Can current crop models be used in the phenotyping era for predicting the genetic variability of yield of plants subjected to drought or high temperature?

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Abstract

A crop model with genetic inputs can potentially simulate yield for a large range of genotypes, sites, and years, thereby indicating where and when a given combination of alleles confers a positive effect. We discuss to what extent current crop models, developed for predicting the effects of climate or cultivation techniques on a reference genotype, are adequate for ranking yields of a large number of genotypes in climatic scenarios with water deficit or high temperatures. We compare here the algorithms involved in 19 crop models. Marked differences exist in the representation of the combined effects of temperature and water deficit on plant development, and in the coordination of these effects with biomass production. The current literature suggests that these differences have a small impact on the yield prediction of a reference genotype because errors on the effects of different traits compensate each other. We propose that they have a larger impact if the crop model is used in a genetic context, because the model has to account for the genetic variability of studied traits. Models with explicit genetic inputs will be increasingly feasible because model parameters corresponding to each genotype can now be measured in phenotyping platforms for large plant collections. This will in turn allow prediction of parameter values from the allelic composition of genotypes. It is therefore timely to adapt crop models to this new context to simulate the allelic effects in present or future climatic scenarios with water or heat stresses.

Key words: Crop model, drought, temperature, tolerance, genetic variability, yield, phenotyping.

Introduction

Genetic progress is based on the pyramiding of alleles that confer advantages in plant production. Semi-empiric breeding has been extremely efficient in achieving this, with a genetic progress of about 1% per year in several species (Cooper et al., 2009; Brisson et al., 2010), even under water deficit (Cooper et al., 2009). However, yields have tended to reach a plateau for the last ten years, largely linked to increasingly adverse environmental conditions, in particular water and heat stresses (Brisson et al., 2010; Lobell et al., 2011, 2012). Furthermore, such adverse conditions tend to increase the genotype by environment interaction (G×E) (Cooper et al., 2001), thereby contributing to the slowing down of genetic progress. Indeed, quantitative trait loci (QTLs) have non-stable effects on yield of plants subjected to drought, with negative, positive, or no effect of a given QTL in different locations and years (Maccarelli et al., 2008; Bonneau et al., 2013). A breeding programme based on phenotypic values may therefore result in the oscillation between years of allele frequencies in the breeding population, following year-to-year climatic variations (Chapman et al., 2003; Hammer et al., 2005, 2006). A widely accepted idea is that G×E increases with the degree of integration and complexity, so underlying traits contributing to yield have a lower G×E than yield does (Fukai et al., 1999; Price and Courtois, 1999; Hammer et al., 2005). Selecting for traits has been successful in several cases (Richards, 2006; Edmeades et al., 1999).
Nevertheless, a given trait itself confers positive or negative effects on crop production depending on the environmental scenario (Tardieu, 2012).

To solve the difficulties linked to high G×E, it has been proposed to simulate the yield of virtual plants characterized by their allelic values at QTLs in a large set of environmental scenarios (Chapman et al., 2002; Tardieu, 2003; Yin et al., 2000; Hammer et al., 2006). A crop model with genetic inputs potentially indicates where and when a given combination of alleles confers a positive or negative effect on plant performance (Tardieu and Tuberosa 2010; Messina et al., 2011). This use of modelling differs from that of the first crop models (de Wit et al., 1970, 1978; Duncan et al., 1967), which simulate the consequences of crop management and climatic conditions on yield (i.e. sowing dates, Acosta Gallegos et al., 1996; row spacing, Egli and Bruening, 1992; Whish et al., 2005; irrigation, Chauhan et al., 2013; or diverse climatic conditions, Kumar et al., 2009; Kim et al., 2010). Recently, crop models have also been used for predicting the trends of yield as affected by climate change in different regions (Brisson et al., 2010; Asseng et al., 2013; Harrison et al., 2014; Rosenzweig et al., 2013; Potgieter et al., 2013), or for environment characterization (Chen et al., 2011).

