Using Biotechnology-Led Approaches to Uplift Cereal and Food Legume Yields in Dryland Environments

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Drought and heat in dryland agriculture challenge the enhancement of crop productivity and threaten global food security. This review is centered on harnessing genetic variation through biotechnology-led approaches to select for increased productivity and stress tolerance that will enhance crop adaptation in dryland environments. Peer-reviewed literature, mostly from the last decade and involving experiments with at least two seasons’ data, form the basis of this review. It begins by highlighting the adverse impact of the increasing intensity and duration of drought and heat stress due to global warming on crop productivity and its impact on food and nutritional security in dryland environments. This is followed by (1) an overview of the physiological and molecular basis of plant adaptation to elevated CO₂ (eCO₂), drought, and heat stress; (2) the critical role of high-throughput phenotyping platforms to study phenomes and genomes to increase breeding efficiency; (3) opportunities to enhance stress tolerance and productivity in food crops (cereals and grain legumes) by deploying biotechnology-led approaches [pyramiding quantitative trait loci (QTL), genomic selection, marker-assisted recurrent selection, epigenetic variation, genome editing, and transgene] and inducing flowering independent of environmental clues to match the length of growing season; (4) opportunities to increase productivity in C₃ crops by harnessing novel variations (genes and network) in crops’ C₃, C₄ germplasm pools associated with increased photosynthesis; and (5) the adoption, impact, risk assessment, and enabling policy environments to scale up the adoption of seed-technology to enhance food and nutritional security. This synthesis of technological innovations and insights in seed-based technology offers crop genetic enhancers further opportunities to increase crop productivity in dryland environments.

Keywords: adoption and impact, applied genomics, gene editing, global warming, phenomics, photosynthesis, stress-tolerant cultivar, transgene
INTRODUCTION

Global warming overall is predicted to have negative effects on agricultural output and productivity. The current world population of 7.2 billion people is projected to increase to between 9.6 and 12.3 billion by 2100, mostly occurring in Africa and South Asia (Gerland et al., 2014). Current yield growth trends are insufficient to match the growing demand for food (Ray et al., 2013). Hence, meeting the dietary and nutritional requirements of an increasing population remains an enormous challenge.

Changes in weather pattern, erratic and uncertain rainfall, and rises in temperature have led to more frequent and longer dry spells and heat waves in many places. In addition to impacting crop growth and yields, such changes may affect crop performance by increasing infestations of insects and other pests, disease epidemics, and weed prevalence, and decreasing pollinating insects (Myers et al., 2017). Declining food quality and increased risk of food and feed contaminated with mycotoxin-producing fungi have the potential to adversely impact human and animal health (Dwivedi et al., 2013).

Agriculture accounts for 70% of freshwater use by humans, which is expected to increase by 17% by 2025 (Molden, 2007). Underground aquifers are rapidly being depleted due to excessive water use (Morison et al., 2008). The acreage of dryland agriculture will expand due to global warming (Challinor et al., 2014). Thus, drought and heat stress present critical challenges for enhancing crop productivity to ensure global food security (Lesk et al., 2016).

There are more than 160 million hectares of dryland cereal and legume crops worldwide. The regions where these crops are grown are prone to drought and heat stress, having limiting soil constraints, contain half of the global population, and account for 60% of the planet’s poor and malnourished people (Hyman et al., 2016). A recent study involving six major crop commodity groups in 131 countries reported losses from 1961–2014 of 1.6% in cereal production, 0.5% in oil crops, 0.6% in pulses, 0.2% in fruits, and 0.09% in vegetables due to drought and heat disasters. Estimated global production losses were US$ 237 billion (using 2004–2006 as a baseline), with the United States, the former Soviet Union, India, China, and Australia being the most adversely affected nations (Mehrabi and Ramankutty, 2017).

Three crop groups (cereals, legumes, and roots/tubers) are the major source of human food worldwide (1271.4 million tons), with root/tuber crops contributing to 65% (825 million t), cereals 26% (332 million t), and legumes 9% (114 million t) (http://www.fao.org/faostat/en/#data/QC, accessed on June 12, 2018). The major cereal crops are barley (Hordeum vulgare L.), maize (Zea mays L.), pearl millet (Pennisetum glaucum (L.) R. Br.), rice (Oryza sativa L.), sorghum (Sorghum bicolor (L.) Moench) and wheat (Triticum aestivum L.). The major legume crops are chickpea (Cicer arietinum L.), common bean (Phaseolus vulgaris L.), cowpea (Vigna unguiculata (L.) Walp.), faba bean (Vicia faba L.), groundnut (Arachis hypogaea L.), lentil (Lens culinaris Medikus), peas (Pisum sativum L.), pigeonpea (Cajanus cajan (L.) Millsp.), and soybean (Glycine max (L.) Merr.). Groundnuts and soybeans are also the main sources of edible oil. Both cereals and legumes are covered in this review because they not only represent worldwide the most important crops, but both are also very similar in their responses to drought and heat stress (Nuñez Barrios et al., 2005; Prasad et al., 2008; Lopes et al., 2011; Daryanto et al., 2017).

In comparison to recent reviews with focus on understanding physiological and genetic basis of drought and heat stress tolerance (Kaushal et al., 2016; Dwivedi et al., 2017; Sita et al., 2017), assessing impact of drought stress on productivity of food crops at global level (Daryanto et al., 2017) and on germplasm mining using SNPs-based arrays and GWAS to identify SNPs/candidate genes associated with plant phenology, architecture, productivity, and stress tolerance (Dwivedi et al., 2017), this review has the unique focus on the use of genetic and genomic resources to enhancing stress [drought, heat, elevated CO₂ (eCO₂)] tolerance and productivity using biotech-led approaches in addition to the uptake and adoption of seed-based technology to enhancing food and nutritional security in dryland environments.

SYNTHESIS

Physiological Basis of Adaptation to Stress Tolerance

Drought and Heat

Natural variation in response to drought or heat stress among and within crop species has been reported elsewhere (Dwivedi et al., 2010, 2013; Kaushal et al., 2016; Sita et al., 2017). The major physiological traits associated with drought or heat stress tolerance, both in cereals and legumes, include abscisic acid, canopy temperature, chlorophyll content, chlorophyll fluorescence (Fᵥ/Fₘ), early vigor, harvest index (HI), membrane integrity, normalized difference vegetation index (NDVI), osmotic adjustment, photochemical efficiency, relative water content, restricted transpiration at high vapor pressure deficit (RT-HVPD) controlled by variation in hydraulic conductance and stomatal conductance, root architecture, stomatal conductance, stay-green (Stg), total transpiration (Tr), transpiration efficiency (TE), and water use efficiency (WUE; Tables 1, 2). Differences in the root profile, Stg, Tr, HI, WUE, and RT-HVPD, among others, were associated with enhanced adaptation to drought and heat stress. Furthermore, the surrogate traits such as carbon isotope discrimination (δ¹³C), specific leaf area, and SPAD chlorophyll meter reading (SCMR) that determine WUE have been deployed in many breeding programs to enhance drought tolerance in both cereals and legumes (Rebetzke et al., 2002; Condon et al., 2004; Tausz-Posch et al., 2012; Cossani and Reynolds, 2015; Reynolds and Langridge, 2016).

Drought and heat stress often occur together. Is tolerance to both genetically distinct from tolerance to either? Prasad et al. (2011) reported that heat reduced photosynthesis more than drought in wheat, while the lowest leaf photosynthesis observed was due to combined heat and drought stress. Each stress had similar effects on spikelet fertility, grain number, and yield...
Elevated CO$_2$ (eCO$_2$)

Atmospheric carbon dioxide (CO$_2$) may increase from the current level (~400 µmol mol$^{-1}$) to 600 µmol mol$^{-1}$ by 2050 (Ciais et al., 2013). eCO$_2$ is associated with increased global warming (de Conto et al., 2012). Natural variation in grain yield in response to eCO$_2$ has been noted in trials with cereals and grain legumes in controlled greenhouses or free-air CO$_2$ enrichment (FACE) systems (Table 3), indicating the feasibility of exploiting genetic variation to develop cultivars responsive to eCO$_2$. Reduced subsets (Frankel, 1984; Upadhyaya and Ortiz, 2001), representing the diversity of the entire collection of a given species in a genebank, are available for most cereal and grain legume crops (Dwivedi et al., 2006), and are excellent resources for identifying CO$_2$-responsive germplasm.

Establishing and operating CO$_2$-fumigation facilities are costly. An alternative method is needed where large numbers of germplasm can be accommodated to assess genotype responses under eCO$_2$. In multi-year and multi-location trials involving 127 diverse rice accessions, two planting densities (normal and wider spacing), Shimono et al. (2014) identified two _japonica_ types most responsive to wider spacing as candidates to support the pre-screening CO$_2$-responsiveness in a FACE system and temperature-gradient chambers under eCO$_2$. The results from FACE confirmed that responsiveness to wider spacing density, as measured by changes in panicles plant$^{-1}$, is positively associated with responsiveness to eCO$_2$ across both temperate and tropical surroundings, suggesting that wider spacing density in rice would be a useful prescreen for testing diverse germplasm at low cost for responsiveness to eCO$_2$ (Shimono et al., 2014). Finlay–Wilkinson’s regression coefficient (RC) approach has also been suggested as a preliminary evaluation to select accessions responsive to eCO$_2$. In rice and soybean RCs and

