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An integrated approach to maintaining cereal productivity under climate change



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ABSTRACT

Wheat, rice, maize, pearl millet, and sorghum provide over half of the world's food calories. To maintain global food security, with the added challenge of climate change, there is an increasing need to exploit existing genetic variability and develop cultivars with superior genetic yield potential and stress adaptation. The opportunity to share knowledge between crops and identify priority traits for future research can be exploited to increase breeding impacts and assist in identifying the genetic loci that control adaptation. A more internationally coordinated approach to crop phenotyping and modeling, combined with effective sharing of knowledge, facilities, and data, will boost the cost effectiveness and facilitate genetic gains of all staple crops, with likely spill over to more neglected crops.

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1. Introduction

Climate change impacts cereal production mainly through heat and water stress but is also associated with waterlogging, frost, and disease and pest dynamics (Porter et al., 2014). Under climate change scenarios, and without adaptation, yields of wheat, maize and rice are predicted to decrease in both tropical and temperate regions (Challinor et al., 2014). For example, wheat yields are already slowing in most locations, and model ensembles show that for each 1 °C increase in global mean temperature, grain yields may decline by 6% (Asseng et al., 2014; Porter et al., 2014)

Not only are temperatures predicted to increase generally (Battisti and Naylor, 2009), short periods of extreme heat are expected to become more frequent. Some models estimate that by the end of the 21st Century, a current 1-in-20 year hottest day will become a 1-in-10 year event, or even occur annually or bi-annually in many regions (Stocker et al., 2013). Frequent short episodes of high temperature stress could have adverse effects on seed number, seed weight, and thus cereal yields (Jagadish et al., 2010, 2007; P. V. V. Prasad et al., 2008a, 2008b). This can have devastating effects on crop production, as seen in Russia during 2010 when the hottest summer experienced in 130 years contributed to a 30% reduction in the predicted grain harvest (Wegen, 2011).

Rainfall patterns are less confidently predicted than temperature, although it is likely that the frequency of heavy precipitation (i.e. the proportion of total rainfall from heavy falls) will increase in many regions (Stocker et al., 2013), leading to run-off and therefore reducing water availability to crops while increasing the risk of soil erosion. At the same time, the frequency of drought stress is likely to increase in many regions, thus diminishing the ability to plan for any given crop season (Hochman et al., 2009). Combined heat and drought stress is generally more detrimental than either stress alone (Pradhan et al., 2012) and is much harder to control in field trials.

Even without accounting for climate change, diminishing water supplies, increasing populations, urbanization, shifting diets, and the additional demand on cereals like maize for fodder and fuel pose significant challenges for cereal production over the coming decades (Hubert et al., 2010). Global demand for cereals is expected to reach 3 billion tons in 2050 – an increase of 940 million tons from 2005/07 – with almost all the increased demand coming from developing countries, especially Asia and Africa (Alexandratos and Bruinsma, 2012). The area under cereal cultivation is increasing worldwide, but the current rates of yield growth and overall production are not sufficient to satisfy future demand (Grassini et al., 2013). These patterns are predicted to result in significant price rises by 2050: more than 50% for maize and 25–50% for other crops, without accounting for climate change (Rosegrant et al., 2013), or 60–97% if climate change is considered (Hubert et al., 2010). With agricultural systems already affected by climate variability – particularly in semi-arid regions (Keating et al., 2010) – climate change is acting as a threat multiplier for the issues normally faced by crop production. Accounting for the negative effects of climate change, yield growth rates of 1.2–1.7% will be required for cereal crops if future demand is to be satisfied and malnutrition reduced (Nelson et al., 2010; Rosegrant pers comms).

Traditionally, breeding efforts have rightly focused on crop yield rather than survival under stresses (Barnabás et al., 2008), but there is an increasing need to identify, develop, and deploy germplasm that can withstand extreme weather events with yield stability in both “good” and “bad” years (Chapman et al., 2012; Fischer and Edmeades, 2010; Keating et al., 2010), despite the fact that variability in crop yields may increase due to climate change (Porter et al., 2014). Researchers are therefore working intensively to exploit and extend existing genetic variability to develop high-

yielding, stress-tolerant cultivars (Djanaguiraman and Prasad, 2014a, 2014b; Reynolds et al., 2015; Valluru et al., 2014).