The use of crop models in a genetic context became possible when model parameters began to be estimated at high throughput in phenotyping platforms (Yin et al., 2000; Reymond et al., 2003; Tardieu 2003; Hammer et al. 2006). A conceptual framework has been proposed for this by Tardieu and Tuberosa (2010). (i) The first step aims at dissecting raw traits obtained in phenotyping platforms, which rapidly vary with the plant environment, into a set of model-based “hidden traits” that characterize each genotype as independently as possible from environmental conditions (phenotypic profile, Module 1 in Figure 1). Specific ‘dissection’ models are used for this (not reviewed in this paper). (ii) This allows the identification of QTLs of model parameters such as the sensitivities of flowering time to photoperiod and temperature (Nakagawa et al., 2005), of leaf growth to water deficit (Reymond et al., 2003; Welcker et al., 2011) or of fruit quality to carbon availability (Quilot et al., 2005). The allelic profile of any genotype can in this way be connected to a phenotypic profile via a matrix of additive QTL effects (Module 2 in Figure 1). (iii) Climatic series, or models of climate change, feed the crop model with environmental scenarios (Module 3 in Figure 1). (iv) Finally, the crop model predicts the performance of genotypes characterized by a given combination of alleles at QTLs of model parameters, under a range of climatic scenarios (Chapman et al., 2002; Chen et al., 2009, Module 4 in Fig. 1).

The purpose of this paper is to discuss to what extent current crop models are adequate to simulate the performances of a large number of genotypes under a variety of environmental scenarios (Module 4 Fig. 1), in particular those scenarios involving water or heat stresses. The paper first reviews the ways in which 19 crop models (Table 1) take into account the effects of temperature and water deficit, with a special focus on seven widely used models presenting marked differences in principles. It then discusses the consequences of these differences for predicting the effect of the genetic variability.

Fig. 1. Conceptual framework for estimating the effects of the genetic diversity on crop performance. Each module involves a different category of models, but only models in Module 4 are reviewed in this paper. Module 1 (Phenotyping) dissects plastic physiological traits measured in phenotyping platforms into a set of environment-independent physiological traits characterizing each genotype (the phenotypic profile). See Tardieu and Tuberosa (2010) for detail. Module 2 (Genetics) links the allelic profile to a vector of parameters specific of a genotype through a genetic model (for example, a matrix of additive QTLs). See Yin et al. (2000) or Raymond et al. (2003) for detail. Module 3 (climate) generates environmental variables from climatic series or models of climate change. See Harrison et al. (2014) or Chen et al. (2011) for detail. Module 4 (Crop model) calculates yield in a large range of environmental conditions from the matrix of environmental variables, the genotype-dependent vector of parameters and the phenotypic profile (reviewed here).

We are aware that the models reviewed here represent a small fraction of available models in the literature and that several versions of each model have been developed, with sometimes appreciable differences between versions. The aim is here to show that different principles coexist for modelling the same effects and to discuss the consequences of this fact.

Response to temperature in current crop models

A consensus among crop modellers is that the growth rates of different organs and the rate of progression of plant cycle from germination to maturity are driven by time corrected for the effect of temperature (thermal time, Bonhomme, 2000; Boote et al., 2013). Several methods have been proposed...
for calculating thermal time. They differ in the formalism describing the response to temperature of different developmental processes and in the coordination between processes.

**Formalism of responses**

The responses to temperature are common to developmental processes such as the expansion or division rates of several organs, or the rate of progression of organ development or plant cycle, as shown in Fig. 2a that presents response curves normalized by the value of each process at 20 °C (Parent et al., 2010b). The diversity of temperature response in 18 species is described by a thermodynamic-based equation with two species-dependent parameters, in addition to the scaling parameter (Parent and Tardieu, 2012, Fig. 2b). Most current models have adopted simplifications with different principles (Fig. 3).

Several models assume a linear relation between temperature and developmental rates or leaf expansion (Fig 3 Development, Leaf expansion, e.g. Sirius, CERES-Wheat, CSM-IXIM, SUNFLO), thereby limiting the domain of validity of the model to the range of temperature in which the response is approximately linear. This results in the expression of thermal time in degree days because integration of this linear equation results in cumulating temperatures above a threshold. This formalism has been widely used in crop models for 30 years (Hammer et al., 1993; Sinclair, 1994). It involves one parameter, the x-intercept of the linear relationship, plus the scaling factor that results in the slope of the relationship.