### Table 1 | Physiological basis of drought and heat stress tolerance in grain legumes from 2005–2017.

| Species                | Physiological traits associated with stress tolerance                                                                 | Reference                                                                 |
|------------------------|------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|
| **Drought stress**     |                                                                                                                        |                                                                          |
| Common bean ( _Phaseolus vulgaris_ L.) | Drought avoidance root traits (DART), water use efficiency (WUE), harvest index (HI), relative water content (RWC), stomatal conductance, pod harvest index | Beebe et al., 2013; Rosales et al., 2013; Polania et al., 2016; Medina et al., 2017 |
| Chickpea ( _Cicer arietinum_ L.) | Canopy temperature, carbon isotope discrimination ($\delta^{13}$C), DART, early vigor, HI, low transpiration rate, restricted transpiration rate at high vapor pressure deficit (VPD), SCMR, photosystem II | Kashiwagi et al., 2005, 2010, 2013; Zaman-Atah et al., 2011a,b; Krishnamurthy et al., 2012; Sivasakthi et al., 2017 |
| Cowpea (_Vigna unguiculata_ (L.) Walp) | Chlorophyll content, delayed leaf senescence, non-photochemical quenching, photosystem II, RWC, restricted transpiration rate at high VPD, TE | Kumar et al., 2008; Muchero et al., 2008; Belko et al., 2012; Mwale et al., 2017 |
| Groundnut (_Arachis hypogaea_ L.) | Chlorophyll content, HI, specific leaf area, SCMR, restricted transpiration rate at high VPD, TE, WUE | Upadhyaya, 2005; Devi et al., 2009, 2010; Devi and Sinclair, 2011; Hamidou et al., 2013; Vadez and Rathnakumar, 2016 |
| Soybean (_Glycine max_ L.) | Restricted transpiration rate at high VPD, slow wilting at high VPD associated with low leaf hydraulic conductance and early stomatal closure | Fletcher et al., 2007; Sinclair et al., 2008, 2010; Sadok and Sinclair, 2009; Severske et al., 2013; Medina et al., 2017 |
| **Heat stress**         |                                                                                                                        |                                                                          |
| Chickpea               | Chlorophyll content, membrane integrity, photochemical efficiency, pollen viability, RWG, seed setting, stigma receptivity, stomatal conductance | Kaushal et al., 2013 |
| Cowpea                 | Membrane integrity, photosynthesis, pollen viability, stigma receptivity                                               | Lucas et al., 2013; Angira, 2016 |
| Groundnut              | Efficient partitioning of photosynthate leading to high pod growth rate                                                | Akbar et al., 2017 |
| Soybean                | Antioxidant metabolites (tocopherols, flavonoids, phenylpropanoids, and ascorbate precursors) confer tolerance to high temperature during seed development | Chebrolu et al., 2016 |
TABLE 2 | Physiological basis of drought and heat stress tolerance in cereals from 2005–2017.

| Drought stress | Physiological traits associated with stress tolerance | Reference |
|----------------|-----------------------------------------------------|-----------|
| Barley (Hordeum vulgare L.) | Biomass, chlorophyll content, osmotic adjustment (OA), flag leaf photosynthesis rate, relative water content (RWC), stay-green, stomatal conductance | González et al., 2010; Vaizzi et al., 2010; Gous et al., 2015; Sharma et al., 2016 |
| Maize (Zea mays L.) | Restricted transpiration rate at high vapor pressure deficit (VPD) associated with low hydraulic conductance, root architecture, anthesis-silking interval (ASI), stay-green, water use efficiency (WUE) | Hund et al., 2009; Gholipoor et al., 2013a,b; Choudhary and Sinclair, 2014; Li et al., 2015; Messina et al., 2015; Maazou et al., 2016 |
| Pearl millet (Pennisetum glaucum (L.) R.Br.) | Restricted transpiration rate at high VPD, tolerant and sensitive genotypes had similar total water extracted under drought stress; however, tolerant genotypes extracted less water prior to anthesis, and more water after anthesis | Khrotavá et al., 2010; Vadez et al., 2013; Medina et al., 2017 |
| Rice (Oryza sativa L.) | Abscisic acid, carbon isotope discrimination (δ13C), chlorophyll content, membrane stability, photosynthesis rate, photosystem II activity, root architecture, RWC, stomatal conductance, transpiration rate, WUE | Kumar S. et al., 2014; Pandey and Shukla, 2015; Sandhu et al., 2016 |
| Sorghum (Sorghum bicolor (L.) Moench) | Chlorophyll content, restricted transpiration rate at high VPD, stay-green, stomatal conductance | Xu et al., 2000; Gholipoor et al., 2010; Choudhary and Sinclair, 2014; Shekoofa et al., 2014 |
| Wheat (Triticum aestivum L.) | Biomass, canopy temperature, chlorophyll content, δ13C, membrane integrity, HI, normalized difference vegetation index (NDVI), root architecture, small canopy, stay-green, stomatal conductance, water-soluble carbohydrate, WUE | Rizza et al., 2012; Nawaz et al., 2013; Wilson et al., 2015; del Pozo et al., 2016; Reynolds and Langridge, 2016; ElBasyoni et al., 2017; Nakhoferoosh et al., 2017 |

| Heat stress | Physiological traits associated with stress tolerance | Reference |
|-------------|-----------------------------------------------------|-----------|
| Barley | Chlorophyll content, stay-green | Gous et al., 2015 |
| Maize | ASI, Canopy temperature, chlorophyll content, chlorophyll fluorescence(Fv/Fm), leaf firing, leaf senescence, membrane integrity, pollen shedding, seed setting, stigma receptivity, tassel blast, tassel sterility | Yadav et al., 2016; Alam et al., 2017 |
| Pearl millet | Membrane integrity, percent seed setting | Yadav et al., 2014; Gupta et al., 2015 |
| Rice | Anther and stigma characteristics, better antioxidant scavenging ability, membrane stability, photosynthesis, pollen development, RWC, seed setting | Jagadish et al., 2007, 2009; Bahuguna et al., 2014 |
| Sorghum | Leaf firing, leaf blotching, floret fertility, individual seed weight, reduced seed setting | Prasad and Djanaguiraman, 2014; Prasad et al., 2015; Chen et al., 2017 |
| Wheat | Canopy temperature, cell membrane stability, chlorophyll content, floret fertility, Fv/Fm, high early biomass, high grain filling rate, lower respiration rate, reduced seed weight, stay-green, stomatal conductance, transpiration | Prasad and Djanaguiraman, 2014; Kumari et al., 2013; Pandey et al., 2015; Sharma et al., 2015; Pinto et al., 2016, 2017; ElBasyoni et al., 2017 |

The responsiveness of yield to eCO2 were positively associated (Kumagai et al., 2016), suggesting that RCs may be initially used to discard accessions not responsive to eCO2. The reason for these relationships may be due to the high CO2-responsive accessions exhibiting high plasticity in resource-rich environments (Shimono, 2011; Shimono et al., 2014; Kumagai et al., 2015). Additional research is required to assess the validity of these methods in diverse crops.

Biomass, HI, heads per unit area, spikelet density, grains per panicle, and grain weight under eCO2 environments contributed to increased yield in cereals (Shimono et al., 2009; Shimono, 2011; Tausz-Posch et al., 2012; Thilakarathne et al., 2012; Shimono and Okada, 2013; Bunce, 2017), while increased biomass, HI, and pods and grains per plant enhanced yields in legumes (Bunce, 2008; Bishop et al., 2015; Kumagai et al., 2015; Bourgault et al., 2016, 2017). A detailed meta-analysis involving 79 species and eight reproductive traits showed that CO2 enrichment (500–800 µl l−1) across all species produced a greater proportion of flowers (19%), fruits (18%), and grains (16%), increased individual grain weight (4%) and test weight (25%), and lowered grain N (−14%). Crops and wild relatives showed a similar response for biomass; however, crops under eCO2 had higher HI and yielded more fruits (28% vs. 4%) and grains (21% vs. 4%) than the wild relatives. Thus, crops were more responsive to eCO2 than wild relatives (Jablonski et al., 2002).

Elevated CO2 is associated with increased atmospheric temperature. Both eCO2 and heat stress strongly affect crop production. There is a need to understand the genotypic response to such an interaction to identify genotypes responsive to eCO2 and heat stress. Rice and wheat grown under two levels of CO2 (ambient and enriched up to 500 µmol mol−1) and temperature (ambient and increased 1.5–2.0°C) in FACE systems increased grain yield, while an increase in temperature reduced yield (Cai et al., 2016). These authors noted a differential response in the treatment combining eCO2 and temperature: greater reductions (17–35%) in wheat than rice (10–12%), and the number of
TABLE 3 | Cultivars response to elevated carbon dioxide (eCO$_2$) relative to ambient carbon dioxide (aCO$_2$) in barley, common bean, lentil, maize, pea, rice, soybean, and wheat from 2007–2017.

