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CGIAR modeling approaches for resource-constrained scenarios: II. Accelerating crop breeding for a changing climate

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Abstract

Crop improvement efforts aiming at increasing crop production (quantity, quality) and adapting to climate change have been subject of active research over the past years. But, ‘to what extent can breeding gains be achieved under a changing climate, at a pace sufficient to usefully contribute to climate adaptation, mitigation and food security?’. Here, we address this question by critically reviewing how model-based approaches can be used to assist breeding activities, with particular focus on all CGIAR (formerly the Consultative Group on International Agricultural Research but now known simply as CGIAR) breeding programs. Crop modeling can underpin breeding efforts in many different ways, including assessing genotypic adaptability and stability, characterizing and identifying target breeding environments, identifying tradeoffs among traits for such environments, and making predictions of the likely breeding value of the genotypes. Crop modeling science within the CGIAR has contributed to all of these. However, much progress remains to be done if modeling is to effectively contribute to more targeted and impactful breeding programs under changing climates. In a period in which CGIAR breeding programs are undergoing a major modernization process, crop modelers will need to be part of crop improvement teams, with a common understanding of breeding pipelines and model capabilities and limitations, and common data standards and protocols, to ensure they follow and deliver according to clearly defined breeding products. This will, in turn, enable more rapid and better-targeted crop modeling activities, thus directly contributing to accelerated and more impactful breeding efforts.

1. Introduction

Global change projections indicate that many parts of the world will continue to face extreme and erratic climate trends, as a result of rapid population growth, and increasing greenhouse gas (GHG) emissions (IPCC, 2014). Model-based projections indicate greater heat and drought stress during the 21st Century (Teixeira et al., 2013; Gourdji et al., 2013b; Li et al., 2015a), especially (though not only) if no major GHG emission reduction strategies are implemented at scale (Betts et al., 2011; Schleussner et al., 2016; Rogelj et al., 2016). Compounded by other drivers of global change (e.g. population growth, changing economic structures, and changing land use), these changes will reduce crop productivity and increase crop yield variability of many crops (Li et al., 2009; Deryng et al., 2014; Campbell et al., 2016), with major implications on farmer livelihoods (Morton, 2007; Jones and Thornton, 2009) and global food security (Wheeler and von Braun, 2013; Campbell et al., 2016). In light of these projections, crop improvement efforts aiming at increasing crop production (quantity, quality) in a sustainable and efficient way have been subject of active research over the past years.

Crop breeding programs have contributed to farmers achieving higher yields, food security and income by developing and delivering varieties with higher yield potential, as well as greater resistance to pests and diseases, tolerance to abiotic stresses, and desirable market quality and nutritional characteristics in the public (Evenson and Gollin, 2003; Pfeiffer and McClafferty, 2007) and private sectors (Cooper et al., 2014b; Voss-Fels et al., 2019d). Moreover, the use of varieties resistant to heat stress, drought, and possible future pests and diseases can also contribute to climate change adaptation (Takeda and Matsuoka, 2008; Habash et al., 2009; Gourdji et al., 2013a; Gaffney et al., 2015). A key question is, however, ‘to what extent can breeding gains be achieved under changing climates, at a pace sufficient so as to usefully contribute to climate adaptation, mitigation and food security?’. Here, we address this question by reviewing how model-based approaches can assist breeding activities, with particular focus on the CGIAR (formerly the Consultative Group on International Agricultural Research but now known simply as CGIAR). We critically discuss limitations and opportunities in light of the need for greater breeding gains under changing climates. Since the body of published literature (especially in some thematic or geographic areas) is substantial, we concentrate on the most relevant examples, aiming at discussing their strengths and weaknesses, in order to ultimately determine the main crop modeling gaps and strategies for collaboration with researchers, crop improvement teams, farmers, and decision and policymakers. We first review the importance of genotypic adaptation in delivering climate change adaptation outcomes (Sect. 1.1), as well as the challenges in converting potential adaptations into actual genetic improvement (Sect. 1.2). We then review tools and approaches for accelerated breeding (Sect. 2), including modeling of environment- and management- specific yield responses (Sect. 2.1), environmental characterization (Sect. 2.2), ideotype design (Sect. 2.3), the linking of crop modeling and genetic data (Sect. 2.4), and simulation methods for optimizing breeding pipelines (Sect. 2.5). Finally, we discuss limitations in terms of data, models, and approaches (Sect. 3), and conclude by proposing a set of next collaborative research activities that can contribute to maximizing breeding gains under climate change.

1.1. The importance of genotypic adaptation under climate change

Modern varieties developed through years of crop improvement have contributed to large increases in crop production in the last 60 years, and they will continue to do so. Evenson and Gollin (2003) reviewed breeding gains during and after the Green Revolution for 11 major food crops, estimating that the contribution of modern varieties to yield growth is in the range 17–50 % in the period 1961–2000. One notable example is the 70 % yield potential increase from the release of the semi-dwarf rice variety IR8 by the International Rice Research Institute (IRRI) in the 1950s and 1960s (Peng et al., 2008). Fischer et al. (2014) indicate a rate of progress in potential yield of 0.5 to 1.08 % per year for wheat, rice, maize and soybean, as a result of crop improvement. Genotypic adaptation to climate change –that is, the process of designing and developing novel crop varieties to enhance productivity and stability under future climates, has the potential to continue delivering productivity gains under changing climates (Rötter et al., 2015; Ramirez-Villegas et al., 2015).

Evidence of how genotypic adaptation can effectively contribute to climate change adaptation generally arises from two types of studies: those in which models are used to simulate future growing conditions with and without adaptation; and those that quantify the yield benefit of climate-adapted genotypes by means of field experimentation. Model-based studies generally indicate potential for substantial gains in both yield and yield stability. A systematic review of the literature (by searching the keywords ‘climate change’, ‘genotypic adaptation’, and ‘ideotype’ in http://scholar.google.com in June 2019) identified 19 studies, from which 389 individual data points for eight crops were drawn. While some publication bias is expected in the meta-analysis, the identified studies indicate that gains from genotypic adaptation are positive for a number of crops (Fig. 1). For instance, modelling by Semenov and Stratonovitch (2013) suggested that if certain traits could be improved adequately, wheat ideotypes could outperform current cultivars in Europe by up to 65 % under future climates. Similarly, simulations by van Oort and Zwart (2018) showed that favoring varieties with greater thermal time can compensate for climate change-induced yield reductions in African rice systems. Similar findings have been reported for Asian rice (Li and Wassmann, 2010; Mottaleb et al., 2017), groundnut (Singh et al., 2012, 2014b), sorghum (Singh et al., 2014c), pearl millet (Singh et al., 2017), chickpea (Singh et al., 2014a), maize (Tesfaye et al., 2017), and wheat in China (Challinor et al., 2010).

