating senescence (Stöckle et al. 2003). CropSyst, on the contrary to the other crop models, considers a constant specific leaf area for the whole growing season (Confalonieri et al. 2009). Moreover, CropSyst contemplates actual leaf biomass production, the standing leaf biomass, and the partitioning coefficient describing the biomass produced to leaves and stem for computing the actual green area index (Castañeda-Vera et al. 2015).

4.3.3 Other crop organs growth rate

In **ORYZA2000**, the crop organs weight is “diluted” once seeds are transplanted in the field with a lower density compared to the seedbed. In the model, this dilution parameter is considered for the first day only. Then, the crop organs growth rate is computed. The roots are the first organ receiving the dry matter which is ready to be used for the initiation of growth. Here, the weight reduction due to transplanting is considered. Leaves, stems and storage organs compose the shoot fraction. Even for stems and green leaves, the weight reduction is examined. The net growth rate of leaves and of structural stem material and the growth rate of the stem reserves are scrutinized by the crop model. All dry matter partitioned to the storage organs is assumed to move to the grains just before flowering. In ORYZA2000 it is possible to estimate grain and spikelet formation rate. For the spikelet, the fertility is calculated based on the temperature that is measured around flowering (Bouman et al. 2001). When the grain is being filled, the production of carbohydrates in grain crops can result higher compared to the grain storage capacity. The storage capacity is established by the grain number counted in one m² and by the maximal grain growth rate. As a consequence, assimilates can concentrate in the leaves and due to a feedback mechanism, the CO₂ assimilation rates can decrease (Barnett and Pearce 1983). When grown

in an extreme environment, this characteristic can be relevant since too low or too high temperatures before flowering can lead to spikelet sterility and also to a low sink capacity (Yoshida 1981). The spike's size of wheat during the flowering phase is proportional to the grain number that have been generated. Moreover, the size of the spike is strictly related to crop growth until the spike formation. The amount of crop growth during this interval is defined by how long this period lasts and by the growth rate of the crop. The length of the period is altered by environmental factors such as temperature, while the growth rate of the crop is affected by temperature and radiation (Fischer 1985). Rice has similar relationships (Yoshida and Parao 1976). The total crop growth measured within the time span from the initiation of the panicle until the beginning of flowering and the number of spikelets during flowering are in a relationship under some conditions: dry and wet seasons with the level of N treatment up to 285 kg ha⁻¹, for planting densities between 25 and 125 plants m⁻², and for severe stress due to drought. Analogously, it happens at tiller level: every single tiller growth throughout the panicle development can explain the number of spikelets per tiller. This process is influenced by water on spikelet formation, solar radiation, nitrogen, temperature, and competition. This relationship is called spikelet formation factor. In ORYZA2000 this factor is considered. However, some differences according to varieties can modify the value. Not all the spikelets turn into grains since some are sterile due to too low or too high temperatures (Bouman et al. 2001). Especially during anthesis, high temperatures can damage the pollen if higher than 35°C (Satake and Yoshida 1978). The spikelet sterility is increased by drought stress, particularly during flowering (O'Toole et al. 1984). This process, together with temperature increase, are related and also influence the leaf rolling. The proportion is of 1.6°C increase with every unit of leaf rolling (Turner et al. 1986). ORYZA2000 takes into account this relationship between leaf rolling and temperature in order to reproduce the increased spikelet sterility. The only variety-specific stem growth parameter is the specific green stem area, which depends on the development stage like the leaf growth parameter for the specific leaf area (Bouman et al. 2001).

In **CERES-Wheat**, under normal conditions, more tillers develop at terminal spikelet formation than tillers maturing with heads. According to Ritchie and Otter (1985), this was the most complex part to simulate with wheat growth modelling. Even Ritchie et al. (1998) mentioned the complexity of the simulation of tiller leaf area expansion and tillering for CERES-Wheat due to the vast spatial variability in field crop tiller numbers and area. Nevertheless, the error is not so great for yield or grain number since the number of tillers expanding stems is regulated by a source-sink equilibrium. Therefore, when tiller number prediction is high, tiller size is low and vice-versa. During the terminal spikelet until the end of the leaf growth, when stems are expanding, tiller loss happens. The model computes the potential growth rate of a stem according to a genetic-specific characteristic able to recognise wheat stem growth trends. The distributed biomass for stem growth for one plant on a specific day is divided by the biomass necessary per single stem in order to define how many stems are able to extend with the accessible assimilates (Ritchie and Otter 1985).

In **CROPSIM-Wheat**, the emergence of 2.5 leaves on the principal stem is required for tillering to start. However, this value can change since it is species dependent. Afterwards, tillers are produced on each axis at a specific rate according to the species and if assimilates are available in the reserve pool. After the last leaf stage, tillering stops. During the terminal spikelet stage, tiller senescence can start. The number of dying tillers depends on the average amount of assimilates that is accessible per stem and on the specific critical assimilate amount for the cultivar. A part of the dry matter belonging to the dead tillers turns back to the reserve pool and a part of the N returns to the stem. Leaf area as well as the leaf and stem weight belonging to the senesced tiller are subtracted from the living sum of the crop. Stem expansion is not reproduced by the model. However, stem and spike are evaluated by the stem dry weight. The stem and spike dry matter accumulation are calculated from the stem as the total above-ground dry matter increment ratio. After the last leaf expansion is completed, all assimilates move to the stem until it stops growing (Hunt and Pararaiasingham 1995).

4.4 Partitioning

4.4.1 Biomass and dry matter partitioning

In **ORYZA2000**, shoots and roots divide, based on partitioning coefficients, the dry matter supplied by the crop. The phenological development stage defines the partitioning coefficients. The effect of drought on the partitioning of assimilates is estimated by **ORYZA1** from the leaf expansion factor (Bouman et al. 2001). Under water-stress, leaves do not expand anymore but the photosynthesis continues. Therefore, carbohydrate availability rises privileging the growth of the roots against the shoot biomass (van Keulen and Seligman 1987; O'Toole and Moya 1981). Dry matter destined to the shoot is divided among other plant organs such as leaves, stems, and storage organs. Sink limitations to grain filling appear when the daily growth rate of grains drives to higher total grain weight than the maximum total grain weight. The weight increase cannot exceed the maximum total grain weight and so it limits the partitioning coefficient for the storage organs. Stems receive source-determined growth rate surplus belonging to the organs (Bouman et al. 2001). During grain-filling, the carbohydrate production (source) can result to be superior or inferior compared to the grains storage capacity (sink). The grains number and the maximal grains growth rate determine the storage capacity. The total biomass that has been accumulated from the initiation of the panicle until flowering permits to calculate the number of spikelets (Kropff et al. 1994; Bouman and van Laar 2006). Excessive high or excessive low temperatures, which cause spikelet sterility, are adjusted. The assimilates fill the fertile spikelets until reaching the maximal grain weight. If sink assimilation is present, the extra assimilates are used as structural carbohydrates to the stems (Bouman and van Laar 2006). Variety-specific parameters for partitioning are the fraction of total dry matter allocated to the shoot, and the fraction of shoot dry matter allocated to the leaves, panicles, and stems. All of them depends on the development stage. The mass fraction of carbon in leaves, stems, panicles (storage organs), roots and stem reserves are also a variety-specific parameter. Additionally, the portion of carbohydrate that are distributed to the stems and then stored as reserves, the time coefficient regarding losses of the stem reserves, the spikelet growth factor, and the maximum

individual grain weight are variety-specific partitioning parameters. Eventually, the leaf death coefficient depends on the development stage and is a variety-specific growth parameter (Bouman et al. 2001).

In **CERES model**, which considers the three crops, all crops have a period during the early development in which the only aboveground sink are the green leaves. Later, the stem grows and consequently switch to be the principal assimilates sink. In wheat as well as in rice, the elongation of stem internodes takes place after the induction of flowering. In maize, the elongation of the stem starts only at a specific developmental stage independently if floral induction has started. Once stems start elongating internodes, assimilate partitioning varies quickly. The model assumes that leaves expand and that during the same time leaves and stems mass growth are proportional to each other. Therefore, the rate of the leaf growth defines the growth rate of the stem. The proportional relationship among leaf and stem varies in time when the elongation of the stem starts to become a significant portion of the plant and the growth of the leaves is finishing. Stems are the primary organs storing assimilates which are then used during grain filling. Approaching anthesis, the only organ able to store assimilates are the roots. Thus, deposited stem assimilate rates are limited. All this is considered by CERES. Ears or panicles start expanding fast once leaf growth finishes. After floral induction, the part of the crop assigned for reproduction grows with a slow trend. However, the capacity of the sink to receive assimilates is limited, so it can be ignored until the end of the leaf growth. After that, active sinks for assimilates are stem and ear or panicle. Wheat and maize have a joined pre-anthesis ear growth as well as a joined stem growth, while rice has a separated panicle and stem growth. The number of grains available per ear or panicle that will later develop into the mature kernel are supposed to be associated with the growth of ears and stems directly preceding anthesis. Hence, assessing the growth of the stem and the ear or the panicle is relevant during this phase. Sink capacity can limit the growth of the panicle or the ear if the source is enough. Growing reproductive parts have a sink capacity and is computed similarly to the sink capacity of the leaf expansion because it is connected with temperature and depends on relative crop size, water and N deficiencies (Ritchie et al. 1998).

IXIM completely replaced the code used for simulating partitioning in CSM-CERES. Before the crop starts flowering, growth partitioning distributes biomass to sole leaf blades and ear structure. For IXIM, only leaf blades are recognized as leaf whereas stem tissue contains leaf sheaths and tassel. Before the initiation of the tassel can start, root tissue receives one-third of what has been accumulated daily as plant biomass. The proportion is reduced linearly in time until reaching the point in which the grain starts to be filled: this is when the growth of the roots end, and the grain is the principal sink for assimilates. Both leaves and stems use the dry mass until the start of the ear growth. For the growth of each leaf the assimilate demand is assessed, while stems receive the remaining dry mass. New leaf tissue biomass requirement is computed dividing the expansion rate of the leaf with the specific leaf area. The specific leaf area is predicted daily and for each leaf the effect of the mean air temperature, the light intensity, and the position of the leaves in the canopy is considered. Therefore, carbon partitioning is

different between leaf and stem. If the shoot growth is limited due to daily carbon assimilation, then leaf dry matter growth is consequently restricted by the available carbon supply. Hence, the specific leaf area is computed again, through the division of the updated version of the leaf surface by the leaf weight. Daily assimilate partitioning is altered if there are soil water and nitrogen stress conditions, in which case roots receive a larger portion of carbon compared to the shoot. Shoot partitioning can be diminished by up to 50% if stress conditions are extreme (Lizaso et al. 2011).