Together, the five major cereal crops (wheat, rice, maize, pearl millet, and sorghum) make up approximately 44% of the calories consumed per capita worldwide, with this figure rising to approximately 55% in least developed countries (FAOSTAT, 2011). Strategic research collaborations across these crops and across disciplines have the potential to accelerate genetic, physiological, and molecular understanding of important traits. Such collaborations would increase the opportunities to enhance genetic gains, since many of the problems faced by cereal crops have a common physiological basis. Furthermore, new tools in genomics, transgenics, and phenomics are playing an increasingly important role in improving cereal crop yields (Tester and Langridge, 2010). Sharing these research outputs and achieving synergies across crops would help accelerate their development, deployment, and adoption, as well as push back frontiers of the physiological and genetic bases of crop adaptation (Valluru et al., 2014). The CGIAR centers have a distinct advantage in undertaking research-for-development on climate resilience in cereals due to their substantial collections of crop genetic resources, extensive stress phenotyping networks around the globe, and well established research collaborations that link public and private entities across continents (Braun et al., 2010). National programs in target regions, on the other hand, have the advantage of access to different ecologies, providing ideal opportunities for screening and phenotyping in target environments, as well as in-depth knowledge of local adaptive needs. Advanced research institutions provide advances in basic understanding of plant adaptation and new technologies especially in the area of genomics. International collaboration between these different types of organization, as well as the private sector, will therefore be vital in developing and evaluating germplasm for improved adaptation to biotic and abiotic stresses.

This paper describes the outcomes and recommendations of a meeting held in New Delhi, India, during November 2013, in which experts from the five major cereal crops met – at the invitation of the U.S. Agency for International Development (USAID) and the Bill & Melinda Gates Foundation – to discuss how research effort and resources that are currently expended largely in a crop-specific context might be combined in more synergistic ways.

2. Defining heat and drought stress

While many aspects of climate change affect crop production, the two primary threats are heat and drought stress, neither of which has been unanimously defined in the literature, largely because crops vary in terms of absolute stress thresholds. Therefore, at the New Delhi meeting experts from different cereals agreed on the following definitions for heat and drought stress, based on plant response:

- **Heat stress:** Supra-optimal temperatures occurring at any plant growth stage that can result in $\geq 10\%$ yield loss. This is typically characterized by accelerated plant development resulting in reduced photosynthetic area, plant biomass, and seed set. It may also result in reduced harvest index (HI) where heat stress inhibits reproductive success by affecting gametogenesis, pollination-related processes, and grain set. Where heat stress occurs during grain-filling, reduced grain weight (and therefore HI) will result from inhibition of starch synthesis, increased starch breakdown, and/or premature and rapid increase in senescence.
- **Drought stress:** Water deficit at any plant growth stage – though with more impact during reproductive and grain filling

Table 1

Crop-wise criteria for heat stress during the day at reproductive stages, as compiled by participants at the meeting in New Delhi.

Crop	Air temp (°C)	Most sensitive growth stage/stress duration	Qualitative indicators of heat stress
Wheat (Pradhan and Prasad, 2015; Prasad and Djanaguairaman, 2014)	≥ 32	Flowering stage for approx. 7 days prior to anthesis and pollination/ fertilization	Reduced seed set; shriveled seed; reduced grain size; quality; pollen sterility; stigma drying
Rice (Jagadish et al., 2007; Prasad et al., 2006)	≥ 33	Approx. 7–10 days prior to anthesis pollination/ fertilization	Inviabile pollen; poor anther dehiscence; reduced pollen deposition on stigma; poor pollen growth; asynchrony between pollen deposition and stigma receptivity; early embryo abortion
Maize (Herrero and Johnson, 1980; Ordóñez et al., 2015)	≥ 35	Approx. 7 days prior to anthesis and silking; flowering/reproductive stage	Leaf firing; tassel blast; pollen sterility; accelerated senescence; barren plants; reduced seed set
Pearl millet (Gupta et al., 2015)	≥ 40	Approx. 7–10 days prior to anthesis and pollination/fertilization	Reduced seed set; pollen sterility; stigma drying
Sorghum (Djanaguairaman et al., 2014; Prasad et al., 2015)	≥ 38	Approx. 7–15 days prior to anthesis and pollination/ fertilization and up to one week after	Reduced seed-set, pollen sterility, and ovule sterility

stages – that results in $\geq 10\%$ yield loss compared to an adequately-watered control. Symptoms are similar to those described above under heat stress, namely accelerated plant development resulting in reduced biomass, decreased seed set probably associated with plant signaling in response to a dry soil profile, and reduced grain size and HI due to early grain filling and premature senescence, triggered by the lack of water.

Temperature thresholds for heat stress vary according to the crop itself, its developmental stage, and the timing, duration, and intensity of the stress (Porter and Semenov, 2005). Various qualitative indicators of heat stress are shown in Table 1, based on experimentation in a limited number of environments (often not in the field) and compiled by experts at the meeting in New Delhi. For most crops there are two critical stages during reproductive growth that are the most sensitive to temperature: the first at micro- or mega-sporogenesis (in the week prior to anthesis), leading to loss of fertility; and the second at pollination/fertilization, leading to decreased levels of pollen shed, pollen reception on stigma, pollen tube growth, and fertilization, as well as early embryo abortion (Djanaguairaman and Prasad, 2014a, 2014b; Prasad and Djanaguairaman, 2014; Prasad et al., 2008a, 2008b).

