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REVIEW PAPER

Use of crop simulation modelling to aid ideotype design of future cereal cultivars

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Abstract

A major challenge of the 21st century is to achieve food supply security under a changing climate and roughly a doubling in food demand by 2050 compared to present, the majority of which needs to be met by the cereals wheat, rice, maize, and barley. Future harvests are expected to be especially threatened through increased frequency and severity of extreme events, such as heat waves and drought, that pose particular challenges to plant breeders and crop scientists. Process-based crop models developed for simulating interactions between genotype, environment, and management are widely applied to assess impacts of environmental change on crop yield potentials, phenology, water use, etc. During the last decades, crop simulation has become important for supporting plant breeding, in particular in designing ideotypes, i.e. 'model plants', for different crops and cultivation environments. In this review we (i) examine the main limitations of crop simulation modelling for supporting ideotype breeding, (ii) describe developments in cultivar traits in response to climate variations, and (iii) present examples of how crop simulation has supported evaluation and design of cereal cultivars for future conditions. An early success story for rice demonstrates the potential of crop simulation modelling for ideotype breeding. Combining conventional crop simulation with new breeding methods and genetic modelling holds promise to accelerate delivery of future cereal cultivars for different environments. Robustness of model-aided ideotype design can further be enhanced through continued improvements of simulation models to better capture effects of extremes and the use of multi-model ensembles.

Key words: Cereals, climate extremes, crop growth simulation, ensemble modelling, future cultivars, genetic modelling, ideotype breeding, model improvement, model-aided design.

1. Introduction

1.1 Food security challenges

Future food security will be challenged by the likely increase in demand, changes in consumption patterns, and the effects of climate change. Global demand for agricultural crop production is expected to roughly double by 2050 according to the projected increases in population, consumption, and changes in diets (Kastner *et al.*, 2012; Tilman *et al.*, 2011). A high percentage of this demand needs to be met by the main staple crops, wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), and barley (*Hordeum vulgare* L.). Concurrently, there have been alarming reports in the last decade of stagnating crop yield growth rates in various important agricultural regions around the world, such as rice in China (Lobell *et al.*, 2009; Ray *et al.*, 2012) and wheat in Europe (Brisson *et al.*, 2010; Lobell *et al.*, 2009; Ray *et al.*, 2012), due to changes in agronomic management and climatic conditions (Brisson *et al.*, 2010; Ray *et al.*, 2012). Moreover, there are increasing concerns about severe constraints to increased cereal production related to competition for resources (e.g. land allocation between food and biofuel

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Abbreviations: GP, growing period; IRRI, International Rice Research Institute; LER, leaf elongation rate; NPT, new plant type; QTL, quantitative trait loci.

production), increasing water scarcity, declining cropland (e.g. due to urbanization), and quality of the soil resource base (Carberry *et al.*, 2013).

Increased climate variability and more frequent extreme weather events further exacerbate constraints to increasing food supplies and food security (Coumou and Rahmstorf, 2012). Increased frequency of extreme weather events such as heat waves and prolonged droughts has already been observed (Christidis *et al.*, 2015; Gourdji *et al.*, 2013; IPCC, 2012), with major negative impacts on agricultural production in broad regions of the world. In 2007, 2010 and 2012, for example, there were simultaneous occurrences of adverse weather events in important agricultural regions (Lobell and Gourdji, 2012). Future projections of a significantly higher frequency of very unfavourable years for crop production may result in poor economic returns in many agricultural regions (Gourdji *et al.*, 2013; IPPC, 2012).

Adaptation of crop production systems to better cope with the challenges of future climate change and increasing weather extremes is, therefore, of key concern (Battisti and Naylor, 2009; Tester and Langridge, 2010; Trnka *et al.*, 2014). In addition, climate smart agriculture requires that climate adaptation and mitigation measures are combined (FAO, 2010). Furthermore, uncertainties of climate change projections are posing particular challenges to plant breeders and crop scientists (Semenov *et al.*, 2014).

Plant breeding is mostly based on 'selection for yield' or 'defect elimination'—breeding for crop 'ideotypes' has been a valuable alternative (Peng *et al.*, 1994; 1998; Sharma *et al.*, 2013). A crop ideotype is a model plant that is expected to yield a greater quantity or quality of grain, oil, or other useful product when developed as a cultivar (Donald, 1968). A similar concept of (new) plant type was introduced in 1964 by Jennings in relation to rice breeding, and was still being used in the 1990s (section 5) (Peng *et al.*, 2008). In ideotype breeding, goals are specified for each plant property, resulting in a description of a model plant for the properties of interest (Rassmusson, 1991). Recently, Martre *et al.* (2015; p 350) defined the term ideotype as 'a combination of morphological and/or physiological traits, or their genetic bases, optimizing crop performance to a particular biophysical environment, crop management, and end-use'. In crop simulation models, an ideotype is defined as a set of crop or cultivar parameters that define growth and development of a crop with the given environmental conditions.

Framing food availability requires adequate planning and agricultural production modelling. Decision-making can benefit from improved understanding of what is known and what is uncertain (Rötter, 2014). Ignorance about future crop varieties and their phenological features is a significant source of uncertainty in the future agricultural socio-economic context for adaptation to climate change. While most crop models are not yet fit for accurately capturing effects of adverse weather or extremes (Rötter *et al.*, 2011), since the 1990s crop simulation modelling has proven to be an important tool for supporting plant breeding (e.g. Boote *et al.*, 2001; Dingkuhn *et al.*, 1991; Hammer *et al.*, 2006; Tardieu, 2003).

1.2 Review objectives

The objectives of this review are:

1. to examine the basic limitations of crop simulation modelling for supporting ideotype breeding;
2. to describe developments in cultivar traits in response to climate variations in recent decades;
3. to review how crop modelling studies have supported evaluation and design of cereal cultivars for future conditions, and draw conclusions on fruitful future directions for collaborative research on ideotype breeding, with a focus on new climate-resilient cultivars.

We start in section 2 with an overview on capabilities and limitations of crop models with respect to supporting ideotype breeding. Section 3 illustrates the development of cereal cultivars and yield trends over last few decades. Section 4 provides a summary on mid-century climate change projections, with special reference to climate extremes. Our review of key modelling studies on the evaluation and design of new cereal cultivars for future environments is presented in Section 5. Section 6 concludes with a synthesis, including a critical review of progress made in model-aided ideotype design and future research challenges and potential solutions through collaborative research.

2. Capabilities and limitations of crop models in supporting ideotype breeding

Crop simulation models have been applied in various ways to support plant breeding, e.g. to design crop ideotypes for different environments aimed at minimizing resource use per unit of dry matter produced and to increase crop yield potential (Aggarwal *et al.*, 1997; Dingkuhn *et al.*, 2007). Particularly promising has been the application of crop simulation to estimate yield potential in crop ideotypes designed for projected future climates. For example, Semenov *et al.* (2014) applied wheat simulation model Sirius across Europe to optimize wheat ideotypes for future climate scenarios, whereby a wheat ideotype was defined as a set of selected cultivar parameters related to photosynthesis, phenology, crop canopy characteristics, and water relations. By changing parameters from given value ranges and optimizing them for yield in response to changing climate or environmental conditions, ideotypes were defined that showed best yield performance under well-defined future conditions.