In **APSIM-Maize**, the daily biomass production is partitioned in various proportions depending on the plant organs and the crop stage. The root/shoot ratio is 1 until the end of the juvenile phase and decreases with flowering. Once leaves appear, the biomass produced for the leaves rises exponentially between emergence and flag leaf appearance (APSIM 2020; Soufizadeh et al. 2018). In general, extreme weather combination such as high radiation and low temperature affects the allocation to various plant parts and also the leaf growth. For instance, the re-translocation of the biomass into new leaves can diminish during days in which the radiation is high and temperature is low due to the fact that the expansion of the leaf is more influenced than the production of the assimilates (Soufizadeh et al. 2018). The remaining biomass after its distribution in the leaves goes between stem and the developing ear, during the period between the floral initiation and the appearance of the flag leaf. The biomass is then subdivided among ear and stem until the grain starts to be filled, once the leaf growth terminates at flag leaf appearance. Thereafter, only grain partitioning is shown. The total re-translocation to the grain of the maize module is no more than 15% of leaf and 20% of stem biomass which is already accessible when the grain starts to be filled (APSIM 2020; Soufizadeh et al. 2018).

In **CROPSIM-Wheat**, the dry matter is mainly used for the aboveground growth, and roots collect accumulated surplus in an assimilate reserve. Aboveground organs can use only a specific amount of assimilates and once reached the maximal value, the surplus is given to the roots. In this manner, roots always are ensured to receive some assimilates. This depends on the developmental stage and is an input value. An assimilate pool regulates possible fluctuations within root and canopy growth (Hunt and Pararaiasingham 1995).

In **APSIM-Wheat**, wheat is composed of four parts, namely root, head, leaf and stem. This is derived from a more generic plant module, so that some components are not used. In fact, leaf applies only to leaf blades, while the stem is mainly considered as functional rather than morphological and includes only the plant stem and the leaf sheaths. The head is composed of grain and pod (spike without grain), while the grain is divided into meal and oil (the latter is not considered in APSIM-Wheat). The biomass in all the plant components mentioned is initiated on the day of emergence. The daily production of the biomass is subdivided according to diverse plant components as well as into diverse proportions adapted to the crop stage. Root biomass is computed by the ratio of shoot from the aboveground biomass to the root. Thereafter, aboveground biomass is divided into the various part of the plants according to a hierarchy (first head, then leaf and finally stem). Hence, if biomass production is limited, not all the

components can be satisfied based on their demand. The biomass separated into pod and grain is considered structural and also is not possible to re-translocate it. In general, the non-structural biomass can be used for re-translocation. The non-structural biomass belonging to the pod can be re-translocated into the grain. The biomass in the roots (which is independent of microclimatic factors within the soil) and in the leaves is defined as structural. If there is any available remaining biomass, this is partitioned into the stem. In the beginning, 65% of the biomass is structural, and the rest is non-structural. After reaching this percentage, none of the stem biomass is structural. Re-translocation occurs when there is a shortfall and the grain demand is higher than the daily assimilate supply. The re-translocation starts from the non-structural stem biomass of up 20% of its daily biomass. If necessary, the non-structural biomass of the pod can be used for grains demand (Zheng et al. 2015).

The accumulation of the dry matter in **APSIM-Nwheat** is caused by the potential accumulation per kernel. The potential kernel growth rate is reduced with extremely high temperature. In the model, the grain filling dry matter supply is provided by the photosynthesis and by the re-allocation of dry matter stored previously. When the grain is being filled, the photosynthesis depends on weather conditions and LAI. The latter depends on environmental effects such as nitrogen supply and water. The model does not consider the temperature of the canopy (Asseng et al. 2011). When transpiring for evaporative cooling, the temperature of the canopy can be colder than the temperature of the air (Kumar and Tripathi 1991). On the other hand, when there is no water available in the soil, the temperature of the canopy can reach higher values than the temperature of the air (Turner and Kramer 1980). Therefore, this omission could lead to an over- or underestimation of the influence of temperature on crop processes. Various processes such as senescence, leaf area, growth, rooting depth elongation, photosynthesis, and phenology are influenced by the air temperature. High temperatures in the model lead to an increment in the rate of the grain filling over the day. However, the final weight of the kernel is reduced since the grain filling duration is shorter. First, in the model the temperature alters the growth of the leaf area, which is lowered when the temperature is below 11°C and above 24°C. Second, the photosynthesis is reduced with mean temperatures below 17°C and above 19°C. Third, with a temperature higher than 34°C, senescence is accelerated. In relation to the photosynthesis, peduncle, leaf sheath and spike are recognized as green LAI by the model (Asseng et al. 2011).

4.4.2 Grain yield and its components – kernel number and kernel weight

In **CERES-Maize**, the growth of the cob starts during silking with an initial amount of biomass fixed to 17% of the total stem biomass. The growth of the cob stops when effective grain filling starts. The daily rate for filling the grain is obtained by the potential rate as well as of the efficiency in filling the grain. The latter is dependent on the temperature, but not on the density of the plants. Consequently, when reproducing the individual grain weight, the value results to be constant across broad variations in plant density. Normally, the grain weight of only one grain for cereal crops is an inverse function and reduces when plant density rises, especially if under high plant population (Yang et al. 2004).

In maize, the yield has a strong relationship with the number of the kernel obtained per unit area (Ritchie and Alagarswamy 2003). The kernel number per plant is obtained from GxE since it considers G2, which is the genetic coefficient for the maximum kernel number per plant under optimal conditions (Du Toit and Prinsloo 2000; Ritchie and Wei 2000). Defining kernel number per plant and its genetic differences are essential for accurately simulating yield. However, it proves to be one of the least accurate elements in modelling yield (Ritchie and Alagarswamy 2003). Ritchie and Alagarswamy (2003) modified CERES-Maize 3.5 in order to predict kernel number per plant. They accounted for a critical window of 327 degree days for number of kernels per plant, which consists of 227 degree days before and 100 degree days after silking with a base temperature of 8°C as demonstrated by Otegui and Bonhomme (1998). The kernel number set per plant is curvilinearly connected with the cumulative IPAR during the critical window. Ritchie and Alagarswamy (2003) adjusted the equation for grains per plant. Genetic differences are reported between the maximum kernel number of apical ear (KN₁) and the production of kernels on the second ear (KN₂). In order to simulate KN₁, two genetic coefficients are used. One is G_k, namely the potential kernels per plant. Its definition is almost the same to the G2 of the original CERES-Maize, but in this adaptation of the model it is related to KN₁ only. The other coefficient, G_e, describes the efficiency of the nonlinear setting of the kernel per unit of cumulative IPAR. KN₂ is computed by adopting a threshold of 64 MJ and considering G_k, G_e, and G_p (prolificacy coefficient). Therefore, with KN₂ is possible to estimate the prolificacy of the crop since at an IPAR of 64 MJ, apical ears produce the maximum kernel number per plant. Additionally, a secondary ear can be produced with higher values of IPAR (Ritchie and Alagarswamy 2003). Du Toit and Prinsloo (2000) reported that the grain yield of the secondary ear can account for more than 50% of the total yield. At an IPAR below 11 MJ, all crops are barren. Barrenness is more common when plant density is over 10 plants m⁻², but also various other factors such as small variations in the space between the plants, missing plants within a row, diversities in leaf orientations among rows as well as during the emergence of the seeds can generate differences in the interception of the radiation for single crops within a canopy, causing diversities in kernel number per plant. In the revision of the model, barrenness takes place when the cumulative IPAR is below 11 MJ and is simulated by using G_b, which is the genetic coefficient considering differences between hybrids in tolerating plant densities without barrenness. Eventually, yield could be reproduced relatively well compared to the original CERES model (Ritchie and Alagarswamy 2003).

CERES-Maize reproduces the final grain yield per plant from the number of kernels that have been generated by each plant and the potential rate of the kernel growth. The number of the kernel per plant depends on the rate of the photosynthesis when the grain starts to be filled. The model estimates the daily crop growth, which is used to obtain the photosynthetic rate. Instead, the potential rate of the kernel growth is an input coefficient with genotype-specific characteristics. The model predicted yield correctly in various environmental conditions, but the accuracy of grain number predictions was lower since the number of grains generated per plant had a less precise range of variability (Lizaso et al. 2001). Environmental constraints influence differently kernel number and the kernel growth rate, which are the two

principal elements of yield. Environmental stresses influence more kernels number than kernel growth rate, in particular when the stress happens before and/or during the early reproductive phase. For instance, kernel number is sensitive to drought, nitrogen deficiency and flooding (Lizaso and Ritchie 1997; Uhart and Andrade 1995). In order to define an adequate kernel number prediction in different environments as well as the relationship between potential kernels number produced per plant and IPAR, Lizaso et al. (2001) compare two methods: the double-curve and the line-cutoff. The double-curve method explains kernel number based on the mean shoot growth rate around silking time, considering the period between one week before and three weeks after it takes place (Tollenaar et al. 1992). The line-cutoff method sets a maximum potential kernel number per plant within a linear function describing the pre-plant relationship among IPAR (when averaged over 15 days after silking) and kernel number (Kiniry and Kniewel 1995). Both approaches are incorporated in the CERES-Maize version 3.1. The original CERES-Maize has six genetic coefficients, of which half of them describe the plant development (P1, P2, and P5), two are used to reproduce grain yield (potential kernel number G2 and kernel growth rate G3), and one controls the leaf appearance rate (also called phyllochron interval, PHINT). In order to incorporate the two methods into CERES-Maize, G2 changed definition, i.e. potential kernel number per ear instead of per plant. G5 is the potential number of kernels per plant in prolific genotypes. When cultivars have G2 smaller than 710 kernels per ear, they create a second ear. So, the model code considers the possible second ear according to G2-values. Consequently, it is possible to control the maximum number of kernels that can develop in each ear, the threshold of the IPAR at which kernels are set on each ear, and the efficiency of the kernel set. Eventually, the double-curve method resulted to predict kernel numbers better than the original version, which forecasts kernel number depending on the average rate per plant of the photosynthesis during the grain filling lag phase, as well as the line-cutoff method integrated into the model (Lizaso et al. 2001). However, Lizaso et al. (2003b) found that the double-curve method suggested by Lizaso et al. (2001) overestimates the IPAR, while the curvilinear model is more accurate. Therefore, Lizaso et al. (2003b) attempt to predict IPAR around silking taking into consideration relevant components of IPAR namely the LAI, the light extinction coefficient and the PAR but the results were not fully successful.

After Lizaso et al. (2001) demonstrated that models with a curvilinear trend are more precise for forecasting the number of the kernel per plant than models with a linear trends and with different range of IPAR values, it has been shown that obtaining the right amount of assimilates produced close to flowering is critical in defining the set kernel numbers of maize (Lizaso et al. 2007; Lizaso et al. 2001). It is expected that kernel set is always source limited. Here, crops produce excessively fertilized ovaries and the actual assimilate flow defines how many of them have the possibility to continue the development. Under critical circumstances, such as limited supply of the pollen and stress factors blocking the anthesis-silking synchrony, a small number of fertilized ovaries is still produced. Hence, kernel set evolves into sink limited as described by Lizaso et al. (2003c). CERES-Maize simulates the number of the kernel taking into account its limitation to the source per plant and later modifying the value with stress factors.

