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Title: Identifying traits for genotypic adaptation using crop models

Running title: Modelling traits for adaptation

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Significance statement

We review state-of-the art genotypic adaptation modelling and suggest potential avenues to better realise the potential of model-based studies of genotypic adaptation for guiding future crop breeding efforts.

Abstract

Genotypic adaptation involves the incorporation of novel traits in crop varieties so as to enhance food productivity and stability and is expected to be one of the most important adaptation strategies to future climate change. Simulation modelling can provide the basis for evaluating the biophysical potential of crop traits for genotypic adaptation. This review focuses on the use of models for assessing the potential benefits of genotypic adaptation as a response strategy to projected climate change impacts. We first review some key crop responses to the environment as well as the role of models and model ensembles for assessing impacts and adaptation. Finally, we describe how crop-climate models can help focus the development of future-adapted crop germplasm in breeding programs. While recently published modelling studies have demonstrated the potential of genotypic adaptation strategies and ideotype design, we argue that for model-based studies of genotypic adaptation to be used in crop breeding, it is critical that modelled traits are better grounded in genetic and physiological knowledge. To this aim, two main goals need to be pursued in future studies: (1) a better understanding of plant processes that limit productivity under future climate change; and (2) a coupling between genetic and crop growth models –perhaps at the expense of number of traits analysed. Importantly, the latter may imply additional complexity [and likely uncertainty] in crop modelling studies. Hence, appropriately constraining processes and parameters in models and a shift from simply

quantifying uncertainty to actually quantifying robustness towards modelling choices are two key aspects that need to be included into future crop model-based analyses of genotypic adaptation.

Keywords: climate change, impacts, genotypic adaptation, ideotypes, crop models

1. Introduction

Agriculture is one of the most vulnerable sectors to changes in climates, due to its reliance on adequate environmental conditions for achieving high productivity (Huntingford *et al.*, 2005). Crops are affected by shortages or excesses of water or excessively high or low temperatures during key periods of their growing cycle (Porter and Semenov, 2005). Effects from adverse environmental conditions have been largely studied and reported by several authors, using combinations of models and data (Allen *et al.*, 2005; Boote *et al.*, 2005). This understanding, in addition to well-constrained and skilful simulation models can provide insights on what could happen under future climate scenarios of higher temperatures, changing precipitation patterns and increased likelihood of extremes.

Although figures are varied, recent literature indicates that negative impacts are expected to affect the basic food basket (i.e. wheat, rice, maize and grain legumes), as well as major cash crops (i.e. sugarcane, coffee, cocoa) at moderate or low (≤ +3 ºC) levels of warming if no adaptation actions are taken (Lobell *et al.*, 2008; Porter *et al.*, 2014; Challinor *et al.*, 2014*b*). Evidence from regional and local studies as well as global meta-analyses of modelling studies indicates that adaptation strategies are critical in countering any negative and/or capitalising positive effects that may arise as a result of climate change (Claessens *et al.*, 2012; Challinor *et al.*, 2014*b*). Adaptation strategies are likely the only means by which food availability and stability can be maintained and/or increased so as to meet future food security needs. In fact, recent model-based global estimates indicate that even incremental adaptation strategies could result in mean yield increases of ~7 % at any level of warming (Porter *et al.*, 2014; Challinor *et al.*, 2014*b*). This suggests that substantial opportunities may exist if deeper (i.e. systemic and transformational) changes in cropping systems are implemented.

This review focuses on one such strategy, namely, genotypic adaptation. Genotypic adaptation involves the incorporation of novel traits in crop varieties so as to enhance food productivity and stability and, more broadly, also the design of crop ideotypes (i.e. crop plants with ideal traits) for future climates (Donald, 1968; Semenov and Stratonovitch, 2013). Specifically, we review the use of models for the development of genotypic adaptation options. We first examine some important crop responses to key environmental factors. Secondly, we examine two aspects of climate impacts research: (1) the different approaches to climate change adaptation, and (2) the importance of models for developing adaptation options. We then describe existing models and provide recommendations so as to capitalise on the potential of using crop model ensembles for understanding crop responses and adaptation options under future climate scenarios. We finally describe how crop-climate models can help focus the development of future-adapted crop germplasm in breeding programs. In doing so, we review past experiences and recent trends in the crop modelling literature. We conclude by proposing a framework that mainstreams crop model-based analyses into future breeding strategies.

2. Key plant processes and crop responses to varying environmental factors

In large areas, climate signals are discernible for many crops and regions even when aggregated growing season information is used (Fig. 1). Signals in such areas reflect crop plant responses to variations in weather and climate at local scale. Some of these responses are discussed in detail below.

[Figure 1 here]

A balance exists in the plant-soil-atmosphere interaction so as to allow enough carbon uptake for plant growth, prevent desiccation due to excess transpiration, and maintain canopy and leaf temperatures at near-optimum levels (Huntingford *et al.*, 2005; Lobell *et al.*, 2013). Stomatal conductance, a key factor regulating plant growth, is highly correlated with net photosynthesis (Wong *et al.*, 1979) and is affected by air moisture deficit (i.e. vapour pressure deficit –VPD), radiation intercepted, leaf temperatures, ambient CO_2 concentrations, and soil moisture. However, both temperature and air and soil moisture conditions operate against plant growth and also against each other in ways that are often difficult to understand.

Mean air temperatures drive canopy and leaf temperatures, which are determinant for photosynthesis. Photosynthetic efficiency varies with temperature in all crop species because it affects RuBisCO (Ribulose 1,5 biphosphate carboxylase oxygenase) activity, and in turn intercellular CO_2 concentration and stomatal conductance (Hew *et al.*, 1969; El-Sharkawy, 2014). Response of photosynthesis to temperatures varies by species (Fig. 2A). Mean temperatures also drive crop development rates and thus define crop duration (Fig. 2B), which in turn affects total photosynthetically active radiation (PAR) intercepted –