[Figure 1 near here]

Experimental studies also provide robust evidence on the benefits of genotypic adaptation, corroborating or extending model-based findings. On-farm maize trials in Africa have shown that drought-tolerant maize can yield between 20–25 % more than current commercial varieties, with no yield penalty in ‘good’ years (Setimela et al., 2017; Cairns and Prasanna, 2018). Suarez Salazar et al. (2018) identified common bean lines adapted to a heat-stress environment in the Colombian Amazon, where commercial bean varieties show low yield. Mondal et al. (2016) estimated genetic yield gains in the range 0.5–0.8% per year when breeding short-cycle heat-adapted wheat varieties in South Asia. Success has also been reported for drought tolerance in maize for the United States corn belt (Cooper et al., 2014a;

Messina et al., 2015) and other regions and crops (Sinclair et al., 2020). These studies provide initial evidence that genotypic adaptation can indeed deliver greater yields in stress-prone environments, thus likely contributing to future adaptation outcomes.

1.2. Current warming rates will reduce yields unless breeding and seed system efficiency is enhanced

The process of breeding a novel cultivar, increasing seed availability and achieving significant adoption often takes more than a decade (Langyintuo et al., 2008; Challinor et al., 2016). This means that temperature increases during the breeding cycle can lead to a systematic (and unintended) yield reduction due to decreases in the duration of the growing cycle (Zheng et al., 2016; Challinor et al., 2016). Researchers confirmed that the challenge is more critical in many subtropical areas with emerging precipitation trends under climate change (Rojas et al., 2019). The breeding of climate-ready crops should, therefore, seek to deliver more productive and resilient crops that keep pace with climate change (Ramirez-Villegas et al., 2015; Challinor et al., 2016). In doing so, it is important to implement a wide range of solutions aiming at making the breeding process more effective and efficient. Anticipatory and predictive tools using crop-climate models (reviewed in Sect. 2 and 3) can enable preemptive breeding and can help enhance and accelerate breeding gains, ultimately ensuring crop improvement contributes effectively to addressing major challenges for agriculture within the context of climate change.

2. Tools and approaches for accelerating trait discovery in target environments

For plant breeding, multi-environment trials (METs) are conducted regularly to study Genotype (G) × Environment (E) × Management (M) interactions (G×E×M), assess genotypic adaptability and stability, and make predictions about the breeding value of the genotypes in other environments and years that will allow crop improvement teams to accurately select the parents for the next breeding cycle. This section reviews modeling approaches to assess G×E interactions (Sect. 2.1), characterize target breeding environments (Sect. 2.2), understand ideal plant types for such target environments (Sect. 2.3), predict breeding values (Sect. 2.4), and breeding cycle optimization (Sect. 2.5). We review both process-based eco-physiological models as well as statistical approaches to G×E prediction.

2.1. Modeling Genotype × Environment × Management

Accurately predicting G×E responses allows identifying well-adapted genotypes for specific sites or stress situations (Hammer and Broad, 2003; Banterng et al., 2006), or testing 'virtual' genotypes to inform breeding programs (Cock et al., 1979; Suriharn et al., 2011; Bogard et al., 2020; Hammer et al., 2020). Similarly, predicting management responses allows identification of appropriate levels of fertilization, tillage, irrigation, weed control, amongst others, for a given set of genotypes (Boote et al., 1996; Artacho et al., 2011; Deryng et al., 2011). Accurate prediction of genotype performance across environments and management options is contingent on various elements, including (i) the development of a model with the necessary physiological processes represented at an appropriate level of complexity (Challinor et al., 2009; Boote et al., 2013; Hammer et al., 2019); (ii) the development of a well-constrained parameter set (Iizumi et al., 2009; Angulo et al., 2013); and (iii) high quality environmental (soil, climate) data to drive the model (Lobell, 2013). As discussed below, the CGIAR has made major contributions in these three areas. The use of models for analyzing G ×E × M interactions for accelerating breeding is described in Sect. 2.1.2.

2.1.1 Model development, parameterization and input data

Model development requires the acquisition of a deep understanding of the biological basis of G×E interactions (i.e. crop physiology), and the translation of such understanding into computer code. Physiological processes of interest, and approaches to model those processes, can vary, sometimes substantially, between contexts. During the early 1980s, progress in process understanding by CGIAR scientists led to the development of three crop models that ably captured G×E×M responses, while also contributing data and knowledge to many other models. Perhaps the earliest crop model developed and used in the CGIAR was the cassava model developed by the International Center for Tropical Agriculture (CIAT) (Cock et al., 1979), upon which various components of the GUMCAS model (Matthews and Hunt, 1994), the CROPSIM-

Cassava model (Jones et al., 2003), the model of Gabriel et al. (2014), and the MANIHOT model (CIAT, unpublished), were later developed. The ORYZA1 rice model (Kropff et al., 1993a, 1994), developed at the International Rice Research Institute (IRRI), incorporated many years of eco-physiological research from IRRI and elsewhere. ORYZA1 quickly evolved into ORYZA2000 (Bouman et al., 2001), and later into ORYZAv3 (Li et al., 2017). The International Potato Center (CIP) has also led the development of the SOLANUM and the dynamic carbon photosynthesis model (DCPM) models for potato (Condori et al., 2010; Quiroz et al., 2017) and sweet potato (Ramírez et al., 2017). Lastly, CIAT also led the early development of the BEANGRO model, which is currently part of the 'CROPGRO' module within DSSAT (Decision Support System for Agrotechnology Transfer) (White and Izquierdo, 1991; Hoogenboom et al., 1993; White et al., 1995). The International Center for Agricultural Research in the Dry Areas (ICARDA) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) have extensively contributed to the development and improvement of the Simple Simulation Model (SSM) (Soltani and Sinclair, 2012; Sinclair et al., 2020), the CROPGRO for peanut and chickpea, and the CERES model for sorghum and pearl millet, also available in DSSAT.