Other models use bilinear (e.g. STICS, CropSyst) or trilinear equations (e.g. APSIM-maize, CropSIM) to approximate the non-linear shape of the responses (Fig. 3 Development, Leaf expansion). This also results in expression of thermal time in degree days, which accumulate differently in the two or three domains of temperature considered by the model. These formalisms involve three to five parameters, respectively, in bilinear and trilinear equations, plus the scaling factor.

Finally, a few models consider the response as intrinsically curvilinear via either (i) a beta function with four parameters that results in the expression of thermal time in modified degree days (GECROS), (ii) or specific equations as the one used by CSM-IXIM for leaf expansion rate or in CROPGRO for reproductive development (Hoogenboom et al., 1992; Boote et al., 1998; Hartkamp et al., 2002) (iii) or the equation presented in Fig. 2 (Parent et al., 2010b). The last two options result in virtual days whose duration is normalized by temperature (‘physiological
### Table 1: Three components of the different models presented: responses of the progression in the crop cycle (development); responses of leaf expansion rate; and response of biomass accumulation. The response is replaced by a text when relevant. (1) Linear, with one parameter ($T_{bp}$). (2) Linear + plateau, with two parameters ($T_{bp}$, $T_{opt}$). (3) Bi-Linear with three parameters ($T_{bp}$, $T_{opt}$, $T_{max}$). (4) Tri-linear with 5 parameters ($T_{bp}$, $T_{opt}$, $F_{int}$, $T_{opt}$, $T_{max}$). (5) Hyperbola with two parameters ($b$, $T_{opt}$, see Eq. 2). (6) Trapezoid with four parameters ($T_{bp}$, $T_{opt1}$, $T_{opt2}$, $T_{max}$). (7) Lizaso et al. (2011) equation with 5 parameters ($a$, $b$, $T_{bp}$, $T_{opt}$, $T_{max}$), see Eq. 3. (8) Beta function with four parameters ($\alpha$, $\beta$, $T_{bp}$, $T_{c}$). $\mu$ is the scaling coefficient, see Eq 4. SLA, specific leaf area.

### Figure 3: Formalisms of temperature effects on crop development, leaf expansion, and biomass accumulation in the crop models presented in Table 1.

Three components of the different models are presented: responses of the progression in the crop cycle (development); responses of leaf expansion rate; and response of biomass accumulation. The response is replaced by a text when relevant. (1) Linear, with one parameter ($T_{bp}$). (2) Linear + plateau, with two parameters ($T_{bp}$, $T_{opt}$). (3) Bi-Linear with three parameters ($T_{bp}$, $T_{opt}$, $T_{max}$). (4) Tri-linear with 5 parameters ($T_{bp}$, $T_{opt}$, $F_{int}$, $T_{opt}$, $T_{max}$). (5) Hyperbola with two parameters ($b$, $T_{opt}$, see Eq. 2). (6) Trapezoid with four parameters ($T_{bp}$, $T_{opt1}$, $T_{opt2}$, $T_{max}$). (7) Lizaso et al. (2011) equation with 5 parameters ($a$, $b$, $T_{bp}$, $T_{opt}$, $T_{max}$), see Eq. 3. (8) Beta function with four parameters ($\alpha$, $\beta$, $T_{bp}$, $T_{c}$). $\mu$ is the scaling coefficient, see Eq 4. SLA, specific leaf area.

\[
F(t) = 1 - b(T - T_{bp})^2
\]

\[
F(t) = a(1 - \exp(-b(T - T_{opt}))) \quad \text{if } T < T_{opt}
\]

\[
F(t) = \frac{(T - T_{max})}{(T_{opt} - T_{max})} \quad \text{if } T_{opt} \geq T < T_{max}
\]

\[
F(t) = \exp(\mu)(T - T_{bp})^\alpha(T_c - T)^\beta
\]
days’ in CROPGRO; ‘biological days’ in CropSim; ‘equivalent days at 20 °C’ in Parent et al., 2010b).