linearly related to total biomass production. Daily extremes of temperature reduce crop yield mostly through damage to plant reproductive organs (Fig. 2C) (Peng *et al.*, 2004) and hastened senescence (Asseng *et al.*, 2011). However, complex responses and interactions occur throughout the cropping cycle. For an example: under optimal temperatures and water availability, photosynthesis and transpiration from leaves occur at normal rates; however, under high temperatures plants open their stomata to avoid heat stress, which increases within-leaf CO_2 concentrations and thus biomass accumulation (exception being made under high VPD conditions –dry air, as in such a case stomata would remain closed to avoid excessive transpiration). If the available soil water is limited, this induces desiccation and stomata are then closed. Drought causes desiccation and stomatal closure, but at the same time water is a direct input of photosynthesis and so the effects on carbon fixation are more direct than those of temperature. In addition, stomatal closure causes within-leaf CO_2 concentrations to decrease, thus decreasing inputs to photosynthesis, in some cases also increasing photorespiration (Kobza and Edwards, 1987). This causes lower biomass production and limits growth (Hew *et al.*, 1969; Huntingford *et al.*, 2005). Low light incidence (i.e. solar radiation) also reduces photosynthesis, whereas winds increase transpiration. Drought stress may be induced by increased osmotic pressure in saline soils. Many limiting conditions can occur simultaneously in a given site [e.g. Trnka *et al.* (2014)], thus making any prediction of their effect a challenging task.

[Figure 2 here]

The effects of increased CO_2 are beneficial for almost any food crop, with increased CO_2 concentrations thought to increase dry matter and thus yield (Leakey *et al.*, 2009).

However, there is contrasting experimental evidence on crop responses to enhanced CO_2 concentrations across varying degrees of soil water and air moisture availability (Long *et al.*, 2006; Tubiello *et al.*, 2007; Ainsworth *et al.*, 2008), despite advances in theoretical understanding (Ghannoum *et al.*, 2000; Leakey, 2009). Underlining experimental evidence on crop responses to elevated CO_2 concentrations is therefore needed, since most models incorporate effects in a fairly basic fashion –mainly through empirical factors to reduce assimilation. Particular attention must be placed on understanding the interactions between enhanced [CO_2] and other environmental controls (particularly drought and high temperatures), as these remain only partially understood (White *et al.*, 2011; Asseng *et al.*, 2013).

A large number of other factors exert control on plant growth and, particularly, on photosynthesis, biomass accumulation and yield. Leaf nitrogen (N) content is strongly and positively associated with carbon exchange rates (CER), radiation use efficiency (RUE) and total plant biomass (Sinclair and Horie, 1989). Similarly, low phosphorous (P) and potassium (K) contents can also lead to limited CER and biomass production (Longstreth and Nobel, 1980; Fredeen *et al.*, 1990). Limited availability of other nutrients (e.g. calcium, magnesium, sulphur, zinc, and iron, among others) can limit plant growth and reduce the nutritional quality of the harvested product, but research on their effects on plant processes is sparse. Responses to ozone concentrations (O_3) are expected to negatively affect leaf area dynamics, light interception and biomass allocation and accumulation, but data scarcity has precluded accurate simulation of this process (Ewert and Porter, 2000). Understanding, parameterising, and evaluating many of these responses in models is essential for impacts science.

3. Approaches for assessing climate impacts

Methods to assess impacts can be classified in projection-based approaches and utility-based approaches. Utility-based approaches (also known as decision-based approaches) focus on making decisions that are robust against the known uncertainties. This is usually done by exploring the outcomes of decisions under a number of plausible scenarios and then choosing those decisions whose outcomes are not affected by the underlying uncertainties (Vermeulen *et al.*, 2013). Projection-based approaches (also known as predict-then-act approaches) are based on the use of models and data to produce projections of a given system's future state that can be used by decision makers. Projection-based approaches therefore focus on reducing uncertainties in order to provide decision-makers with information that can be directly used to make a decision. As with most of the modelling literature, this review focuses on projection-based approaches. In the following sections, a summary of related methods is provided. For further discussion on decision-based approaches the reader is referred to Vermeulen *et al.* (2013).

In projection-based frameworks, typically, global climate model projections for one or more given forcing scenarios are first scaled and/or bias-corrected to produce climate scenarios. Crop models are then forced using these climate scenarios to produce a range of projections that are then used to conceptualise and develop adaptation strategies to be tested or implemented at different scales (from global to the field) (Fig. 3). Modelling choices across the framework shown in Fig. 3 are thus varied and can produce differing responses, thus causing uncertainty. It is expected for almost all steps in the impact assessment process that uncertainty will increase, although it can be reduced via model calibration and evaluation. The global meta-analysis of Challinor *et al.* (2014*b*) is particularly useful portraying some of the uncertainties to which impact projections are subjected.

[Figure 3 here]

4. The role of process-based models in estimates of climate change impacts and adaptation

The choice of both crop models and climate model projection types for climate change impact assessment varies substantially across modelling studies (White *et al.*, 2011). Nevertheless, the vast majority of projection-based studies focus on a site-specific scale and use process-based simulation models, though a recent trend exists for regional-scale studies that use simple (yet process-based) or statistical models (Ramirez-Villegas and Challinor, 2012). Rivington and Koo (2011) report the existence of 122 crop models –from which roughly a half are process-based. Due to the focus of this review, in this section, emphasis is placed on process-based models.

Process-based models are both the most diverse and the most complex of the two model types reviewed here and can themselves be divided into two categories according to scale and level of complexity: (i) regional-scale and (ii) field-scale. Regional-scale models have been designed to capitalise on large-scale crop-climate relationships and thus operate at scales commensurate with those of global and regional climate models (i.e. 25 – 100 km). Despite their reduced complexity, regional-scale models retain enough mechanistic detail in plant growth processes as to be used with reasonable confidence under future climate scenarios, including increased CO_2 concentrations, and higher rates of extreme temperature and drought events (Challinor *et al.*, 2004, 2007). Conversely, field-scale crop models are tools aimed to simulate growth processes in plants so that technological changes and environmental effects at the farm level can be assessed (El-Sharkawy, 2005). Initially, field-scale models were conceived with the objective of being perfect and comprehensive, and able to reproduce all plant functions [the 'universal model' myth, see Sinclair and Seligman (1996)], though they rapidly evolved into approaches that were theoretically coherent, yet different in their implementation and purpose (Affholder *et al.*, 2012). While the choice of which processes to represent in detail, and the level of detail achieved for a given process is limited by an understanding of crop physiology derived from available data (Craufurd *et al.*, 2013), it is also governed by research focus and intended model use. The guiding principle for designing abstractions in such models is to "*Use the right level of description to catch the phenomena of interest. Don't model bulldozers with quarks*" (Goldenfeld and Kadanoff, 1999).