Sink limited kernel set is not directly considered. Therefore, Lizaso et al. (2007) developed an algorithm for estimating kernel set in maize under sink-limited conditions contemplating quantitative interactions of flowering dynamics among male and female flowers as described by Westgate et al. (2003). This algorithm is added into CERES-Maize in order to reproduce source- and sink limited conditions for the kernel set. A double curve for apical and subapical ears simulated the source limited process where the number of kernels is computed based on the average light captured by the plant around flowering (-250 to +100 GDD after silking). Reproduced field mechanisms of pollen release and silk exertion are used to predict sink limited kernel numbers. The model can compute kernel set for both situation-limited conditions and choose the more extreme case in order to determine final number of kernels per plant. Prolificacy and/or barrenness are obtained by the average IPAR during the same time span. The proposed model gives a better range of variability for the processes regulating kernel set. The only limitation is that the simulation of female and male inbreds regarding growth and development is not separated (Lizaso et al. 2007). Lastly, James et al. (2011) tried to evaluate kernel number and yield by using CERES-Maize introducing four kernel number equations. The equations were incorporated in CERES-Maize version 3.51. However, none of the proposed equations resulted competent in simulating kernel number throughout plant population, location, and hybrids for irrigation or dryland (James et al. 2011).

López-Cedrón et al. (2005) compared CERES-4.0 with CERES-Maize-2003 and CERES-3.5. In general, the RUE is used to estimate potential biomass accumulation per plant, which depends on IPAR and plant population. In turn, IPAR depends on LAI and the extinction coefficient of the canopy. In all CERES-Maize models, water, nitrogen deficiencies and temperature can lead to have an actual daily biomass production per plant that is lower compared to the potential one. From emergence to tassel initiation, assimilates are partitioned between roots and leaves. When tassel initiates until silking, the partitioning is between roots, stems, and leaves. When silking is starting, ear growth is calculated. Here, stem and roots can carry on their growth if assimilates are accessible, while biomass accumulation in leaves finishes. Then, the number of grains per plant is estimated by the average plant dry weight growth over the day between silking and when the grain starts to be filled. Once the grain starts to be filled, the grain filling rate over the day is determined through a source-sink reserve operation. The reproductive growth is calculated by multiplying the cultivars' potential growth of the kernel at the most favourable temperature by the relative rate of grain filling if there are enough assimilates. Some dissimilarities are already mentioned in subchapter 4.1.3, while the relative rate of grain fill, the efficiency of conversion of mobilized vegetative dry matter to grain, the grains per plant computation, and the LAI computation are discussed here. The relative rate of grain filling depends on temperature, is calculated daily, and influences the daily kernel growth. In CERES-Maize-2003 and CERES-3.5, eight factors related to temperature corrections are computed every three hours and the relative rate of grain filling is obtained by summing some equations. CERES-4.0 uses 5.5°C, 16.0°C, 39.0°C, and 48.5°C as base, first optimum, second optimum, and maximum temperature respectively for obtaining the relative rate of grain fill. The efficiency of conversion of mobilized vegetative dry matter to grain starts when actual production of

biomass per day per plant is lower than the grain growth rate. Thereafter, only a restricted quantity of vegetative dry weight can be moved from leaves and the stem. In CERES-2003, a decrease of 1.0 g of stem reflects a gain of 0.36 g of grain weight, while in the other two models a decrease of 1.0 g of stem reflects a gain of 1.0 g of grain weight. In CERES-2003, the grain per plant computation is obtained with the daily average biomass accumulation rate during 75% silking to the start of grain filling. Moreover, the potential kernel number per plant coefficient is not considered. In CERES-3.5 and -4.0, the grain per plant is obtained with a different formula in which both the coefficient and the daily average biomass accumulation rate are considered. The LAI in the three models is fundamentally the same as the one in the original version, but CERES-4.0 and -3.5 have slightly different coefficients resulting in a little greater LAI, while in CERES-2003 they are the same as in the original version. According to López-Cedrón et al. (2005), CERES-4.0 results in a better simulation of biomass and grain yield in environment with low temperature than CERES-2003 and -3.5 (López-Cedrón et al. 2005). Indeed, López-Cedrón et al. (2008) used CERES-Maize version 4.0 successfully in order to predict biomass and grain yield when the water availability is restricted by using the Penman-Monteith and Priestley-Taylor equations to determine the potential ET. In CERES-4.0, when anthesis and the effective grain filling are taking place, the average photosynthesis rate is estimated so to define the number of kernels per plant. The average rate of photosynthesis is connected with values of daily biomass accumulation per plant and consequently influenced by the actual soil water stress factor affecting photosynthesis. The rate of the grain growth per day depends on the number of grains per plant, the temperature, the rate of the potential kernel growth per day, and the water stress factor in the soil on photosynthesis. Better biomass and grain yield predictions were obtained by using the Penman-Monteith equation (López-Cedrón et al. 2008).

The main differences between **CSM-CERES-Maize** and **CSM-IXIM** concerning grain yield are due to the computation of the number of kernels. Both models use a source-limited kernel set, but CSM-CERES uses the growth over the day to compute the daily average photosynthesis when the lag phase is taking place after silking. This average is used to produce a linear function to define the number of kernels. While IXIM considers the average growth rate at critical TT interval around silking together with a double curve function in order to obtain the number of kernels in the apical and subapical ears (Yakoub et al. 2017; Lizaso et al. 2011). In **CSM-IXIM**, ear growth begins 250 GDD before silking. How much of the daily mass that is given to the ear depends on the rate of the plant growth over the day, the TT after the ear growth starts and the ear partition parameter. Moreover, it is possible to reproduce a reduction of assimilates partition going to the ear when conditions are unfavourable for the plant. The ear tissue (composed of ovaries, and later kernels after fertilization, cob, rachis and husks) grows until reaching the end of the lag phase, which is defined at 170 GDD after half of the silking process took place. Differently to these tissues, when the grain filling phase is occurring only seeds can grow. If conditions are favourable, excessive assimilates for the sink capacity of the grain are moved into the stem. The number of kernels for one plant is obtained through a curvilinear function representing the

mean shoot growth rate over the day. This is calculated with the same TT interval used for growth of the ear. Kernel number is simulated by two equations considering the number in the uppermost ear (KN1) and the number in the second ear (KN2) if the shoot growth rate is broad as often happens under low population densities. Both equations consider G2, the definition of which differs from the original CERES, being here the potential number of seeds of a specific cultivar on its uppermost ear and is considered a genetic coefficient. Furthermore, barrenness, defined as less than one ear per plant, and prolificacy, which is more than one ear per plant, are simulated as two equations based on shoot growth rate. The threshold of 3.6 g per plant and per day is defined for the shoot growth rate for a second kernel when the kernel set critical period is present (Lizaso et al. 2011).

In **APSIM-Maize**, the grain yield comes from the number and the size of the grain. The number of the grain is obtained from the rate of the average daily growth per plant when tassel initiates and the grains start to be filled, and from the potential number of grains obtainable per ear. The grain demand for carbohydrate is dependent on the number of grains and on the rate of the potential grain growth. The latter is established by potential size reached by the grain and by the time necessary to fill the grain. The current assimilation is the first source of carbohydrate supply to the grain. Carbohydrates first come from the stem and only later from the leaves leading to an acceleration of the leaf senescence process. The excessive assimilates are translocated to the stem, and later to the roots when the daily assimilation is higher than the demand of the grain mass (Soufizadeh et al. 2018).

In **CERES model**, which considers all the crops, the most relevant determinant for crop yield is the grain number per unit area as already mentioned under CERES-Maize (Ritchie and Alagarswamy 2003; Ritchie et al. 1998). The final grain weight and number depend on cultivar variability and plant population (Ritchie et al. 1998; Rinaldi 2004). CERES-Wheat considers proportional stem weight at anthesis and grain number according to Fischer (1985), which established that 30 days before starting the anthesis the number of the kernel and the incident solar radiation are correlated. During this process, the majority of the stem weight is developed (Ritchie et al. 1998; Ritchie and Otter 1985). During the stage of grain filling, the maximal possible kernel growth rate is considered an input parameter. In CERES-Wheat, when temperatures are less than 17°C or when the total kernel sink demand for assimilates is higher than the available assimilates, the kernel growth rate can be lower than the maximum (Ritchie and Otter 1985). CERES-Maize defines grain number by using the photosynthesis average rate per plant during a phase close to silking. For rice, the weight of the panicle is established during the grain filling phase and does not take into account the number of the grains produced before they start to be filled. Then, an approximation of the panicle weight once reached maturity is done in order to establish the number of grains. Crop models computing grain number before starting the grain filling process calculate the kernel filling rate daily, considering a source-sink-reserves operation. The capacity of the sink is computed according to cultivar coefficient and temperature. The cultivar coefficient is the potential growth rate of a single kernel over the day and under optimal temperature. The fraction regarding the temperature has

a vast optimum spectrum so that only an uncommonly high or low temperature reduces the kernel growth rate. Grain filling source is defined as the addition of the production of biomass over the day and the assimilates stored in the stem. Once the minimal stem weight is reached, stored assimilates are exhausted (Ritchie et al. 1998). The grain filling rate is not altered by water and nutrient deficiencies (just indirectly if assimilates are diminishing during the phase); while stresses normally do not influence the partitioning process: the movement of the assimilates due to stresses from storage in the stem into grains is low (Ritchie et al. 1998; Ritchie and Otter 1985). When the yield and the grain weight are reduced as a result of the presence of stress, the underlying mechanism consists on a decrease in assimilates production when the grain is filled. The final yield is established by the number of grains grown per plant, the weight of the individual kernel grain and the number of crops available per unit area. Any adjustment is done under severe stress during grain filling and some kernels are aborted (Ritchie et al. 1998; Ritchie and Otter 1985). However, as stated in the description of CERES-Wheat of Moreno-Sotomayor and Weiss (2004) and to what was reported by Ritchie et al. (1998), wheat grain yield is principally connected with the number of kernels than its weight as mentioned for CERES-Maize (Ritchie and Alagarswamy 2003). CERES-Wheat calculates kernel per plant as the product of stem dry matter during anthesis and is a cultivar specific coefficient. To obtain the kernel number, the kernel per plant is multiplied by plant population. The number of kernels can be diminished when temperature between anthesis and the beginning of grain filling is high, but CERES-Wheat does not consider this reduction. The model hypothesized that every single kernel has a weight of 3.5 mg when the grain starts to be filled independently of the cultivar. During maturity, the mean kernel weight is calculated based on the grain-filling period duration, the cultivar specific kernel filling rate under optimum conditions, temperature, actual assimilates, and assimilate reserves stored in the stems. The site of the reserve stem coincides with all the stem grown after the emergence of the spike is finalized. The multiplication of the number by weight of kernels defines the grain yield (Moreno-Sotomayor and Weiss 2004). Improvement of kernel number and weight calculations have been attempted without significant results (Moreno-Sotomayor and Weiss 2004).

In **APSIM-Wheat**, the stem weight at anthesis determines the number of grains that will grow per plant. The grain demand, or also meal demand, is computed from flowering until the conclusion of grain filling. This is influenced by the daily mean temperature, which pertains to the grain filling rate. Moreover, it is dependent on a nitrogen factor. This latter depends even on CO₂ for leaves. The demand of the grain is however restricted by the maximal size of the grain. The pod demand is computed by the grain demand or by the daily biomass accumulation (Zheng et al. 2015).