| Germplasm no. (year/season) | Evaluation conditions | CO$_2$ treatments | Summary of response at elevated CO$_2$ (eCO$_2$) | Reference |
|-----------------------------|-----------------------|-------------------|-------------------------------------------------|-----------|
| Barley (Hordeum vulgare L.) | Open-top chambers     | aCO$_2$: 400 ppm; eCO$_2$: 700 ppm | eCO$_2$ increased aboveground biomass on average by 15% (range: 36% to 95% among genotypes) | Mitterbauer et al., 2016 |
| Common bean (Phaseolus vulgaris L.) | Field open-top chambers | Ambient CO$_2$ (aCO$_2$): 370 µmol mol$^{-1}$; eCO$_2$: 550 µmol mol$^{-1}$ | Significant cultivar × CO$_2$ interaction; seed yield at eCO$_2$ was 0.89–1.39 times that of ambient CO$_2$ (aCO$_2$); pod/seed numbers at eCO$_2$ the main determinant of response to seed yield | Bunce, 2008 |
| Lentil (Lens culinaris Medik.) | FACE facility          | aCO$_2$: 400 µmol mol$^{-1}$; eCO$_2$: 550 µmol mol$^{-1}$ | eCO$_2$ increased yields by about 0.5 t ha$^{-1}$, with greatest increase noted during terminal drought; relative increase among cultivars ranged from 18–138%; biomass increased by 32% and harvest index up to 60% | Bourgault et al., 2017 |
| Maize (Zea mays L.)         | Field open-top chambers | aCO$_2$: 390 µmol mol$^{-1}$; eCO$_2$: 550 µmol mol$^{-1}$ | Biomass, grain yield and harvest index in relation to aCO$_2$ improved by 32–47%, 46–57%, and 11–68%, respectively, under eCO$_2$; grain number and test weight contributed to improved yield under eCO$_2$ | Vanaja et al., 2015 |
| Pea (Pisum sativum L.)      | FACE experiments       | aCO$_2$: 390–400 ppm; eCO$_2$: 550 ppm | eCO$_2$ significantly increased seed yield by 26% due to increased pods per unit area, with no effect on grains per pod, grain size, or harvest | Bourgault et al., 2016 |
| Rice (Oryza sativa L.)      | Controlled environment chambers | Three temperature regimes (29/21, 31/23, 33/25°C) | eCO$_2$ increased biomass and seed yield, however, response reduced due to increasing air temperature; weedy rice showed increased yield with eCO$_2$ at all temperatures; ratio of tiller production between CO$_2$ treatments at 30 DAS a significant predictor of seed yield in response to eCO$_2$ at all temperatures | Ziska et al., 2014 |
| 3 cultivated and 1 wild rice (1) | Controlled environment chambers | Three temperature regimes (29/21, 31/23, 33/25°C) | eCO$_2$ increased biomass and seed yield, however, response reduced due to increasing air temperature; weedy rice showed increased yield with eCO$_2$ at all temperatures; ratio of tiller production between CO$_2$ treatments at 30 DAS a significant predictor of seed yield in response to eCO$_2$ at all temperatures | Ziska et al., 2014 |
| 24 (1) | Sunlit temperature-gradient chambers | aCO$_2$: 377 µmol mol$^{-1}$; eCO$_2$: 568 µmol mol$^{-1}$; temp: 23 and 18°C | eCO$_2$ increased biomass by 27%, with tiller numbers the main driving force to increased biomass; significant genotype × temperature interaction; genotypes with higher biomass response to eCO$_2$ had smaller reduction of biomass under low temperature | Shimono and Okada, 2013 |
| 4 (2) | FACE experiment; two planting density | aCO$_2$: 383–385 µmol mol$^{-1}$ eCO$_2$: 576–600 µmol mol$^{-1}$ | eCO$_2$ at low planting density increased biomass by 36–64%; significant cultivar × density interaction; panicle number and grain weight had similar response to eCO$_2$; low planting density emulates eCO$_2$ effects which could be used to select germplasm responsive to eCO$_2$ | Shimono, 2011 |
| 16 (2) | Field open-top chambers | aCO$_2$: 370 µmol mol$^{-1}$ eCO$_2$: 570 µmol mol$^{-1}$ | Genotypes responded differently to eCO$_2$: yield increase ranged from 4–175% and 3–64% in two seasons; panicle number and grains per panicle contributed to greater yield at eCO$_2$ | de Costa et al., 2007 |

(Continued)
TABLE 3 | Continued

| Germplasm no. (year/season) | Evaluation conditions | CO2 treatments | Summary of response at elevated CO2 (eCO2) | Reference |
|-----------------------------|-----------------------|----------------|------------------------------------------|-----------|
| Soybean (<i>Glycine max</i>) | Temp. gradient chambers in greenhouse | aCO2: 400 µmol mol−1; eCO2: 600 µmol mol−1; temp: 28°C | eCO2 increased seed yield up to 62% among cultivars, with aboveground biomass and pods plant−1 contributed most to the yield; low density (LD) increased yield by 5% to 105% owing to increased biomass and pods plant−1; yield increase in LD significantly associated with eCO2, suggesting biomass and pods plant−1 at LD could be used to select eCO2 responsive germplasm | Kumagai et al., 2015 |
| 18 (4)              | FACE                  | aCO2: 380–990 ppm; eCO2: 550 ppm | Biomass and seed yield under eCO2 increased by 22% and 9%, respectively, but with reduced harvest index (HI); however, genotypes with highest HI under eCO2 also had highest HI in eCO2, suggesting HI could be used select for CO2 responsive germplasm | Bishop et al., 2015 |
| Wheat (<i>Triticum aestivum</i> L.) | 4 (2) and 9 (1) FACE | aCO2: 422 µmol mol−1; eCO2: 628 µmol mol−1 | Significant differences among cultivars, evaluated on large and small plots in FACE, were detected, with some more responsive to eCO2; no loss in precision when response to eCO2 assessed on small plots | Bunce, 2017 |
| 2 (2); 3 growth stages | FACE                  | aCO2: 390 µmol mol−1; eCO2: 550 µmol mol−1 | Drysdale (high transpiration efficiency, TE) responded more favorably to eCO2 than Hartog (low TE), with former yielding ~19% more than Hartog; more green leaf mass (~15%) and greater spike (~8%) and tillers (~11%) contributed to increased yield in Drysdale, suggesting cultivars with superior TE perform better under eCO2 | Tausz-Posch et al., 2012 |
| 7 (1); 4 growth stages | Glasshouse             | aCO2: 384 µmol mol−1; eCO2: 700 µmol mol−1 | Grain yield increased by 38% under eCO2, correlated with spike number (γ = 0.868) and aboveground biomass (γ = 0.942); leaf mass per unit area (LMA) associated with increased N content on an area basis ([N]LA) and positively correlated with grain yield; differences in LMA could be used to select eCO2 responsive germplasm | Thilakaratne et al., 2012 |

aCO2, ambient carbon dioxide; eCO2, elevated carbon dioxide.

filled grains per unit area accounted for most of the effect of eCO2 and high temperature. Similar antagonistic effects of eCO2 and high temperature were noted among diverse rice accessions (Wang D.R. et al., 2016). Rising CO2 may compensate for losses due to drought in some situations. However, a recent study – conducted over eight years under varying precipitation and with year-to-year variation in weather at a unique open-air field facility – revealed that stimulation of soybean yield by eCO2 diminished to zero as drought intensified and eCO2 interacted with drought to modify stomatal function and canopy energy balance (Gray et al., 2016). eCO2 did not stimulate photosynthesis, biomass or grain yield, whereas the treatment combining eCO2 and high temperature reduced grain yield in maize (Ruiz-Vera et al., 2015). The above examples show the negative impact of rising CO2 on crop productivity due to changes in the intensity of drought and heat stress. Careful selection of crop cultivars responsive to eCO2 under drought and heat stress is needed, therefore, to minimize the negative impacts from interacting climatic factors in key crop production areas.

**Molecular Basis of Adaptation to Stress Tolerance**

**Drought**

**Legumes**

A "quantitative trait loci (QTL) hotspot" region bearing 12 QTL for drought tolerance explained up to 58% of the variation in chickpea (Varshney et al., 2013). Further research involving this region unlocked two subregions enriched with 23 genes, of which four were functionally validated for drought tolerance in chickpea (Kale et al., 2015). Eighteen single nucleotide polymorphisms (SNPs) from five genes (ERECA, ASR, DREB, CAP2, and AMDH) significantly contributed to enhanced drought and heat tolerance in chickpea (Thudi et al., 2014b). Roorkiwal et al. (2014) generated 1.3 Mbp of sequence data on 300 chickpea reference set accessions (Upadhyaya et al., 2008) using 10 genes known to confer drought adaptation, and noted 79 SNPs and 41 indels in nine genes, with the maximum number of SNPs in ASR gene, grouped into two distinct haplotypes.

In common bean, 19 WRKY genes, 11 downregulated and eight upregulated, responded to drought stress (Wu et al., 2017) and eight significant marker-trait associations under drought stress were noted on chromosome 9 and 11 (Hoyos-Villegas et al., 2017).

The stay-green QTL <i>Dro-1</i>, <i>Dro-3</i>, and <i>Dro-7</i> were noted in recombinant inbred lines and diverse germplasm, with a map resolution equal to or below ≤3.2 cM, suggesting valuable targets for marker-assisted genetic enhancement in cowpea (Muchero et al., 2013). Furthermore, the co-location of a stay-green trait with biomass and grain yield QTL (Muchero et al., 2009) opens up the opportunity to select for stay-green at the seeding stage as a rapid screening tool for selection of terminal drought tolerance in cowpea.

In pigeonpea (<i>Cajanus cajan</i> (L.) Millsp.), U-Box protein-coding genes, <i>uspA</i> domain genes, <i>CHX</i> gene, and an uncharacterized
polymorphisms (16 SNPs and 25 indels) at the induced under water-deficit conditions. Xia et al. (2017) detected tolerant accessions (Guo et al., 2009). 

reproductive stage that were exclusively expressed in drought-varying levels of drought response unraveled 34 genes at the both types contribute adaptation to drought stress in barley. 

In barley, 17 constitutively expressed (exclusively in tolerant accessions) and 18 drought-responsive (differential expression under drought among tolerant and intolerant accessions) genes have been reported (Guo et al., 2009). This suggests that both types contribute adaptation to drought stress in barley. 

A gene expression study involving barley accessions with varying levels of drought response unraveled 34 genes at the reproductive stage that were exclusively expressed in drought-tolerant accessions (Guo et al., 2009). P5CSI is the key gene involved in the biosynthesis of proline and is significantly induced under water-deficit conditions. Xia et al. (2017) detected 41 polymorphisms (16 SNPs and 25 indels) at the HvP5CSI locus among barley accessions, with 13 distinct haplotypes; of these, five polymorphisms in HvP5CSI were significantly \( (P < 0.001) \) associated with drought tolerance. Wild barley provided new genes and differentially expressed alleles for adaptation to drought. These genes appear to be more conserved than non-associated genes, while those tolerance genes evolved more rapidly than other drought-associated genes (Hübner et al., 2015).

Anthesis–silking interval (ASI), ears per plant, plant height, and stay-green traits were correlated with drought tolerance in maize (Messmer et al., 2009, 2011). Chromosome 3 bears a QTL hotspot region (~8 Mb) harboring QTL for traits related to drought tolerance (Almeida et al., 2014). Many drought-tolerant candidate genes (271) and non-synonymous protein-coding SNPs (nsSNPs) (524), with most nsSNPs in bin 1.07 region harboring known drought-tolerant QTL, are reportedly involved in physiological and metabolic pathways in response to water deficit in maize (Xu et al., 2014). Li et al. (2016) detected numerous SNPs, located in 354 candidate genes, associated with drought-related traits. More recently, 77 SNPs associated with ten drought-responsive transcription factors involved in stomatal closure, root development, hormonal signaling, and photosynthesis were found in maize (Shikha et al., 2017). In a multi-environment study, Millet et al. (2016) noted a pattern of QTL effects expressed as functions of environmental variables, of which eight were associated with tolerance to heat and 12 with drought in maize.