4.2.1. Designing models for extensibility and correctness

There are three key aspects involved in the development and use of well-established process-based crop models – (1) the modelling of biophysical processes, (2) the selection and maintenance of technical methodologies, and (3) collaborative community support. Modelling biophysical processes involves choosing the right abstractions to map the interactions of genotype, management and environment to phenotypic traits of interest. The selection of technical methodology involves choosing programming languages, software environments, data formats, collaboration software, computing hardware, and protocols for maintaining model quality (e.g., automated testing) and uncertainty (e.g., model ensembles). Collaborative community support includes communication between developers of the model, between the modelling team and other expert modelling groups, and between model developers, users and the wider community of stakeholders (such as farmers, consultants and policy makers).

These key modelling aspects have been traditionally undertaken within individual research groups, often using ad hoc procedures –although with exceptions [e.g. the International Consortium for Agricultural Systems Applications, ICASA, White *et al*. (2013)]. However, two relatively recent developments have had a significant impact on the design and development of process-based crop models. First, a significant increase in available computer processing power has enabled ever-increasing complexity in the processes being modelled. 'Next generation' frameworks spanning processes from gene expression to climate change are becoming available (Holzworth *et al.*, 2014). Second, the rapid adoption of online tools has enabled global collaborative model development (McLaren *et al.*, 2009) and inter-comparison [AgMIP; Rosenzweig *et al.* (2013)], and changed expectations regarding the availability of model source code and data.

Contemporary process-based crop models are increasingly being used to combine sub-components (such as different crop types and genotypic traits) in novel ways. These models are typically not developed in isolation, but are the refinement and integration of pre-existing algorithms, data, and models [Fig. 1 in Holzworth *et al.* (2014)]. In addition, they are developed and tested in a variety of programming languages and computing environments, utilizing agronomical and climate data provided in a wide variety of formats.

This increased complexity of processed-based crop modelling, and the global, cross-disciplinary nature of model development, assessment, and use, has led to modelling groups adopting more formal techniques to support their research. In particular, to facilitate scientific reproducibility, sharing, inter-comparison and integration of sub-models and data, the crop modelling community is increasingly relying on tools and techniques from the software development community. The use of support tools such as wikis, source code version control and issue tracking (as in the GLAM, DSSAT and APSIM communities), online user interfaces (Hochman *et al.*, 2009), and the adoption of modular source code frameworks, is becoming more frequent. For example, the current APSIM process-based crop modelling framework (Holzworth *et al.*, 2014) employs (1) a modular software structure that allows components to be combined in novel ways at runtime, and to be improved and tested in isolation, (2) XML configuration files allowing model parameters and custom logic to be shared in a standardized way, and (3) the integration of scripting language control (including the R and C# languages) that facilitates quick prototyping and sharing of model logic.

While such developments are significant steps towards improved model sharing, uncertainty analysis, and code correctness, more work needs to be done. Automated testing, source code version control, and modular model structure are not yet ubiquitous process-based modelling practices. Standardization of common parameter names and their definitions would facilitate more complete model intercomparisons. Significant gains can be achieved through the adaptation of the software design patterns process (Gamma *et al.*, 1994) to document key crop modelling components such as biophysical processes, model structure, ensemble design, and model intercomparison, in a form independent of any specific implementation or programming language. The development of such patterns would help reduce the reinvention of solutions, encourage the use of state of the art procedures, and provide a community platform for crop model improvement.

4.2.2. The use of ensembles for informing impacts and adaptation

The aforementioned increase in the complexity and number of models, along with significant advances in the climate models used to drive regional-scale yield projections, has led to greater confidence in our model projections. However, increasing model detail has meant that uncertainty in projections is not being reduced [see, for example, Knutti & Sedlacek (2012)]. In addition, model simplifications (such as regional scale process-based, statistical, and niche-based models) have introduced their own uncertainties in terms of spatio-temporal scaling and specificity, and the inter-related lineage of process-based crop models complicates assessments of model uncertainty. As a result, an emphasis on quantifying the uncertainty in projected yields has become prevalent (Iizumi *et al.*, 2009; Asseng *et al.*, 2013). Crop predictions based on single parameter sets or single model output values are no longer good enough.

Consequently, projecting crop responses under future climate scenarios requires careful treatment of issues related to parameter uncertainty, structural uncertainty (model discrepancy), algorithmic uncertainty (code uncertainty), parametric variability, experimental uncertainty (observation error), and interpolation uncertainty (Kennedy and O'Hagan, 2001; Challinor *et al.*, 2009*a*). While accounting for all of these uncertainty sources is critical for the robust use environmental models in general, the tendency for crop models to be developed using information from one spatial scale, and applied at another, means that crop modellers must pay particular attention to parameter, structural, and interpolation uncertainty. An assessment of 178 published studies on climate change impacts (sourced by searching the keywords 'climate change impacts' in http://scholar.google.com in June 2014) indicates that field-scale, regional-scale process-based models, and statistical models are used at a variety of spatial scales (Fig. 4). For field-scale process based models, the fact that ca. 50 % of studies use the models at scales other than those for which the models were originally designed suggests some potential for model vs. study scale mismatch or even model misuse (Fig 4A). While mathematically one-dimensional models can be used across different spatial scales, remarkably, virtually no study using field-scale process-based models at scales beyond individual fields assesses parameter uncertainty or parameter scaling issues [Fig. 4B, e.g. Iizumi *et al.* (2014)]. More importantly, the implications of model misuse, including the use of models that lack key processes and scale mismatches, may impact further estimates of adaptation (Challinor *et al.*, 2014*a*; Lobell, 2014). This is of particular importance since about one in every three studies does not conduct model evaluation regardless of the type of model used (Fig. 4C).