Heat stress at other crop stages may also have devastating impacts. During crop establishment, drought may result in poor stands and heat will accelerate development and reduce leaf area, which reduces the capacity to intercept light. The greatest challenges may come from an increased frequency of extreme high temperatures of short duration, which can have a major impact on yield without much difference in the average temperature (Gourdji et al., 2013) since they may damage the crop at key sensitive stages such as flowering or trigger premature senescence during grain-filling (Porter and Semenov, 2005; Prasad and

Djanaguairaman, 2014) (Fig. 1). In the case of rice, diurnal temperature variation can impact yields (Welch et al., 2010) and the effect should be studied in other cereals in the context of climate change.

Common strategies for heat adaptation include: (i) stress avoidance by ensuring flowering during a relatively cooler period, either agronomically through changing planting dates (Gourdji et al., 2013) or genetically by modifying phenological patterns; (ii) reduce exacerbation of heat stress effects by avoiding nutrient or water deficiency (for example through good agronomic management); and (iii) via genetic adaptation. Strategies for adapting crops to heat stress have been reviewed recently e.g. Jha et al. (2014), including for wheat (Cossani and Reynolds, 2012), rice (Jagadish et al., 2015), maize (Cairns et al., 2013), pearl millet and sorghum (Rattunde et al., 2012).

In most crops (excepting some that mature into autumn/winter), both drought and heat stress tend to intensify as the crop cycle progresses. This is especially the case for drought because: i) in most rainfed environments, precipitation tends to decrease as the cycle progresses; ii) stored soil moisture becomes increasingly depleted over time; and iii) rising temperatures increase vapor pressure deficit (VPD) and therefore crop evaporative demand for water (Table 2). Cereal crops are increasingly being subjected to a combination of stresses. It is important to remember that tolerance to heat + drought stress may be genetically distinct (Barnabás et al., 2008; Cairns et al., 2013), placing a premium on traits that help adapt to both heat and drought stress, e.g. prolific root growth (Pinto and Reynolds, 2015). The development and deployment of climate change resilient cereal cultivars requires:

- i. A better understanding of the physiological and genetic bases of tolerance to key abiotic stresses;

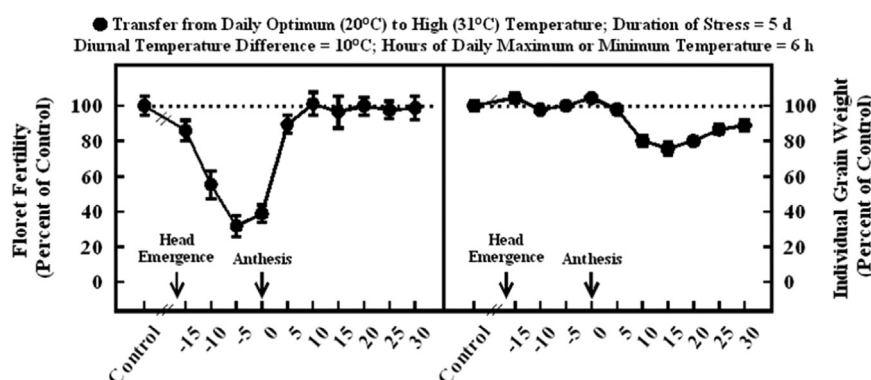


Fig. 1. Impact on floret fertility and individual grain weight caused by short episodes of high temperature stress imposed on spring wheat during various stages of reproductive development. Data are presented as a percentage of control at optimum temperature (redrawn with permission from Prasad and Djanaguairaman, 2014).

Table 2
Crop-wise criteria for drought stress, as identified by participants at the meeting in New Delhi.

Crop	Critical stage	Qualitative indicators of drought stress
Wheat (Saini and Westgate, 1999)	Continuous two weeks during critical stage-starting with onset of flowering	Early flowering; poor grain filling
Rice (Liu and Bennett, 2011; Prasad et al., 2008)	Heading and two to four weeks during critical stages-starting on set of flowering till early to mid-grain filling stages	Poor panicle emergence; decline in leaf expansion rate and tiller number; early senescence; inferior grain-set; reduced grain weight; increased chalkiness; lower head rice recovery
Maize (Prasad et al., 2008)	Four-week period beginning with pre-flowering (at least one week) through the flowering (anthesis-silking) stage, and during grain-filling	Leaf senescence; increase in anthesis-silking interval; barren plants; reduced grain set; poor tip filling of the ears
Pearl millet (Winkel et al., 1997)	Two weeks during critical stage-starting on set of flowering, and during grain-filling	Reduced seed size and seed set; poor tillering; early flowering
Sorghum (Prasad et al., 2007)	Panicle emergence, development and flowering stages, as well as grain-filling	Inhibits panicle exertion; decreased seed set; poor grain filling; smaller grain size

- ii. High-quality phenotyping at sites representative of target production environments, where stresses can be well managed at scales that fit breeding efforts;
- iii. Identification of hot spots of climate vulnerability for research, and germplasm screening at future climate analog sites;
- iv. Incorporation of modern/efficient breeding tools;
- v. Public-private partnerships that accelerate impacts in climate-vulnerable farming communities

3. Priority traits across crops and comparative biology

The team of experts attempted to determine the priority traits across all cereals (Table 3), based on an extensive body of

literature, some of which is cited herein (e.g. (Barnabás et al., 2008; Cairns et al., 2013; Cossani and Reynolds, 2012; Dreccer et al., 2014; Jha et al., 2014; Pradhan et al., 2012; Valluru et al., 2014; Zaman-Allah et al., 2011)). They also evaluated the current protocols to measure these traits, and suggested areas for further investigation.