A SNP related to a putative acetyl CoA carboxylase gene and an indel associated with a putative chlorophyll a/b binding protein gene, near a major drought-tolerant QTL, are linked with stay-green, grain yield, and HI in pearl millet under drought (Dwivedi et al., 2017).

In rice, several large-effect QTL have been reported in multiple genetic backgrounds and production environments (Kumar A. et al., 2014). In a study involving N22 (drought tolerant) and IR64 (drought intolerant) rice cultivars, Shankar et al. (2016) detected 801 transcripts that were exclusively expressed in N22 under stress conditions, with a larger number encoding NAC and DBP transcription factors. Transcripts encoding for thioredoxin and involved in phenylpropanoid metabolism were upregulated in N22. This suggests that cultivar-specific stress-responsive transcripts may serve as a useful resource to explore novel candidate genes for abiotic stress adaptation in rice. Plant phenotypic plasticity refers to producing a distinct phenotype in response to changing environments (Nicotra et al., 2010). Seventy-six SNPs and 233 priori candidate genes associated with root plasticity traits regulate root growth and development, which upon validation can be deployed in breeding to enhance abiotic stress adaptation in rice (Singh et al., 2015). Using image-based traits (i-traits) – non-destructive phenotyping as a measure of response to drought – Guo et al. (2018) noted high heritability and large variation and discovered previously unknown genes associated with drought resistance. For example, OsPP15 is associated with a hub of i-traits, whose role was further confirmed by genetic transformation.

The reduction in canopy size associated with Stg QTL in sorghum reduces water demand prior to anthesis, thereby saving more water for plants during post-anthesis. Over expression of P5CS2, mapped within the Stg1 QTL (Subudhi et al., 2000), in the stay-green line relative to the senescent line was correlated with higher proline (Johnson et al., 2015). Polymorphisms at cis-elements in the putative promoter region of P5CS2 probably caused a difference in the expression of this gene, which may facilitate sorghum improvement by marker-assisted selection (MAS). Fracasso et al. (2017) assessed the gene expression dynamics of five drought-related genes in sorghum and found increased expression levels of all genes under drought in tolerant compared with sensitive genotypes, and identified three candidate genes (SbDREB1F, SbERECTA, and SbDHN) that may be deployed to assess drought adaptation in sorghum. Five to nine SNPs near the 14 candidate genes conferred heat stress tolerance in sorghum (Chen et al., 2017).

Variation in water-soluble carbohydrates in stems confers stress tolerance in wheat (Blum, 1998). Polymorphisms of trait-associated SNPs unraveled eight candidate genes grouped into two distinct classes – defense response proteins and proteins...
triggered by environmental stress – which provide opportunities for selecting for stress tolerance in wheat (Dong et al., 2016). Meta-analysis unraveled 43 co-localized QTL for both drought and heat stress, and 20 drought and two heat stress QTL (Acuña-Galindo et al., 2015). Furthermore, integration of 137 SNP markers for drought- and heat-responsive candidate genes identified 50 candidate SNPs within MQTL confidence intervals, including genes involved in sugar metabolism, reactive oxygen species scavenging, and abscisic-acid-induced stomatal closure (Acuña-Galindo et al., 2015). More recently, three major QTL for drought-responsive traits, one each for days to anthesis (QDa.ccsu-5A.1), plant height (QHt.ccsu-5A), and 100-grain weight (QTgw.ccsu-7A), were reported under rainfed conditions among double haploid lines in wheat (Gahlaut et al., 2017). The maximum quantum efficiency of photosystem II, measured as Fv/Fm, is the most widely used parameter for the rapid non-destructive measurement of stress response in plants. Major QTL on chromosome 3B (two) and chromosome 1D (one), explaining 13–35% of the variation for Fv/Fm, involved in heat stress response were noted in wheat (Sharma et al., 2017).

Emmer wheat (Triticum dicoccum Schrank ex Schübl) – the durum wheat (T. durum Desf) ancestor – harbors a rich source of allelic diversity for abiotic stress adaptation (Peng et al., 2012). Near-isogenic lines (NILs) of durum and bread (T. aestivum L.) wheats containing wild emmer QTL alleles enhanced productivity and yield stability across environments, thereby enriching their gene pools with diversity for improving drought adaptation (Merchuk-Ovnat et al., 2016). Wheatgrass (Agropyron elongatum (Host) P. Beauv.) and wild barley (Hordeum spontaneum (K. Koch) Thell.) also provided genes for drought adaptation: KNAT3 and SERK1 in wheat (Placido et al., 2013) and Hsdr4 in barley (H. vulgare L.) (Suprunova et al., 2007).

Heat

Legumes

Tolerance to heat stress is associated with browning (Hbs) of seed coats in cowpea. Five QTL associated with heat stress tolerance accounting for 11–18% phenotypic variation were tagged with 48 SNP in cowpea (Lucas et al., 2013). Hbs-1 contributed 28–73% phenotypic variation associated with heat stress tolerance and segregated with SNPs, 1_0032 and 1_1128 (Pottorff et al., 2014).

Cereals

Genomic regions on chromosome 2H and 7H at elevated temperature and 17 root/shoot trait QTL have been found in barley (Dwivedi et al., 2017). Six heat stress tolerant and 112 heat-responsive candidate genes were co-located within two QTL hotspot regions (Frey et al., 2015) – reported to contain three heat tolerance and 23 heat-responsive genes – for grain yield under heat stress in maize (Frey et al., 2016). Of interest is the heat tolerance gene GRMZM2G248866, present in both QTL hotspot regions, which encodes a calcycin-binding protein involved in calcium signaling in response to external stress (Frey et al., 2016).

Using NILs differing in heat sensitivity and cDNA-AFLP analysis, Liao et al. (2012) reported 54 transcript-derived fragments (TDFs), 45 of which were mapped to rice chromosomes, mostly in heat-tolerant lines. Twenty-eight of these homologous sequences encoding proteins were associated with signal transduction, oxidation, transcriptional regulation, transport, and metabolism; thus, they are good candidates for studying the molecular basis underlying adaptation to heat stress in rice. Five to 14 loci including qHTSF4.1, qSTIPS9.1, and qSTYS.5/SSIY5.2, which are major QTL associated with heat tolerance at the reproductive stage, are known in rice (Lafarge et al., 2017; Shanmugavadivel et al., 2017). A novel QTL on chromosome 9 for percent spikelet fertility at the reproductive stage and one known QTL on chromosome 5 for heat tolerance mapped to 331 kbp genomic regions, comprised 65 and 54 genes, respectively (Shanmugavadivel et al., 2017).

**Elevated CO2 (eCO2)**

The eCO2 in the atmosphere, which enhances CO2 fixation, plant growth, and production (Xu et al., 2013), is the major driving force behind global warming. The global surface temperature may rise between 2.6 and 4.8°C by the end of this century, depending on greenhouse gas emission pathway (IPCC, 2013). Stomata on the surface of plant leaves balance the uptake of CO2 with evaporation. How plants regulate their stomata in response to environmental stimuli may have important implications for future crop production. Stomata responds to eCO2 by partial closing, and large variation in response to eCO2 was noted among crop species [see section "Elevated Carbon Dioxide (eCO2)"]

The decrease in stomatal conductance, the rate at which CO2 enters the leaves, under eCO2 reduces water consumption and increases WUE. Stomatal function is regulated by genetic variation such as stomatal development, density, and trade-off, and molecular mechanisms regulating guard cell movement under eCO2, and its interactive effects with environmental factors such as vapor pressure deficit, temperature, CO2 concentrations, and light either alone or in combination (Xu et al., 2016). The genetic basis for inter- and intraspecific variation in the response of stomata under eCO2 and the mechanisms for sensing and responding to eCO2 are poorly understood in plants. To date, 16 genes (HIC, GT1, EPF2, STOMAGEN, OST1, CA1, CA4, SCAP1, HT1, APRC2, SLAC1, PATROL1, AILM1A12/QAC1, QAC1, AtABC14, and ROP2), two (EP3 and SLAC1) in rice, and one (ROP2) in faba bean, controlling stomatal development and movement response to eCO2 in Arabidopsis, have been discovered (Xu et al., 2016). Johansson et al. (2015) noted two genetic loci and candidate genes involved in the stomatal response to eCO2 in Arabidopsis. Furthermore, a MATE-type transporter associated with eCO2 concentration in the repression of HT1, which negatively regulates CO2-induced stomatal closing, was found in Arabidopsis (Tian et al., 2015). It was also shown that ABA in guard cells or their precursors mediate the CO2-induced stomatal density response in Arabidopsis (Chater et al., 2015).

**High-Throughput Phenotyping to Study Phenomes and Genomes and Their Use in Plant Breeding**

High-throughput precision phenotyping (HPP) facilitates measurements within a wide spectrum of light reflectance
wavelengths that should correlate significantly with a trait of interest to assess phenotypes (White et al., 2012; Yang et al., 2013). HPP and other phenomic methods and tools are becoming available to predict edible yield, nitrogen use efficiency, host plant resistance in early development stages, as well as for large-scale multi-environment trials (Furbank and Tester, 2011; Araus and Cairns, 2014). Phenomic platforms were first validated for their use in biotrons, growth chambers, and screenhouses, or for field testing using cameras attached to tractors and harvesters. Nonetheless, HPP remains limited in large-scale field trials because of the related costs and logistics involved in its implementation. The availability of relatively cheap unmanned aerial vehicles provides an opportunity for developing and adopting HPP to screen many genotypes evaluated in field trials. Adopting new technologies with efficient phenotyping may lead to larger genetic gains and reduce the time needed to breed climate-resilient cultivars. Phenomic tools such as digital imaging allow the screening of physiological traits that are difficult to measure in the field. Likewise, HPP platforms are facilitating functional genetics as noted in rice (Yang et al., 2013). Today selections are made that consider both the genotype and the resulting phenotype, which increases the speed and efficiency of selection.