Combining this simulation approach with new breeding methods and strategies (e.g. Yang *et al.*, 2013) could significantly enhance ideotyping in support of well-targeted breeding, and thus accelerate delivery of future cereal cultivars adapted for different environments with their typical current and expected future exposure to extreme and adverse weather events (Table 1).

The potential of process-based crop models to be effective tools for ideotype breeding is because the model's purpose is to describe the causal relationships between crop growth and factors driving them. The models' limitations are also linked to their potentials: the accuracy of the process descriptions

Table 1. *Type of extreme events important for cereal crops in Europe to receive first priority for model improvement (based on Rötter et al., 2013a).*

Extreme event	Development stage	Main physiological processes affected	Cereals
Drought, high temperature	Vg	Tillering and leaf expansion/senescence, carbon and nitrogen assimilation and partitioning, vernalization, phenology	Wheat, barley
	Rg	Canopy senescence, carbon and nitrogen assimilation and partitioning, anthesis/silking interval, grain development	Wheat, barley, maize, rice
Heat shocks	An	Floret mortality, pollen viability (maize), potential grain size	Wheat, barley, maize, rice
	Rg	Starch granule and gluten protein size distribution	Wheat
Cold spells	Vg-An	Cold hardening, frost damage or winter-kill	Wheat, barley
Heavy rain and storm	Vg/Rg-RP	Stem lodging, interaction with nitrogen fertilization, water logging-oxygen stress, post-maturity losses from delayed harvest, disease losses from wet conditions	Wheat, barley

An, anthesis; Rg, reproductive growth; RP, ripeness; Vg, vegetative growth.

and uncertainties related to their parameters affect their usability for ideotype design. The availability of high-quality, long-term empirical data sets for model calibrations and testing is a prerequisite for ensuring the quality of simulation results. The robustness of model-based cultivar design will need to be enhanced by improving models to better capture the effects of climatic variability and extremes. Although a few years ago, most crop simulation models failed to accurately capture effects of adverse weather and extremes (Rötter *et al.*, 2011), considerable progress regarding model improvement has been made in the framework of The Agricultural Model Intercomparison and Improvement Project (AgMIP; www.agmip.org) and Modelling European Agriculture with Climate Change for Food Security (MACSUR; www.macsur.eu). Most notable is the progress in adequately describing the impacts of heat shocks around flowering on floret mortality (e.g. for wheat and barley) (Moriondo *et al.*, 2011; Nendel *et al.*, 2011), and effects of heat waves during reproductive stages on leaf senescence and grain filling (Asseng *et al.*, 2011). Moreover, judicious use of multi-model ensembles for assessing uncertainties in climate change–impact projections for various cereals (e.g. Asseng *et al.*, 2013; Bassu *et al.*, 2014; Li *et al.*, 2014) has led to more robust estimates of impacts of heat stress on yields, water use, etc. under very diverse agro-ecological conditions. Even though most cereal crop models are not yet fit to capture all relevant stresses (Table 1), realized model improvements hold promise for using many of them in the near future for supporting the breeding of crop ideotypes for future climates with more extreme weather.

3. Development of cereal cultivars and yield trends over recent decades

There is evidence of shifts in crop cultivar characteristics and their responses to weather in past few decades from different parts of the world. In Asia, the increase in rice grain yield has resulted from the development of new varieties such as semi-dwarf varieties in the 1960s and hybrid rice varieties in the 1970s. For instance, rice yield potential in China increased by about 30% because of the development of semi-dwarf varieties in (Fang *et al.*, 2004). An additional 15–20% increase was achieved by the use of heterosis (Yuan, 2003) combined with the International Rice Research Institute's (IRRI's) design of a new plant type (NPT) into super hybrid rice (Peng *et al.*, 2008).

In a country-wide study on wheat in China (Tao *et al.*, 2012), based on comprehensive observations for 1981−2009, it was found that warming had caused a significant decrease in lengths of growing period (GP, from sowing to maturity) and vegetative GP (from sowing to heading) at about 30% of the investigated stations (n = 108), especially for spring wheat. By contrast, lengths of reproductive GP (from heading to maturity) increased at 60% of the investigated stations. Thermal requirements for completing the various phenological phases generally increased. However, thermal requirements to complete each single development stage changed differently with most substantial increases for reproductive GP. The harvest index also increased steadily. The rice transplanting date was advanced significantly at about 20% of over 100 stations. The duration of vegetative GP increased significantly at 26.1% of stations for single-crop rice; however, in double-crop rice, it decreased significantly for early rice at 19.7% of stations and for late rice at 16.2% of stations. The duration of reproductive GP increased significantly at 21.8% and 17.0% of stations for single-crop rice and early rice, respectively, but decreased at 21.4% of stations for late rice (Zhang *et al.*, 2014).

Based on maize phenology observations taken in 1981–2009 at 112 national agro-meteorological experiment stations across China, Tao *et al.* (2014) found that cultivar shift delayed heading date and maturity date and prolonged the duration of whole GP at 75.0%, 94.6%, and 92.9% of stations on average by 1.5, 6.5, and 6.5 days/decade, respectively.

In studies on cultivar development of spring cereals in Finland and in other Nordic countries, negative impacts on yields have been reported under increased temperatures and reduced water availability both during pre- and post-anthesis phases (Peltonen-Sainio *et al.*, 2011). Various papers resulting from the Adaptive Capacity and Resilience of Finnish Agrifood Systems project report that there has been a decline over the last decade in the response diversity to weather of the various cultivars used by farmers in the main barley cultivation areas of Finland (e.g. Kahiluoto *et al.*, 2014).

In high latitude countries like Finland it has been indicated that yield growth rates on farmers' fields have nearly stagnated. This, however, is mainly due to socio-economic developments because the genetic yield potential of cereal crops during the last 25 years reportedly increased, without any signs of slowed pace of increase in recent years (Peltonen-Sainio *et al.*, 2009). The latter is in line with the continuous increase in yield potential of cereal cultivars reported elsewhere (Rijk *et al.*, 2013).

According to a study on Nordic wheat cultivars in 1901–1993 (Ortiz *et al.*, 1998), on average, the absolute genetic gain for grain yield was about 18.5 kg ha^{-1} year^{-1}. Negative changes in days to heading (at a rate of −0.06 year^{-1}) and plant height (−0.5 cm year^{-1}), and positive changes in harvest index (0.06% year^{-1}) and kernels m^{-2} (45 year^{-1}) were associated with early flowering, less straw, but many fertile tillers.. Overall, this resulted in gains in observed grain yield. Particularly, breeding has reduced plant height in recently released cultivars, thereby reducing lodging in this germplasm. Related relative genetic gains during the 20th century were significant for agronomic characteristics, such as grain yield (20%), harvest index (19%), and number of kernels per unit area (18%).