The determination of parameters for crop models, whether they are statistically- or process-based, is crucial to ensure that the model correctly captures genotype behavior across different combinations of climate, soils, and management options. This is especially important for process-based crop models, since the sometimes large number of parameters required means that there can be many more degrees of freedom in the model than can be constrained by the available data (Challinor et al., 2014; Wallach et al., 2016). Progress in model parameterization has been enabled by extensive eco-physiological trials conducted by the CGIAR. Notably, recent progress in characterizing yield changes in response to heat stress for wheat, at least in part, was possible due to data collected in the International Heat Stress Genotype Experiment (IHSGE) carried out by the International Maize and Wheat Improvement Center (CIMMYT) (Asseng et al., 2014). Based on CIMMYT data, too, statistical models by Lobell et al. (2011) and Gourdji et al. (2013a) assessed maize and wheat genotype responses to temperature, respectively. Li et al. (2015b) used IRRI trial data from Los Baños (Philippines) and Ludhiana

(India) to calibrate and evaluate 13 different rice crop models, and Fleisher et al. (2017) used an experiment from Bolivia conducted by the International Potato Center (CIP) as part of the calibration and evaluation dataset for nine potato crop models. The use of remote sensing has also been tested for the estimation of crop model parameters at a low cost (Quiroz et al., 2017).

Attempts to estimate model parameters from genetic information date to work in the 1990s at CIAT on common bean, where simulations from gene-based estimates of model parameters were generally as accurate as manually estimated parameters (White and Hoogenboom, 1996; Hoogenboom et al., 1997). Similar work in collaboration with CIMMYT, showed that differences in phenology of winter wheat cultivars could be simulated based on genetic information (White et al., 2008). Work also extends into the development of a gene-to-phenotype model for common bean based field trials conducted by CIAT and the University of Florida (UF) (Hwang et al., 2017). Compared to success in linking gene-to-phenotypes achieved by other institutions (Messina et al., 2006; Chenu et al., 2009; Bogard et al., 2020), progress in the CGIAR remains slow.

The CGIAR has also contributed to the development of key spatially-explicit climate datasets that are used as inputs into crop models. These include WorldClim (Hijmans et al., 2005) and the Climate Change, Agriculture and Food Security (CCAFS)-Climate database (Navarro-Racines et al., 2020), as well as methods to generate daily weather data for crop model simulations (Jones and Thornton, 2000, 2013). Contributions to soil (Jones and Thornton, 2015; Vågen et al., 2016; Piikki et al., 2017) and crop geography (You et al., 2009, 2017; IFPRI, 2019) for crop modeling have also been made in recent years. By contrast, CGIAR work on developing datasets that characterize crop management for crop modeling is limited to specific regional or national studies (see Sect. 2.1.2).

2.1.2 Explaining and simulating G×E×M interactions

Using available data and models, CGIAR modelers have studied G×E×M interactions extensively in close coordination with breeding programs. Virtually all centers have done modeling for their mandate crops. Use of models has focused on assessing the stability of economically important traits and predicting the performance of newly developed genotypes evaluated under varying environmental conditions and management practices.

Statistical approaches have the longest history in plant breeding. These models can be used to study both univariate (Crossa et al., 2004) and multivariate responses (Montesinos-López et al., 2018d). A recent study with on-farm wheat trials (Vargas-Hernández et al., 2018) used a univariate model to assess the combined effects of the wheat lines and their interactions with the farmer-irrigation-year combinations for several traits. For single trait grain yield, the study identified stable wheat lines across all environments, as well as the environments that caused most of the G×E interaction. Multivariate models, though less used, are particularly useful when measurements are available for multiple response variables (i.e. multi-trait), and the objective is to increase our understanding of the complex nature of particular phenomena under field conditions. Many studies have shown that a multivariate approach is better than univariate approaches because it identifies the existing (co)variation between the response variables (Xiong et al., 2014). Moreover, the multivariate analysis also improves accuracy when classifying and identifying superior genetic components (Montesinos-López et al., 2018d). In addition, it increases the precision of genetic correlation parameter estimates between traits, which helps crop improvement teams perform indirect selection. Multivariate models have been implemented using Bayesian analysis (Montesinos-López et al., 2016b) as well as deep machine learning regression (Montesinos-Lopez et al., 2018; Montesinos-López et al., 2018c). Notably, Montesinos-Lopez et al. (2018) report that the performance of multi-trait and multi-environment deep learning (MTDL) is commensurate with that of the Bayesian multi-trait and multi-environment approach. Erzos et al. (2020) and Washburn et al. (2020) review machine-learning approaches in crop improvement.

Process-based crop models have also been used for assessing G×E×M interactions within the CGIAR. At ICRISAT, crop models are used to investigate whether and how changes in G and M result in positive change in yield across different environments, as a way to prioritize breeding and agronomic intervention decisions, including sowing density (Vadez et al., 2017), irrigation (Vadez et al., 2012), the combination of better-adapted genotypes and irrigation (Soltani et al., 2016), and different traits and combinations of traits (Kholová et al., 2014). ICARDA has employed the Simple Simulation Model (SSM) to characterize the stress scenarios in target regions of focus, as well as to explore plant traits and/or management to be exploited in stress-adapted cultivars for specific target environments (Ghanem et al., 2015; Guiguitant et al., 2017). CIP has used the SOLANUM (Condori et al., 2010) and LINTUL (Spitters, 1988, 1990) models to compare the performance of native and hybrid potato genotypes under extreme climatic conditions (Condori et al., 2010, 2014) and climate change (Quiroz et al., 2018), demonstrating that appropriate choice of germplasm and crop management practices could significantly secure and increase potato production under future climate conditions.

Similar work has been conducted by IRRI, whereby high yielding and stable genotypes were identified using the ORYZA2000 crop model (Li et al., 2013a). At IRRI, simulations have also been used to simulate potential yield across environments (Kropff et al., 1993b), identify ideotypes for increasing rice yield potential (Kropff et al., 1995; Aggarwal et al., 1997; Dingkuhn et al., 2015, 2016), and to inform national certification processes for the release of crop varieties (Li et al., 2016). At CIMMYT, grid-based global-scale simulations are used to assess the value of certain traits. This modeling capacity was developed in a consortium of UF, CIMMYT, and the International Food Policy Research Institute (IFPRI) that incorporated three crop models, including CERES-wheat, CROPSIM, and NWheat (Gbegbelegbe et al., 2017; Hernandez-Ochoa et al., 2018). At CIAT, crop models have been used to understand drought responses across G and M for rice and beans (Heinemann et al., 2016; Ramirez-Villegas et al., 2018), as well as to assess the value of drought tolerance traits (Heinemann et al., 2019). At IFPRI, a grid-based crop modeling framework was developed and linked with the IMPACT global trade and economic model (Robinson et al., 2015) to simulate the potential impacts of adopting agricultural technologies (e.g. precision agriculture), management practices (e.g. integrated soil fertility management), and breeding target traits (e.g. drought and/or heat tolerance) on global food security and economic implications under climate change scenarios (Rosegrant et al., 2014; Islam et al., 2016). Analyses of climate risk for rice in Africa have also been possible by crop simulation at the Africa Rice Center (van Oort et al., 2015b; a).