Traits of importance across crops can generally be classified as relating to:

1. **Photosynthesis, biomass, and metabolism:** Recent genetic progress in yield may be linked to greater radiation use efficiency (RUE) at the canopy level and/or an increase in maximum photosynthesis (Fischer and Edmeades, 2010). For wheat and rice, current RUE is well below the theoretical limit

Table 3
Priority traits determining crop yields under heat and drought stress under field conditions, as defined by participants at the meeting in New Delhi (pers comms).

Class of trait	Specific trait	Application
Photosynthesis/biomass/metabolism	Canopy temperature (CT)	High through-put phenotyping (HTP) proxy for gas exchange
	NDVI (Ground cover/biomass/stay-green)	HTP for early establishment and stay-green
	Final biomass	Useful screen of genetic resources; NDVI can provide semi-quantitative estimates during season
	Spike photosynthesis	Unexplored genetic variation
	Night respiration	Role needs greater understanding (under heat)
	Chlorophyll fluorescence	HTP screen for photosynthesis (under heat); spike/flag leaf senescence
	Starch synthesis	Important in hot humid environments where evaporative cooling cannot occur and nights are hot
	Membrane thermostability	Possible proxy for respiration
	Spectral indices for pigments	HTP for photo-protective pigments
	Water relations	Canopy temperature
Wax/glaucousness		Reflects excess light; reduces water loss
Transpiration response to vapor pressure deficit		HTP screens available, but may also be able to use temporal CT (response as VPD increases)
Leaf area/leaf expansion rate		Primary indicator of growth under drought
Soil moisture extraction		Laborious, CT is a potential proxy
Root depth/root dry matter		Highly laborious, CT is a potential proxy
Carbon isotope discrimination		Indicator of intrinsic transpiration efficiency if measured under well-watered conditions
Osmotic adjustment		Associated with leaf survival (and growth) under drought
Leaf Water Status		Measured precisely as leaf water potential or estimated as relative leaf water content
Water index (spectral)		HTP proxy for leaf water status, based on spectral reflectance
Fertility/partitioning	Time of day of flowering (diurnal)	Early morning anthesis to escape heat impacts
	Grain-filling rate	Terminal stress escape strategy
	Pollen viability	Not HTP, but possible to measure if good sample collection and image analysis available
	Harvest Index	Trait integrating all processes that determine partitioning to grain
	Fruiting efficiency/panicle HI	Possible proxy for 'opportunistic' versus 'conservative' adaptive strategies
	Phenology (days to anthesis/maturity)	Important reference point when interpreting interactions of trait expression with growth stage and environment
	Tillering	Tillering patterns need better understanding to fine tune their dynamics with environment and management (e.g. wide vs. close plant spacing)
	Sugar and starch production and remobilization	Permit grain-filling to continue even when stress precludes net assimilation
	Plant growth regulators	Important role in need of further clarification and development of HTP tools
	Coleoptile length	Important for early establishment

(Reynolds et al., 2012a, 2012b), indicating an opportunity to increase yields even under climate change.

- Water related traits:** A plant's capacity to extract soil moisture is a key factor determining drought adaptation (Pinto and Reynolds, 2015). Periods of drought vary in timing and intensity and water is not used equally efficiently during all crop stages, availability during grain filling being especially critical (Vadez et al., 2013). Research into generic drought tolerance using single-gene transformations has typically concentrated on survival of plants suffering from severe water stress, rarely an important trait in crops (Richards et al., 2010). The authors agree that understanding efficient use of water is key to improving crop performance, which is likely to be achieved through improved exploration of soil water combined with good water budgeting over the crop cycle, more than increasing water use efficiency per se (Blum, 2009).
- Flowering/partitioning:** Flowering is usually timed to occur during stress-free periods in order to prevent reduced floret fertility that can lead to decreased seed set (e.g. (Barnabás et al., 2008; Prasad and Djanaguiraman, 2014)

These commonalities in key traits across the five cereal crops provide further opportunities for sharing knowledge and technologies across disciplines. Nonetheless, there is a general lack of comparative biology studies on the major cereal crops. Wheat and rice have been compared recently for their physiological and genetic architecture (Valluru et al., 2014), though less so at a metabolic level (Kadam et al., 2015). Some of their loci and genes linked to environmental adaptation appear to share high sequence similarity (Valluru et al., 2014), and there are many similarities between RUE-related yield in the two crops (Fischer and Edmeades, 2010). Traits for both wheat and rice have been explored through breeding, physiological, and molecular approaches (Table 4), though sharing research hotspots would improve the yield potential of the two crops (Valluru et al., 2014).