APSIM-Nwheat computed the accumulation and remobilization of stored assimilates. Water-soluble carbohydrate and carbon skeletons belonging to amino acids are incorporated in the assimilates. After 50% of the anthesis stage, grain growth begins and finishes after reaching maturity. Grain filling duration depends on temperature. Grain filling duration is a cultivar-specific input parameter. Calculating

the actual rate of the grain filling as the minimum of assimilate demand or supply considers the source and sink limitations. The supply is accounted as a limiting factor for the growth of the grain when it takes place during the maturity phase. The assimilate demand represents the daily grain yield growth rate and is temperature dependent. In the model, grain filling assimilates supply comes from the direct photosynthesis and the remobilization from assimilates that were stored preceding grain filling. During grain filling, photosynthesis is based on weather conditions and green LAI, which in turn depends on environmental effects and phenological stages. When grain growth demand is higher than the supply of the assimilates from the photosynthesis, the extra request can be provided by assimilates that were stored preceding the grain filling phase. Contrarily, when the photosynthesis request during the grain filling is higher than the demand of assimilate accumulation of the grain, extra assimilates are collected in the stem. Kernel weight of the dry matter is 3.5 mg at grain filling (Asseng and van Herwaarden 2003). To obtain the initial weight of the grain per area unit, the set weight is multiplied by the number of kernels per unit area (Asseng and Milroy 2006). Eventually, the number of grains, the grain filling, and the carbohydrate remobilization influence grain yield. The carbohydrate remobilization has the potential to move into grain. This takes place when 75% of biomass accumulation is reached between 150 °C days before and until the initiation of grain filling (Asseng et al. 2011). Similarly to CERES, APSIM-Wheat and APSIM-Nwheat cultivar coefficients related to grain yield are the coefficient of the number of kernels per stem weight when the grain starts to be filled (Grno), the rate of the potential kernel growth (Fillrate), and the potential final dry weight of a single stem excluding grain (stwt) (Asseng and van Herwaarden 2003; Asseng et al. 1998; Asseng et al. 2004; Keating et al. 2001).

In **CROPSIM-Wheat**, the number of grains is defined by the difference among aboveground dry matter when anthesis is finished and the aboveground dry matter at emergence: by doing so, the factor of dry matter is the same as the total aboveground dry weight when anthesis concludes (Hunt and Pararaiasingham 1995). The number of grains and potential growth of a single grain determine potential daily accumulation of the grain dry matter. The potential growth of a single grain is specific for a cultivar and consequently depends on the maximum weight that the grain of the cultivar can reach, the time necessary to fill the grain, and the number of grains per plant. If the temperature reaches values outside the optimum or if available assimilates are scarce, the actual growth is less than the potential (Hunt and Pararaiasingham 1995). CROPSIM-Wheat, like CERES-Wheat, use genotype parameters for grain characteristics such as G1, G2, and G3 (Li et al. 2018; Gbegbelegbe et al. 2017).

Differently from CERES-Wheat, in which aboveground biomass and yield are source and sink limited, in **CropSyst** the yield is obtained from the accumulation of the total biomass during the maturity and from the harvest index (Castañeda-Vera et al. 2015; Stöckle et al. 2003). The latter corresponds to the division between harvestable yield and aboveground biomass. The base harvest index is unstressed and is adapted according to the intensity of water and nitrogen stress and to the sensitivity of the crop to stresses especially when it flowers and the grain is being filled (Stöckle et al. 2003).

4.4.3 Grain protein in wheat

CERES-Wheat (as well as APSIM-Nwheat) nitrogen availability and crop nitrogen demand determine the grain protein concentration. Nitrogen demand is founded on the expansion of the leaf area and consequently regarding the capacity to store nitrogen of the leaf biomass. The model considers source-limited conditions for grain protein deposition. Here, LAI is the main factor for nitrogen available as a source for transfer (Orlando et al. 2017). CERES-Wheat calculates grain protein concentration from dry matter and from the accumulation of nitrogen into the grain. The latter is altered by N uptake by crops and N distribution into the grains. It is supposed that the starch deposition duration rate during grain filling depends mainly on factors related to the grains themselves and are consequently sink-limited (Fischer et al. 1977; Orlando et al. 2017). To the contrary, the protein deposition rate and duration depend on factors external to the grain and are considered source-limited (Jenner, C. F., Ugalde, T. D., Aspinall, D. 1991; Orlando et al. 2017). Nitrogen assimilation is established by the supply of the N from the soil and on the expansion of the leaf area. Therefore, it is defined by the leaf biomass capable of storing nitrogen and relocate it into the grain when the grain filling phase is taking place. Hence, source-limited premise indicates that grain protein accumulation is defined by nitrogen content of the above-ground biomass when the grain is being filled. Under optimal conditions, the nitrogen is moved into the grain. When the grain filling phase is taking place, the model computes the nitrogen of the grain according to the size of the sink. The latter is dependent on accumulated dry matter rate over the day and the number of grains per crop (Orlando et al. 2017). Orlando et al. (2017) proposed a new equation for determining the concentration of the grain proteins in order to improve its simulation but the results did not reach the expected target.

APSIM-Nwheat can simulate grain protein (Asseng and Milroy 2006; Asseng et al. 2002). Daily potential grain growth and grain nitrogen accumulation are obtained according to a single kernel basis. However, the simulation of the actual growth of the grain and also the accumulation of the grain N is computed per unit area through the multiplication of the number of kernels per area by the sole kernel rate. In the model, the grain growth begins together with the start of the linear phase, i.e. when the grain weight increases in a linear way, and finishes together with the maturity phase, i.e. when the grain weight decreases its increment. The model includes the actual rate of accumulation regarding grain dry matter as the minimum demand or the minimum supply (sink or source respectively) according to a time step over the day considering thus source and sink limitations. The demand restricts the growth of the grain when it is in the linear phase, while commonly supply is the limiting factor regarding the growth of the grain when maturing. The basic elements are the dry matter (including several carbon-based compounds such as sucrose and starch) and N. The model does not consider various energy costs necessary for the production of distinct types of tissue and conversions between them. To obtain the total protein concentration, the concentration of grain N is multiplied by a factor of 5.7. The dry matter as well as the N accumulation into the grain define the concentration of grain proteins in the model. Both are stimulated by the supply available and potential kernel accumulation rate. The potential rates of the dry matter

accumulation and the N in the grain come from diverse temperature operations, in which nitrogen relocation to the grain has higher temperature optimum compared to the dry matter. With an average temperature up to 23°C over the day, the potential dry matter accumulation in the grain increases. It is different for the potential nitrogen accumulation rate which continues to rise above the average temperature of 23°C. In APSIM-Nwheat, the dry matter supply used to fill the grains comes from the actual photosynthesis and re-allocation of the accumulated dry matter during the anterior anthesis phase. When the grain is being filled, photosynthesis depends on weather conditions and green LAI. The latter depends on the phenological stage and on environmental effects such as temperature and nitrogen supply. In the model, the nitrogen supply in the grain comes from various organs (roots, stem and leaves). This continues until the N levels in the tissue are lowered to a minimum concentration which is dependent on phenology. The tissue nitrogen derives from the uptake that takes place before and until the end of grain filling and also depends on the soil characteristics of the crop (Asseng and Milroy 2006). In the simulation, the amount of protein in the material that is moved to the grain ranges from 7% to 23%, then dry matter and nitrogen delivery are separated into different operations (Jenner, C. F., Ugalde, T. D., Aspinall, D. 1991). Differently, when the protein concentration is below 7 or above 23%, the relocation into the grain of dry matter or nitrogen is limited to keep the protein content within this spectrum (Asseng et al. 2002).

5 Varietal responses to the environment

5.1 Rice

Rice (*Oryza sativa* L.) is a tropical, annual, short-day C3 grass (Hodges and Doraiswamy 1979). The main climatic factors influencing rice growth and development are day-length and temperature, but even precipitation, solar radiation, and wind are relevant (Vergara 1991; Chang and Oka 1976). Physiological stresses such as diseases, drought, extreme heat, and chilling, strongly determine the growth duration of a variety (Dingkuhn and Kropff 1996). Rice plant life cycle is between 100 and 210 days. The development of the rice plant is based on vegetative phase (from seed germination to panicle initiation), reproductive phase (from panicle initiation to anthesis), and ripening phase (from anthesis or heading to full maturity). During the vegetative phase, the sowing method defines the growth of the seedling, which can vary between 0 to 90 days. Tillers and leaves are then produced. Leaf growth can be affected by environmental conditions (Vergara 1991). The vegetative growth is divided into two phases: the basic vegetative phase (or juvenile phase) and the photoperiod-sensitive phase. Generally, the very young plant is insensitive to photoperiod. The basic vegetative phase length varies between 10 and 63 days. After that, the photoperiod-sensitive phase starts, and floral initiation begins. This phase lasts less than 30 days for photoperiod-insensitive varieties, while more than 31 days for sensitive varieties. Photoperiod-insensitive varieties can flower and ripen during the entire year if irrigation is available. Therefore, based on cultivation plans, insensitive varieties are more flexible and more suitable in multiple cropping systems. Nevertheless, photoperiod-sensitive varieties are advantageous in some environments since they have a long growth period, and floating rice needs 180-200 days after sowing to produce grain when the water diminishes (Yoshida 1981). Short-day plants are photoperiod-sensitive and normally belong to traditional cultivars (Vergara 1991). In general, cultivars belonging to Japonica result to be more responsive to temperature and less to photoperiod compared to Indica cultivars (Fukai 1999). After the vegetative phase is concluded, the reproductive phase can start. In the reproductive phase, beginning once the maximal tiller number is reached, panicle initiation begins. Internode elongation depends on cultivars. Heading can then start, but it may be affected by low temperature. All spikelets on a panicle can complete anthesis within seven days. After that, the ripening phase starts. Once the caryopsis is developed and hard, without any green colour, the grain is mature (Vergara 1991). Every development process has specific temperature preferences and thresholds, also depending on varieties, as reported by Sánchez et al. (2014).

Low temperature leads to anthesis failures, low germination, delayed heading, increased spikelet sterility, stunting, incomplete panicle exertion, changes in leaf colour, increased degenerated spikelets, and increased grain shattering. During panicle initiation and anthesis, low temperature is highly damaging to grain yield (Vergara 1991). However, according to Pereira Da Cruz et al. (2013), the most important limiting factor for rice when under low-temperature is spikelet sterility. Exposure to chilling, which depends on cropping calendars, phenology, and varietal response to chilling, determines the occurrence

of spikelet sterility (Dingkuhn 1995; Dingkuhn et al. 2015). High temperature can reduce tiller production and degenerate the young leaf tips if occurring during the vegetative phase; during the initiation of the panicle and its formation, spikelet numbers can be lowered, while during flowering it leads to spikelet sterility. High temperature can also accelerate grain ripening leading to prematurity. However, low temperature reduces the speed of the translocation of carbohydrates and as well as the respiratory consumption of carbohydrate, contributing to a prolonged ripening phase and therefore generating more filled spikelets (Vergara 1991). Nevertheless, temperature perception of the rice crop can be complex since it is defined by the plant system. Temperature perception relies on the developing organs and their location within the soil-water-canopy-atmosphere continuum respectively. Here, thermal gradients can take place (Yoshimoto et al. 2011; Julia and Dingkuhn 2013). According to Yoshimoto et al. (2011), as a measured variable, panicle temperature gives more precise information than air temperature about daily maximum heat-induced spikelet sterility. Hence, referring to panicle temperature instead of air temperature is more precise in this context (Yoshimoto et al. 2011).