[Figure 4 here]

In the last ten years, the critical task of quantifying and accounting for the full range of uncertainty sources in models has been recognized by the weather, climate, and hydrological communities (Stainforth *et al.*, 2005; Beven, 2006). However, there has been limited applied appreciation for these issues in the crop modelling community besides quantifying parameter (Iizumi *et al.*, 2009; Tao and Zhang, 2013) and structural uncertainty in impacts projections (Ruane *et al.*, 2013; Asseng *et al.*, 2013). While many crop-climate impact studies include some treatment of modelling uncertainty (e.g. by using various future climate projections, crop parameters, and crop models), sampling of the entire model and parameter space is fundamentally incomplete, and is likely to underestimate the importance of uncertainty in model-based projections of impacts and adaptation. Therefore, in order for the crop modelling community to move towards ensembles that better sample the uncertainty space and provide useful information for food security assessments, platforms that allow model, parameter and input transferability between groups and regions so as to facilitate ensemble simulations for both site- and regional-scale assessments need to be developed (also see Sect. 4.2.1). Additionally, characterising the crop model space [e.g. Angulo *et al.* (2013)] and better understanding of parameter and process scaling (Iizumi *et al.*, 2014) will ultimately allow for a better understanding and sampling of the model and parameter uncertainty space.

5. Design of genotypic adaptation strategies using crop models

5.1. The importance of genotypic adaptation

Genotypic adaptation is expected to be one of the most important adaptation strategies to future climate change (Challinor *et al.*, 2009*b*; Semenov and Stratonovitch, 2013). For instance, Challinor *et al.* (2014*b*) indicated that switching from currently grown to better-adapted varieties that are cultivated elsewhere or stored at genebanks ('cultivar adjustment') is a more effective adaptation strategy than adjusting planting dates, improving irrigation and enhancing fertilisation (Fig. 5). In addition, increased evidence exists that climate change stresses can, to a large extent, be managed or completely offset through the breeding of new "climate-smart" cultivars with improved yield potential and stability (Ortiz *et al.*, 2008; Semenov and Stratonovitch, 2013). Progress in crop breeding demonstrates the scales of potential yield gains. In Africa, two decades of maize breeding have led to mean genetic gains of 14 kg ha^{-1} year^{-1} under drought and 40 kg ha^{-1} year^{-1} under optimum conditions (Badu-Apraku *et al.*, 2013). Similarly, global mean wheat breeding gains in the last 25 years are about 100 kg ha^{-1} year^{-1} under drought and 25 kg ha^{-1} year^{-1} under optimum conditions (Gourdji *et al.*, 2013). For rice, genetic gains have been estimated in 45 kg ha^{-1} year^{-1} for Brazilian upland systems in the period 2002-2009 (Breseghello *et al.*, 2011), whereas in irrigated rice in Asia solely the release of the semi-dwarf rice variety IR8 produced an increase of almost 70 % in rice potentials during the 1950s and 1960s (Peng *et al.*, 2008).

[Figure 5 here]

Under future climate scenarios, ideotype design appears as key strategy to drive breeding decisions, since breeding towards a crop ideotype is more efficient than breeding to remove undesired characteristics one at a time (Peng *et al.*, 2008). Crop ideotypes are idealised plant types that have the greatest effectiveness in producing dry matter and yield under given environmental conditions (Donald, 1968). Defining a crop ideotype involves a definition of the physical-morphological (e.g. height, maximum leaf size, leaf thickness and positioning) and physiological (e.g. stomatal conductance, photosynthetic efficiency) characteristics of a given crop plant, that would allow such a plant to respond well under certain conditions (e.g. in a drought-prone environment). Breeding programmes are currently challenged with having to set priorities based on climate change impacts projections [see e.g. Cairns *et al.* (2013)]. Decisions of which traits to breed and by when would varieties need to hold such traits are expected to be largely influenced by the type (e.g. increase in mean, increase in extreme events), direction (e.g. drier and warmer, wetter and warmer), and extent (how warmer, how drier) of the projected climatic changes in a given area (Stamp and Visser, 2012). Many breeding programs, however, already work towards achieving crop ideotypes for different agro-environmental zones (Berry *et al.*, 2007; Peng *et al.*, 2008). Hence, progress towards better future food security prospects of increased food availability and stability through breeding better adapted crop varieties seems, at least in principle, possible to achieve.

5.2. The potential role of crop models for developing genotypic adaptation options

Process-based crop models can help make informed decisions with regards to genotypic adaptation options and ideotype design both under current and future climates (Baenziger *et al.*, 2004; Banterng *et al.*, 2004). The main challenge, however, is to carefully interpret modelling outcomes so as to provide information that is of use for breeders. Recent experiences in the use of crop model simulated ideotypes for crop breeding in rice as well as existing model-based investigations of genotypic adaptation and ideotype design reveal encouraging results with regards to increasing food availability and stability in the context of climate change adaptation.

Under current climates, probably the most notable example of ideotype design for increasing yield potential is the New Plant Type (NPT) proposed and developed by the International Rice Research Institute (IRRI) and the subsequent establishment of the *super* rice program in China inspired by the NPT (Cheng *et al.*, 2007; Peng *et al.*, 2008). IRRI's NPT had its origins on the work of Dingkuhn *et al.* (1991), who used a process-based growth simulation model to propose a rice ideotype. Based upon model simulations, they hypothesised that 25 % productivity gains could be achieved by increasing the length of the grain filling phase, maintaining high concentration of nitrogen in the leaves, increasing the vertical gradient of nitrogen in the foliage (so that top leaves have more N, and lower leaves have less), enhancing leaf growth in early stages and reduced leaf growth in later stages, larger panicles but reduced tillering capacity (i.e. lower number of panicles), more assimilates in the stems and longer life span and larger size of flag leaves (Dingkuhn *et al*., 1991). Since morphological characteristics are easier to select for in breeding trials, a more precise definition of these was done in a subsequent study (Khush, 1995) (Fig. 6). Two breeding cycles then led to the development of NPT varieties that outyielded check varieties (Peng *et al.*, 2008). Following IRRI's promising results, the *super* rice program in China was established (Cheng *et al.*, 2007). In addition to what had been proposed by IRRI's NPT breeding program, a more specific definition of the position and size of the flag leaves and an optimisation of photosynthetic efficiency were done. Newly developed *super* rice varieties reportedly outyielded commonly cultivated rice hybrids by 15-25 % in many regions of China (Peng *et al.*, 2008). Further research and development of ideotype rice cultivars and hybrids is currently being pursued both in China and internationally by IRRI.