Developing a comprehensive dynamic mechanistic model of C3 photosynthesis is a priority for both wheat and rice for the genetic and molecular exploration of photosynthesis and its associated traits (Gu et al., 2014). Researchers predict that exploring rubisco nucleotide diversity and identifying key residues of carboxylation rate could result in improvements in rubisco activity of the two crops (Valluru et al., 2014), and that these genes could be transferred to next generations via marker-assisted selection, similar to incorporating the maize ZmC4Ppc gene into rice (Xiang et al., 2007). While the genetic and molecular regulation of grain development is generally less well studied, genes controlling grain architectural traits such as grain number (GN1), weight (GW2), and size (GS3) were used in marker-assisted selection in rice (Song

et al., 2007), and could be applied to wheat, though generally seed appearance is less important for milled grains. Furthermore, identifying the novel genetic loci controlling harvest index and utilizing metabolomics-assisted crop breeding will also need to be a key part of future breeding programs (Valluru et al., 2014). These examples also illustrate the potential value of comparative crop biology especially using model species like rice, as an alternative to non-crop models such as Arabidopsis.

While breeders are often skeptical about using exotic germplasm (except for introducing disease resistance), interspecific hybridization has achieved impressive yield gains in wheat for example (Ortiz et al., 2008). Landraces also represent alternative pools of allelic diversity that have been used successfully in breeding for abiotic stress (Reynolds et al., 2015), and techniques such as Focused Germplasm Identification Strategy (FIGS) help identify accessions originating in conditions of relevance to breeding targets.

4. Modeling trait responses to the environment

Models allow crop researchers to see the 'big picture' by looking at the pattern and frequency of drought or heat events, predicting crop adaptation, and evaluating hypothetical trait values and trade-offs (Kholová et al., 2014, 2013; Porter and Semenov, 2005). Using models to predict crop adaptation under various environmental and climate change scenarios is therefore an essential part of assessing future food security (Challinor et al., 2014; Chapman et al., 2012; Grassini et al., 2013; Porter et al., 2014) and they have been successfully used to advance germplasm within the commercial sector (Cooper et al., 2014). Process-based crop simulation models offer the benefit of decades of data on the response of crop phenology and yield to environment and are thus an important validation tool to understand the potential effects of increased heat or drought stress on crops (Asseng et al., 2014), enabling both researchers and farmers to plan responses to environmental changes, and more importantly to set the most critical breeding and agronomic management targets.

Efficient and reliable models for predicting crop adaptation under climate change are being developed, but need to be further refined. The Agricultural Production Systems Simulator (APSIM) allows for modeling of the entire cropping system (for about 40–50 crops), and can provide a key role in connecting for example genomic data to functional processes (Holzworth et al., 2014). APSIM is used routinely in sorghum (Kholová et al., 2014, 2013), and an upgraded APSIM version of pearl millet using the model architecture of the sorghum APSIM is under development (Kholová, van Oosterom, pers comms), but use of the model in the other crops has been scant, although Pioneer routinely uses APSIM for maize (Messina et al., 2011). However, the precision of models needs significant improvement, especially when it comes to simulating genetic effects and guiding targets for the five crops highlighted here (Chenu et al., 2008). The Agricultural Model Intercomparison and Improvement Project (AgMIP) is currently evaluating the ability of models to quantify crop responses to high temperatures by testing them against field experiments conducted over a wide temperature range (Asseng et al., 2014, 2013).

Table 5 illustrates the current status of models with respect to the key traits identified for the five major cereal crops. Many challenges remain, in particular modeling canopy and panicle temperature dynamics (Julia and Dingkuhn, 2013). A recent rice model has attempted to take into account effects such as transpirational cooling and early morning flowering to reduce heat sterility (van Oort et al., 2015).

Models vary widely in how they simulate dynamic processes (e.g. crop development), which processes they model (for example

Table 4
Key traits and comparisons for wheat and rice (adapted from Valluru et al., 2014).

Wheat	Trait	Rice
25–30 °C	Maximal photosynthesis	30–35 °C
High at < 30 °C	Rate of photosynthesis	High at > 30 °C
High at low temperatures	Photosynthesis per unit leaf area	High at high temperatures
20–25%, greater Kcat (50% high Vmax for carboxylation)	Leaf N to Rubisco	25–30%, high affinity for CO ₂ (20% lower Km for CO ₂)
Higher	Kcat of Rubisco	Lower
Low	Mesophyll conductance	High
8–24%	Total surface of mesophyll cell to leaf area	23–44%
Higher	FBPase, NADP-G3PDH, Cyt f content	Lower

Table 5
Priority traits, importance of future research, urgency of the research (rated as * = least urgent to **** = most urgent), and modeling status, as defined by participants at the meeting in New Delhi.