Crop phenology mainly depends on major variables controlling day-length, planting date, plant genetic components, and temperature. According to the situation, moisture and nutrient availability can play a relevant role (Hodges and Doraiswamy 1979). Since rice genotypes are mainly short-day plants, photoperiod and temperature sensitivity play a crucial role in influencing crop duration (Dingkuhn and Miezian 1995). Crop duration is mostly a result of how long the genotype-specific basic vegetative phase lasts when the conditions are optimal, with a temperature range of 20-30°C and photoperiod of less than 12h (Sié et al. 1998a). According to Dingkuhn (1995), the main element determining agroecological and agronomic suitability of rice cultivars is crop duration, which depends on temperature (Dingkuhn 1995). Crop growth duration is necessary to be properly estimated to avoid the sterility of the spikelet caused by extremely low or extremely high temperatures (Sié et al. 1998b). Two principal conditions based on temperature influence crop duration. The first is the delay between germination and appearance of the first two to five leaves due to the low temperature of the water when the early vegetative growth phase is occurring. The second is the length of the panicle induction phase, that is defined by water temperature and photoperiod (Sié et al. 1998a). The meristem is exposed to a temperature which is determinant for crop development (Ritchie 1993). For rainfed lowland rice, the duration of the growth is the most relevant trait that makes a distinction among cultivars and their acclimatization to various growing conditions. Most rainfed lowland rice cultivars are sensitive to photoperiod, while it is rare to have photoperiod-insensitive cultivars (Mackill et al. 1996). Flowering time defines final crop growth duration (Yoshida 1981). Flowering time is often referred for characterizing a genotype's phenology due to the constant patterns between flowering and maturity in the rainfed lowland, since reproductive and ripening phases are supposed to be invariable within genotype in a specific environment. Flowering time depends on many factors such as the use of old seedling for transplanting, drought, and low soil fertility (Fukai 1999). Developmental phases are delayed when drought appears while the rainfed rice is germinating or flowering (Wopereis et al. 1996). However, this influences the ripening phase which is accelerated

(Dingkuhn and Le Gal 1996). Drought, low soil fertility, and old seedling can influence flowering time together with phenology, which mainly depends on the water environment. The latter is highly variable. The temperature has a lower influence in determining flowering time than photoperiod for rainfed lowland rice in many areas. Altogether, it makes the system of rainfed lowland rice more complex than irrigated rice (Fukai 1999).

Temperature determines rice phenology in irrigated flooded systems since nutrient resources and stress factors and are mainly under control. However, photoperiod can influence the date of flowering regarding the more susceptible cultivars (Craufurd et al. 2003). Physiological component traits of phenology such as temperature (base, optimal and maximal temperature for development), the duration of specific temperature conditions during the basic vegetative and reproductive phase, and components traits for responses to photoperiod (such as the strength of the day-length effect and the critical day-length parameters) diverge genetically between species (Dingkuhn et al. 1995). Irrigated rice is sensitive to extreme temperatures, which lead to spikelet sterility and consequently to yield losses. Air temperature and organ temperature can differ, complicating sterility prediction. Under heat stress, sterility is strongly affected due to the effects of humidity on transpiration cooling. In irrigated rice, the meristem is exposed to a temperature that corresponds to water temperature for most of the time (Sié et al. 1998b). Dingkuhn et al. (1995) report similar information, namely that relevant for rice crop is the meristem temperature. Until the booting stage, water temperature is determinant for the meristem (Dingkuhn et al. 1995). Booting stage is defined as the completion of panicles growth and development as well as of its elements inside the flag leaf sheath (the boot) (Dunand and Saichuk 2014). Once the booting stage started, the meristem is raised over the surface of the water due to the elongation of the internodes. The period in which the meristem is submerged is around 75-85% of the duration from sowing to the half of flowering. The physiological temperature at the meristem is influenced by daily temperature, meristem submergence, and water temperature. Mean water temperature is especially influenced by high LAI and by dry days, which results to be below to air temperature (Dingkuhn et al. 1995). The heat requirement of irrigated rice can vary depending on photoperiodism and transplanting shock. Consequently, crop duration is influenced, particularly at low temperature. Base temperature, optimum temperature, genotype-specific number of heat units (accumulated mean daily temperature), basic vegetative phase and the photoperiodic slope constant are varietal constants that define thermal and photoperiodic responses of flowering (Dingkuhn et al. 1995). Sié et al. (1998b) reported that crop duration variability depends mainly on the thermal delay of germination, on early leaf generation appearance, and on the photothermal delay of floral induction during the inductive period. However, the main determinant for duration variability is temperature and not photoperiodism (Sié et al. 1998b). Therefore, microclimate and organ temperature should be considered in order to predict sterility losses due to high temperature (Julia and Dingkuhn 2013).

During various development phases and growth stages, yield components develop defining the final yield. The number of tillers that are generated when the vegetative growth takes place, the panicles number formed during the end of the vegetative phase, the spikelets number created in every panicle when the panicle develops, the fertile spikelets number defined during flowering and the final grain weight reached once the grain filling phase ends define the yield potential (Dingkuhn and Kropff 1996). Therefore, phenological development is one of the main processes driving partitioning. Crop duration establishes the number of daily increments available in order to produce various organs gradually, and also defines the source and sink potential, which changes in time (Dingkuhn and Kropff 1996). The individual spikelet's sink potential changes depending on genotype. However, it is a stable varietal character since grain size is controlled by hull size (Yoshida 1981). Nevertheless, climatic conditions define all yield components during their developmental phases. Consequently, interactions between genotype, environment and management practices determine final yield (Messina et al. 2009). Hence, G×E defines varietal performance if management is the same (Dingkuhn et al. 2006). For upland rice, it has been demonstrated that sowing date, location, year and genotype strongly alter the duration of the crop, grain yield and its components (grain weight, grains per panicle, panicles per tillers, tillers per hill, and sterility). Individual yield components change according to environmental conditions during development stages influencing final yield more strongly than the genetic regulation of the individual components of the yield (Shrestha et al. 2012). However, crop duration varies according to altitude. Year, sowing date, and genotype selection at high altitude affect crop duration of upland rice in the same pattern. Differently, at mid altitude crop duration is not influenced by genotype, while at low altitude is mainly altered by sowing date. Low temperature at high altitudes has repercussions on grain yield. About 70% of variation regarding spikelet sterility is due to genotype at high altitude, while at mid and low altitude environment is responsible for more than 70% of this variation (Shrestha et al. 2013).

5.2 Maize

Maize (*Zea mays* L.) is a tropical, warm season, short-day C4 cereal grass (Hodges and Doraiswamy 1979). Under favourable conditions, cultivars have a life cycle of 120 to 135 days (Steduto et al. 2012). A single meristem produces the primary axis of the maize shoot. The meristem then generates internodes, leaf, prophyll and bud. The meristem produces vegetative phytomers before seedling maturity (5-6 phytomers) and after germination (10-20 phytomers) until tassel production (Poethig 1994). Shape and size of juvenile and adult leaves is different (Freeling and Lane 1994). Tassel, i.e. the male inflorescence, is generated from the meristem. Later, the tassel develops spikelets. The ear, i.e. the female inflorescence, is the terminal inflorescence and comes from the axillary bud apices (Cheng and Pareddy 1994; Poethig 1994). The shoot growth lasts 3-4 weeks under normal field conditions. At this point, internodes grow, and leaves are produced (Poethig 1994). Maize growth and development stages are divided into vegetative and reproductive. The vegetative stage starts with emergence and finishes once the tassel has developed. The number of vegetative stages depends on the number of leaf collars. The

reproductive stage is composed of six phases starting at silking and concluding with physiological maturity (Nleya et al. 2016).

Temperature is the main factor influencing the corn growth rate (Nleya et al. 2016). Temperature influences the plant dry weight as well as the leaf area and consequently silage and grain yield (Hardacre and Turnbull 1986; Wijewardana et al. 2016; Freeling and Lane 1994). In general, grain yield decreases with high and low temperature or drought (Sánchez et al. 2014). High-temperature stress affects the reproductive stage of maize, especially before and during anthesis, resulting in increased anthesis silking interval and reduced seed setting. The high temperature restricts photosynthesis and pollination because of the desiccation of the silk and the abortion of the pollen. Once leaves reach a temperature above 38°C, photosynthesis is inhibited (Sánchez et al. 2014; Crafts-Brandner and Salvucci 2002). Corn can be planted early in the season in order to adapt corn yield to varying environmental conditions and to prevent drought or excessive heat during the grain filling period (Lauer et al. 1999). During the day, the optimum temperature for maize ranges between 22°C and 32°C (Crafts-Brandner and Salvucci 2002). Below 5°C and above 32°C, the plant is negatively affected (Naveed et al. 2014). Cold temperature can damage the corn depending on the hybrid (Wijewardana et al. 2016). Low temperature diminishes leaf initiation rate and can lead to a reduction of total leaf number (Poethig 1994). Despite this, maize is tolerant to mild frost when the meristem is still underground and before flowering starts (Hodges and Doraiswamy 1979). Nevertheless, as reported for rice, temperature tolerance and preference vary according to the development phase and process (Sánchez et al. 2014).

However, not only the temperature but also the photoperiod influence the vegetative and reproductive development of the shoot. Photoperiod can influence leaf number (Poethig 1994) and, together with temperature, affect the rhythm of development events in maize, namely from sowing until tassel initiation. The sensitivity to these two factors depends on genetic differences (Ellis et al. 1992). Even water stress influences maize, stopping leaf elongation. In case of severe stress, the stomata close causing an increment in leaf temperature compared to air temperature leading to a hastened or delayed development. Moreover, short stress periods during floral initiation and anthesis can lead to yield loss (Hodges and Doraiswamy 1979).

5.3 Wheat

Wheat (*Triticum aestivum* L.) is a cool-season, long-day C3 cereal grass (Hodges and Doraiswamy 1979). Spring wheat is sown in autumn or spring, while winter wheat only in autumn. Winter wheat needs vernalization, namely a cold period when the early growth occurs in order to head under long days. Differently, spring wheat does not need chilling to develop the head. Spring wheat sown in spring has a total growing period between 100 and 170 days, while winter wheat ranges from 180 to 300 days (Steduto et al. 2012). Three main development phases are recognised in wheat. The first is the vegetative phase, in which leaves are initiated. After germination, the shoot apex has a shape of a dome for a period length that depends on GxE. Primarily, tiller growth begins with the appearance of the fourth leaf.

Thereafter, the reproductive phase starts. Leaf initiation stops and floral and spikelet initiation commence. Eventually, the grain filling phase starts (Miralles and Slafer 1999).