[Figure 6 here]

Under future climates, on the contrary, to the knowledge of the authors, no breeding program is currently breeding a model-designed plant type; although the WHEAt and barley Legacy for Breeding Improvement (WHEALBI) appears as a new (started in eearly 2014) promising initiative. Nevertheless, the number of studies investigating genotypic adaptation through introduction of novel traits and ideotype design has been increasing in the last decade. All these studies point to the same direction: that in most situations genotypic adaptation can offset climate change-related losses and even boost crop yields. For instance, studies for wheat indicate that climate-ready varieties would outyield currently cultivated varieties by 25-65 % under future climates (Semenov *et al.*, 2014), and similar figures have been reported for other crops such as groundnut, sorghum and maize (Fig. 7). These figures are, however, contingent on two key modelling aspects:

(i) *The ability of the model to correctly simulate processes that are relevant in future climate scenarios*. The fact that all existing models have been subjected to varying degrees of evaluation mostly against agronomic trial data [e.g. Asseng *et al.* (2013), Bassu *et al.* (2014)] and many individual model components (e.g. water balance, photosynthesis response) are often assessed independently has increased confidence on the capabilities of models to simulate crop responses under varying environmental conditions, including climate change. Recent literature, however, indicates shifting climate distributions and increased likelihood of extreme events (Battisti and Naylor, 2009; Trnka *et al.*, 2014) and this may result in additional and/or different processes constraining future crop yields as compared to present-day conditions. Indeed, a recent review identified that only a handful (≤ 6) of crop models currently used in impact and adaptation studies simulate CO_2 impacts on canopy temperature (by computing a soil-plant-atmosphere energy balance), a key process under climate change (White *et al.*, 2011). It is thus not clear whether models already include sufficient detail so as to simulate any additional processes that may arise from projected climate change. This has in turn resulted in the need for additional field experiments in which novel conditions and their interaction are evaluated and then tested in multi-model intercomparison frameworks (Rosenzweig *et al.*, 2013). While these initiatives are clearly a way forward, individual-study assessments of processes and their interactions in single-model and multi-model ensemble simulations as well as more complete descriptions of model limitations with respect to key missing processes are warranted in future genotypic adaptation studies [see e.g. Fig. 1 in Singh *et al.* (2014)]. Achieving a better representation of future-climate relevant processes will ensure that model-based analyses are more realistic.

(ii) *The correct separation between model parameters that influence yield as a function of crop physiology and those with large impact on simulated yield only due to model specification.* That is, the possibility of relating model parameters to the effect of alleles on given loci or genes controlling key traits (Luquet *et al.*, 2012). Importantly, there is a tight link between such a relationship and model complexity –an overarching issue in climate impacts prediction, because overly simplistic models are unlikely to capture physiological responses with enough level of detail for use in crop breeding (Luquet *et al.*, 2012), but overly complex models are more difficult to constrain at the scales typical of climate prediction frameworks (Challinor *et al.*, 2009*a*). Work towards linking quantitative trait loci information and process-based crop growth modelling, however, shows promise. For example, Chenu *et al.* (2009) used a gene-to-phenotype modelling approach that included a genetic model and a process-based crop model to simulate the impact of leaf and silk elongation traits (as derived from genetic data) on maize yield across different environments. Despite some success, however, the lack of a more thorough consideration of genetic effects [beyond those related to crop development (Messina *et al.*, 2006; Challinor *et al.*, 2009*b*)] on yield and genotype-by-environment interactions in genotypic adaptation studies suggests that appropriate frameworks need to be established [e.g. Chenu *et al.* (2009); Cooper *et al.* (2005)].

[Figure 7 here]

We suggest that in order to mainstream crop-model based analyses of genotypic adaptation into breeding programmes, more research as well as a framework on the coupling of crop and genetic models is needed. Fig. 8, based on the work of Chenu *et al.* (2009) and Cooper *et al.* (2005), is an attempt to such a framework, through which we expect model-based analyses of genotypic adaptation can incorporate genetic information from breeding programs and, in turn, retrieve *ex-ante* assessments of genotypic responses across environments [also see Yin *et al.* (2003, 2004)]. As a starting point, traits that have constant QTLs (and hence constant model parameters) across environments have to be determined. Modular crop models can then be coupled with 'plug-and-play' parameterisations of relevant characteristics for which genetic information is available, with appropriate sensitivity testing to ensure realism. Genetic model simulations of crosses between promising parental lines can then yield crop model parameters and be run through an ensemble of crop models at one or more environments. The resulting crop model simulations can then be used to select promising phenotypes and the process repeated for various steps in the breeding cycle (Fig. 8).

[Figure 8 here]

Additionally, simulation of genotypic adaptation (including ideotype design) for projected weather conditions of uncertain nature means that additional principles may be needed in order to develop robust projections of adaptation. In particular, appropriately constraining processes and parameters in models across scales [cf. Iizumi *et al.* (2014)] and a shift from simply quantifying uncertainty to actually quantifying robustness (i.e. the relationship between uncertainty and the climate change signal) towards modelling choices [cf. Ramirez-Villegas and Challinor (2014)] are two key aspects that need to be included into crop model-based analyses of genotypic adaptation. Two key initiatives toward these aims include the AgMIP (Rosenzweig *et al.*, 2013) and FACCE-MACSUR (http://www.macsur.eu) projects.

Conclusions

The challenges ahead with regards of developing genotypic adaptation strategies that can then be implemented in breeding programs are substantial. On one hand, climate change impacts are projected to pose significant challenges to agriculture and genotypic adaptation strategies are critical for responding to such challenges. On the other hand, uncertainties in climate and crop modelling are substantial and poorly explored in studies of genotypic adaptation to future climates that use process-based simulation models, particularly at field scales. While uncertainties need to be better understood and quantified (see Sect. 5), it is important to note that a shift in focus from solely quantifying output variance to quantifying robustness is required in order so as to facilitate assessments and interpretation of confidence levels in crop model-based projections of genotypic adaptation. In addition to this, it is critical that genotypic adaptation options are grounded in genetic and physiological knowledge that can be mainstreamed in real-world breeding programs. To this aim, while recently published studies have demonstrated the potential of genotypic adaptation strategies and ideotype design, two main goals need to be pursued in future studies: (1) a better understanding of driving processes under future climate change; and (2) a coupling between genetic and crop growth models –perhaps at the expense of number of traits analysed. Importantly, the latter may imply additional complexity [and likely uncertainty] in crop modelling studies. Therefore, modularity in crop models as well as individual component testing against observational data would be critical components in any attempts to simulate crop breeding strategies under future climate scenarios.