2.2. Environmental characterization for setting breeding priorities

The existence of significant G×E×M interactions can slow plant breeding progress for broad adaptation and/or for adaptation to specific conditions within a region (Löffler et al., 2005; Chenu et al., 2011). The Target Population of Environments (TPE) approach aims at addressing G×E×M through model-based environmental characterization (Lacaze and Roumet, 2004; Chenu, 2015). In the TPE approach, process-based crop models are used to assess and detect stress patterns and their impacts. This, in turn, allows prioritizing stress types by their intensity and frequency across geographies, as well as identifying sites where selection for given stresses is likely to be more successful. Thus, TPEs offer a concrete way to aid breeding programs through effectively setting trait and geographic priorities. The TPE approach has been used with success by wheat breeding programs in Australia (Chenu et al., 2011, 2013; Lobell et al., 2015), and more recently has been applied to maize in Europe (Harrison et al., 2014).

Compared with the applications described in Sect. 2.1, CGIAR’s work on TPEs for breeding programs is less in terms of number of crops covered and published studies (Fig. 2A, B). CGIAR’s collaborative efforts include studies addressing drought for rice (Heinemann et al., 2015; Ramirez-Villegas et al., 2018) and beans (Heinemann et al., 2016, 2017) under current and future climate in Brazil. Significant breeding progress has resulted from these studies, including improvements in drought phenotyping in a drought-prone environment which allows controlling the timing, intensity, and duration of drought, reducing the uncertainty associated with climate variability trials in the main season (Martinez et al., 2014).

[Figure 2 near here]

For rainfed beans, EMBRAPA (*Empresa Brasileira de Pesquisa Agropecuaria*) initiated a drought tolerance breeding program following the results of Heinemann et al. (2016, 2017), though its implementation was halted due to the Brazilian economic crisis. For post-rainy sorghum in India, Kholová et al. (2013) report five main types of stress conditions requiring different breeding/agronomic approaches (Fig. 2B). A related larger-scale method, referred to as Mega-Environments, has been used by CIMMYT to target breeding since the 1990s (Rajaram et al., 1994; van Ginkel et al., 2002; Cairns et al., 2013). Though less mainstream in the CGIAR in terms of centers and traits, TPE and Mega-Environment work has the potential to help better-target breeding programs across scales (see Fig. 2C). Similar TPE analysis has also been done for chickpea in India (Hajjarpoor et al., 2018).

The first step across breeding programs should be to map what stresses exist currently (in recent decades) to then analyze changes in stress patterns under future climates (Harrison et al., 2014; Lobell et al., 2015). Using TPE results to stratify the target geographic area of the breeding program, in combination with socio-economic (e.g. farmer preference) studies, breeding programs can then decide which products are most relevant and impactful. Contrary to the private sector (Cooper et al., 2014a; Voss-Fels et al., 2019a; c), however, to the best of our knowledge, the extent to which this is currently done in a systematic way across the CGIAR system is very limited. Yet, taking into account the TPE definition as part of the definition of the breeding products will allow modelers to impact breeders, while allowing breeders to discuss model results from the start of the breeding process.

2.3. Design of ideotypes for future target environments

With a clear understanding of the target stresses for breeding, a key use of process-based crop models is to determine which traits can maximize yield in each target environment. When applied to a range of traits simultaneously, this then becomes a process referred to as ideotype design (Donald, 1968; Rasmusson, 1987). Ideotypes can be developed for current as well as for future climates via a variety of methods ranging from iterative testing changes in model parameters (Suriharn et al., 2011; Dingkuhn et al., 2015), optimization to maximize mean yield and minimize yield variability (Semenov and Stratonovitch, 2013; Hammer et al., 2020), or by developing gene- or trait × gene-specific components into the crop models (White and

Hoogenboom, 1996; Hoogenboom et al., 2004; Messina et al., 2006). Modeling in this case is based on traits that have previously indicated promise for example in boosting yield potential (Reynolds et al., 2012), adaptation to heat stress (Cossani and Reynolds, 2012), amongst others. Table 1 summarizes all existing studies in which models have been used to design ideotypes within the CGIAR; that is, conducted by CGIAR scientists on CGIAR mandate crops and geographic areas.

[Table 1 near here]

The 12 studies listed in Table 1, published in a span of 9 years, indicate that CGIAR Centers are very active in this area of work. The list, while not extensive in terms of crops or countries (i.e. covers five crops across five countries), offers valuable insights as to the methods used and the potential value of these analyses for breeding programs. Foremost, we note that all studies use systematic parameter modifications to create ideotypes, which suggests opportunities to explore optimization methods as well as more direct gene-to-phenotype modeling (e.g. van Eeuwijk et al., 2019). Additionally, the similarity in the ideotypes proposed for different studies (e.g. chickpea, sorghum and groundnut) suggests the need for refinement in the traits assessed through discussion with crop improvement teams, or through the use of more detailed eco-physiological models (Rebolledo et al., 2015; Dingkuhn et al., 2016). Such similarity could also suggest that the models may fail to capture cropping system dynamics realistically when subjected to these parameter modifications. Furthermore, little connection is seen in most studies between the parameter variations proposed and existing ideotypes for these crops, except for the study of Mottaleb et al. (2017). Additionally, there is a need to ensure that parameter modifications, especially when several traits are simulated simultaneously, are done within realistic biological bounds (Koornneef and Stam, 2001).

Finally, we note that moving from a set of prescribed changes in model parameter values (as reported in the studies listed in Table 1) to a range of phenotypic screens that can be feasibly measured and selected for in breeding trials is not a trivial process. Most notably, it requires delivering information on (i) the available genetic diversity, (ii) heritability, and (iii) high-throughput phenotyping methods for the trait in question. Future research within and outside the CGIAR will need to capitalize on existing well-calibrated models, results from environmental characterization, methods to connect eco-physiological models with genetic data (see Sect. 2.4), in better connection with existing ideotypes and crop improvement teams and their knowledge, needs and priorities.