Day-length and temperature are relevant aspects when selecting cultivars. As mentioned before, wheat cultivars are defined as winter or as spring types depending on their sensitivity to day-length, chilling requirements, and winter hardiness. However, some winter and spring cultivars are photoperiod sensitive, even if crop development depends above all on temperature (Steduto et al. 2012). From sowing to seedling emergence and from anthesis to maturity, the plant is insensitive to photoperiod and vernalization, while temperature influences all the cultivars during all the phases (Miralles and Slafer 1999). For the growth of spring and winter wheat, 5°C are required as minimum mean daily temperature, while the optimum ranges between 15°C and 23°C. The requirements for vernalization and the sensitivity to photoperiod change among cultivars and can shift the tillering phase duration (Steduto et al. 2012). Temperature is the main influencing factor for leaf primordia initiation and leaf appearance. Even spikelet primordia are susceptible to temperature (Miralles and Slafer 1999). According to the process, the minimum, optimum and maximum temperature of wheat varies as reported by Sánchez et al. (2014) and Porter and Gawith (1999). The grain filling process can be halted by severe water stress and heat shock (Miralles and Slafer 1999). High temperature significantly reduces the dry weight of the kernel at maturity (Wardlaw and Moncur 1995). Indeed, grain-set, size of the grain and milling yield can decrease if excessive temperatures prevail when the post-anthesis period is occurring (Nuttall et al. 2017). The importance of the loss depends on the cultivars, with a loss in kernel dry weight ranging between 30% and 60% (Wardlaw and Moncur 1995). How long each phase lasts can be influenced by a change in sowing date or location. Even if photoperiod and temperature are the main components changing the development of the plant, nutrition, water availability, plant density, radiation, and CO₂ concentration can influence the crop but with a smaller effect (Miralles and Slafer 1999). However, an high level of CO₂ increases wheat yields up to 36% but consequently grain protein concentration diminishes reducing their functional properties (Nuttall et al. 2017).

Rainfed wheat, which is sown from October to December, is altered by high-temperature stress at germination, weed infestation, and the risk of lacking the appropriate grain moisture when sown too early. When sown too late, wheat can be injured by chilling, be exposed to less solar radiation or to temperatures that are too high and low moisture during reproductive development (Cao and Moss 1994). Temperature and solar radiation have a considerable impact on crop performance, especially temperature in terms of the dynamics of leaf appearance and phenophase duration. However, the response to environment changes dependent on the variety (Ahmed and Farooq 2013).

Similarly as to what has been reported with irrigated rice (Dingkuhn 1995), it was supposed that soil temperature gives an improved indication of shoot apex TT compared to air temperature until the elongation of the internode increases the apex above the soil surface (McMaster and Wilhelm 1998).

However, McMaster and Wilhelm (1998) demonstrated that the temperature of the soil does not enhance the prediction of winter wheat phenology and that air temperature is a reliable source for wheat phenology.

Grain protein concentration is altered by various environmental factors (van Herwaarden et al. 1998). The definition of the concentration of the grain protein corresponds to the grain N/grain yield ratio. Grain yield, which is based on carbohydrates, is produced from sucrose in the grain originated from the assimilation of CO₂ when the grain is being filled (Rawson and Evans 1971) and also from the transfer of stored soluble carbohydrate in leaves, stems, and spikes (van Herwaarden et al. 1998). Proteins are synthesized from amino acids generated principally from the repurposing of proteins in the vegetative organs like roots, shoots, and leaves, and partially from the actual uptake of nitrogen (Spiertz and Ellen 1978). Grain yield and N content of the grain are affected by mechanisms regarding uptake and plant growth taking place before and after anthesis as well as transfer mechanisms after the anthesis cycle (Flood and Martin 2001). Therefore, grain proteins are affected by any environmental factor affecting these processes. Environmental parameters with a direct influence on the concentration of the grain protein are post-anthesis water availability (van Herwaarden et al. 1998), nitrogen supply (Anderson et al. 1995), light intensity and temperature while the grain filling period is taking place (Spiertz 1977).

6 Discussion

6.1 Crop responses simulation

Photosynthesis is simulated by all the models with some small differences. The biomass and dry matter production is obtained by multiplying the RUE by the IPAR in most of the simulation models (Asseng et al. 2011; Bouman et al. 2001; Hunt and Pararaiasingham 1995; López-Cedrón et al. 2008; Ritchie et al. 1998; Yang et al. 2004; Zheng et al. 2015; Soufizadeh et al. 2018). However, the calculation of biomass production changes for IXIM and CropSyst. In IXIM, more components regarding assimilation and respiration are considered instead of the PAR (Lizaso et al. 2011). In CropSyst, water availability and the minimum of the radiation and transpiration dependent biomass growth are taken into account. Moreover, it focuses more on the green area index than on the general LAI (Stöckle et al. 2003). CERES-Maize obtained some more attention in successfully improving the biomass simulation by modifying the photosynthesis submodels as reported by Lizaso et al. (2005a). Additionally, various versions of CERES-Maize were compared to each other, including some photosynthetically relevant aspects (López-Cedrón et al. 2005), but it is not clear which version came first. Due to the awareness obtained by CERES-Maize in order to improve the equations and by the different calculation used from IXIM and CropSyst, it is suggested that the biomass production calculation is still an open process in crop modelling, where improvements or adjustments are necessary. However, since it is not reported if the proposed modifications are integrated into the new versions and, more in general, since there is no overview of the crop model versions that have been released, it is not definite if the actual stand of the last released models is accurate enough or if more research is needed. The ET is computed by using Penman-Monteith preferably, otherwise by Priestley-Taylor (Bouman et al. 2001; López-Cedrón et al. 2008; Kang et al. 2009; Hunt and Pararaiasingham 1995; Asseng et al. 2011; Stöckle et al. 2003). Only ORYZA considers even Makkink as a possible alternative for the calculation. However, the most suggested method is Penman-Monteith it since uses more parameters and the result is consequently more accurate (Bouman et al. 2001). Therefore, if it is possible according to the access to weather parameters, Penman-Monteith is the recommended equation for computing ET. The CO₂ assimilation is described just for ORYZA1, ORYZA2000 and CERES-Rice (Bouman et al. 2001; Wikarmpapraharn and Kositsakulchai 2010). There are some differences about this topic between CERES-Rice and ORYZA2000, in which CERES-Rice results to be more sensitive to photosynthesis than ORYZA2000 (Wikarmpapraharn and Kositsakulchai 2010). However, due to the scarce and missing information for the models described, it is hazardous to give a conclusion about which of the mentioned models is better in simulating the CO₂ assimilation. This is valid for the biomass and dry matter production part as well as for the photosynthesis, in which without comparing each model according to their outputs and the statistic is not possible to select the most accurate model. For the photosynthesis, in no model is mentioned that some processes are directly affected by genotype, only ORYZA2000 is reported by Bouman et al. (2001) to use some variety-specific parameters for simulating it. The influence of environment on photosynthesis is considered in every model.

Phenology is a relevant topic in crop model simulation as mentioned by Aggarwal and Mall (2002). Indeed, the topic received lots of awareness compared to the other simulation aspects, with the exception of IXIM, about which no information is available. For phenology, the number of development phases considered depends on the crop model and not on the crop self. In all CERES models, the number of the phenological phases are 9 (Ritchie et al. 1998; Kiniry 1991; Yang et al. 2004; Ritchie and Otter 1985), with exception of CROPSIM-wheat with 8 phases (Hunt and Pararaiasingham 1995). In APSIM models, 11 growing phases are considered (Soufizadeh et al. 2018; Zheng et al. 2015), while in ORYZA 4 (Bouman et al. 2001). Apart from CropSyst, which does not mention any phase, all the other models structured and subdivided the phenological stages according to their calculation system. Temperature is always the main driving factor influencing phenology, but even photoperiod and, in case of wheat, vernalization are essential factors. The TT changes among crops, crop genetics and slightly among crop models (Bouman et al. 2001; Kiniry 1991; Ritchie and Otter 1985; Gbegbelegbe et al. 2017; Zheng et al. 2015). Thermal time depends on environment and genotype (Stöckle et al. 2003; Soltani and Sinclair 2015). The temperature which TT is based on is often proposed as a fixed value by the models as reported in the literature review. However, these values are supposed to be input parameters and they will be considered as aforementioned. Besides CropSyst that does not have a classification for the input parameters (Soltani and Sinclair 2015), in the other models some phases are characterized by cultivar-specific parameters in order to simulate the GxE (Soltani and Sinclair 2015; Gbegbelegbe et al. 2017; Porter et al. 1993; Román-Paoli et al. 2000; Yang et al. 2004; Kiniry 1991). The CERES family uses the same phenological cultivar-specific input parameters for each model with additional parameters for the vernalization of wheat (Ritchie 1991; Kiniry 1991; Román-Paoli et al. 2000; Yang et al. 2004), while APSIM-Wheat and Nwheat use similar parameters as CERES (Asseng and van Herwaarden 2003; Asseng et al. 1998; Asseng et al. 2004; Keating et al. 2001). Even ORYZA2000 has variety-specific development rate constants for each phase but does not clearly mention which ones they are (Bouman et al. 2001). Nowadays, crop models simulating production are faced with the high number of new cultivars introduced. Therefore, the estimation of parameters is essential for each of them. Phenology is one of the main differences between cultivars and many of the principal physiological processes depend on it (Nissanka et al. 2015). Consequently, it is important to simulate phenology accurately since outputs are sensitive to this (van Oort et al. 2011). However, the estimation of phenological parameters with tolerable error margin is complicated in crop modelling (Aggarwal and Mall 2002). Moreover, trials and errors estimation has disadvantages, as mentioned in the introduction (Nissanka et al. 2015). From the results of the literature review, it is suggested that the more parameters are used in one model, the more accurate will be the output. Meanwhile, the complexity of the model increases by adding processes and parameters. As mentioned by Soltani and Sinclair (2015), model complicatedness is based on two aspects. The first is the number of processes that the model can simulate. The more processes, the more intricate is the simulation model. The second point is the number of equations or parameters used by the model in order to reproduce a specific process. The more parameters, the more complex is the model

(Soltani and Sinclair 2015). Furthermore, Ahmed et al. (2013) believe that in order to improve the prediction accuracy, further researches for individualizing more input parameters simulation cofactors are necessary. Consequently, it is proposed that it is possible to achieve better results with a more complicated model. According to these criteria, DSSAT and APSIM families would be more accurate crop models than ORYZA and CropSyst; while ORYZA would be more accurate than CropSyst. However, Stöckle et al. (2003) pointed out that spatial variability in fields is enormous making the evaluation among the simulated outputs with data collected in field trials complex and limited since the performance of models is hard to establish. Moreover, some model outputs are not comparable due to the complexity of obtaining the corresponding measures. There is another problem in evaluating models: model performance is compared statistically with field trial results, but measurement errors and variations in field experiments are often not considered (Stöckle et al. 2003). Therefore, even if the number of parameters used in the models is high, error sources due to the high intricacy of field variabilities can occur leading to imprecise outputs and output comparisons. Due to the differences in GxE interactions such as cultivar-specific input parameters for distinct models and due to some lacking information, a comparison within diverse models regarding phenology is impeded. Moreover, similarly to the photosynthesis section, a comparison of their outputs and related statistic with field trials would better judge which model simulates phenology more accurately. Additionally, the points mentioned above by Stöckle et al. (2003) should be taken into consideration in order to have a more precise comparison of outputs.