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Figure captions

Figure 1 Percentage variance in historical crop yields explained by seasonal mean temperature and seasonal total precipitation across (A) crops and (B) regions. Variance explained is measured using the coefficient of determination (R^2) as derived from the statistical models in Lobell *et al.* (2008). Both panels show the same data, but pooled differently. Variation for each crop in panel A reflects differences between regions and variation for each region in panel B reflects differences between crops. Thick red lines are the medians, boxes represent the interquartile range, whiskers extend to 5-95 % of the data, and red dots are outliers.

Figure 2 Responses of (A) net photosynthesis to leaf temperature, (B) development rates to mean daily air temperature, and (C) crop yield to temperature during reproductive period. Data in panel A have been derived from the study of Nagai and Makino (2009) for wheat and rice, and from Bird *et al.* (1977), Schmitt *et al.* (1981), Crafts-Brandner and Salvucci (2002), and Labate *et al.* (1990). Solely for illustrative purposes, maize data were fitted to a spline curve with 5 degrees of freedom. Rice and wheat data were fitted to 3rd order polynomials as in Nagai and Makino (2009). Curves in panel B were plotted following Parent and Tardieu (2012). Development rates at each temperature in their models have all been normalised by development rates at 20 ºC. Data from panel C were derived from Peng *et al.* (2004) for rice [hence *x*-axis for rice is minimum growing season temperature], from Gibson and Paulsen (1999) for wheat [hence *x*-axis is mean temperature during grain-filling], and from Wilhelm *et al.* (1999) for maize [hence *x*-axis is mean temperature post-anthesis]. For panel C all data were linearly scaled so that the maximum yield corresponded to a value of 1. Fits in panel C all follow a linear regression except for rice where the original 2nd degree polynomial of Peng *et al.* (2004) was used.

Figure 3 Ways in which impact assessment is typically approached in projection-based frameworks. Red arrows indicate flow of information. The black hollow arrow in the bottom shows that as long as more information is derived from climate projections, uncertainties are likely to increase, as a result of what is known as “cascade of uncertainties”.

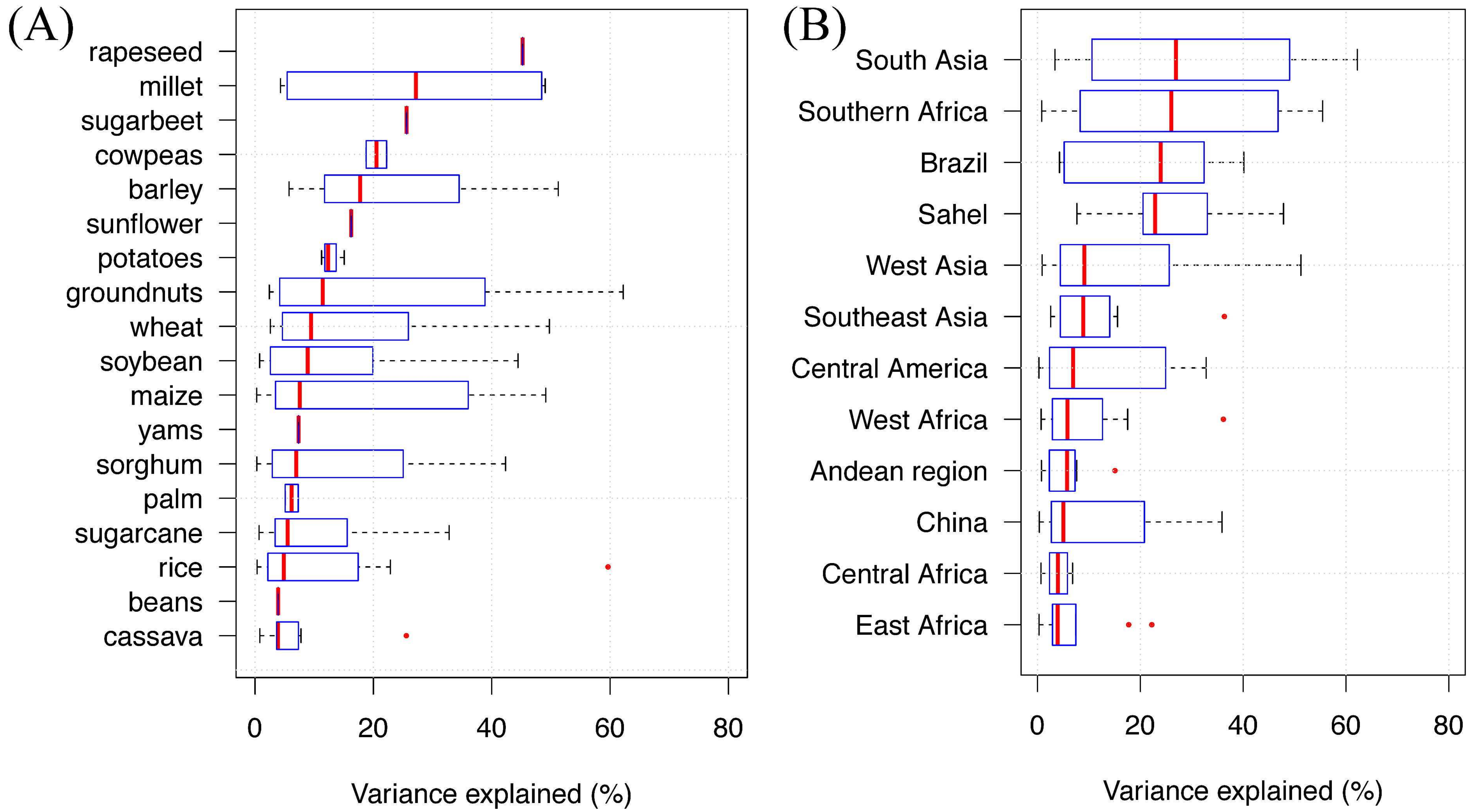
Figure 4 Use and misuse of crop models, based on 178 model results published in climate change impacts studies between 1994 and 2014, and disaggregated by model type. (A) Fraction of results that perform simulations at the scale for which the model was designed; (B) fraction of results (at scales other than field) for each model type that use multiple parameter sets (i.e. account for parametric uncertainty); and (C) fraction of studies that state model evaluation procedures for their locations or areas of interest. Model types are as follows: CSM-FS: field-scale crop growth simulation model; CSM-RS: regional-scale crop growth simulation model; E/S: empirical and/or statistical. Note that field scale models are used above field scale in roughly 50 % of the cases.