Depending on the chosen formalism, one will detect (or not) the presence of a variability in temperature response between genotypes or between organs. For instance, with the equation presented in Fig. 2, Parent and Tardieu (2012) found no significant genetic differences between lines of different origins (tropical, temperate, or highlands) in maize, wheat, and rice. Because the range of temperatures in which a linear temperature response is fitted usually differs between genotypes, the fitting of a linear equation on an essentially curvilinear response can provide different x-intercepts for each genotype, with higher x-intercepts for genotypes analysed in warmer temperature ranges. The same applies to linear equations fitted to the growths of different organs. Organs growing later in the season are generally subject to warmer conditions, resulting in higher x-intercepts. This results in different intercepts depending on plant stage as in ARCWHEAT or in CropSim-wheat.

Finally, the respective effects of temperature and other variables (in particular light or vapour pressure deficit, VPD) have different weights depending on the formalism of temperature response. The usual procedure for calculating the effects of light or vapour pressure deficit (VPD) is to first take into account the temperature effect, and then to consider the effects of other environmental cues as deviations from the tendency (Ben Haj Salah and Tardieu, 1996; Sadok et al., 2007; Parent et al., 2010a). Hence, the parameterization of VPD or light effects, which have an appreciable genetic variability in maize and rice (Welcker et al., 2011, Parent et al., 2010a), depends on the model formalism for temperature responses.

Coordination between the temperature responses of growth, development, and biomass accumulation

Models also diverge in the way in which the temperature responses of different processes are coordinated. Experimental

**Fig. 4.** Flowcharts of water deficit effects on leaf area and biomass in two classes of crop models. (a) Models ‘in parallel’ in which leaf expansion and biomass production are essentially independent. (b) Models ‘in series’ in which leaf area index (LAI) depends directly on biomass accumulation, partitioned to leaves and calculated from the specific leaf area (SLA). In both groups, the main feedback is the effect of leaf area index (LAI) on light interception and conversion to biomass. In “in parallel” models, expansion can be limited by biomass accumulation through the maximum specific leaf area, SLA\textsubscript{max}, in STICS and APSIM, or the effect of water deficit on partitioning to leaves as in CSM-IXIM, CropSyst or GECROS. In CropSyst and APSIM, biomass accumulation is calculated as the minimum of biomass accumulation when calculated from radiation use efficiency (RUE) or transpiration efficiency (TE). Water stress index differs between models: available water content in STICS and Sirius, and ratio of actual/potential transpiration in CERES Wheat, CropSyst, CSM-IXIM, GECROS, and APSIM.
evidences suggest common temperature responses for expansion rate and the reciprocal of durations of cycle phases, phyllochron, or duration of the vegetative phase (Warrington and Kanemasu, 1983a; b; Parent et al., 2010b). This is not the case for the temperature response of photosynthesis or respiration, and more generally for carbon metabolism (Parent et al., 2010b).

The coordination of the temperature responses of biomass accumulation (Fig. 3, Biomass accumulation) and leaf expansion (Fig. 3, Leaf expansion) differs between models. In GECROS and CropSyst, leaf expansion is driven by biomass allocation to leaves (Fig. 4b) and therefore directly depends on the temperature response of photosynthetic activity. Hence, no specific temperature response is implemented for leaf expansion rate. All other models consider different responses for leaf expansion and biomass accumulation, the latter with quite different formalisms between models.

The coordination of development and leaf expansion also differs between models (Fig. 3, Development, Leaf expansion). In APSIM-Maize, Sirius, and CERES-Wheat, the temperature response of leaf expansion rate is common to that of the rate of progression in the cycle (Fig. 2). Conversely, STICS and CSM-IXIM consider different responses, either sharing a similar equation with different parameters (STICS), or using a different equation (CSM-IXIM).

Emergent properties that can affect traits and performances of genotypes result from the modes of coordination chosen by models. Experimentally, expansion is more affected than biomass accumulation by low temperatures (Parent et al., 2010b), resulting in an increase in mass per unit leaf area (Atkin et al., 2006). In the same way, high temperatures result in a reduction in carbon accumulation during the crop cycle (Peng et al., 2004) because cycle duration is more shortened than photosynthesis is increased. These experimentally observed emergent properties can be predicted if shoot biomass on one hand and developmental processes on the other hand have independent temperature responses (as in APSIM, CSM-IXIM, or STICS), but not if leaf expansion and biomass accumulation have common temperature responses, as in CropSyst or GECROS.