As stated for the sections photosynthesis and phenology, missing information about most of the crop models regarding crop growth rate and other crop organ growth rates limit the evaluation and comparison between them. Even leaf-related variables are not easily comparable between models due to the generic or lacking information. However, LAI and senescence are computed by each model. First temperature and then light intensity are often mentioned as the main influencing factors. Environmental stresses such as nitrogen, water, and extreme temperature are generally considered (Ritchie et al. 1998; Bouman et al. 2001; Zheng et al. 2015; Hunt and Pararaiasingham 1995; APSIM 2020; Lizaso et al. 2003a). Nevertheless, only CROPSIM-Wheat is clearly reported to consider extreme shading as a limiting growing factor (Hunt and Pararaiasingham 1995), while ORYZA2000 differentiates among direct-seeded rice and transplanted rice and considers transplanting shock and drought. Consequently, it contemplates leaves rolling effects and different LAI values according to the stress or to planting pattern (Bouman et al. 2001). Nevertheless, not all possible stresses are represented by the models. For instance, APSIM-Wheat does not consider phosphorous stress (Zheng et al. 2015). Often, values under unlimited water and nitrogen situations are used, so that soil properties and initial conditions can influence less the inaccuracy. Indeed, when results do not match, the error can be due to the imprecision of one or more functions. However, this is more often due to inaccurate input data as well as to initial conditions (Basso et al. 2016). In CERES the difficulty of simulating sink-limitations during the vegetative phase and of collecting LAI values is mentioned. There is much variability in fields tiller number and area. Therefore, it is complicated to simulate them (Ritchie et al. 1998). As a matter of facts, APSIM-Wheat does not

consider tillering (Zheng et al. 2015), simplifying the simulation. Nevertheless, CERES-Maize pointed out the relevance of the green leaf area in order to properly simulate crop growth. Green leaves area changes between genotype, but its simulation is a limiting factor: its prediction is not precise and various effects of stresses on expansion and senescence are not considered (Lizaso et al. 2003a). Hence, Lizaso et al. (2003a) introduced a new model, CERES-LA, with 3 new cultivar specific parameters for simulating leaf area. The prediction resulted to be better than in CERES-Maize (Lizaso et al. 2003a). Similarly, IXIM does the calculation as proposed by Lizaso et al. (2003a) for CERES-Maize, with extra modifications and the introduction of 2 additional cultivar specific parameters (Lizaso et al. 2011). So, it is able to simulate the seasonal leaf area (Yakoub et al. 2017). However, even if the prediction of CERES-LA is more precise than the original CERES-Maize model, it is not clear if the simulation has been introduced in the model. If the proposed adjustment is not introduced in a current CERES-Maize version, also IXIM can better forecast leaf area. Since the CERES family considers specific genotype parameters for the leaf growth and efforts are done in improving its simulation (for instance Lizaso et al. (2003a)), this family appears to be more reliable and accurate in simulating maize and wheat leaf-area variables than others crop models. On the other hand, it seems that the topic is still open and further researches are necessary. For rice, ORYZA2000 appears to be a reliable crop model in simulating the growth. CropSyst, which considers a constant specific leaf area for the entire growing season (Confalonieri et al. 2009), is a simplified version for simulating leaf area but is not so accurate like the other models. Like for phenology, it seems that the more cultivar-specific parameters are available, the more accurate is the simulation. This leads to a higher level of complexity of the crop models which require lots of field experiments in order to obtain such values. Moreover, growth and development, as defined by Ritchie et al. (1998) in chapter 4.3, are often considered together without making a distinction between them. This is because the processes are strongly related and considering them in this chapter as single processes was not possible.

Partitioning coefficients between roots and shoots determine biomass allocation in a similar manner in all the models under biomass and dry matter partitioning (for example Bouman et al. (2001)). The coefficients depend on phenological development stages and plant organs part. Extreme weather affects the distribution privileging the root instead of the shoot biomass (for example Bouman et al. (2001)). Regarding grain yield and its components, lots of efforts have been made to improve the grain yield prediction of maize (Ritchie and Alagarswamy 2003; Lizaso et al. 2001; Lizaso et al. 2003b; Lizaso et al. 2007; James et al. 2011; López-Cedrón et al. 2008). Grain yield in maize is strongly connected with the number of kernels per unit area, which is dependent on GxE interactions. Grain yield is established by genetic factors and in crop models like CERES genetic coefficients are necessary for its simulation. Even the environment strongly affects the final grain yield (Ritchie and Alagarswamy 2003; Lizaso et al. 2001). According to Ritchie and Alagarswamy (2003), kernel number is essential for simulating yield accurately but meanwhile it is one of the most inaccurate factors in modelling yield. Ritchie and Alagarswamy (2003), Lizaso et al. (2001), Lizaso et al. (2003b), Lizaso et al. (2007), James et al. (2011),

and López-Cedrón et al. (2008) proposed more adaptations to the CERES-Maize model in order to enhance kernel number simulation. However, it is not definite if some of the proposed improvements have been integrated into the model or into a new version of the model. IXIM mentioned to compute differently kernel number (Lizaso et al. 2011; Yakoub et al. 2017) but it is not clear if its simulation is more accurate than the CERES-Maize model. APSIM models for maize and wheat also consider kernel number, kernel size and the GxE interactions for defining total final yield (Soufizadeh et al. 2018; Asseng et al. 2011; Zheng et al. 2015), while CropSyst uses the total biomass accumulated at physiological maturity and the harvest index for determining yield. The harvest index can be adjusted according to water and nitrogen stress and to crop sensitivity to stress as mentioned by Stöckle et al. (2003). Using the harvest index as an input parameter for defining the final yield is easier than defining kernel number per unit area, which needs various equations and genetic specific parameters. As mentioned by Dingkuhn and Kropff (1996), by using the harvest index, which just represents the final redistribution of source and sink relationships during the growing season, temporal information about the source and sink exchanges is lost. Therefore, using the harvest index instead of considering single components and interactions like in other models simplifies the equations for the final yield assessment but meanwhile the results are more imprecise. Grain protein in wheat is considered by CERES-Wheat and APSIM-Nwheat. In both models, the environment influences it and affects source and sink relationships (Orlando et al. 2017; Asseng et al. 2002). This topic should be described more in depth and linked to nitrogen interaction with plant growth and development, which is not considered in this literature review.

6.2 Varietal responses to the environment

Comparing varietal responses to the environment in field trials with the simulation models, information is based on phenology only (see chapter 5). Regrading rice, Vergara (1991) considers 3 phenological phases with the first stage divided into two, namely vegetative phase (divided into basic vegetative phase or juvenile phase and photoperiod-sensitive phase), reproductive phase, and ripening phase. Analogously, ORYZA2000 counts four phenological phases (Bouman et al. 2001), while CERES-Rice has nine phases not defined here (Wikarmpapraharn and Kositsakulchai 2010). ORYZA2000 simulated development phases and their variability by using variety-specific parameters that are photoperiod and temperature dependent (Bouman et al. 2001). Bouman et al. (2001) reported that most of the crop parameters regarding rice are generic. Therefore, they can be adopted for a wide range of varieties. Some of them are variety as well as environment specific. The parameters are necessary for simulating the fraction of stem reserves, development stages, partitioning factors, specific leaf area, relative leaf growth rate, and leaf death rate. These parameters are obtained by field experiments under potential conditions devoid of any stress factor, limitation or infestation (Bouman et al. 2001). However, as mentioned in the subchapter regarding phenology, these parameters are not clearly defined in Bouman et al. (2001). If their meaning was better explained the quality of the information would be increased and updating them would be easier. In ORYZA2000, various effects due to drought such as leaves rolling are considered. Nevertheless, even if temperature is considered the main influencing factor followed by photoperiod

(Bouman et al. 2001), less crop parameters are contemplated compared to field realities. Vergara (1991) properly explained various effects of high and low temperature on crop development. For instance, Vergara (1991) mentioned leaf discoloration, increased degenerated spikelets, and increased grain shattering due to low temperature, while in ORYZA2000 these are not mentioned (Bouman et al. 2001) and therefore probably not accounted for in any simulation. This can lead to false values regarding the green area index and yield prediction. On the other hand, the mentioned processes would be complex to simulate with crop modelling since they are not only a direct consequence of low temperature only, but also interactions with the microclimate. Moreover, in irrigated rice, air temperature differs from organ temperature, making sterility prediction complicated. More in general, for lowland rice, Yoshimoto et al. (2011) suggested panicle temperature as a more accurate measure for determining heat-induced sterility than air temperature. As reported by Yoshimoto et al. (2011) and Julia and Dingkuhn (2013), temperature perception depends on the organs and their position in the soil-water-canopy-atmosphere. Indeed, Sánchez et al. (2014) reported how each process and development phase has its own variety-dependent optimum temperature range. If a crop model would simulate rice growth and development in the most precise way possible, it should follow the temperature ranges proposed by Sánchez et al. (2014) for each process and development phase and also consider the consequences when the temperature is not within the proposed range. Moreover, for predicting (and maybe possibly preventing) the heat-induced sterility in lowland rice, panicle temperature should be considered and monitored by crop models. Nevertheless, ORYZA2000 takes into account TT (Bouman et al. 2001). Drought, low soil fertility, and old seedling affecting the crop growth duration of rainfed lowland rice (Fukai 1999). Crop duration is dependent on the genotype-specific basic vegetative phase under optimum conditions (Sié et al. 1998a) and defines the agronomic suitability of a crop. Temperature influences crop duration (Julia and Dingkuhn 2013). Indeed, the growth duration of rainfed lowland rice is considered the most relevant trait for distinguishing cultivars and their acclimatization to different growing conditions (Mackill et al. 1996). For irrigated rice, the main determiner for crop duration is the temperature (Sié et al. 1998b). Besides, microclimate and organ temperature are to be considered (Julia and Dingkuhn 2013). Even in upland rice crop duration plays an important role and is affected by genotype selection, sowing date and year (Shrestha et al. 2013). Therefore, considering crop duration in modelling could help to find the right cultivar for a specific place. As reported by Julia and Dingkuhn (2013) and later by Sánchez et al. (2014), focus on the temperature is necessary. Crop simulation models should be able to reproduce organ temperature and also the microclimate in order to improve their predictions. However, the rainfed lowland system is more complicated than irrigated rice (Fukai 1999), since this latter is mainly affected by temperature while stresses and nutrients are mostly under control (Craufurd et al. 2003). Indeed, Li et al. (2017) mentioned that irrigated lowland rice has easier dynamics than rainfed, upland and aerobic rice. Due to the presence of standing water, soil moisture and temperature fluctuate less compared to other systems with higher vulnerability to abiotic stresses and climate (Li et al. 2017). Therefore, Sié et al. (1998b) and Dingkuhn et al. (1995) suggested using the temperature at meristem for irrigated rice until booting,

which corresponds to water temperature. Fukai (1999) even highlighted the dependence of water for the phenology of rainfed lowland rice. These approaches differ from ORYZA2000, which considers air temperature as general weather data for the entire growing period (Bouman et al. 2001). Therefore, water temperature for irrigated and rainfed rice until the beginning of the booting stage should be taken into account instead of using air temperature. After this stage, air temperature is to be considered. Nevertheless, even if what is contemplated by ORYZA2000 is less accurate, the value of air temperature is easier to obtain than the water temperature. Moreover, it is easier to define one single temperature for the entire growing period than determining when the booting phase initiates and adapt the measurement according to it. In ORYZA2000, the system considered is irrigated lowland rice (Bouman et al. 2001; Li et al. 2017), and its parametrisation is mainly based on tropical environments (Shrestha et al. 2013). Hence, the prediction quality of other ecosystems and environments results to be poor (Shrestha et al. 2013). Instead, ORYZA(v3) is able to represent even other production environments such as upland and aerobic rice due to the addition of modules and routines (Li et al. 2017). Thus, in order to increase cropping system variabilities, ORYZA(v3) is recommended since it is a more suitable model for simulating rice in various ecosystems. Additionally, comparisons between the ORYZA family and CERES-Rice are not possible due to the very scarce information about the latter (only in chapters 4.1.1 and 4.2). For the numerous versions of ORYZA mentioned in chapter 3.1, no information has been found for comparison among versions.