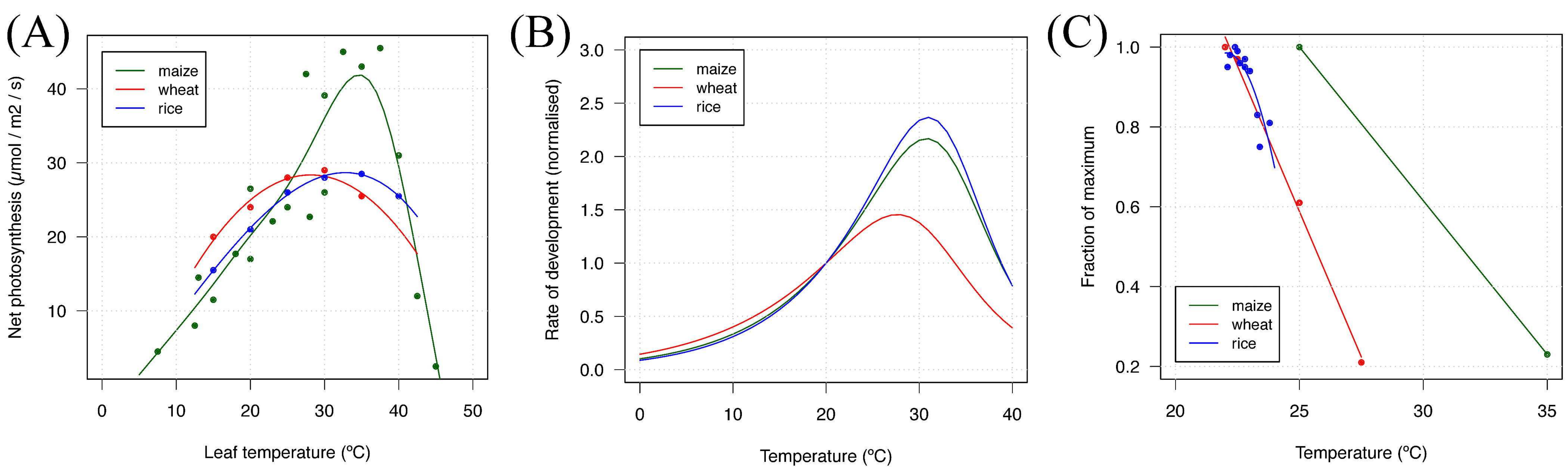
Figure 5 The benefit of different adaptation practices expressed as percentage change, from the baseline, in yield with adaptation minus that without adaptation, adapted from Challinor *et al.* (2014*b*). Data in this figure consists of yield changes from 32 simulation studies for various crops as described in Challinor *et al.* (2014*b*). Bars are means for each category and red lines indicate standard error. Note that the vast majority of data in the second category come from a single study (Deryng *et al.*, 2011).

Figure 6 Different plant types of rice. Left: tall conventional plant type. Centre: improved high-yielding and high-tillering plant type typical of the green revolution. Right: low-tillering ideotype (new plant type) with larger sink capacity (larger panicles and grains) and sturdier stems. Taken from Khush (2001).

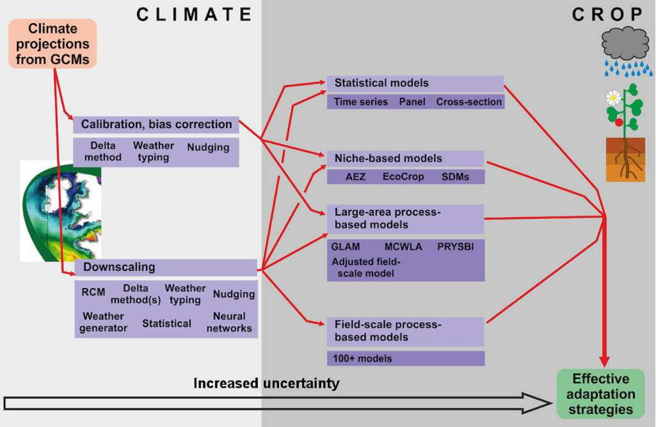
Figure 7 Simulated future potential benefits from genotypic adaptation (including ideotype design) as derived from available modelling studies for four different crops in different sites. Studies are as follows: Semenov and Stratonovitch (2013) and Challinor *et al.* (2010) for wheat; Singh *et al.* (2014) for sorghum; Singh *et al.* (2012, 2013) and Challinor *et al.* (2007, 2009*b*) for groundnut; and Lobell *et al.* (2013) for maize. The benefit of genotypic adaptation has been calculated as the difference between yield changes under adaptation and that under no adaptation, except in the case of Challinor *et al.* (2010) for which the relative change in crop failure rate between adaptation and no-adaptation results was used. Thick red lines are the medians, boxes represent the interquartile range, whiskers extend to 5-95 % of the data, and red dots are outliers.

Figure 8 Proposed framework for incorporating genetic information into simulation studies of genotypic adaptation. Figure derived from the practical example of Chenu *et al.* (2009). The dashed line that links the genetic portion of the diagram with the environment indicates that analyses are needed to identify traits whose QTLs are constant across environments.