While phenotypic diversity of spring barley cultivars has been actively maintained and also consistently enlarged by Nordic plant breeders after the Second World War (Ortiz *et al.*, 2002), the picture is not so clear for genotypic diversity. While the latter authors suggested no signs of the Nordic germplasm being of too limited diversity for the future, other studies (e.g. Tondelli *et al.*, 2013) concluded that the direction and type of breeding programmes of the 20th century have contributed to a narrowing of gene pools in cultivated barley, which is to be overcome by new breeding strategies (Henry, 2014).

Crop yields worldwide have increased noticeably over the last half of the 20th century with fairly linear growth rate; however, there are signs that this trend is not likely to continue at the same rate as shown for the first decade of the 21st century–except for maize in the USA (see Fig. 1).

Rice yield growth rates in China have slowed down (Peng *et al.*, 2009; Ray *et al.*, 2012); wheat yields in France, the most important wheat producer in the European Union, have stagnated or even decreased since the late 1990s (Brisson *et al.*, 2010); and the growth rate of barley yields in Germany has weakened since the late 1990s (Höhn and Rötter, 2014).

Maize yields in the USA grew fairly linearly until the end of the 2000s, with an observed record yield of 10.3 tons ha^{-1} in 2009. This great accomplishment must be attributed to the exceptional efforts and successes with respect to both maize breeding and US maize agronomic research and its implementation in the field (Dobermann *et al.*, 2011). Recently, however, this trend has slowed down: the exceptionally dry year of 2012 (Lobell *et al.*, 2013) had the lowest maize yield since 1995.

While cultivar traits related to crop phenology and yield components have developed continuously for the various cereals—partly in response to climatic variations —there is serious concern about the resilience of current genotypes under future conditions. This is especially true when considering recent more frequent climatic extremes that have already negatively impacted crop productivity, slowed yield growth, and reduced the benefits of continued gains in genetic yield potentials (Brisson *et al.*, 2010; Challinor *et al.*, 2014; Lobell and Gourdji, 2012).

4. Climate change projections for mid-century

4.1 Changes in climatic means

The observed global mean change since pre-industrial times currently amounts to 0.8–0.9°C and is fairly large compared to temperature variability over comparable time spans (Rummukainen, 2014). Projected climate change for the mid-century show wide variations depending on the climate models (global or regional) and emissions scenarios considered (e.g. IPCC, 2013; Rötter *et al.*, 2012). According to the fifth Assessment Report of the Intergovernmental Panel on Climate Change, global temperature increases of 0.3–4.8°C are projected for the end of the century (IPCC, 2013). Global warming will increase global precipitation, whereby global climate model simulations suggest an increase in the global mean of precipitation by about +1% for each 1°C increase in temperature (Rummunkainen, 2014). However, projected changes are quite heterogeneous across climatic zones. While there are exceptions from the rule, the general tendency for large-scale precipitation projections is that the 'wet gets wetter' and the 'dry gets drier' (Held and Soden, 2006).

It has been reported that the intensity, length, and frequency of heat waves is very likely to increase (Christidis *et al.*, 2015; Coumou and Rahmsdorf, 2012; Tebaldi *et al.*, 2006). Changes in climate extremes can result from either changes in means, in variance, and/or changes in a combination of the mean and distribution of climate variables (IPCC, 2012; Porter and Semenov, 2005). Studies that only consider changes in the mean are likely to arrive at incorrect conclusions about how changes will evolve (Ballester *et al.*, 2010; Rummukainen, 2012).

4.2 Changes in climatic variability and extremes

A significantly higher frequency of extremely unfavourable years under future climate conditions is projected, as illustrated for summer temperature in Fig. 2. Gourdji *et al.* (2013) showed that, by 2030, we can expect a 2-fold increase in the global wheat-growing area threatened by extremely high temperatures during critical developmental stages in a typical year, and, by 2050, a more than 3-fold increase of the area at risk. Expected changes in agricultural drought (as indicated by changes in soil moisture) are presented in Fig. 3.

A promising approach to assess the future climate-driven challenges in agricultural production is the use of so-called agroclimatic indicators. Instead of quantifying climate change impacts on crop yields, this approach examines the essentials of climate-induced stresses for crop production by capturing climatic risks, e.g. heat, drought, frost, and waterlogging, during sensitive crop growth stages and impacts on

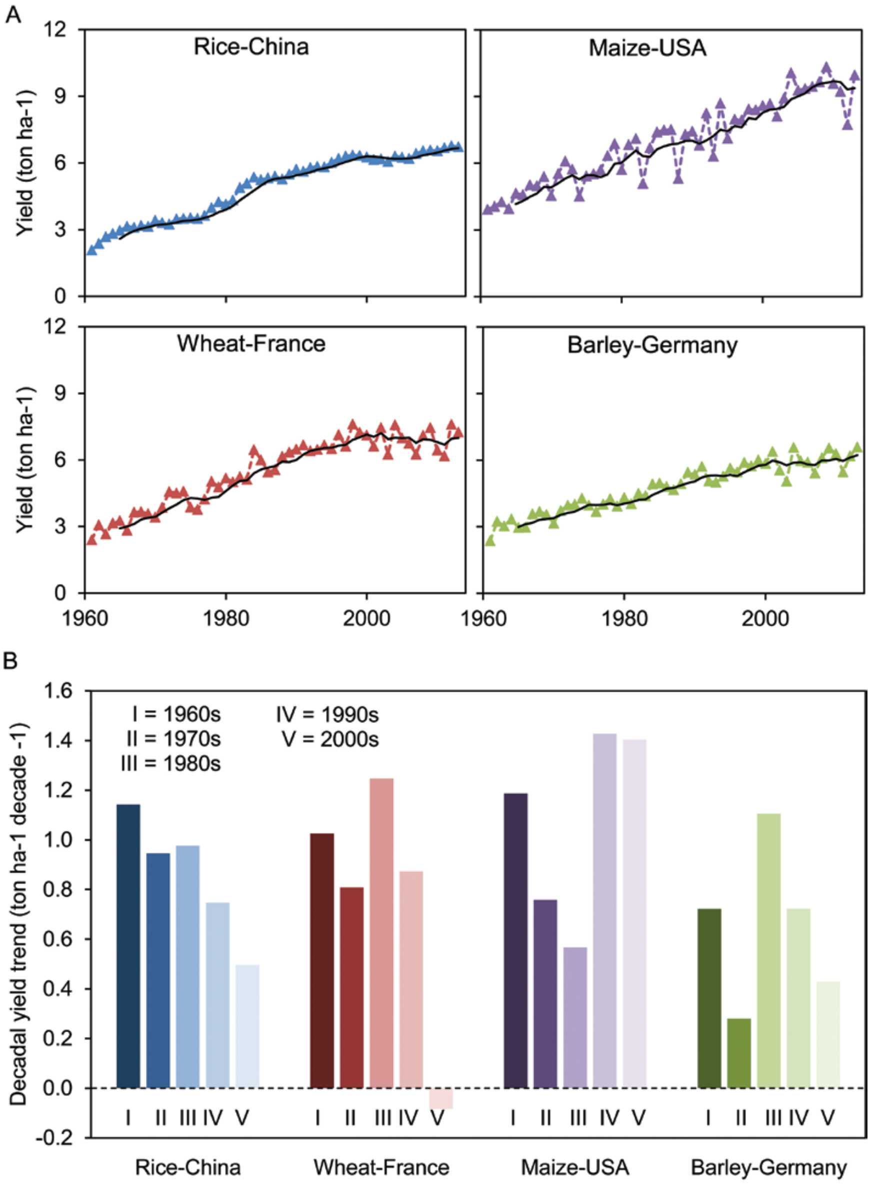

Fig. 1. Yield trends for selected cereal crops and countries from 1961 to 2013 (based on FAOSTAT 2014). **(A)** Annual (triangles) and 5-year moving average (black line) yields and **(B)** decadal yield changes (based on the linear regression line fitted to 10 years of data, see also Lobell and Gourdji, 2012). (This figure is available in colour at JXB online.)