Sir Ronald A. Fisher, Sewall G. Wright, and J. B. S. “Jack” Haldane defined quantitative genetic models that included various genes with large or small effects as well as non-genetic factors influencing the phenotype of complex traits, using variance components, resemblance between relatives, and the mathematical theory of selection, respectively (Ortiz, 2015). Large datasets of precise phenotypic measurements in early generation testing and large multi-environment trials are becoming available after using HPP methods to measure canopy temperature, or to obtain spectral reflectance indices and associated information, which can be used to predict grain yield and its components, as well as abiotic stress tolerance and host plant resistance to pathogens and pests.

Biometrics explains complex quantitative traits with continuous variation to understand the action of multi-genes and the genotype by environment interaction controlling phenotypic variation measured across environments. Furthermore, data from genome sequencing on genetic resources and breeding lines or populations along with HPP are increasing the knowledge base regarding specific genomic regions, loci, and alleles therein, haplotypes, linkage disequilibrium blocks, and gene networks contributing to specific phenotypes (Xu et al., 2012). This approach has changed plant breeding by enlarging it to a three-dimensional concept that includes genotype, phenotype and environment. Moreover, prediction models using high-density DNA markers offer promising results in terms of prediction accuracy (Abera Desta and Ortiz, 2014). Genomic prediction (GP) based on genotyping with genome-wide SNPs along with pedigree and phenotypic data is indeed powerful for capturing small genetic effects across the genome, thus allowing the prediction of breeding values or the genetic merit of an individual. Breeding values result from the parents’ average component and the Mendelian sampling of the parents’ genes. Genetic gains due to the response to selection depend on the accuracy and time taken to estimate the Mendelian sampling. The factors affecting the accuracy of GP are model performance, sample size and relatedness, DNA marker density, gene effects, trait heritability, and genetic architecture. Bayesian statistics can effectively estimate breeding values and may be coupled with geo-statistics for modeling multi-environment trials.

**Biotechnology-Led Methods to Enhance Crop Adaptation to eCO₂, Drought, and Heat Stress**

Limited progress has been made on enhancing abiotic stress adaptation in crops through crossbreeding largely because of low heritability, genetic (epistasis) and genotype by environment interactions, and multigenic effects (Dwivedi et al., 2010). **Figure 1** shows how biotechnology may assist in developing cereal and legume-bred germplasm. Considerable progress has been made in developing genetic resources (i.e., diversity panels to identify new sources of variations and mapping populations to unravel the molecular basis of trait expressions) and genomic resources (i.e., high-density SNPs arrays, genetic maps, and reference genomes to unravel QTL and candidate genes associated with agronomically beneficial traits) for crop breeding. Transgenic research has moved from discovering protocols, promoters (constitutive or tissue-specific), and transgenes to developing appropriate technology to generate stress-tolerant GM crops without yield penalty under optimum agronomic conditions. Both genomic-assisted breeding and transgenic approaches can enhance the adaptation of cereal and legume crops to drought and heat stress, as detailed here.

**Pyramiding Quantitative Trait Loci**

**Drought Stress in Grain Legumes**

A few chickpea introgression lines (ILs) harboring drought-tolerant QTL for root traits produced deeper roots, better root length density, and higher root dry weight than their recurrent parent J 11 or drought-tolerant donor parent ICC 4958 (Varshney et al., 2014), with some lines in national trials prior to release in India (Thudi et al., 2014a). Three backcross-derived cowpea (V. unguiculata L. Walp.) lines containing drought-tolerant QTL under water-deficit conditions produced on average 48% more seed yield (990–1185 kg ha⁻¹) than the drought-tolerant cultivar Gorom (728 kg ha⁻¹) in Burkina Faso (Batieno et al., 2016).
Drought Stress in Cereals

Six of 14 large-effect QTL associated with drought adaptation in rice were effective across genetic backgrounds and environments (Kumar S. et al., 2014). Pyramiding large-effect QTL enhanced drought adaptation of rice cultivars in Asia (Uga et al., 2013; Shamsudin et al., 2016; Dixit et al., 2017). Lines with two-qDTY combinations were more drought tolerant and productive than lines with three-qDTY combinations, suggesting a differential synergistic relationship among QTL (Shamsudin et al., 2016).

NILs containing Stg QTL in sorghum increased water uptake during grain filling relative to RT × 7000, and produced higher biomass, grain numbers, and grain yield without yield penalty across Australian environments (Borrell et al., 2014). In India, ILs containing Stg QTL in R16 (highly senescent but adapted to the post-rainy season) and ICSV 111 (dual purpose, grain and sweet sorghum types, open-pollinated cultivar) genetic backgrounds improved stover and grain yields as well as stover quality, with no tradeoff (Dryland Cereals and Archival Report, 2012–2013). A large-scale MABC program involving promising ILs and SSRs flanking Stg QTL was initiated to transfer stay-green trait into other sorghum cultivars adapted to the post-rainy season in India. Likewise, 1-2 Stg QTL was successfully transferred via marker-assisted breeding into a farmer-preferred sorghum cultivar E36-1 in Kenya (Ngugi et al., 2013).

The IL S42IL-121 containing major QTL from wild barley (H. vulgare ssp. spontaneum) produced 36% more biomass under drought-stressed conditions than recurrent parent Scarlet (Honsdorf et al., 2014). ILs containing major drought-tolerant QTL in pearl millet (Pennisetum glaucum (L.) R. Br) in the genetic background of a drought-sensitive parent (H 77/833-2) tolerated drought better and significantly out-yielded testcross hybrids made with the original recurrent parent under varying water deficits (Serraj et al., 2005).

Heat Stress in Cereals

Oryza officinalis contributed the major QTL qEMF3 (on chromosome 3) for flower opening time in rice. NILs containing qEMF3 in IR64 genetic background shifted flower opening time 1.5–2.0 h earlier in the tropics, thereby escaping heat stress (≥35°C causes spikelet sterility) at flowering. Thus, qEMF3 has the potential to advance flower opening time in current cultivars to mitigate the effect of heat stress at flowering (Hirabayashi et al., 2015). O. glaberrima contributed a major QTL for heat tolerance Thermotolerance1 (TT1), that protects cells from heat stress. NILs containing TT1 allele had higher thermotolerance than the recurrent parent (WYJ) at flowering and grain filling (Li X. M. et al., 2015). Thus, pyramiding qEMF3 and TT1 is expected to enhance adaptation to heat stress in rice.

Drought Tolerance in Marker-Assisted Breeding in Maize

Ziyomo and Bernardo (2013) noted that indirect selection based on secondary traits or grain yield in maize under irrigation was not more efficient than selecting directly for grain yield under drought, while genomic selection (GS) was more efficient, with predicted relative efficiency of 1.24, for grain yield under water deficit. ASI, ear girth, ear length, 100-kernel weight, and grain yield in maize, on the other hand, had the highest prediction accuracies (0.95–0.97) across drought-stressed environments (Shikha et al., 2017). Furthermore, 77 SNPs distributed across the genomes were associated with ten drought-responsive transcription factors related to stomatal closure, root development, hormonal signaling, and photosynthesis (Shikha et al., 2017). A more recent study in maize revealed higher prediction accuracy of GS than phenotypic variance explained by the sum of QTL for individual traits following MAS. This suggests that using QTL-MAS in forward breeding will enrich allelic frequency for a few desired traits with strong additive QTL in early selection cycles while GS-MAS will additionally capture alleles with smaller additive effects (Cerrudo et al., 2018).

Marker-assisted recurrent selection (MARS) has been successfully employed to enhance genetic gains in maize, with greater genetic gains (105 kg ha⁻¹ year⁻¹) in well-watered (WW) than water-stressed (51 kg ha⁻¹ year⁻¹) plants in sub-Saharan Africa (Beyene et al., 2015). Likewise, test crosses derived from the second selection cycle (C₂) had higher grain yield under drought stress than those coming from the original population, with a relative genetic gain of 7% per cycle, while test crosses of inbred S₁ lines from C₂ had an average genetic gain of 1% per cycle under WW and 3% per cycle under irrigated (Bankole et al., 2017). Hence, both GS and MARS were more effective at increasing genetic gain in maize under both irrigated and drought-stressed environments.

Epigenetic Variation and Abiotic Stress Adaptation

Epigenetics is “the study of mitotically and/or meiotically heritable changes in gene function that cannot be explained by changes in DNA sequences” (Russo et al., 1996). Epigenetic changes contribute to gene expression under environmental stress and are regulated by processes such as DNA methylation, histone modification, and RNA interference (RNAi; Meyer, 2015). Increasing evidence shows that changes arising from DNA methylation or histone acetylation are heritable (Zheng et al., 2013; Wang W. et al., 2016) and may be exploited in plant breeding. Cytosine methylation polymorphism, as indicated by hypermethylation or hypomethylation under stress (Gaycharan and Joel, 2013), plays a key role in the expression of genes in plants (Shen et al., 2012). Hypermethylation and hypomethylation of DNA under drought are indicators of stress susceptibility and tolerance, respectively. The most commonly used assays to assess cytosine DNA methylation are methylation-sensitive amplified polymorphism (Xiong et al., 1999), bisulfite sequencing (Li et al., 2010), and methylated DNA immunoprecipitation sequencing (Taiwo et al., 2012).

DNA Methylation

DNA methylation is chemical modification arising from addition of a methyl group to the nitrogenous base in the DNA strand in a sequence-specific manner (Law and Jacobsen, 2010). Cytosine DNA methylation is a major epigenetic modification affecting gene regulation in response to environmental stress. Drought-induced genome-wide epigenetic modification accounted for ~12% of the methylation differences in the rice genome,
which were genotype-, tissue-, and developmental stage-specific (Wang et al., 2011), while Xia et al. (2016) noted greater DNA methylation (52.9–54.3%) under drought stress among diverse rice ecotypes adapted to upland (rainfed) and lowland (irrigated) sites. Moreover, adaptation-specific highly divergent epiloci confer adaptation to drought in both rice ecotypes (Xia et al., 2016). Gayacharan and Joel (2013) noted a positive correlation between spikelet sterility and methylation (%), whereas panicle length and weight, seeds per panicle, 100-seed weight, and grain yield were negatively correlated, suggesting the role of epigenetic regulation in grain-yield-attributing traits in response to drought in rice.