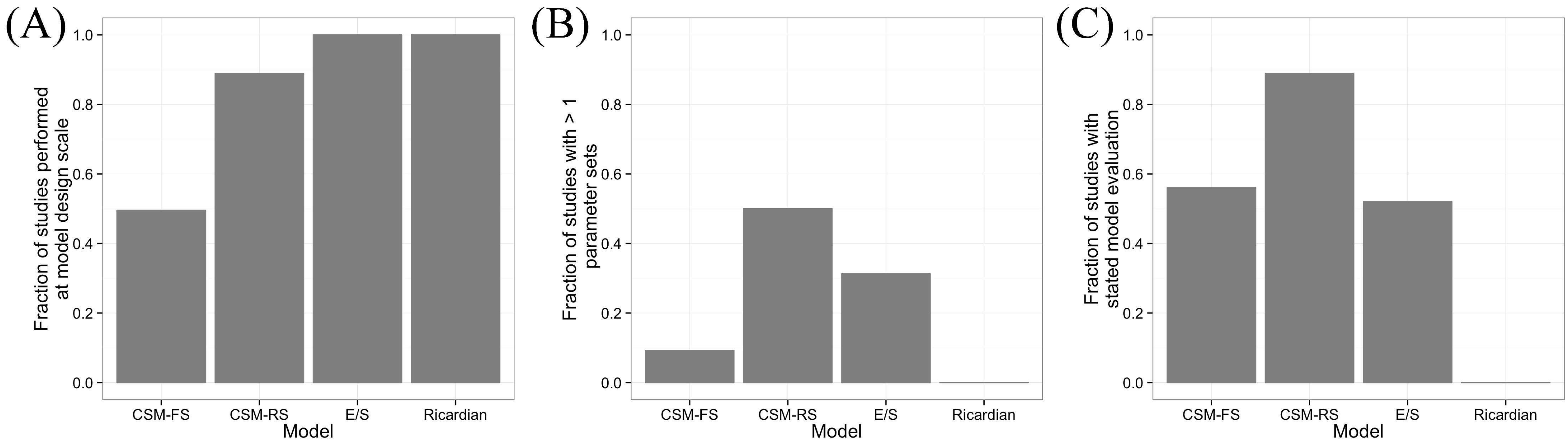

(A)
rapeseed
millet
sugarbeet
cowpeas
barley
sunflower
potatoes
groundnuts
wheat
soybean
maize
yams
sorghum
palm
sugarcane
rice
beans
cassava
0
20
40
60
80
Variance explained (%)
(B)
South Asia
Southern Africa
Brazil
Sahel
West Asia
Southeast Asia
Central America
West Africa
Andean region
China
Central Africa
East Africa
0
20
40
60
80
Variance explained (%)

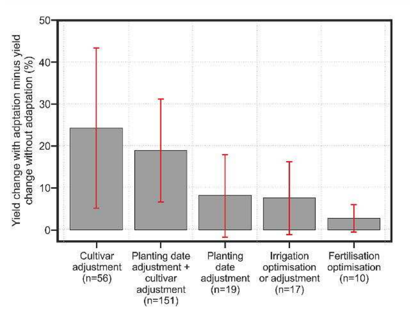


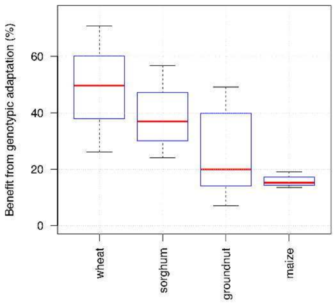
(A)
maize
wheat
rice
Net photosynthesis (μmol / m2 / s)
Leaf temperature (ºC)
0
10
20
30
40
50
(B)
maize
wheat
rice
Rate of development (normalised)
Temperature (ºC)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
(C)
maize
wheat
rice
Fraction of maximum
Temperature (ºC)
0.2
0.4
0.6
0.8
1.0
20
25
30
35



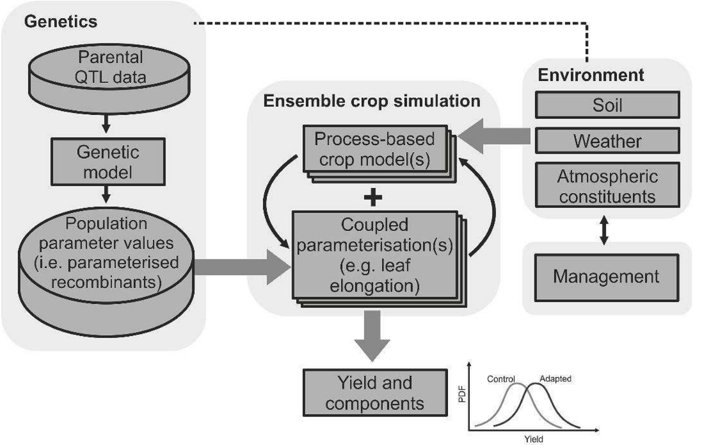
CLIMATE
CROP
Climate projections from GCMs
Calibration, bias correction
Delta method
Weather typing
Nudging
Downscaling
RCM
Delta method(s)
Weather typing
Nudging
Weather generator
Statistical
Neural networks
Statistical models
Time series
Panel
Cross-section
Niche-based models
AEZ
EcoCrop
SDMs
Large-area process-based models
GLAM
MCWLA
PRYSBI
Adjusted field-scale model
Field-scale process-based models
100+ models
Increased uncertainty
Effective adaptation strategies


(A)
Fraction of studies performed at model design scale
1.0
0.8
0.6
0.4
0.2
0.0
CSM-FS
CSM-RS
E/S
Ricardian
Model
(B)
Fraction of studies with > 1 parameter sets
1.0
0.8
0.6
0.4
0.2
0.0
CSM-FS
CSM-RS
E/S
Ricardian
Model
(C)
Fraction of studies with stated model evaluation
1.0
0.8
0.6
0.4
0.2
0.0
CSM-FS
CSM-RS
E/S
Ricardian
Model


50
40
30
20
10
0
Yield change with adptation minus yield change without adaptation (%)
Cultivar adjustment (n=56)
Planting date adjustment + cultivar adjustment (n=151)
Planting date adjustment (n=19)
Irrigation optimisation or adjustment (n=17)
Fertilisation optimisation (n=10)



Benefit from genotypic adaptation (%)
0
20
40
60
wheat
sorghum
groundnut
maize


Genetics
Parental QTL data
Genetic model
Population parameter values (i.e. parameterised recombinants)
Ensemble crop simulation
Process-based crop model(s)
+
Coupled parameterisation(s) (e.g. leaf elongation)
Environment
Soil
Weather
Atmospheric constituents
Management
Yield and components
PDF
Control
Adapted
Yield