crop management, like unfavourable weather conditions, during sowing and harvest. Agroclimatic indicators analyse the broad-scale sensitivity of agricultural systems to climate change, examine shifts in agricultural conditions, and quantify the challenges of agricultural production under climate change, thereby providing valuable information about effective crop management, breeding, and adaptation strategies. Applications of this approach can be found in studies at the national scale by Hakala *et al.* (2012), Lalic *et al.* (2013), and Rötter *et al.* (2013b), and most recently by Trnka *et al.* (2014) for wheat cultivation in Europe. The last study specifically evaluates the changing frequency of the occurrence of multiple climate-related stresses during the growing season and draws a comprehensive picture of the climatic challenges crops have to cope with under a changing climate.

The study by Rötter *et al.* (2013b) used the agroclimatic indicator approach to assess climatic risks (heat, drought, frost, etc.) to barley cultivation in Finland for current and future climates. Fig. 4 presents a synthesis with focus on shifts of climate risk zones as defined by combinations of different heat and drought stress levels—from current (1971–2000) to a future (a projection for 2041–2070) climate. Such mapping of climate risk zones can guide ideotype breeding.

5. Model-aided evaluation of cultivar suitability and ideotype design for the future

5.1 Summary

Here, we first report evaluations of cultivar suitability under projected future climatic conditions using crop simulation models (subsection 5.2). We then present selected studies

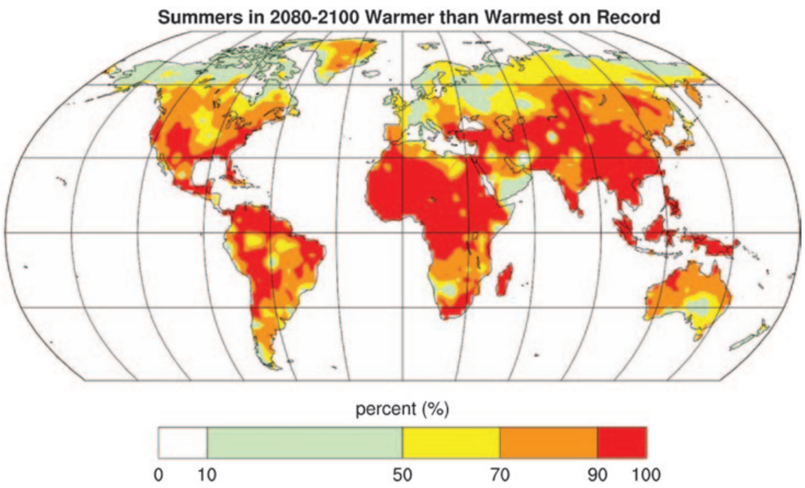

Fig. 2. Likelihood (in percent) that future summer average temperatures (for 2080–2100) will exceed the highest summer temperature observed on record. For example, for places shown in red there is greater than a 90% chance that the summer averaged temperature will exceed the highest temperature on record (1900–2006). From Battisti and Naylor. 2009. Historical warnings of future food insecurity with unprecedented seasonal heat. Science, **323**, p 242. Reprinted with permission from AAAS.