The molecular basis of DNA methylation at the genome level may unravel the regulatory mechanisms associated with abiotic stress adaptation. Wang W. et al. (2016) detected 1190 differentially methylated regions (DMRs) between drought-tolerant (IL_DK151) and intolerant (IR 64) lines under irrigation. The IL_DK151 plants under drought had more stable methylome (only 92 drought-induced DMRs) than IR64 plants (506 DMRs). Epigenetic regulation of drought responses was associated with changes in DNA methylation of genotype-specific genes. A set of 12 and 23 DMR-associated genes were differentially expressed in IL_DK151 and IR 64, respectively, under drought (Wang W. et al., 2016). Previous research found numerous DMRs among rice cultivars with distinct responses to drought and salinity, many of which were associated with the differential expression of genes associated with stress tolerance (Garg et al., 2015). Five of the six drought-stressed DMRs reported in faba bean (V. faba L.) had higher expression in drought tolerant (Bachar) than sensitive (F177) cultivars, suggesting their role in faba bean drought tolerance (Abid et al., 2017). DNA methylation polymorphism can, therefore, be effectively deployed to develop crops with enhanced drought tolerance.

**Histone Modification**

Histones are proteins associated with DNA in the nucleus that condense it into chromatin. Histone modifications may regulate gene expression in plants under abiotic stress. Post-translational modification of histones includes acetylation, methylation, phosphorylation, and ubiquitination (Chinnusamy and Zhu, 2003). Histone acetyltransferases (HATs) and histone deacetylases (HDACs) are involved in histone acetylation homeostasis. Eight HATs, grouped into four families, are known in rice. When investigating the response of four HATs, one from each family in rice, Fang et al. (2014) noted that drought significantly increased the expression of OsHAC703, OsHAG703, OsHAM701, and OsHAM701. They further showed that the acetylation level on certain lysine sites of H3 and H4 increased with OsHATs expression, suggesting that OsHATs is involved in the response of rice to drought. Previous research also identified that the modification in H3K4me3 was positively correlated with a subset of genes showing changes both in modification and expression under drought (Zong et al., 2013).

Programmed cell death (PCD) plays a prominent role in plants during development and in response to stress (Danon et al., 2000; Jones, 2001). Wang P. et al. (2015) showed significantly increased levels of total acetylation of histones H3K9, H4K5, and H3, whereas the di-methylation level of histone H3K4 remained unchanged and H3K9 decreased in maize seedlings under heat stress. Furthermore, maize seedlings treated with “trichostatin A” resulted in histone hyperacetylation caused by increased levels of the superoxide anion (O_2·-) within the cell, leading to PCD in association with histone modification changes under heat stress in maize leaves.

**RNA Interference (RNAi)**

MicroRNAs (miRNAs) are single-stranded RNA molecules (20–24 nt) that affect the expression of genes at the post-transcriptional level and are involved in plant development and a wide array of stress responses (Zhang et al., 2006). Many of the drought and heat stress-responsive miRNAs and their target genes associated with plant development, metabolism, and stress tolerance has been found in cereals and grain legumes. Drought-associated miRNAs include 11 in cowpea (Barrera-Figueroa et al., 2011), five in maize (Chen et al., 2015), and 10 and 12 in wheat (Xin et al., 2010, 2011), whereas 20 and 12 in common bean (Jyothi et al., 2015), 11 and 26 in rice (Liu et al., 2017), and 6 and 12 in wheat (Xin et al., 2010, 2011). Changes in miRNAs under stress correlate well with increased expression of stress-related genes in tolerant genotypes. For example, Liu et al. (2017) reported eight target genes that correspond with 26 miRNAs within the four QTL regions associated with heat stress in heat-tolerant rice. This relationship of miRNAs with their target genes, however, may not be one-to-one (i.e., negative or positive) and may vary between miRNAs of the same gene family or even for the same target miRNAs at various development stages (Lopez-Gomollon et al., 2012; Zhang et al., 2012). Identification of differentially abundant miRNAs in stress-tolerant germplasm may thus provide molecular evidence that miRNAs contribute to stress tolerance and so are good candidates for enhancing stress tolerance in crops by transgenic breeding.

**Genome Editing to Harness Novel Allelic Variations in Stress Adaptation**

Genome editing brings changes in DNA that are smaller than those from genetic engineering (Ainsworth, 2015). Rice and
wheat showing host plant resistance to pathogens (Wang et al., 2014; Wang F. et al., 2016) or potato with improved cold storage and processing (Clasen et al., 2016) became available using genome editing.

Targeted modification of specific genes using CRISPR and CRISPR-associated protein9 (Cas9) leads to useful genetic variations for improving plants (Feng et al., 2013). Indeed, plant breeding enterprises are beginning to exploit genome editing with CRISP/Cas9 to develop genetically enhanced seed-embedded technology showing new traits. Avoiding off-target mutations during genome editing may be achieved using protocols to eliminate off-target effects and improve the specificity of the CRISPR/Cas9 system (Pattanayak et al., 2013).

The open stomata2 (OST2) gene encodes the major plasma membrane H^+-ATPase (AHA1) in Arabidopsis (Palmgren, 2001). Using CRISPR/Cas9 and the tissue-specific promoter EF1 (germline- and meristematic cell-specific), Osakabe et al. (2016) generated a new mutant allele for OST2/AHA1 (ost2_crispr-1) without off-target effects in Arabidopsis. Such plants did not show any significant differences in plant growth compared to wild-type (WT) plants. Furthermore, ost2_crispr-1 plants exhibited higher leaf temperature and lower water loss than WTs, suggesting enhanced stomatal closure upon abiotic stress.

Maize plants overexpressing ARGOS8 produced high grain yields under water deficit (Shi et al., 2015). Endogenous expression of ARGOS8 mRNA in maize is low and spatially non-uniform. Using CRISPR/Cas9 technology and the GOS2 promoter, Shi et al. (2017) obtained heritable novel variants with enhanced expression of ARGOS8 transcripts relative to the native allele in all maize tissues tested. Furthermore, such variants produced higher grain yield than their WT under water deficit at flowering, without any grain yield penalty under irrigation.

Rodriguez-Leal et al. (2017) recently proposed the engineering of beneficial quantitative variation for plant breeding through genome editing of promoters that leads to the generation of diverse cis regulatory alleles. They successfully generated tomato mutants from genome editing with variation in fruit size, inflorescence branching, and plant architecture. Their findings provide the underpinning for dissecting intricate interactions between gene regulatory changes and quantitative phenotypic variation, including adaptation to stress-prone environments.

**Inducing Flowering Independent of Environmental Clues to Match Growing Season**

West Africa and South Asia are among the regions worst affected due to climate change and variability effects. Farmers in West Africa have experienced a shortening of the rainy season. Climate models have projected the late onset, early cessation of rainfall, and reduction in length of growing season, which will negatively impact agriculture in West Africa (Sarr, 2012) although there is high uncertainty about shifting rainfall patterns and amounts. In South Asia, by the end of the 21st century, models project a delay in the start of rainy season by 5–15 days and an overall weakening of the summer monsoon precipitation (Ashfaq et al., 2009). A reduction in the length of the growing season has direct impacts on the adaptation of current cultivars. There is thus a continued need to breed cultivars adapted to a shortened growing season. An alternative to crossing is to engineer flowering time along with the external application of flower-inducing compounds (Ionescu et al., 2017).

Enhanced expression of the Ghd7 gene under extended photoperiod delays flowering and increases plant height and panicle size in rice (Xue et al., 2008). Such orthologous floral repressor systems also exist in maize (ZmCCT) and sorghum (SbPRR37 and SbGHD7) (Hung et al., 2012; Yang et al., 2014). Okada et al. (2017) produced non-flowering rice after overexpressing the Ghd7 gene that inhibits environmentally induced spontaneous flowering. Thereafter, they isolated a promoter responsive to agrochemical spraying. Next, Hd3a was introduced under the control of an agrochemical-responsive promoter, which was already co-transformed with Ghd7. Such plants reacted to chemical spraying by beginning their floral transition, thus flowering earlier than the non-transgenic control, with no adverse impact on plant growth and development. This result shows that flowering time can be manipulated independently from the environment in which the plant grows, leading to the possibility of engineering crops with suitable growth in different climates (Okada et al., 2017).

Pyramiding QTL has been successful for combining tolerance to drought and heat stress into bred-germplasm for both cereals and legumes. Both GS and MARS, in contrast to QTL pyramiding by MAS, have been more effective at enhancing gains in maize productivity, both in drought-stressed and irrigated environments. The proof of concept also indicated the usefulness of deploying epigenetic variation or genomic editing to create new variation for agronomic traits and drought tolerance in some crops. As noted above, use of agrochemicals to induce flowering independent of environmental signals has also been effective, as evidenced in rice, thereby suggesting the utility of this approach in other crops.

**Stress-Tolerant Genetically Modified Crops**

Plant adaptation to abiotic stress is achieved by genes associated with stress tolerance. The coordinated involvement of these genes and their interaction with the timing and intensity of the stress make it difficult for plant breeders to develop stress-tolerant crops by crossing. Advances in genomics are allowing researchers to identify tissue-specific expression of genes under abiotic stress. The transfer and expression of such candidate genes into crops through genetic engineering offer considerable promise.