2.4. Assisting varietal selection through linking crop models and genetic information

A more recent area of work aims at directly linking crop model and genetic information with the aim of addressing two different, but related, questions (i) what is the phenotypic response of a set of genotypes for which the genetics are known, but on which no phenotyping has been conducted?; and (ii) what is the phenotypic response of a set of genotypes (with known genetics) in a location where environmental (soil, climate) characteristics are known, but no phenotyping has been conducted? As the methods to be used may depend on the crop and geographic areas of interest (e.g. due to differences in data availability, targets, and breeding methods), several potential avenues need to be explored to address these questions (Asseng et al., 2019a). These are discussed below.

2.4.1 Link environmental information into genomic selection models

Genomic selection (GS) that leverages genome-wide molecular marker information to select individuals based on their predicted genetic merit (Meuwissen et al., 2001) is a promising tool for accelerating crop genetic gains in the face of climate change. In a recent paper, Zhang et al. (2017) reported genetic gains of 0.225 ton ha^{-1} per cycle (or 0.100 ton ha^{-1} $year^{-1}$) from rapid cycling genomic selection for four recombination cycles in a multi-parental CIMMYT tropical maize population (Fig. 3). However, in spite of these early findings and the fact that GS has revolutionized animal breeding by increasing the accuracy of selections and reducing cycle time and cost (Hayes et al., 2013; Hickey et al., 2017), its implementation in CGIAR crop breeding programs is still limited (focusing primarily on the major cereals), in part due to costs associated with routine evaluation and relatively low prediction accuracy due to G×E.

[Figure 3 near here]

CGIAR has done extensive research to evaluate the genomic predictabilities of several traits including phenology, grain yield and its components, disease resistance, quality and micronutrients (Grenier et al., 2015; Crossa et al., 2016a; Juliana et al., 2017a, 2018; Sukumaran et al., 2018). The accuracy of forward predictions for grain yield (using a previous nursery/year to predict the next nursery/year) is, however, low and highly influenced by the environment (Juliana et al., 2018), thereby highlighting the importance of incorporating environmental data in genomic prediction models for grain yield (van Eeuwijk et al., 2019; Bhandari et al., 2019). Several novel methods and statistical models for modeling genomic relationships, pedigree relationships, environmental data and genomic × environment (Gi×E) interactions have been developed and evaluated in the CGIAR. These methods (see Table 2) vary in the type of information they use as input, the way they assess Gi×E interactions, and their prediction purpose and accuracy. Notably, studies comparing the predictive abilities of some of these approaches have also been conducted (Pérez-Rodríguez et al., 2012; Juliana et al., 2017b; Montesinos-López et al., 2018a).

[Table 2 near here]

While GS models are promising tools to accelerate breeding gains, further research is needed to understand how they fit in different stages of the breeding cycle, their comparative advantage over conventional breeding, their integration with rapid cycling technologies such as speed breeding (Voss-Fels et al., 2019b), and the type of approach used to integrate crop and genomic models (Messina et al., 2018; Voss-Fels et al., 2019a; van Eeuwijk et al., 2019). Experience for hybrid maize breeding in the private sector, however, offers evidence of the potential of GS for enhancing breeding gains (Cooper et al., 2014b, 2020).

2.4.2 Models that capture trait-trait relationships

Crop models aimed at capturing trait-trait relationships, developed with sufficient simplicity to be understandable, yet with enough mechanistic detail to be robust, can also help crop improvement teams in the selection process. CGIAR involvement and leadership in this area is very limited. These models can be useful in situations where a trait is too difficult to screen but is clearly predictable on the basis of other, more easily measurable, traits. Fundamental changes in the structure of current crop models would, however, be required for this approach to be implemented. That is, models should be sufficiently generic to be applicable across genotypes with limited or no calibration requirements (Soltani and Sinclair, 2012; Kholová et al., 2014; Holzworth et al., 2014). More flexibility in the types of model inputs may also be required when dynamic changes in certain plant traits are used as predictors. For instance, prediction modeling for genotype values can use correlated physiological traits measured using high-throughput phenotyping (HTP) platforms. This, in turn, facilitates indirect selection for grain yield in early-generations. Integration of HTP data for canopy reflectance and vegetation indices in genomic and pedigree-relationship based prediction models has proven to increase prediction accuracies in several studies (Rutkoski et al., 2016; Sun et al., 2017, 2019; Juliana et al., 2019).

2.4.3 Gene-based crop simulation models

Another way to couple crop models and genetic data is to develop models or model components that, from the start, use genetic and environmental information and are based on empirical relationships from available agronomic trial and marker data. This can be achieved through a highly dynamic approach (Hwang et al., 2017), at the expense of increasing uncertainty, or through prediction of crop state variables at coarser time scales, at the expense of mechanistic detail. Dynamic approaches that link genetic information with crop simulation models have proved successful for crop development variables (i.e. phenology) (White and Hoogenboom, 1996; Yin et al., 2004; White et al., 2008) as well as for more complex traits (Chenu et al., 2009; Bertin et al., 2010). The current level of direct engagement and leadership by the CGIAR in this line of work is very limited, likely due to a combination of CGIAR center-specific focus, funding sources for modelers, and limited uptake and applicability of these models in CGIAR breeding programs.

2.5. Optimization of breeding methods through genetic modeling and simulation

In addition to modeling of cropping systems and trait-specific responses, simulation work also extends to the design of breeding pipelines. While not directly related to crop modeling, we include this area of work in our review as constitutes part of the simulation tools available to crop improvement teams. These computer tools are capable of simulating the performance of a breeding strategy. For instance, QuLine, can simulate the selection of inbred lines, which means most major food cereals in the world, plus basically all leguminous crops (Wang et al., 2003, 2005; Wang and Pfeiffer, 2007). QuLine has been used to compare and optimize conventional selection strategies (Wang et al., 2003, 2009; Li et al., 2013b), to predict cross performance using known gene information (Wang et al., 2005), and optimize marker assisted selection to pyramid multiple genes (Wang et al., 2007).