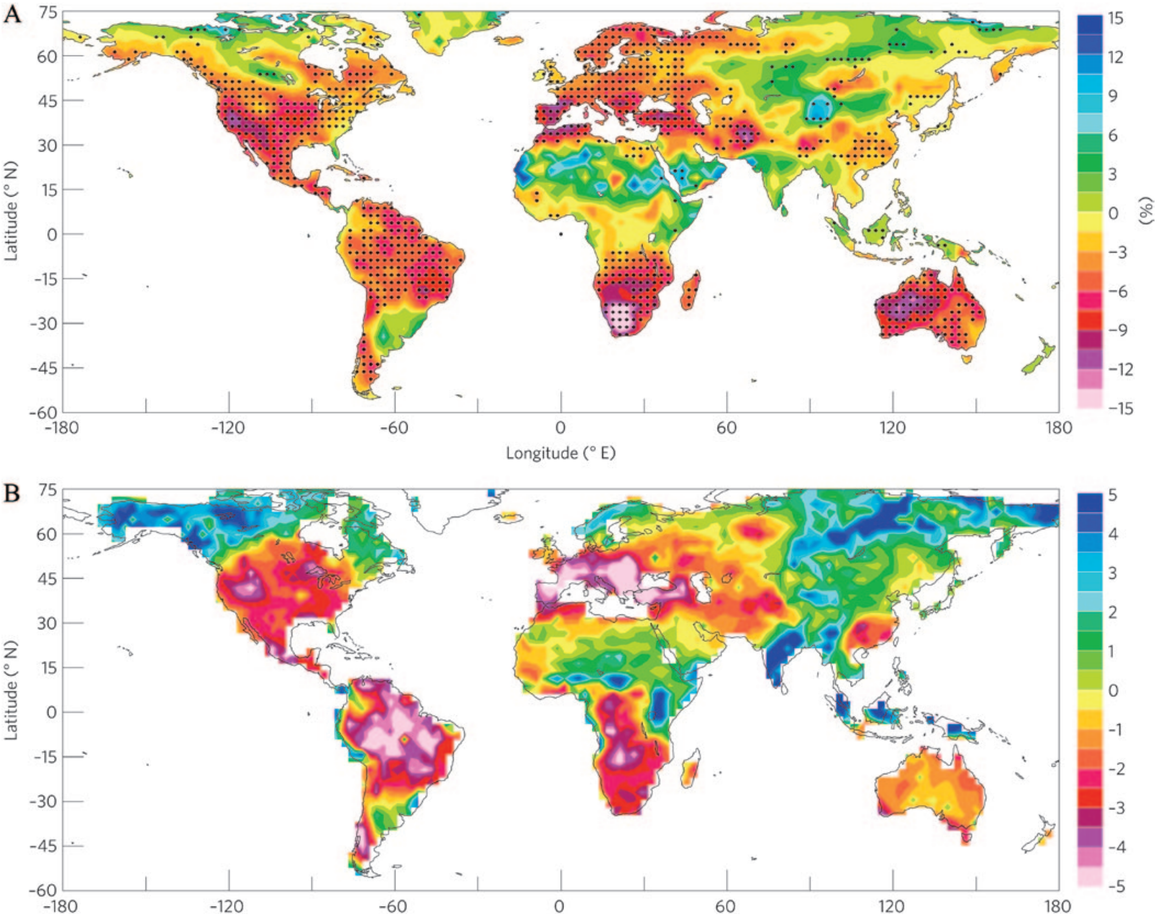

Fig. 3. Future changes in soil moisture and the self-calibrated Palmer drought severity index (PDSI) with potential evapotranspiration estimated using the Penman-Monteith equation (sc_PDSI_pm). **(A)** Percentage changes from 1980–1999 to 2080–2099 in the multi-model ensemble mean soil-moisture content in the top 10 cm layer (broadly similar for the whole soil layer) simulated by 11 Coupled Model Intercomparison Project Phase 5 (CMIP5) models under the representative concentration pathway 4.5 (RCP4.5) emissions scenario. Stippling indicates at least 82% (9 out of 11) of the models agree on the sign of change. **(B)** Mean sc_PDSI_pm averaged over 2090–2099 computed using the 14-model ensemble mean climate (including surface air temperature, precipitation, wind speed, specific humidity, and net radiation) from the CMIP5 simulations under the RCP4.5 scenario. A sc_PDSI_pm value of −3.0 or below indicates severe to extreme droughts for the present climate, but its quantitative interpretation for future values in B may require modification. From Dai. 2013. Increasing drought under global warming in observations and models. Nature Climate Change, **3**, 54. Reprinted with permission from Macmillan Publishers Ltd: Nature Climate Change, copyright 2013.

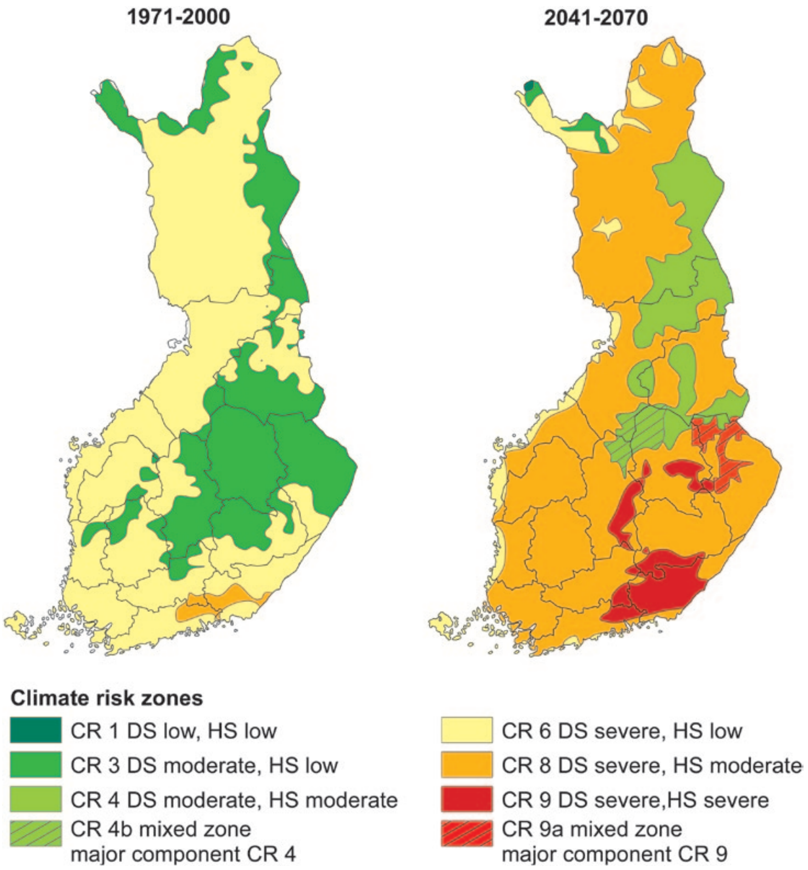

Fig. 4. Illustrative example of shifts in climate risk zones for cereal cultivation in Finland (constructed based on Rötter *et al.*, 2013b. Modelling shifts in agroclimate and crop cultivar response under climate change. Ecology and Evolution **3**, 4197–4214).

on model-aided crop ideotype design, and conclude with a success story of communication and collaborative research among crop modellers, agronomists, and plant breeders for rice ideotype breeding (1991–2005). Whereas only a few selected ideotype modelling studies are presented here, a more comprehensive overview of related studies and papers is provided in Supplementary Table S1. Finally, an outlook is provided on possible future expansions of modelling, from mere simulation of phenotypic traits to linkages with genetic modelling and quantitative trait loci (QTL) mapping in order to establish a modelling platform allowing more effective support to ideotype breeding.

5.2 Evaluating performance of different cereal cultivars under climate change

Tao and Zhang (2010) applied a super-ensemble-based probabilistic projection system (SuperEPPS) to estimate maize productivity and actual evapotranspiration over the GP in the 2050s in the North China Plain, and to examine the relative contributions of various adaptation options. Based on a large number of simulation outputs from SuperEPPS, results showed that without adaptation maize yield could decrease on average by 13–19%, and evapotranspiration during the GP could decrease by 16–22%, relative to 1961–1990. In comparison to this simulation experiment without adaptation, the yield of high-temperature-sensitive varieties of maize could on average increase by 1–6% when adopting early planting, 10–15% by fixing variety growing duration, and 4–6%, by adopting late planting. Using high-temperature-tolerant varieties would increase average maize yield even more. The spatial patterns showed that the relative contributions of adaptation options can be geographically quite different, depending on the climate and crop cultivar properties. Suitable cultivars and adaptation options should be defined for a target environment. The biggest benefits will result from the development of new crop varieties that are high-temperature tolerant and concurrently have higher thermal requirements.

Hybrid vigour may help overcome the negative effects of climate change in rice. Madan *et al.* (2012) tested a popular rice hybrid (IR75217H); a heat-tolerant check (N22); and a common, wide-spread rice cultivar (IR64) for tolerance of seed-set and grain quality to high-temperature stress at anthesis at ambient and elevated [CO_2]. Under an ambient air temperature of 29°C (tissue temperature 28.3°C), elevated [CO_2] increased vegetative and reproductive growth, including seed yield, in all three genotypes. Seed-set was reduced by high temperature in all three genotypes, with the hybrid and IR64 equally affected and twice as sensitive as the tolerant cultivar N22. No interaction occurred between temperature and [CO_2] for seed-set. The hybrid had significantly more fertile spikelets at all temperatures than IR64 and at 29°C this resulted in a large yield advantage. At 35°C (tissue temperature 32.9°C) the hybrid had a higher seed yield than

IR64 due to the higher spikelet number, but at 38°C (tissue temperature 34–35°C) there was no yield advantage anymore. Grain gel consistency in the hybrid and IR64 was reduced by high temperatures only at elevated [CO_2], while the percentage of broken grains increased from 10% at 29°C to 35% at 38°C in the hybrid. It was concluded that seed-set of hybrids is susceptible to short episodes of very high temperature during anthesis, but that at intermediate tissue temperatures of 32.9°C higher spikelet number (yield potential) of the hybrid can compensate this to some extent. If the heat tolerance from N22 or other tolerant donors could be transferred into hybrids, yield could be maintained under the higher temperatures predicted with climate change (Madan *et al.*, 2012).