The overexpression of transgenes enhances abiotic stress adaptation, both in model plants and cereals (Dwivedi et al., 2010). Grain yield penalty is often associated with the introduction of transgenes that improve plant responses to abiotic stress adaptation (Campos et al., 2004). Overexpression of HvEPF1 in barley, TPP in maize, OeERF48, OsKAT2, AtGoLS2, OsERF71, OsNAC9, and OsNAC10 in rice, AtGoLS2 in soybean, and ScCspA and TaNAC69-I in wheat enhances drought...
Overexpression of transgenes enhances drought adaptation and increases grain yields under field-drought environments in barley, maize, rice, soybean, and wheat from 2010–2018.

| Species            | Gene       | Effect of transgene                                                                 | Reference                        |
|--------------------|------------|--------------------------------------------------------------------------------------|----------------------------------|
| Barley (Hordeum vulgare L.) | HvEPF1     | Reduced stomatal density and enhanced water use efficiency, drought tolerance, and soil water conservation properties with no yield penalty | Hughes et al., 2017              |
| Maize (Zea mays L.) | OsMYB55    | Increased plant biomass and reduced leaf damage under drought and heat stress (individual or combined) during or after recovery from stress | Casaretto et al., 2016           |
| Rice (Oryza sativa L.) | TTP        | Enhanced grain yield by 9–49% under moderate or 33–123% under severe drought conditions | Nuccio et al., 2015              |
| Soybean (Glycine max L.) | OsERF48    | Root-specific (RXO1) or whole-body specific (RXO1) overexpression resulted longer and denser roots compared to wild-type; RXO1 plants exhibited higher grain yield than RXO1 or wild-type plants under field-drought conditions | Jung et al., 2017                |
| Maize (Zea mays L.) | OsKAT2     | Delayed photo-induced stomatal opening, reduced water loss, and increased drought tolerance, with no yield penalty | Moon et al., 2017                |
| AtGoLS2            |            | Conferred drought tolerance and increased grain yield under drought-stressed conditions in two genetic backgrounds | Selvaraj et al., 2017            |
| OsERF71            |            | Enhanced drought tolerance at reproductive stage and increased grain yield by 23–42% over wild-type | Lee et al., 2016                 |
| SNAC3              |            | Enhanced tolerance to drought and high temperature                                    | Fang et al., 2015                |
| HYR                |            | Improved photosynthesis leading to increased grain yield under drought and heat stress conditions | Ambavaram et al., 2014           |
| OsNAC9             |            | Enhanced drought tolerance and increased grain yield by 28–72% under field-drought conditions | Redillas et al., 2012            |
| OsMYB55            |            | Improved tolerance to high temperature and increased plant biomass                    | El-Kereamy et al., 2012          |
| OsNAC10            |            | Improved drought tolerance and increased grain yield by 25–42% and by 5–14% over controls under drought and irrigated conditions, respectively | Jeong et al., 2010               |
| Soybean (Glycine max L.) | AtGoLS2    | Enhanced drought tolerance and improved seed yield under field-irrigated and drought-stressed environments | Honna et al., 2016               |
| Wheat (Triticum aestivum L.) | TaFER-5B   | Exhibited enhanced drought and thermotolerance                                         | Zang et al., 2017                |
| SeCspA              |            | Enhanced drought tolerance and increased seed weight (19–20%) and seed yield (24%)     | Yu et al., 2017                  |
| TaNAC69-1           |            | Enhanced primary root length and root biomass, produced 32 and 35% more aboveground biomass and grains, respectively, under water-deficit conditions | Chen et al., 2016                |

adaptation and increases grain yield under field drought, without yield penalty under WW conditions (Table 4). Overexpression of OsMYB55 enhances adaptation to drought and heat stress in maize and rice (El-Kereamy et al., 2012; Casaretto et al., 2016). Furthermore, OsMYB55 under individual or combined (drought and heat) stress during or after recovery of stress produced more plant biomass with less leaf damage in maize (Casaretto et al., 2016). It appears that using a tissue-specific promoter (i.e., root-specific or seed-specific), rather than whole body (plant)-specific promoters, containing a transgene had no or relatively fewer adverse effects on plant growth and development, leading to no yield penalty.

Selection criteria in breeding programs will benefit from insights on the molecular and physiological basis for adaptation to increased grain yield under stress. For example, HvEPF1 significantly reduced stomatal density but enhanced WUE and soil water conservation properties, thus enhancing drought adaptation and productivity in barley (Hughes et al., 2017). Likewise, improving sucrose supply or altering sucrose metabolism in developing ear spikelets improved kernel set in maize under drought (Zinselmieer et al., 1995; Boyer and Westgate, 2004). Furthermore, EPP increased sucrose content in spikelet and kernel set in maize, leading to increased HI and grain yield under drought, without yield penalty under WW conditions (Nuccio et al., 2015). Similarly, in rice, OKAT2 delayed photo-induced stomatal opening and enhanced drought adaptation without grain yield penalty (Moon et al., 2017), while tolerance to heat stress seems to be related to enhanced amino acid metabolism by OsMYB55 (El-Kereamy et al., 2012).

Environmental stress reduces photosynthetic carbon metabolism (PCM) and limits grain yield in cereals. For example, increased expression of HYR, which is associated with PCM, enhanced photosynthesis, leading to high grain yield in rice under stress (Ambavaram et al., 2014). Overexpression of OsERF48, OsERF71, OsNAC9, and OsNAC10 enhanced grain yield under water scarcity by altering root architecture (Jeong et al., 2010; Redillas et al., 2012; Lee et al., 2016; Jung et al., 2017). In contrast, increased grain yield in transgenic rice overexpressing AtGoLS2 under drought was related to higher panicle numbers, grain fertility, and biomass (Selvaraj et al., 2017). Enhanced thermotolerance due to overexpression of TaFER-5B in wheat was due to ROS scavenging (Zang et al., 2017). Overexpression of TaNAC69-1 under drought promoted root elongation in drying soils, producing more aboveground biomass and grain in wheat (Chen et al., 2016), while overexpression of SeCspA under drought increased test weight and grain yield (Yu et al., 2017).
Monsanto’s “DroughtGuard” maize (MON87460) expressing *Bacillus subtilis* cold shock protein B (cspB) (Castiglioni et al., 2008) which produced 6% higher grain yield across years than the control (Monsanto hybrid NH6212) under water-limited conditions (Nemali et al., 2015) was cultivated on $\geq 50,000$ ha in the United States during the first year after release (Marshall, 2014). New genes conferring drought and heat stress adaptation are being discovered and the experimental area soown to drought or heat stress tolerant crops containing transgene(s) is expected to grow as more countries become involved in the development and field testing of such crops. However, the major concern with biotech crops is food safety for humans and animals. A rigorous assessment based on robust, science-based criteria should be in place to assess biosafety issues associated with the use of such crops.

Unlike in the past when the induction of transgenes was often associated with adverse impacts on plant growth and productivity, the proof of concept has been demonstrated for the development of stress tolerant genetically modified crops without yield penalty under agronomically optimal environments, as evidenced both in cereals and legumes.

**Genetic Variation and Candidate Genes Associated With Photosynthetic Traits**

Photosynthesis is a complex process whereby green plants use sunlight to synthesize nutrients (carbohydrates) from carbon dioxide ($\text{CO}_2$) and water, in the process, generating oxygen as a by-product. The process of converting light energy into chemical energy to produce biomass is highly efficient. Over the years, there has been increased understanding of the processes that limit photosynthetic efficiency (PE), paving the way to manipulate light energy into carbon gain in plants. Future increases in biomass production may, therefore, depend largely on increases in PE, with a focus on harnessing cross species ($\text{C}_3$ vs. $\text{C}_4$ crops) as well within-species differences, as detailed below.

**Harnessing Novel Variation for Photosynthesis Traits**

Plant genetic resources are a valuable foundation of natural genetic variation for photosynthetic traits. Rubisco is a target for improving photosynthesis. Prins et al. (2016) measured Rubisco carboxylation velocity ($V_c$), Michaelis–Menten constants for $\text{CO}_2$ ($K_c$) and $\text{O}_2$ ($K_o$), and specificity factor ($S_{c/o}$) for Rubisco diversity in vitro in 25 accessions of the Triticeae tribe at 25 and 35°C and noted a positive association between $V_c$ and $K_c$ and negative association between $V_c$ and $S_{c/o}$. Rubisco from barley increased photosynthesis at 25 and 35°C while Rubisco from jointed goatgrass (*Aegilops cylindrica* Host) increased photosynthesis at 25°C. Thus, naturally occurring Rubisco with superior properties among the Triticeae tribe may be exploited to develop wheats with enhanced photosynthesis and productivity. The $\text{CO}_2$ fixation rate ($K_{\text{cat}}$) for Rubisco from the $\text{C}_4$ grasses (*Paniceae* tribe) with NAD, NADP-ME, and PCK photosynthetic pathways was twofold greater than the $k_{\text{cat}}$ of Rubisco from NAD-ME species across all temperatures, while the declining response of $\text{CO}_2/O_2$ specificity with increasing temperature was less pronounced for PCK and NADP-ME Rubisco, which would be advantageous in warm climates relative to the NAD-ME grasses (Sharwood et al., 2016). Rubisco from certain $\text{C}_4$ species could thus enhance carbon gain and resource use efficiency in $\text{C}_3$ crops.

Driever et al. (2014) reported significant variation in photosynthetic capacity, biomass, and grain yield among 64 wheat accessions, although they noted an inconsistent correlation between the flag leaf photosynthetic capacity and grain yield across accessions, thus suggesting scope for further improvement in photosynthetic capacity. Moreover, Carmo-Silva et al. (2017) compared flag leaf photosynthetic traits, crop development, and grain yield in the same cultivars used by Driever et al. (2014) and noted that pre-anthesis and post-anthesis photosynthetic traits in the field were positively associated with grain yield and HI. Moderate to high heritability for photosynthetic traits suggests that phenotypic variation can be deployed to enhance photosynthesis in wheat.