Responses to water deficit in current crop models

Transpiration and biomass accumulation

Transpiration flux is simulated in similar ways in most models. Transpiration demand is simulated either via a Penman-Monteith-like equation (Penman, 1948; Allen et al., 1998; Priestley and Taylor, 1972) in STICS, GECROS, CROPGRO, CropSyst, and CERES, or by the product of biomass accumulation by transpiration efficiency and air vapour pressure deficit in APSIM-maize. Plant water status and transpiration are simulated based on indices such as a supply/demand ratio in APSIM-maize, the ratio of actual vs potential transpirations in CERES, CSM-IXIM, SUCROS1&2, GECROS, and CropSyst, or directly via available water content in the root zone in STICS. These simplifications avoid complex equations of water transfer in the soil and in the plant, which include complex determinisms of the water transfer in the plant (Tardieu and Davies, 1993, Caldeira et al 2014) and in the soil (Janott et al., 2011).

Biomass accumulation and its dependence on water deficit are modelled in different ways through either (i) the widely used concept of radiation use efficiency (RUE), which relates biomass to intercepted light in CERES, STICS, APSIM, and CropSyst, or (ii) the simulation of photosynthesis and respiration at leaf level in CERES-PR and CSM-IXIM, or (iii) a more mechanistic approach with the integration of a model of leaf photosynthesis (Farquhar, 1980) in GECROS. An effect of water deficit on RUE or on its components is simulated either by reduction factors depending on a drought index, or indirectly as in APSIM-maize where biomass accumulation is calculated as the minimum of “the light-limited biomass accumulation” and “the water-limited biomass accumulation”, which involves transpiration efficiency and available water (Hammer et al., 2010).

Expansive growth

Growth under water deficit is simulated with different principles. Water deficit affects stomatal conductance, photosynthesis, leaf expansion, and the progression in the plant cycle among other traits. A key issue for crop modelling is how these responses are coordinated in the whole plant. Responses can be coordinated in several ways (Tardieu et al., 2011), either (i) via “hubs” that control simultaneously all processes (e.g. due to cascades of transcription factors or common hormonal determinisms), so all of them react in a coordinated way, (ii) in series, with one process governing the others via a cascade of events, or (iii) in parallel, with all processes being affected independently but with feedbacks that coordinate them. It has been argued that the last option better accounts for experimental results than the other two (Tardieu et al., 2011). These options are considered in crop models (Fig. 4, a simplification of the described models that often include more feedbacks than those presented here to ensure model stability).

A coordination ‘in series’ is hypothesized by CropSyst and GECROS (Fig. 4b). In these models, leaf area expansion is directly derived from biomass accumulation in leaves. Water deficit affects biomass accumulation via reductions in either photosynthesis in GECROS or RUE in CropSyst. Simulated changes in photosynthesize availability affect biomass accumulation in leaves, transformed into the increase in leaf area via the specific leaf area (SLA). In this case, SLA is considered as a genotypic parameter used to calculate leaf expansion from leaf dry weight increase.

A coordination ‘in parallel’ is assumed by CERES-wheat, STICS, SIRIUS, and APSIMmaize (Fig. 4a), in which leaf area expansion and biomass accumulation are essentially independent processes with different response to water deficit. CSM-IXIM works in a similar way, but considering photosynthesis and respiration instead of RUE. In these models, SLA is an emerging property resulting from the balance of leaf expansion and biomass accumulation in leaves,
consistent with experimental results (Bertin and Gary, 1998; Tardieu et al., 1999; Tardieu et al., 2011). However the range of SLA is voluntarily limited in these models, in such a way that biomass accumulation becomes the limiting factor for leaf expansion rate if carbon resources are considered as insufficient to build leaves with an acceptable biomass per unit leaf area.