Component	Modeling needs	Urgency	Current status
Phenology	Improved predication of leaf number and sensitive growth stages	***	Good
	Variation associated with development (tillering etc.)	*	Poor
Growth	Expansive growth (leaf, stem, root extension), including CO ₂	**	Moderate
	Photo-system function (leaf and spike function)	**	Poor
	Night-time temperature (development and respiration)	****	Poor
	Grain set and abortion	*****	Varies
Partitioning	Grain expansion (grain size) and filling	****	Poor
	Changes in allocation and senescence of biomass	*	Poor
	Grain quality	**	Varies
Energy balance	Canopy, soil, and irrigation/rainfall effects	***	Poor
	Temperatures of organs	***	Poor
	Diurnal dynamics	**	Moderate
Water balance	Simulation of leaf and root transpirational cooling	****	Poor
	Integration of heat and VPD effects on organ growth	****	Poor

around anthesis and microclimate), how parameters are set (e.g. genetic coefficients or through optimization), and which input variables are required. Development above optimal temperatures is generally not well-defined and crop models vary in the way they model phenology, thus resulting in increased uncertainty with regard to crop development (e.g. (Asseng et al., 2013)). Therefore, results from climate impact studies are contingent on the choice of climate data and the impact model used (Asseng et al., 2014), while several important physiological processes still need to be brought into simulation models, as mentioned above (Eyshi Rezaei et al., 2015). Another example related to environmental cues that elicit plant growth regulator responses, and their sometimes drastic effects on growth and development (Wilkinson et al., 2012) should also be considered, and may well help to explain crop response to extreme weather events, for example. The issue of standardization will be addressed later.

5. Platforms for testing traits

There is a pressing need to establish a global phenotyping network for comprehensive characterization of genetic resources and breeding materials, using harmonized protocols. This will require institutional cooperation (national institutions, CGIAR, and private sector) with a clear focus and deliverables, and standardization of platforms and measurements (Reynolds et al., 2012a, 2012b).

All field platforms should have managed stress environments and precision treatments – including contrasting genotypes to identify tolerance responses – with adequate irrigation options for the range of target environments to be adequately simulated. Access to proximal and/or remote sensing equipment for high throughput phenotyping is necessary for breeding scale field operations, as well as drying ovens and sample processing laboratories for precision phenotyping needs and marker work. For soil characterization, useful protocols have been developed to gather water and nitrogen characterizations (Dalglish and Foale, 1998) that are also sufficiently detailed for simulation modeling. For data to be meaningful, testing locations and their environmental dynamics must be well characterized and representative of the most important aspects of the range of target sites. Defining the target environment requires a minimum dataset consisting of the following (including long term weather variables):

- Air temperature (daily, or hourly if possible; minimum/maximum)
- Wet and dry bulb temperature (to calculate relative humidity/

VPD); or canopy temperature depression on well-watered plots as a proxy

- Pan evaporation (daily in mm) to estimate transpiration demand
- Sunshine hours/radiation intensity (Mj/m²/day)
- Plant available moisture in the rhizosphere (i.e. depth to which roots penetrate, typically approx. 1 m) when the cycle starts and ends
- Rainfall (daily in mm) and water application from irrigation.
- Soil physical and chemical properties, including micronutrient deficiency/toxicity in rhizosphere
- Potential rooting depth of soil (e.g. it may be limited by rock, or toxic subsoil, etc.)
- Altitude
- Longitude, and latitude (from which photoperiod can be calculated)
- Wind speed
- Control measures used for prevalent diseases (to avoid confounding factors)
- Management practices (rotation, residues, tillage, fertilizer use, weed control)

Most crop research institutes already use managed experimental phenotyping sites, but there is a general need for further investment to meet all of the requirements outlined above, and to ensure greater standardization of trait measurement. In the last decade or so, major investments have been made to develop controlled environment (CE) phenotyping facilities (e.g. (Cooper et al., 2014)) – with the assumption that work in model species would readily translate to crop plants – and there has consequently been less emphasis on field facilities in international research (though there are exceptions). Limited association between the CE results in model species with crop performance in the field has led to renewed awareness of the imperative for high-quality field experimentation to support crop improvement for heat and drought stress, and the need to re-balance investment in field vs. CE facilities. The trend against field phenotyping in international research has started to be reversed through initiatives such as Drought Tolerant Maize for Africa (DTMA), Improved Maize for African Soils (IMAS), and use of field phenotyping tools being provided by various organizations and developed for ground and aerial sensing (e.g. Chapman et al., 2014). While new field phenotyping platforms are often built with a particular crop in mind, many can be adapted to multiple crops and could be shared across projects and institutes, arguing for investment in better-equipped, centralized platforms.