5.3 Model-aided ideotype design

Crop growth and development results from many interacting (partly counteracting) biochemical, morphological, and physiological processes taking place at different temporal and spatial scales at the plant/crop level (Martre *et al.*, 2015). Crop modellers have in the past collaborated with agronomists, breeders, and geneticists on different cereal crops and developed different approaches for (i) better predicting the performance of given cultivars under different environmental conditions, and/or for (ii) crop ideotyping in order to support design of new cultivars better suited to specified target environmental conditions (e.g. Aggarwal *et al.*, 1997; Haverkoort and Kooman, 1997; Martre *et al.*, 2015; Tardieu, 2003).

The concept of plant type or ideotype breeding was first introduced and applied to rice (Donald, 1968; Jennings, 1964), as was the first model-aided ideotype design (Dingkuhn *et al.*, 1991; Khush, 1995), and, eventually, the first successful realization of ideotype breeding with the super hybrid rice variety 'Lianyoupeijuu' (see Section 5.4). Not surprisingly, the ideotype design was first realized for irrigated rice, as in the absence of water stress ideotyping is easier and more straightforward than for rain-fed cultivation environments (e.g. Semenov *et al.*, 2014).

5.3.1 Ideotype design for irrigated rice

There was a severe and steady yield decline during the late 1970s and 1980s in the Long-Term Continuous Cropping Experiment at IRRI, Los Baños. This is the world's longest-running experiment on triple-cropped rice, started in 1963 and representing the intensive flooded tropical lowland rice systems of Asia (Dobermann *et al.*, 2000). In response to this, scientists at IRRI initiated a research programme on an NPT (or ideotype) with higher yield potential. In this programme, crop modellers, breeders, and agronomists closely collaborated to break the yield barrier for irrigated rice that had existed since the introduction of IR8, the first semi-dwarf, high-yielding rice variety released for the tropical irrigated lowlands (Peng *et al.*, 1994). This indica inbred rice variety has a climatic yield potential of 8–9 tonnes ha^{-1} during the dry season (Dobermann *et al.*, 2000). The research ultimately aimed at enhancing the average farm yield of irrigated rice land to meet future demands (Khush, 1995; Peng *et al.*, 2008).

The major constraints to yield improvement were identified to be limited sink size, too many unproductive tillers, and lodging susceptibility. Based on this, Dingkuhn, together with crop modellers from Wageningen University and breeders from IRRI, developed a narrative of the desired morphological and physiological traits (Khush, 1995). First, computer simulation experiments were conducted for an *ex ante* evaluation on expected yield gains from the 'designed' NPT. Traits were implemented as sets of crop parameters in a Simple and Universal Crop Growth Simulator type of crop growth simulation model for rice (Dingkuhn *et al.*, 1991; Peng *et al.*, 1994). Simulation results suggested that a 25% increase in yield potential was possible by modifying the current indica plant type according to Dingkuhn's storyline or 'wish list' for the NPT, which included (i) enhanced leaf growth with reduced tillering; (ii) reduced leaf growth and greater foliar N concentration, mainly during the reproductive stage; (iii) steeper slope of the vertical N concentration gradient in the leaf canopy, with a greater share of leaf N in the top three leaves; (iv) increased carbohydrate storage in the stem; and (v) greater reproductive sink capacity with extended grain-filling period. (For details, see Dingkuhn *et al.*, 1991; Peng *et al.*, 1998). Fig. 5 (obtained from Sharma *et al.*, 2013, based on Khush, 1995) illustrates rice ideotype changes from traditional or 'pre-green revolution' plant type to the semi-dwarf plant type as, for example, introduced with IR8, NPT as designed in the early 1990s (Dingkuhn *et al.*, 1991), and fully realized in 2001–2005 in China (Yuan, 2001; Peng *et al.*, 2008) (see Section 5.4).

5.3.2 Ideotype design for wheat

Semenov *et al.* (2014) applied wheat simulation model Sirius to optimize wheat ideotypes for the main wheat growing areas in Europe under future climate scenarios. Special attention was paid to ensure that these ideotypes either avoided or better tolerated projected future drought stress by adjusted phenology, as well as exhibiting improved photosynthetic and 'stay green' properties of leaves under drought conditions.

The authors defined a wheat ideotype as a set of selected cultivar parameters related to photosynthesis, phenology, crop canopy characteristics, and water relations. By changing parameters from given value ranges and optimizing them for yield in response to changing climate or environmental conditions, ideotypes were defined that showed the best yield performance under well-defined future conditions. The exercise resulted in the following: while the extension of post-anthesis thermal requirements would allow higher dry matter production and grain yield, exposure to heat stress at anthesis would become more frequent. Presently, use of heat-escaping shorter-duration cultivars comes at the cost of lower yields. Conclusions based on both simulation results and associated controlled heat and drought experiments were that increased wheat yield potential under projected climate change can only be realized by new cultivars with increased tolerance of heat and drought stress.

One shortcoming of the analysis was that in the optimization much attention was paid to increase yield level but little to maintain yield stability. Additionally, only one climate model

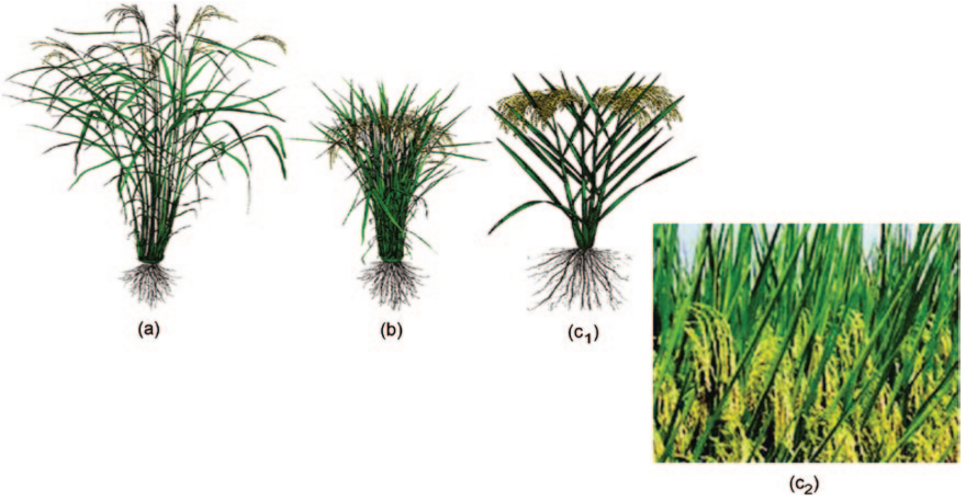

Fig. 5. Suggested ideotype changes for continued improvement of rice yield. (a) Traditional plant type, tall with much biomass allocated to leaves and (weak) stems. (b) Semi dwarf plant type, more tillers, short and sturdy stems. (c_1) New plant type as designed in the early 1990s, reduced tiller number and increased stem sturdiness. (c_2) Fully realized new plant ideotype super hybrid rice variety 'Lianyoupeijiu' with desired properties. Modified from Figure 1 and Figure 3b by Sharma *et al.* 2013. Tailoring rice plants for sustainable yield through ideotype breeding and physiological interventions. African Journal of Agricultural Research **8**, p 5007 and p 5019,

was used for projecting future conditions; hence neglecting the considerable uncertainty range from climate modelling for the ideotyping.