Depending on the model structure, a given trait and the effect of the QTLs that determine it either has a crucial importance in the overall plant response to water deficit, or is one trait among others. ‘In series’ structure results in the fact that crucial traits/parameters are the responses of photosynthesis (or RUE) to water deficit, SLA, and the proportion of biomass allocated to each organ. As a consequence, a QTL affecting RUE under water deficit would have a key effect. ‘In parallel’ structures result in a large effect of water stress indices, largely independently of biomass allocation, resulting in a major effect of QTLs controlling developmental responses to water deficit. Furthermore, the independence of biomass accumulation and leaf expansion results in an increase in carbon availability under water deficit which affects more expansion than photosynthesis, consistent with experimental data (Muller et al., 2011).

An observed genetic variability on a given trait is difficult to simulate if not explicitly present in the model. For instance, it is straightforward to simulate consequences of QTLs affecting leaf expansion (Reymond et al., 2003, Welcker et al., 2011) in an ‘in parallel’ model as in Chenu et al. (2009), whereas inserting them in a ‘in series’ model would require contrived hypotheses. Even so, simulating the effects on yield of QTLs of leaf expansion still required adjustment of the model (Chenu et al., 2008) and new hypotheses, for instance assuming that QTLs involved in leaf expansion affected both leaves, silk growth, and Anthesis-Silking Interval, consistent with experimental evidences provided by Welcker et al. (2007) and Dignat et al. (2013).

Simulating the yield of a reference genotype versus simulating the ranking of yield in a panel of genotypes

In a genetic context, a crop model primarily aims at predicting in which environments a given combination of alleles offers a comparative advantage to plants. This potentially allows one to estimate the agronomic value of a combination of QTLs over a long series of climatic data in a mesh of sites covering the considered region (Messina et al., 2011; Harrison et al., 2014). The most essential output of a crop model is in this case the ranking of genotypes in typical environmental scenarios, whereas the absolute value of the mean yield in each environment is probably less important. Hence, current models simulating the behaviour of a reference genotype in a range of environments have been designed and tested for a purpose that appreciably differs from its purpose in a genetic context.

Are sensitivity analyses based on current crop models suited for designing genotypes in a range of environments? A crucial consequence of the above paragraphs is the large risk associated with sensitivity analyses of traits by using a crop model, in a “you get what you brought” way. Figure 4 strongly suggests that with “parallel” architectures the response of leaf expansion to water deficit is an important trait for improving yield under drought. Because this trait is not explicitly present in ‘series’ architectures, it cannot be identified as a key trait, whereas RUE and carbon partitioning will. Sensitivity analyses therefore may well predict that most important traits are those that have been placed in the model as a central position in the network. A striking example is found in the work of Jamieson et al. (1998a), who showed that a set of crop models provide accurate yield predictions based on the premise that the reduction in biomass accumulation with water deficit is mainly due to changes in photosynthetic efficiency. However, experimental data of the same dataset showed that the decrease in biomass was primarily due to changes in leaf area index. The consistency of observed versus predicted data was based on parameter estimation through model inversion that identifies the parameter value providing the best predictions in a set of experiments. Hence, the studied models provided accurate simulations but a wrong analysis of sensitivity because models would predict better performances for genotypes maintaining a high photosynthetic efficiency at the expense of genotypes maintaining leaf area expansion. In the same way, 27 crop models provide consistent yield predictions (Asseng et al. 2013), although these models are based on markedly different principles, equations, and input variables, as reviewed above. These authors propose that the combination of different models (i.e. the median value of all model outputs in a given site) provides the best yield estimate of a reference genotype in a range of environmental conditions.

Overall, crop models used for genetics need to provide accurate estimates of biological processes. As discussed above, accurate yield prediction from inaccurate algorithms (or combination of different algorithms) is probably a more serious problem if one aims at ranking the performance of genotypes that differ in one or another of the mechanisms implemented in the crop models.