5.1. Phenotyping protocols

Progress in phenotyping can be hastened through adoption of standardized phenotyping protocols. Recent efforts have been made in wheat (Pask et al., 2014) and it is hoped that through the various phenotyping initiatives that have emerged recently (e.g. International Plant Phenotyping Network, European Plant Phenotyping Network, Wheat Initiative), some standards can be agreed upon, at least within crops. High-throughput phenotyping methods exist for several of the traits identified as high priority across the five major cereal crops and are outlined below. (A review of the many low-throughput phenotyping approaches is beyond the scope of this article but see Pask et al., 2014 and references therein for some of the more common low-throughput field measurements)

5.1.1. Photosynthesis and growth analysis

Given the lack of information on what determines genotype level differences in growth rate, it is prudent to work – initially at least – at the integrative plant level using growth analysis and measuring proxies for photosynthesis. Growth rate is the best integrator of net photosynthesis and in relatively closed canopies is an accurate measure of RUE. Although direct measurement through growth analysis is not high-throughput, a number of spectral indices as well as digital imagery can estimate cultivar level differences in biomass when all treatments are at the same growth stage and have similar growth habits (Babar et al., 2006). To estimate short-term and diurnal fluxes in photosynthesis the trait would need to be measured more constantly. Again proxies need to be employed, at least when screening large panels, where the following approaches can be adopted. Thermal imaging of canopies can pinpoint genotypes that contrast in gas exchange rate (of both leaves and spikes), at least in environments where VPD permits evaporative cooling to be associated with gas exchange with adequate resolution. Tactical use (in the sense of well-timed experimental treatments) of applied soil water can permit the distinction between gas exchange limitations associated with vascular capacity, signaling effects on stomatal conductance, or feedback inhibition associated with metabolism and sink limitation. Chlorophyll fluorescence offers a potentially medium-throughput alternative to measure leaf level photosynthetic rate and imaging approaches are in development.

5.1.2. Water relations traits

The fastest and most integrative indicator of crop transpiration is to measure the resultant evaporative cooling, at least in high VPD environments. Again measuring canopy temperature directly using infrared thermometry or through thermal imaging is the best proxy for estimating differences in transpiration rate, which is closely associated with stomatal conductance (Amani et al., 1996). As the soil moisture profile is depleted under drought, cool canopies indicate root access to subsoil water, while under hot-irrigated conditions cool canopies indicate proliferation of roots in the well-watered root zone (Pinto and Reynolds, 2015), or the capacity to transpire under high VPD conditions (Zaman-Allah et al., 2011). Water status of canopies can be estimated remotely with the spectral water index (Gutierrez et al., 2010). There are a few visually assessed traits that can influence water relations, including glaucousness and leaf rolling.

5.1.3. Flowering/partitioning

Remote sensing approaches for phenology are not well established, but a recent study has demonstrated that it is possible to use high-quality image analysis to estimate flowering time (Guo et al., 2015) and that this should be applicable to other crops. Estimation of physiological maturity, and possibly other morphologically distinct growth

stages, may be more challenging, but also achievable through regular monitoring. Remote sensing of stem water-soluble carbohydrates has been shown recently using hyper spectroscopy (Dreccer et al., 2014).

5.2. 6.2. Genotyping platforms

By linking the outputs of phenotyping experiments in a range of environments with molecular markers, genetic bases are revealed including their seemingly complex interaction with environment. The main genotyping systems currently in use are (Lateef, 2015):

- Wheat: 90 K SNP chip/KASP/SSR/GBS/DArT
- Rice: 700 K SNP chip/Multiplex KASP
- Maize: GBS-based SNP genotyping
- Pearl millet: SSR/Cyt/SNP (though no SNP is globally available)
- Sorghum: GBS/SNP

There are several limitations currently facing genotyping systems and services can be expensive and time consuming. Kompetitive Allele Specific PCR (KASP) can take six weeks, and three months is usually required for genotyping-by sequencing (GBS), though this can be reduced to a month for a premium fee. There is currently no regionally centralized genotyping facility, though the International Crops Research Institute for the Semi-Arid-Tropics (ICRISAT) is establishing a genotyping facility for South Asia, with 60–80% of its capacity reserved for organizations other than ICRISAT. There is also perhaps a need for locally developed seed-DNA extraction facilities at a reasonable price, along with automated tissue collection from leaves and seeds (seed chipper, for example). There is currently a lack of trained manpower to analyze and interpret genotyping data, and national agricultural research system researchers often face many administrative restrictions. These are the same limitations that were identified when the Global Challenge Program/Integrated Breeding Platform was first set up, but efforts are being made to improve the system.

Details on how DNA sequence information can be used to develop molecular markers for screening a range of agronomic traits is provided elsewhere (e.g. <http://maswheat.ucdavis.edu/>).

6. Making the most of the data

If the information described above is captured and curated using standardized approaches, and organized using widely available software, it can prove valuable to a wide range of users. Some institutions – such as the CGIAR and any project funded by the Bill & Melinda Gates Foundation, U.S. Department of Agriculture, USAID, or Biotechnology and Biological Sciences Research Council – are now obliged to share their data in a timely way. Data sharing can help in avoiding redundancy, or by adding robustness among data sets, but there are not yet comprehensive policies for sharing data (especially between the public and private sectors). Shared data can be difficult to source, creating challenges for accurate interpretation, and it may be difficult or impossible to use if badly formatted.