The study by Semenov *et al.* (2014) convincingly demonstrates the benefits of conventional crop simulation modelling for breeding as a framework for the design and *ex ante* evaluation of new ideotypes (Zheng *et al.*, 2012) and presents state-of-the-art results for this. While the approach presented in this study has shown to be useful for selecting the most appropriate traits for improving crop performance, it still lacks the connection of model parameters to genetic information—the ultimate goal of model-aided phenotyping (or ideotyping) (Hammer et al,. 2006; Martre *et al.*, 2015). The next two studies on maize and barley, however, go a step further, already illustrating promising future directions for how to expand conventional crop simulation for breeding.

5.3.3 QTL-based model prediction of leaf elongation rate in maize

To design maize ideotypes suited to different climatic conditions, Reymond *et al.* (2003) set out to identify the sources of the genetic variability in maize response to water deficits. Focusing on the trait leaf elongation rate (LER) in maize, Reymond *et al.* (2003) were able to demonstrate the potential of combining process-based crop growth simulation and genetic mapping for predicting genotype–environment interactions. While conventional crop simulation models are able to estimate quantitative traits of one genotype in any environment, QTL models are restricted to estimating the contribution of alleles to quantitative traits for just a few environments. QTL analysis was performed for parameters of a linear model (derived from experimental data) for predicting LER as determined by meristem temperature, water vapour pressure, and soil water status. QTL information was used to determine parameter values of the crop simulation model. Results of this combined approach showed that LER of individuals were well predicted for alternative climatic (i.e. different experimental) conditions: the combined model accounted for 74% of the overall variability of LER.

Although the efficiency of plant breeding has been considerably enhanced by use of molecular markers, which allow complex traits to be deciphered and allocated to QTL (Paterson *et al.*, 1988), a major obstacle still is that QTL mapping is not yet capable of satisfactorily extrapolating QTL information from one environment–management situation to new, independent conditions (Martre *et al.*, 2015), especially for complex adaptive traits (Hammer *et al.*, 2010). This obstacle could be overcome by combining crop growth simulation and genetic mapping into an expanded QTL-based crop model (e.g. Yin *et al.*, 2003) (see also Fig. 6).

5.3.4 QTL-based model prediction of flowering in barley

Schweizer and Stein (2011) reported that barley is emerging as a model for studying the genetics of stress adaptation, because QTL (Paterson *et al.* 1988) and candidate genes for biotic and abiotic stress tolerance (Dawson *et al.*, 2015) have already been identified. Yin *et al.* (2005a,b) present an early example of examining the feasibility of combining crop simulation (ecophysiological) modelling and genetic mapping for predicting or extrapolating the performance of individual spring barley genotypes under new environmental conditions. Similar to Reymond *et al.* (2003), Yin *et al.* (2005b) focused on a relatively simple trait, 'days to flowering'. Based on previous work on coupling information from QTL analysis of traits with simulation models (Yin *et al.*, 2000; 2005a), the phenology sub-model was fed with QTL information to predict flowering time in barley. In the model, flowering was simulated as a function of temperature and photoperiod. A test of the model showed that a high percentage of the observed variation in flowering time of individual genotypes exposed to a range of environmental conditions could be predicted by a combined approach of QTL mapping and simulation

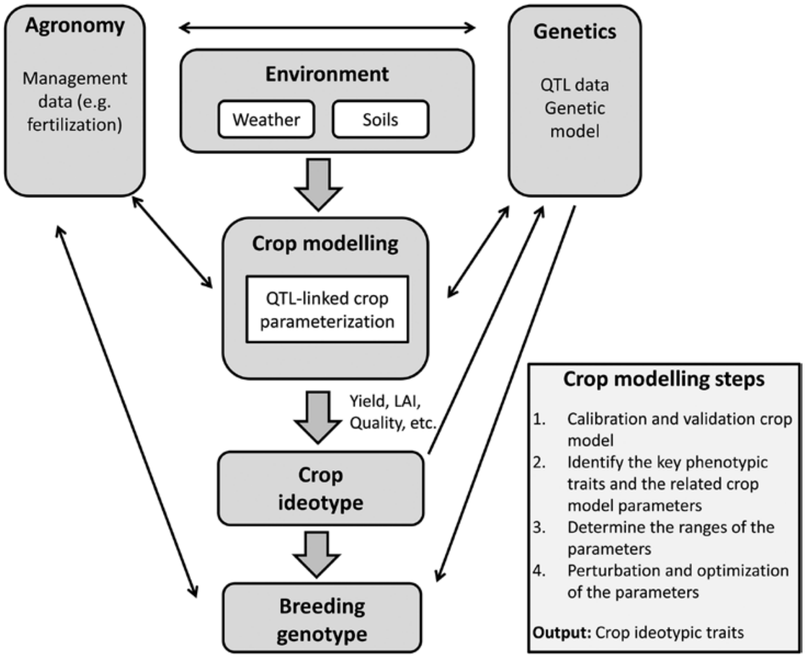

Fig. 6. Proposed model-based framework and its main elements to support effective breeding of climate-resilient crop cultivars. LAI, leaf area index. (This figure is available in colour at JXB online.)

modelling. This demonstrated that the combined approach is, in principle, capable of extrapolating QTL information from one environment to another (Yin *et al.*, 2005a,b).

A wider collection of related modelling studies on phenotyping and ideotype design of cereals and other food crops is presented in Supplementary Table S1.

5.4 Early success story of collaborative research on ideotype breeding

The ideotype approach has been used in breeding programmes at the IRRI and in China, especially since the end of the 1980s, to improve rice yield potential. First-generation NPT lines developed from tropical japonica at IRRI had a low yield because of limited biomass production and poor grain filling (Khush, 1995). This breeding effort had aimed to realize some of the changes in traits suggested by early model-aided ideotype design (Dingkuhn *et al.*, 1991; see Section 5.3.1). But soon thereafter, progress was made in second-generation NPT lines developed by crossing elite indica with improved tropical japonica. Several second-generation NPT lines out-yielded the first-generation NPT lines and indica check varieties (Peng *et al.*, 2008). Inspired by IRRI's NPT breeding, China's super hybrid rice breeding project (Yuan, 2001) developed many F1 hybrid varieties using a combination of the ideotype approach and inter-subspecific heterosis. These hybrid varieties produced grain yield of 12 tonnes ha^{-1} in on-farm demonstration fields, 8–15% higher than the hybrid check varieties. The success of China's super hybrid rice was partially the result of assembling the good components of IRRI's NPT design in addition to the use of inter-subspecific heterosis. For example, both designs focused on large panicle size, reduced tillering capacity, and improved lodging resistance. More importantly, improvement in plant type design was achieved in China's super hybrid rice by emphasizing the top three leaves and panicle position within a canopy in order to meet the demand of heavy panicles for a large source supply. The success of super hybrid rice breeding in China and progress in NPT breeding at IRRI together led to the realization of the NPT in the form of super hybrid rice variety 'Liangyoupeijiu', released in 1999 (Fig. 5) (Yuan, 2001; Sharma *et al.*, 2013). This success gives evidence that the ideotype approach has been effective for breaking the yield ceiling of irrigated rice crop (Peng *et al.*, 2008).