Phenotyping, a key for modelling the responses to water deficit and temperature

The use of a crop model for predicting performance of genotypes in water deficit or high temperature scenarios requires that its parameters are measured for each genotype and not optimized. Genotype-dependent parameters were not measured in the past or at too low throughput for hundreds of genotypes. They can be now directly measured in phenotyping platforms (Sadok et al., 2007; Granier et al., 2006; Berger et al., 2010; Fiorani and Schurr, 2013). First attempts of using measured parameters (or QTL-derived parameters originating from measurements) have until now involved ad hoc models specifically developed for one function such as flowering time (Yin et al., 2005), leaf elongation rate (Reymond et al., 2003), or peach quality (Quilot et al., 2005). To our knowledge, its use in crop models has until now been limited to “proof of concepts” (Yin et al., 2000; Chenu et al., 2009).
Phenotyping methods may influence the structure of crop models aimed at evaluating genotypes, through the choice of algorithms that involve parameters that can be phenotyped. A striking example is the choice of either a simplified model based on light interception and RUE, or a model predicting photosynthesis and respiration of the canopy. The latter better simulates the effects of environmental conditions, because respiration and photosynthesis have different response to environmental conditions (Oberhuber and Edwards, 1993), potentially resulting in apparently erratic variations of RUE (Loomis and Amthor, 1999). However, such models have a parameter estimation that requires the establishment of the response of photosynthesis to internal CO2 for each studied genotype, a task currently impossible to carry out on hundreds of genotypes. By contrast, radiation use efficiency (RUE) can be evaluated in a phenotyping platform (L. Cabrera, personal communication) and its relation with environmental conditions can be modelled (Loomis and Amthor, 1999). Depending on the phenotyping abilities, one can therefore choose either a process-based model (e.g. with submodels of photosynthesis and respiration) if phenotyping allow its parameterization, or a more empiric model (e.g. involving light interception and RUE) whose parameter can be estimated at high throughput in a phenotyping platform.

Recent years have seen the development of functional-structural plant models (FSPM), linking plant architecture to external physiological function (Prusinkiewicz and Rolland-Lagan, 2006; Barczi et al., 2008). These 3D models allow better estimation of light interception (Fourcaud et al., 2008), currently calculated with a coefficient of extinction and the leaf area index (e.g. APSIM and STICS), or through more complex algorithms but still based on a 2D approach (CERES-PR, CSM-IXIM). In the future, it could be conceivable to include such submodels in crop models for genetics if the large number of parameters were phenotyped in imaging platforms.

Progress in the phenotyping of water flux or water content in organs may lead to future changes in the modelling of water flux and water status in planta. Modelling fluxes requires fine time resolutions, a large number of parameters, with differential equation governing flows between reservoirs. This has been considered until now as intractable with a crop model, resulting in the drought indices reviewed above in “responses to water deficit in current crop models”. However, it has become increasingly possible to measure or estimate hydraulic parameters in the plant (Liu et al., 2009; Ehlert et al., 2009) and hydraulic conductivity as a response to several environmental cues (Maurel et al., 2008; Cochard et al., 2007) so they may shortly be evaluated for each genotype. It is therefore tempting to develop a model with hydraulically explicit equations, so QTLs or genes affecting plant hydraulic properties could be accounted for by the model.

Hence, it is proposed here that the level of simplification of any biological process should be based on one’s ability to phenotype and get parameters characterizing this process for hundreds of genotypes.

Conclusion

The above paragraphs show that even if current crop models can be used for different objectives, their characteristics may diverge in the future depending on objectives, either simulating the effects of climate change or crop management on the performance of a reference genotype, or simulating the genetic variability of yield responses to climate changes. For engineering or climate change studies, prediction accuracy is the major criteria of decision, and adequate simplifications of the biological complexity can provide good estimation of yield. Conversely, using a model in a genetic context require flexibility, for adapting it to specific questions, traits, and QTLs. Parallel progress of modelling and phenotyping is required to insert independent and relevant biological parameters with genetic diversity into crop models. This is feasible in the short-term for crop models, but more complex models, including genes and metabolic networks (Keurentjes et al., 2011) or functional structural plant models describing 3D architecture of plants, will remain difficult to parameterize and calibrate for a long period.

Overall, we propose that an adequate estimation of QTL impacts requires crop models with algorithms that are closer to actual plant mechanisms, but in such a way that most parameters would be measurable in phenotyping facilities. A solution will probably rise after tries and errors from the community of biologists/modellers. We hope that thoughts as those presented in this paper would result in the building of integrated modelling views developed together by the biologist community.

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