There is some consensus on what constitutes core data, around which data sharing standards should initially be prioritized. In order to simulate plant growth in models, minimum required information includes daily weather data, soil characterization, basic agronomic inputs, and at least two measures of biomass; while more detailed and time-consuming measurements, such as phenology or leaf appearance rate, vary from model to model. Historical weather and crop performance data are also valuable, but these can be the most difficult (and expensive) datasets to acquire. Better environmental data is required if the effects of climate change are to be properly monitored, though this

needs to represent all countries, not just developed countries that can afford to do it (Cramer et al., 2014). Researchers should avoid assumptions about what data is useful based simply on the priorities in their own field.

All data (phenotypic, functional, genomic) should be properly documented and searchable, ideally with metadata for context. Australian national trial data for the last 10 years is available online (<http://www.nvtonline.com.au>), along with metadata. Raw data is not published due to a high level of variability, so some statistical analyses are conducted first and the data is then published at the trial-trait-treatment level. In the USA, all variety testing data is available and categorized by region (<http://www.nass.usda.gov>). These datasets (with some exceptions for weather data) can be freely accessed and analyzed. Information from other national programs is not always so easily available, or may be in difficult to use formats (e.g. PDF). CGIAR centers handle data across multiple locations and crops and are therefore a mine of useful information, much of which is collated within the AgTrials database.

It is clear that an accessible, searchable, needs-based database is an urgent priority, yet there is currently no work being done to create one. It would be challenging and non-productive to attempt to fit all the required data into a one-size-fits-all format, especially with regard to genotyping markers, but inter-crop and inter-organization data sharing relies on information being in a transferable format. Metadata should also be included for context, but an abundance of raw data is only useful if the technology exists for evaluating it quickly and thoroughly. There are some web tools that can be programmed to extract relevant data from different kinds of databases, but ease of harvesting information is a key issue that will need to be addressed.

Research institutions and funding bodies could facilitate timely sharing of data by further prioritizing publications as research outputs, with the condition that they be accompanied by public access to all relevant data (in supplemental tables and/or public databases). This would require more explicit emphasis on resourcing the necessary steps; namely data curation, collation, statistical analysis, interpretation, literature searches, and writing itself. These activities are not always emphasized in proposals in comparison to data acquisition. Such an intervention would foster a win-win scenario, in the sense that more data would be published, including that associated with the less attractive but fundamentally important 'null hypothesis' outcomes, while allowing data and meta-data to be available that has been interpreted and peer-reviewed. Such an intervention could also lead to greater standardization in the way 'Materials and Methods' sections of publications are presented, leading to more thorough reporting of experimental treatments and conditions by researchers, as well enabling 'data sharing search engines' to more easily identify relevant studies.

7. Conclusions

There is a significant opportunity to improve the global coordination of agricultural research, which will greatly improve our ability to develop crops and cropping systems that will be more resilient in the face of climate change. Such an effort can help identify and address crop level technology gaps that may otherwise slow the adoption or reduce impacts of recent investments in biotechnology. Common examples of technology gaps include incomplete knowledge of target breeding environments, inadequate understanding of key adaptive processes, lack of uniform methodology/protocols, insufficient investment in state-of-the-art phenotyping platforms in the public domain, and duplication of efforts partly due to inadequate access to databases. A better-coordinated and more standardized approach to crop research is proposed, in the following complementary areas:

- **Characterization of target agro-ecosystems** in terms of the physical, biotic, agronomic and socio-economic constraints, now and in future climate scenarios;
- **Standardized experimental environments**, including definitions of crop response and phenotyping protocols, such that data is directly comparable across a wide range of experimental variables including germplasm, environments, and other research interventions;
- **Phenotyping platforms** representative of key ecologies, enabling results to be extrapolated to a wide range of realistic farming systems encompassing multiple crop species;
- **Comparative biology** whereby what is learnt in one crop can be more readily applied to others, especially in terms of adaptive traits and their genetic bases. This could lead to agreement on, among other things:
 - a. *generic traits* that underpin adaptation across a range of crops (e.g. within cereals) and would, for example, represent a first priority in pioneering research such as exploring novel genetic resources or ecologies;
 - b. *minimum data sets* that also lend themselves to crop simulation modeling;
 - c. *standardized protocols* for measuring generic traits so that results are directly comparable across crop species;
 - d. Data sharing in a way that encourages a public goods approach to agricultural research to underpin food security, especially for the most vulnerable sector of the global community.

In summary, better, science-driven coordination of global level crop research efforts would lead to multiple benefits associated with timely identification of constraints, research conducted in environments that best represent target sites, better sharing of expertise, resources, and data, and in the longer term a more efficient use of research funds.

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