3. Limitations of existing approaches and future work

The use of crop models to accelerate breeding under changing climates is a complex and rapidly evolving area of work, especially with regards to linking crop models and genetic data. At the same time, with the availability and affordability of high throughput phenotyping and genotyping technologies, most breeding programs are undergoing major transformations in the way they operate, most notably through the incorporation of genomic selection and modeling. The CGIAR is no exception to these transformations, as shown by the establishment of the Excellence in Breeding Platform and the Crops to End Hunger Initiative[1], and the existing research on genomic selection (Sect. 2.4.1). Under these initiatives, breeding programs are expected to become more focused and impactful, with clearly set product profiles that clearly outline geographic, farmer and consumer, as well as trait priorities. Hence, it is in the context of these transformations that crop modeling needs to operate, in an effective, flexible and agile

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[1] The CGIAR Crops to End Hunger Initiative (CtEH Initiative) seeks to improve and modernize CGIAR crop breeding programs, moving toward using improved breeding approaches. See document of the 8th CGIAR System Council meeting here https://storage.googleapis.com/cgiarorg/2019/04/SC8-08-CtEH-Module.pdf.

way, to provide crop improvement teams with tools and information that can help them make informed decisions.

An emerging result from the review of Sect. 2 is that there is no common protocol or approach in the CGIAR to inform breeding programs. This is in part due to the diversity of methods and approaches used, but also due to the lack of collaboration platforms for crop modelers, as well as between modelers and crop improvement teams. In addition, varying degrees of leadership by the CGIAR and coordination between CGIAR Centers also exists with respect to the integration of modeling into breeding programs. As a result, crop modeling activities have little perceived and actual impact on breeding decisions and the breeding process itself. We highlight four suggestions for targeted joint work across the modeling and breeding communities.

(i) Actively take part in the transformation of the breeding programs. Many CGIAR modeling studies, especially those focused on ideotype design, fail to capture the range of traits relevant in crop improvement, the range of model outputs and spatial and temporal scales that would be useful to them, and the parts of the breeding process that need to be informed (see Sect. 2.3). As breeding programs become more modern (Voss-Fels et al., 2019c), crop modelers need to be an active part of crop improvement, ensuring crop improvement teams are truly multidisciplinary, including crop physiology and modeling, quantitative genetics, genomic prediction and breeding. Given its potential to enhance breeding gains (Messina et al., 2018; Voss-Fels et al., 2019a), a critical part of this endeavor will be the integration of crop modeling with genomic selection (Sect. 2.4.1), and the use of crop models to map and stratify stress variation and response in the target breeding area (Sect. 2.2). As has been demonstrated by some private sector breeding programs (e.g. Cooper et al. 2014), if these tools are integrated to enable the definition and implementation of breeding products, the impact of the breeding programs can be maximized.

(ii) Move towards simpler models that ably simulate key traits and their responses across environments and management conditions. In the last decade, most model improvements have been relatively slow (compared to the rate of knowledge generation), limited by data availability, typically incremental (i.e. without thinking out of the box), and focused on a small range of crops (Challinor et al., 2014; Maiorano et al., 2017). At the same time, because crop models are increasingly being used beyond their original design purposes, they have also tended to become overly complex. Furthermore, as summarized by Rotter et al. (2011) and Challinor et al. (2018), major limitations exist in process-based crop models regarding the processes they consider, the accuracy and precision with which they do so, and the true significance of their parameters. New models need to be designed that specifically incorporate those traits that are of importance to CGIAR breeding programs and crops, as well as their response to key stresses and their interactions, considering the proper balance between parsimony, and biological relevance (Hammer et al., 2019). Leapfrog changes in crop modeling frameworks, such as those proposed by Droutsas et al. (2019) and Soltani and Sinclair (2011, 2012), offer promise in creating models that can be more effectively and rapidly improved to support the breeding process (e.g. by adding new processes and/or traits, or by connecting them with genetic or phenotypic data) [e.g. Messina et al. (2015)]. A documented portfolio of models will allow selection of best-bet models on a case-by-case basis.

(iii) Modernize data storage and interoperability. Collaboration across researchers in crop modeling in global or regional projects, including the Agricultural Model Inter-comparison Project (AgMIP), has helped the crop modeling community to identify high-value datasets (Asseng et al., 2015; Raymundo et al., 2018), resulting in improved models with greater applicability for breeding under future climates, for example for heat stress response on wheat (Asseng et al., 2013, 2014, 2019b), or CO_2 response on maize (Durand et al., 2018). As breeding programs become more data-driven (e.g. through the application of genomic selection), joint efforts between the modeling and breeding communities will help develop and deploy common standards and inter-connected data storage, translation, transfer, and use platforms that enable the seamless integration of crop modeling into breeding methods.

(iv) Fully take advantage of phenotyping and breeding data for modeling key traits. Lack of appropriate documentation and benchmarking and extensive model evaluation across target breeding environments implies that the range of model capabilities is generally poorly understood within the modeling community itself (Ramirez-Villegas et al., 2015; Challinor et al., 2018), and even less so by the breeding community. Testing models against experimental data will generate closer links between crop model parameter sets and specific crop varieties, and enable faster and more targeted model development and improvement.

4. Conclusions

We have reviewed the use of crop models in support of accelerated breeding, with a particular focus on the CGIAR. Crop modeling can support breeding efforts in many ways, including assessing genotypic adaptability and stability, characterizing and identifying target breeding environments, identifying traits and/or eco-physiological characteristics that maximize yield for such environments, and making predictions about the breeding value of the genotypes. Crop modeling science, especially within the CGIAR, has contributed to all of these, with clear strengths around knowledge generation on eco-physiology, the translation of such knowledge into crop model development and evaluation, and the assessment of G×E×M interactions. However, much progress remains to be made if crop modeling is to effectively contribute to the accelerated breeding rates required to adapt to climate change (see Sect. 1.2).

In a decade in which major CGIAR system breeding program transformations are expected, crop modelers will need to be part of crop improvement teams, with a common understanding of breeding pipelines and model capabilities and limitations, and common data and protocols, ensuring they follow and deliver according to common and clearly defined breeding products. Doing so will imply more rapid and better targeted crop model improvement activities, and 'thinking out of the model box' to create novel approaches that capitalize on the availability of genetic data, thus ultimately allowing the use of the knowledge embedded in current models to effectively address breeding program questions. Standard tests of crop model skill, whilst requiring perhaps a little courage on the part of modelers, will ultimately be of great service to the modelling and breeding communities, as well as those who use the results of their work.