6. Synthesis and outlook

6.1 Synthesis

Various lessons can be drawn from this review: one of the biggest current challenges in plant sciences is to establish firm links between genotype and the associated phenotypic variation in different environments. Various studies have shown that process-based crop simulation models can help to build such links. Crop modelling can support breeding with a longer perspective, by showing the alternative and variable future cultivation conditions or future target environments on which the breeding efforts should be focused. While deficiencies in representing phenotypic traits and adequately capturing effects of climatic variability and extremes are still seen as main limitations of crop simulation modelling in the context of aiding ideotype design, there is progress in eliminating these.

As highlighted in this review, studies from different parts of the world have shown that crop cultivar characteristics and cultivar responses to weather have changed considerably in past few decades and that breeding has continued to help adaptation to changed conditions.

A couple of studies have demonstrated that simulation of phenotypic traits can be successfully linked to genetic modelling and QTL mapping. An early success story for rice (section 5.4) underpins the potential of crop simulation modelling for ideotype breeding when used in a collaborative process involving crop modellers, breeders, and agronomists.

Yet, while there has been progress in improving ecophysiologcial crop models and linking them to genetic modelling, the limitations of such linked modelling approaches are still substantial, challenging scientists from the various disciplines to make concerted efforts for overcoming them. In our view, it is not only that these models lack the capability to adequately capture effects of climatic variability and extremes, but also, still in many cases, the accuracy of the process descriptions is inadequate and uncertainties related to the model design and parameters affect their usability for ideotype design.

The *ex ante* analysis of crop phenotypes is a goal that is shared by agronomists, breeders, crop modellers, and geneticists/molecular biologists. However, there have only been a few cases in which scientists representing the different disciplines have communicated and worked together towards this common goal, which has most likely considerably delayed progress in the design and delivery of new crop cultivars.

Thus, a key question is: how can the delivery of new, more climate-resilient cultivars be accelerated and become more effective through collaborative research?

6.2 Outlook

In our view, several gaps need to be overcome in modelling and the integration of data and knowledge from the various disciplines for enhancing design of crop ideotypes.

Current crop simulation modelling considers phenotypic properties only. To better serve the goal of reliably linking genotype with phenotype expressions, crop simulation models need to be refined to account for cultivar traits, especially with respect of those related to various stresses and canopy architecture (for example, a three-dimensional canopy model can be useful). The linkages between crop model simulation of phenotypic traits with genetic modelling and QTL mapping need to be enhanced.

Close collaboration between agronomists, breeders, crop modellers, and geneticists/molecular biologists needs to be enhanced. The Joint Research Programming Initiative on Agriculture, Food Security and Climate Change (FACCE-JPI) project ClimBar, 'An integrated approach to evaluate and utilise genetic diversity for breeding climate-resilient barley', is a recent example where such efforts for strengthening interactions is underway.

Eventually, an ideotype designing platform should be set up, integrating the knowledge of all the stakeholders such as agronomists, breeders, crop modellers, and geneticists/molecular biologists. Such an approach would exploit the potential of crop models as tools for synthesis and planning. A look into the future of linked phenotypic-genotypic simulation modelling is sketched in Fig. 6. Linkages between the elements of a (virtual) modelling platform for crop ideotyping are indicated. The steps of model-aided crop modelling as performed for the barley cultivar design simulation experiment (briefly described below) are shown in the legend to Fig. 6.

In an attempt to further illustrate the way ahead, we refer to a crop simulation exercise that was recently launched in the framework of the European knowledge hub MACSUR (Ewert *et al.*, 2014) that aims at supporting crop ideotyping for future climates in Europe. The novelty of this project is the collaborative modelling with molecular biologists/geneticists. The study is restricted to barley ideotyping and two current target environments, south-west Finland and north-east Spain—with multiple future environments (three climate scenarios for each). Trait goals for the envisaged ideotype are likewise limited to improvements in its ability to cope with only two specific climate-induced stresses, heat and drought. The range of stresses to be considered in model-aided ideotyping can, of course, be varied.

Analytical steps of the barley cultivar design study (Fig. 6) are as follows:

Step 1. Define the most important crop parameters of the simulation model for rough adaptation targets (e.g. heat, drought, frost, or combination of these).
Step 2. Define potential value ranges for each selected parameter based on what is considered to be possible within the given time frame. Ranges are refined in consultation with molecular biologists/geneticists.
Step 3. Perform simultaneous crop parameter perturbations according to a predefined sampling scheme.
Step 4. Run simulations for baseline climate and for three different future climates using perturbed parameter sets.
Step 5. Optimize parameters: this leads to the identification of ideotypes. In the optimization process, certain criteria are taken into account, such as high long-term (30 years) mean yields, subject to the restriction that inter-annual yield variability (coefficient of variation or other) is not higher than for the reference climate, and that water-use efficiency is within a reasonable range.
Step 6. Perform post-model synthesis: identify desirable ideotypes and cross-check on feasibility with breeders and molecular biologists/geneticists.

For steps 1–5 we apply a multi-model ensemble approach to test the robustness of estimates of future traits. In step 6, the results are examined for the ideotypes with the most desirable traits according to performance and optimization. To check for feasibility, crop model-based ideotypes are confronted with results from gene-mapping (by molecular biologists/geneticists) and discussed; infeasible model-based solutions are discarded and the next ideotypes in the ranking are then checked for feasibility.

Rötter *et al.* (2013a) have further suggested the value of combining model-aided crop ideotype design with comprehensive uncertainty analysis comprising three elements: (i) ensemble crop modelling, (ii) climatic sensitivity analysis (perturbations of temperature, precipitation, [CO_2]) with current and new cultivars using the impact response surface method, and (iii) overlaying the impact response surface methods with probabilistic information on climate change.

During 2014, work on model-aided ideotyping in MACSUR was presented to leading molecular biologists from the new FACCE-JPI–funded project ClimBar. Although barley is an important crop of multiple uses, yield increase in Europe has flattened over recent years and future harvests are likely to be threatened by climate change. ClimBar aims to identify genome regions, genes, and alleles conferring the traits needed to breed resilient barley varieties adapted to different climate change scenarios modelled for the main grain-producing zones in Europe (i.e. north-east, north-west, Mediterranean, and Central) by 2070 (Dawson *et al.*, 2015). In this endeavour, ClimBar is establishing high-throughput phenotyping platforms (Yang *et al.*, 2013) that will further the development of genotype–phenotype crop modelling (Fig. 6).

Mutual benefits of collaboration between ClimBar scientists and crop modellers from MACSUR were discussed. The views and expectations substantially helped to shape the proposed model-based framework as well as the envisaged mode of collaborative research depicted in Fig. 6.

Supplementary data

Table S1, containing a collection of studies on phenotyping and ideotype design of cereals and other food crops, adds to the few key studies presented in section 5.

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