In maize, the temperature is reported to be the main factor influencing growth (Nleya et al. 2016). Extreme temperature events and drought negatively influence the crop and consequently reduce the yield (Nleya et al. 2016; Sánchez et al. 2014). Ritchie et al. (1998) also reported the importance of temperature during crop development for CERES models. However, the TT reported in CERES-Maize (Kiniry 1991) differ slightly from the TT reported by Crafts-Brandner and Salvucci (2002). As for rice, Sánchez et al. (2014) proposed an optimum temperature range for each process and development phase. By following these indications, crop models would have a much higher complexity level compared to the use of a single temperature for each process. Nevertheless, its outputs prediction is expected to improve.

For wheat, similarly to maize, temperature is reported to be the main factor affecting every developing phase (Miralles and Slafer 1999), as also highlighted by Ritchie and Otter (1985) for CERES-Wheat. Porter and Gawith (1999) reported optimum temperature ranges for each process of wheat, like later Sánchez et al. (2014) for rice and maize. Nevertheless, in wheat, differently from rice, it has been demonstrated that air temperature is a reliable measure and there is no need to consider soil temperature (McMaster and Wilhelm 1998). Indeed, CROPSIM-Wheat and APSIM-Wheat clearly mention using air temperature (Gbegbelegbe et al. 2017; Zheng et al. 2015). Therefore, air temperature is a good measure to simulate wheat growth and development. However, in order to improve the prediction, the ideal range temperature for each process and development stage should be taken into consideration. As mentioned above, simulating this tendency by using crop models would lead to a higher complexity level but

probably to a more precise prognosis. Photoperiod is relevant but does not influence every phase (Miralles and Slafer 1999). Moreover, depending on cultivar, vernalization and photoperiod sensitivity can change (Steduto et al. 2012). CERES-Wheat, CROPSIM-Wheat, APSIM-Wheat and Nwheat use cultivar-specific parameters in order to simulate phenological development, included vernalization (Ritchie 1991; Gbegbelegbe et al. 2017; Asseng and van Herwaarden 2003; Asseng et al. 1998; Asseng et al. 2004; Keating et al. 2001). Also CropSyst considers vernalization, even if it does not have a parameter classification (Soltani and Sinclair 2015). Hence, crop models seem to simulate vernalization reliably.

6.3 Limitations

The quality of the information given by the websites of the respective crop models is low. ORYZA (IRRI 2020) gives an overview of the various released versions in time and the main differences among them, which is helpful. However, the information given is general and superficial. The book of Bouman et al. (2001) is the only source mentioned that document the model. For the DSSAT family (DSSAT 2020), information is also incomplete and rather superficial. It is not possible to have an overview of the number of existing models and of the main innovative elements of the successively released version. Meanwhile, almost no information is given about a model's functionality and for some models, such as CROPSIM, no information at all is mentioned. The website of the APSIM family (APSIM 2020) is more structured and clearer than the DSSAT and ORYZA websites. On the other hand, finding the information is not always easy or direct. For instance, when searching for information about the crop module documentation, the relative page is not simple to obtain. Moreover, the description quality changes among cultivars. For example, maize is poorly described, while more information is available for wheat. Analogously, CropSyst (Stöckle 2020) has a more structured website but is poor in information quality. In general, all the four websites are inadequately structured, not necessarily visual, not properly communicating with the virtual user, and the information insufficient. Additionally, most of the information is not updated and it is not possible to have an amended overview of the course of each simulation model development. Unfortunately, even papers often do not explain differences between models and model descriptions, leading to a general lack of knowledge and basic information. Sinclair and Seligman (2000) proposed three criteria in order to publish a crop modelling paper. The first point is to clearly define the scientific objective of the model analysis and its relevance; second, the model needs to have a mechanistic framework involved in crop development, growth, and yield; lastly, the model needs to evaluate the scientific innovation proposed using statistical analysis (Sinclair and Seligman 2000). By following these points, the quality of the crop modelling papers would increase. However, these points do not include a complete overview of the model used as well as of the calculation used to obtain the outputs. Additionally to what Sinclair and Seligman (2000) wrote, all models about crop simulation should better specify the version of the model used and the computation followed in order to obtain outputs. It is not clear if suggested adjustments or improvement proposed by some papers are later integrated into the model or in a new released model. This information should be included. Moreover, it is recommended to write a more theoretic paper that just focuses on the various simulation aspects of the crop models

including a timeline development of the model without considering any simulation output. Papers often focus on simulation outputs without considering the general context. This leads to incomplete information with non-reproducible field trials or simulations. For example, from the initial literature research, CERES-Rice was a popular and applied crop model. However, it was not possible to find information regarding the model itself. Therefore, due to the reasons explained above, the method used for choosing the more relevant and actual crop models is not enough in order to obtain a complete overview of the models. It follows that it is important to improve the communication quality of crop modelling papers and websites. Indeed, Stöckle et al. (2003) highlighted the necessity of better communication and exchange of information regarding model development and their applications between various modelling groups. This would contribute to a general benefit and to increased modelling progress (Stöckle et al. 2003).

A further limiting point is the access to various important scientific papers. Papers that are often referred to by other highly regarded papers are not always available. For instance, for CERES-Maize is often mentioned to check the paper “Jones, C.A., Kiniry, J.R., 1986. CERES-Maize: A Simulation Model of Maize Growth and Development. Texas A.M. University Press, College Station”, while for CROPSIM “Hoogenboom, G., J.W. Jones, P.W. Wilkens, C.H. Porter, K.J. Boote, L.A. Hunt et al. 2011. Decision Support System for Agrotechnology Transfer (DSSAT) Version 4.5 [CD-ROM]. Release Version 4.5. Univ. of Hawaii, Honolulu”. Limited access to information leads to a limited comparison potential within models and model functions.

Another crucial point is the language used among crop models, which is not standard. Depending on the paper, it is spoken about “module” as a synonym of “model”. This is the case of APSIM. In chapter 3.2, Asseng et al. (2002), described that APSIM-Wheat is based on the submodel Nwheat. However, the author considers submodel and module as synonyms (Asseng et al. 2002). The use of different terminology between diverse authors and models leads to confusion and misinterpretations. Thus, it is suggested to standardize the terminology used by defining it properly. Moreover, differences between APSIM-Wheat and Nwheat are reported. For example, APSIM-Nwheat has 9 development stages (Keating et al. 2001), while APSIM-Wheat 11 (Zheng et al. 2015). This led to consider APSIM-Wheat and Nwheat as two distinct models for the entire literature review.

In the papers, most of the topics debated under the chapter 4 are summarised and are described grouped together as a unique subject. Consequently, it was complicated to separate some topics from others. For instance, photosynthesis was strongly related to leaf characteristics and partitioning. As a consequence, since separating the subjects according to the chapters was not always feasible, some processes are explained more than once in different subchapters in order to understand the connections with other subjects. Moreover, when the information available is only summarized, the models’ description is general, and many interactions and processes are not illustrated. This contributed to a superficial overview of them. Additionally, some topics are more developed than others or more focused on one crop or model.

For instance, phenology and leaf-related variables generally obtained lots of attention, while grain yield has been widely studied for CERES-Maize. Regarding chapter 5, the focus has been specially given for rice, while maize and wheat are generally poorly described. Thus, the quality and quantity of information varies greatly between subject, crop and crop model. Furthermore, different crop models use distinct approaches and when the information is poor, a comparison among them is not possible.

Lastly, most of the papers regarding crop modelling focus on the crop simulation outcomes, without fully considering all plant x environment interactions, especially GxE, which is mainly implied and general. The environment is taken into account by all the models, especially temperature, radiation, photoperiod and water and nitrogen stresses as shown in chapter 4. However, models often consider just the environment they were calibrated for as cited by Shrestha et al. (2013) for ORYZA2000. The genotype is principally simulated by using cultivar-specific input parameters. As mentioned before, it seems that the more cultivar-specific input parameters are optimized and used, the more precise is the simulation of various cultivars. Consequently, it contributes to an increase in complexity among crop models, without considering the numerous field trials necessary for achieving them. On the other hand, this could be a solution in order to improve GxE simulations. Another important point that could enhance the reliability of the prediction is to use a more mechanistic framework, namely the relationship of influencing dependent variables, as proposed by Sinclair and Seligman (2000).

7 Conclusion

Various crop models belonging to the DSSAT, ORYZA, and APSIM families, as well as CropSyst, were investigated with focus on maize, rice, and wheat. A general lack of information and the use of different approaches among models limited the comparison. In order to improve the quality of crop modelling papers, a standardization of the terminology, and a definite timeline of the released models with a full description of their functions is necessary. Better information exchange and communication are required to enhance the quality and progress of the models. More reliable models in simulating plant x environment interactions are, for rice, ORYZA(v3), which considers various ecosystems; while for maize and wheat are CERES and APSIM family. CropSyst resulted to simulate phenology too superficially and did not focus on a specific crop. Phenology is the key process in order to properly simulate plant responses in GxE context, and therefore to simulate new cultivars. For lowland rice, water temperature is to be considered until booting, thereafter air temperature is reliable. Moreover, for lowland rice panicle temperature is to be monitored in order to predict heat-induced spikelet sterility. Crop duration of rice cultivars, which defines their agronomic suitability, is a relevant characteristic to study in order to find adequate cultivars for a specific location. Rice, wheat, and maize have different optimal temperatures according to the processes and the development phases. In order to improve the simulation outputs, these variations in temperature, and more in general the microclimate, should be considered. Crop parameters need to be simulated as accurately as possible. For instance, leaf discoloration, increased degenerated spikelets, and increased grain shattering of rice lead to a lower green area and consequently to a false grain yield estimation. These processes are not considered by the models. By improving these aspects, it would be possible to better define other varieties in response to environmental conditions and also enable to select a variety that suits a new environment based on crop model outputs.

It is recommended to define more cultivar-specific parameters in order to improve the simulation outputs by adapting the existing functions and integrating the mentioned missing characteristics. However, the more parameters, the more complicated the crop model. Moreover, parameters are obtained by field experiments in which estimation errors can be generated. Additionally, field trials have disadvantages such as being time-consuming, and site-specific locations would restrict the parametrization to a limited environment. A more mechanistic approach should be followed in order to improve the prediction. Nonetheless, field trials are more complex than simulation since unexpected events or abiotic as well as biotic stresses can occur influencing the outputs.

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