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Conflict of interest

The authors declare no conflict of interest

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Figure captions

Figure 1 Average simulated future potential benefits from genotypic adaptation (including ideotype design) as derived from 19 modelling studies for wheat (n=15 simulations), sorghum (n=4), pearl millet (n=48), groundnut (n=12), chickpea (n=48), rice (n=159), maize (n=19), and barley (n=48). The number of data points used to compute means and error bars follows the number of studies, and the number of sites, varieties, and scenarios reported in each study. The height of the bar shows the mean of all reported simulations for each crop, and error bars extend 5–95 % of the data.

Figure 2 Three major CGIAR examples of environmental characterization to support breeding. (A) Drought stress patterns for rice in central Brazil (Ramirez-Villegas et al., 2018); (B) drought stress patterns for post-rainy sorghum in India (Kholová et al., 2013); and (C) map of maize breeding mega-environments from CIMMYT (Cairns et al., 2013). Panels A and B are redrawn from the original studies, and data from C was provided by CIMMYT.

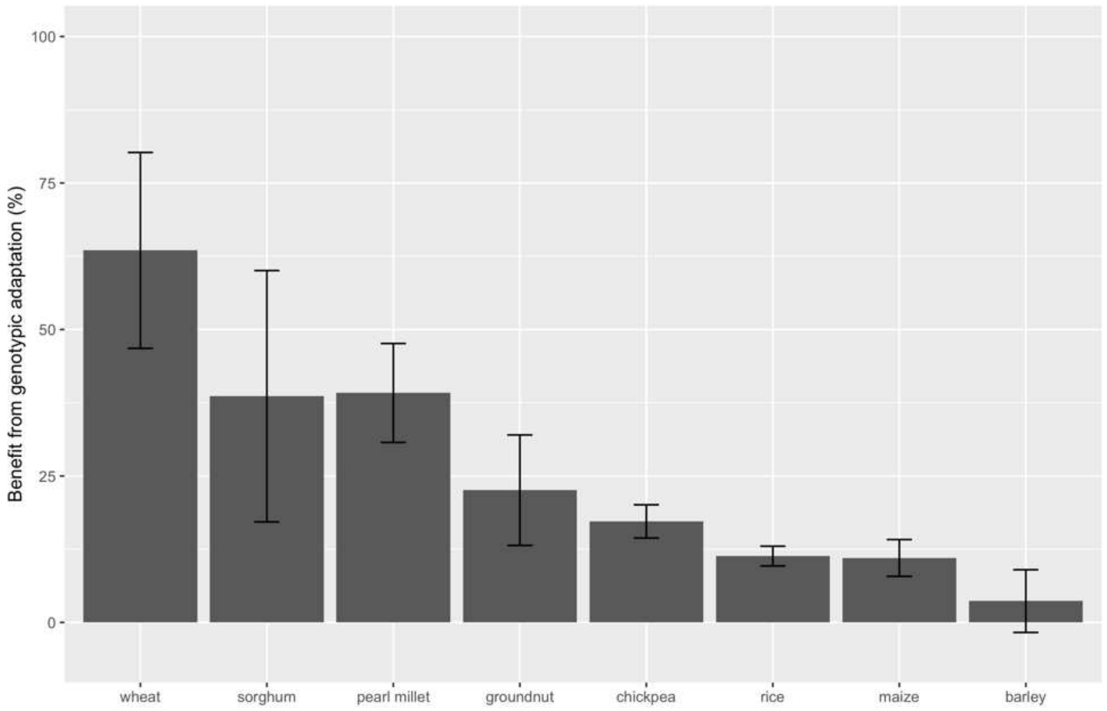
Figure 3 Response to rapid GS cycling for grain yield from the rapid cycling recombination genomic selection for four cycles (C1, C2, C3, and C4). Colored dots indicate means of the checks (red) and of the entries (blue). Figure taken from Zhang et al. (2017).

Table 1 Key CGIAR model-based ideotype design studies

Crop	Region	Model	Proposed ideotype / trait change	Reference
Chickpea	South Asia and East Africa	CROPGRO (DSSAT)	– Increased maximum leaf photosynthesis rate, partitioning of daily growth to pods and seed-filling duration. – Drought and heat tolerance: greater rooting density, water extraction capacity, and lower sensitivity for seed-set, individual seed growth, and partitioning (depending on location)	Singh et al. (2014a)
Peanut	India	CROPGRO (DSSAT)	Longer maturity	Singh et al. (2012)
Peanut	India and West Africa	CROPGRO (DSSAT)	– Increased crop maturity, leaf photosynthesis, partitioning to seeds, and seed filling duration – Greater heat and drought (root traits) tolerance	Singh et al. (2014b)
Peanut	India	GLAM	Increasing maximum photosynthetic rates, total assimilate partitioned to seeds, and, where enough soil moisture is available, also maximum transpiration rates	Ramirez-Villegas and Challinor (2016)
Lentil	East Africa	SSM	– Shorter cycle of lentil – Limited transpiration rates under high vapor pressure deficit	Ghanem et al. (2015)
Lentil	South Asia	SSM	– Shorter cycle of lentil – Limited transpiration rates under high vapor pressure deficit	Guiguitant et al. (2017)
Sorghum	India and West Africa	CERES-Sorghum	– Increased crop maturity, radiation use efficiency, relative leaf size and partitioning of assimilates to the panicle. – Greater heat (lower sensitivity of reproductive processes) and drought (root traits) tolerance	Singh et al. (2014c)
Sorghum	India	APSIM	Limited transpiration rates under high vapor pressure deficit, especially combined with enhanced water extraction capacity at the root level. Smaller canopy size, later plant vigor or increased leaf appearance rate.	Kholová et al. (2014)
Pearl millet	India and West Africa	CERES-Pearl millet	– Increased crop duration and yield potential traits (photosynthesis, partitioning) – Drought and heat tolerance in arid and semi-arid hot tropical climates.	Singh et al. (2017)
Rice	Africa	ORYZA2000	Greater crop duration and increased maximum photosynthetic rate at high temperatures	van Oort and Zwart (2018)
Rice	South Asia	ORYZA2000	Deeper roots (from 45 to 50 cm) to reduce plant sensitivity to drought. Drought onset occurs 3 weeks after transplanting.	Mottaleb et al. (2017)
Rice	Philippines	ORYZA2000	Greater duration and tolerance to extreme temperatures	Li and Wassman (2010)

Table 2 List of statistical approaches that incorporate environmental information into genomic prediction models

	Method description	Reference(s)
i	Prediction model integrating pedigree based additive genetic covariances between relatives and G×E interactions	Crossa et al. (2006)
ii	Multi-environment prediction framework for modeling G×E interactions using pedigree and genomic information	Burgueño et al. (2012)
iii	Reaction norm model for incorporating the main and interaction effects of high-dimensional markers and environmental covariates	Jarquín et al. (2014)
iv	Threshold models incorporating Gi×E and additive × additive × environment (G×G×E) interactions for predicting ordinal categorical traits	Montesinos-Lopez et al. (2015)
v	Bayesian mixed-negative binomial genomic regression model for count data that integrates G×E interactions	Montesinos-Lopez et al. (2016a)
vi	Marker × environment interaction (Mk×E) genomic model for predicting non-phenotyped individuals and identifying genomic regions associated with yield stability and environmental specificity	Crossa et al. (2016b)
vii	Models integrating genomic, pedigree and environmental covariates for predicting grain yield in different agro-ecological zones	Saint Pierre et al. (2016)
viii	G×E interaction kernel regression models using nonlinear Gaussian kernels for modelling marker main effects and marker-specific interaction effects	Cuevas et al. (2017)
ix	Single-step approach incorporating genomic, pedigree and G×E interaction information for predicting wheat lines in South Asia	Perez-Rodriguez et al. (2017)
x	Pedigree-based reaction norm model incorporating G×E interactions for multi-environment trial data	Sukumaran et al. (2017),
xi	Bayesian approach and a recommender systems approach for predicting multiple traits evaluated in multiple environments	Montesinos-Lopez et al. (2016b, 2018b)
xii	G×E interaction model in durum wheat evaluated using three cross-validation (CV) schemes for predicting incomplete field trials (CV2), new lines (CV1), and lines in untested environments (CV0)	Sukumaran et al. (2018); Roorkiwal et al. (2018)



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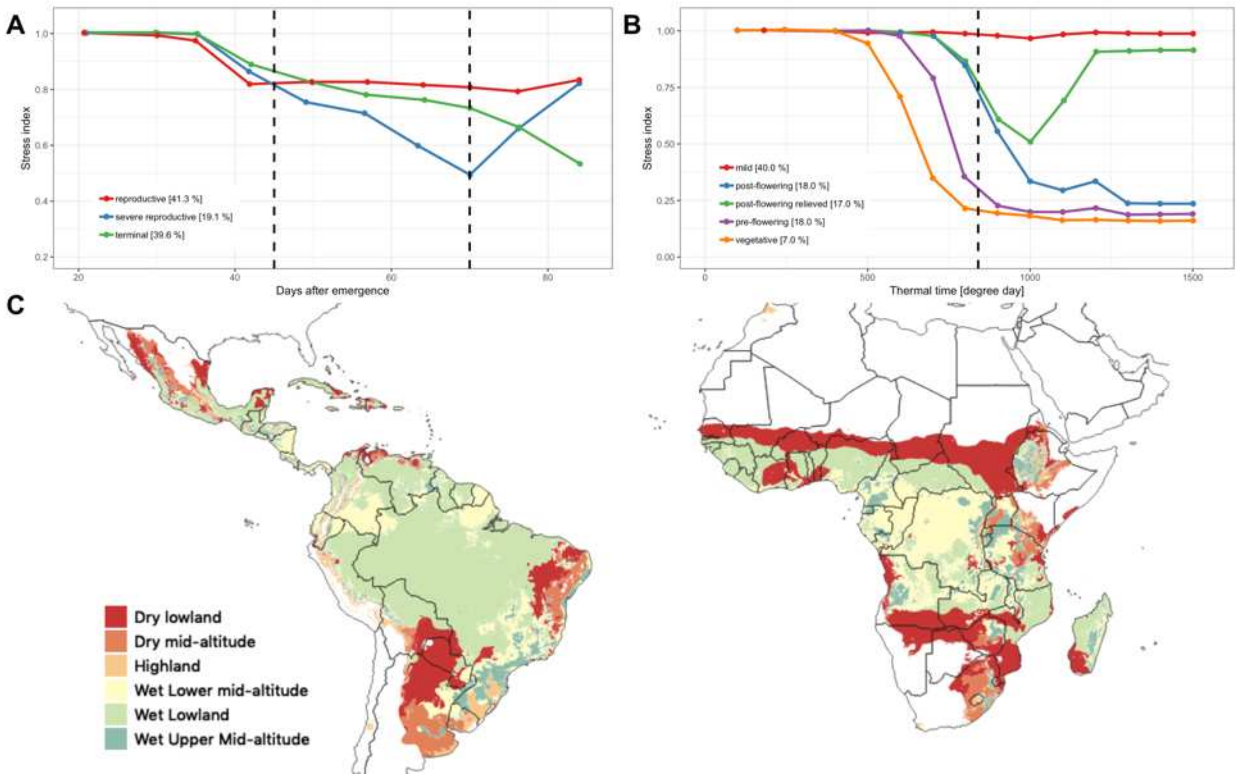

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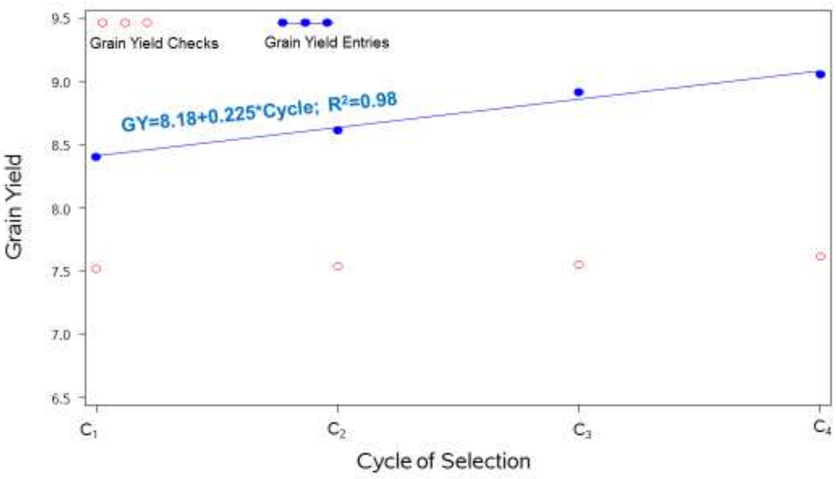

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