Gu et al. (2012a) noted significant genetic variation for stomatal conductance ($G_s$), mesophyll conductance ($G_m$), electron transport capacity ($J_{\text{max}}$), and Rubisco carboxylation capacity ($V_{c}\text{max}$) in rice, although drought and leaf age contributed for a greater proportion of phenotypic variation. The differences in light-saturated photosynthesis and TE were mainly associated with variation in $G_s$ and $G_m$. Further research revealed that a known photosynthesis-QTL is associated with differences in $G_s$, $G_m$, $J_{\text{max}}$, and $V_{c}\text{max}$ at flowering. One to three QTL associated with eight photosynthetic traits contributed 7–30% of the phenotypic variation, with some QTL near the SSR marker RM410 consistent across development stages and moisture regimes (Gu et al., 2012b). Gu et al. (2014) noted a 25% increase in genetic variation in leaf photosynthetic rate ($P_r$) corresponding to a 22–29% increase in crop biomass across locations and years. More recently, Qu et al. (2017) detected large variation in photosynthetic parameters among diverse rice germplasm across environments, and noted that $P_r$ under low light intensity is correlated with biomass accumulation, and the narrow-sense heritability is high, suggesting its potential in breeding for improving biomass and yield potential in rice.

Natural variation in the $\text{CO}_2$ assimilation rate is another promising strategy to identify genes contributing to higher photosynthesis. Adachi et al. (2017) fine mapped a QTL *Carbon Assimilation Rate*8 (CAR8), identical to rice flowering QTL *DTH/Ghd8/LHDI*, that controls flag leaf nitrogen content, $G_s$ and $P_r$ in rice. QTL *GPS* (GREEN FOR PHOTOSYNTHESIS), identical to *NAL1* (a gene that controls lateral leaf growth in rice), controls photosynthesis rate by regulating carboxylation efficiency. The high-photosynthesis allele of *GPS* is a partial loss-of-function allele of *NAL1*, which increases mesophyll cells between vascular bundles, leading to thickened leaves, and pleiotropically enhances $P_r$ with no adverse impact on plant productivity (Takai et al., 2013). Further research on molecular functions of *GPS* and *CAR8* may contribute to enhanced photosynthesis in rice and possibly other crops.

Understanding the genetic basis of PE may contribute to enhanced seed yield. Basu et al. (2018) reported 16 SNPs linked...
to major QTLs underlying 16 candidate genes associated with PE and seed yield in chickpea. Furthermore, they delineated superior haplotypes from a chlorophyll A-B binding protein-coding gene, *Timing of a CAB Expression1*, as the most potential candidates for enhancing PE and seed yield.

Enhancing G_{m} may increase WUE and photosynthetic water use efficiency (WUE_{p}). G_{m} refers to the rate of CO_{2} diffusion from substomatal cavities to the site of carboxylation. To improve WUE, G_{m} should increase without concomitantly increasing G_{s}. Across species, a 24-fold variation was noted in G_{m} (Tomás et al., 2013). Within-species differences in G_{m} were also noticed, e.g., 60% in rice (Gu et al., 2012a), two to threefold in wheat (Jahan et al., 2014; Barbour et al., 2016), and twofold in soybean (Tomeo and Rosenthal, 2017). A QTL for G_{m} on chromosome 3A contributes to 9% variation in wheat (Barbour et al., 2005). Fixation of CO_{2} in C_{4} crop. Rangan et al. (2016a,b) discovered a C_{4} photosynthesis pathway restricted to wheat grain and identified six genes (PPc, aat, mdh, me2, gpt, ppa) specific for C_{4} photosynthesis and only expressed in the photosynthetic pericarp of the caryopsis of wheat exhibiting dimorphism related to the mesophyll- and bundle sheath cells of the chloroplasts in the leaf of C_{4} plants. Hence, it is feasible to genetically engineer C_{4} photosynthesis in wheat due to the available expression of the whole pathway in its grain, though some researchers are skeptical of this approach.

Maize is a C_{3} crop. The foliar leaf blade is a Kranz (C_{4}) type, while the husk leaf sheath is a non-Kranz (C_{3}) type (Wang et al., 2013). Sixty-four of the 124 C_{4} specific genes showed differential expression between the foliar leaf blade and husk leaf sheath, of which 57 were highly expressed in the foliar leaf blade but not the leaf primordia, suggesting their involvement mainly in C_{4} photosynthesis in leaves (Ding et al., 2015). Further research on gene expression in husk leaf sheath tissues may unlock candidate genes associated with C_{3}-type photosynthesis and the subsequent comparison and cross-talk between candidate
genes (C₄ and C₃ photosynthetic pathways in maize) may unravel a cascade of genes and networks to guide further improvements in photosynthesis and productivity.

The introduction of Krantz anatomy into C₃ leaves is a major challenge. The genes that control Krantz anatomy are unknown. Screening large-scale mutagenized populations identified variants with altered leaf anatomical structure, e.g., maize mutants with bundle sheath and mesophyll sheath specific pathways, sorghum mutants with variation in vein spacing, or rice mutants with closure vein spacing (Hall et al., 1998; Covshoff et al., 2008; Kajala et al., 2011; Rizal et al., 2015). More importantly, Scarecrow and Shrl which regulate structural differentiation of the root endodermis also contribute to the development of Krantz anatomy in maize (Slewinski et al., 2012, 2014). Thus, the discovery of such structural variation in leaf and Scarecrow and Shrl genes may provide an opportunity to introduce Krantz anatomy into C₃ leaves.

Research to transform rice with C₄ photosynthesis began in the last decade (Covshoff and Hibberd, 2012; von Caemmerer et al., 2012; Babege and Magule, 2017). While researchers are getting closer to unraveling the complex C₄ photosynthesis, the pathways for such transformation will not be easy and may take another decade before this innovation can be used to introduce C₄ photosynthesis into C₃ crops.

Sourcing diverse germplasm pools has unraveled natural genetic variation for photosynthetic traits, both in cereals and legumes. A few QTLs and candidate genes associated with enhanced PE are known in chickpea, rice, and wheat. Significant knowledge on Krantz anatomy and key genes (and their differential expression between C₃ and C₄ plants) and pathways involved in the evolutionary transition from C₃ to C₄ photosynthesis have been unlocked. The discovery of a C₄ pathway in wheat grain (or C₃ pathway in maize husk) may further unravel a cascade of genes and networks to improve photosynthesis and productivity. The introduction of Krantz anatomy into C₃ leaves is a major challenge. However, the discovery of genetic variants with altered leaf anatomical structure or genes (Scarecrow and Shrl) regulating structural differences in the root epidermis may provide opportunities for introducing Krantz anatomy into C₃ leaves.

ADOPTION, IMPACT, RISK ASSESSMENT, AND ENABLING POLICY ENVIRONMENTS

Genetically enhanced seed-embedded technology is an important innovation leading to gains in crop productivity. Both crossbreeding and biotechnology have been used to enhance tolerance to drought and heat stress in food crops. Bred-cultivars may substantially reduce projected yield losses under climate change in the tropics and subtropics (Challinor et al., 2014) while improving food self-sufficiency of smallholders and increasing their incomes without the need to cultivate extra land. Changing crop cultivars will continue to be among the first lines of defense for improving productivity and resilience in farming systems (Thornton et al., 2017).

Drought tolerant maize (DTM) cultivars developed by crossbreeding have been released in sub-Saharan Africa, while in South Asia, efforts are underway to scale up cultivation of heat stress tolerant maize hybrids. Likewise, a genetically modified drought-tolerant maize-derived hybrid, DroughtGuard (MON 87460), has been approved for cultivation in the United States (Marshall, 2014). DTM hybrids may bring benefits ranging from US$362 to 590 million for consumers and producers and could reduce poverty by 5% within 13 countries in sub-Saharan Africa (Kostandini et al., 2013). Wossen et al. (2017) showed that the adoption of DTM cultivars in rural Nigeria increased grain yields by 13.3%, and reduced grain yield variance and risk by 53 and 81% among adopters, respectively. Furthermore, productivity gains and risk reduction due to adoption reduced the incidence of poverty by 12.9% and increased the probability of food security among adopters by 83.3%. In rural Zimbabwe, adoption of DTM hybrids significantly enhanced maize productivity, allowing farmers to set aside enough produce for personal household consumption and excess for sale (Makate et al., 2017).

Adoption rates of improved seeds, regardless of their origin, in areas where those seeds are available can be as high as 85% among smallholder farmers, if awareness is high (Kyazze and Kristjanson, 2011). Many situations exist, however, where few farmers have access to improved seeds in the developing world. In sub-Saharan Africa, for example, 68–97% of seed grown by smallholder farmers comes from informal sources or local markets (McGuire and Sperling, 2015). Seed availability thus constitutes a primary barrier to the adoption of bred cultivars (Fisher et al., 2015; Lunduka et al., 2017).

DTM hybrid cultivars with big cob size, good tip cover, resistance to lodging, and good grain quality are the most preferred types in Eastern and Southern Africa (Setimela et al., 2017). Female farmers have much lower adoption of DTM, mainly due to differences in resource access, notably land, agricultural information, and credit. Male farmer age or economic status (poor or rich) has no significant influence on adoption of DTM. Young but poor female household heads are least likely to adopt DTM, while wives strongly influence the adoption of DTM on plots controlled by their husbands (Fisher and Carr, 2015). Are the farmers willing to invest more to purchase DTM seeds? Kassie et al. (2017) noted that farmers in rural Zimbabwe are willing to pay three to seven times higher premiums for drought-tolerant hybrids giving an additional metric ton of yield per acre and possessing bigger cob size, covered cob tip, and larger grains.

The environmental risks associated with the cultivation of MON 87460 are no different from the risks associated with crossbred maize (Sammons et al., 2014). Are GM crops safe for human consumption? No major differences on compositional profile were noted between GM and their counterpart, non-GM crops (Venkatesh et al., 2015; Herman et al., 2017); minor differences, however, typically reflect changes associated with crossbreeding practices (Venkatesh et al., 2015; Herman et al., 2017). Thus, GM crops are as safe and nutritious as currently
consumed food crops. Robust and science-based criteria should, however, be in place to assess any biosafety issues associated with the use of such transgenic crops.

Improved understanding of how policy environments can support the widespread adoption of bred cultivars is greatly needed. There is only limited quantitative information available to guide national investment and policy choices (Vermeulen et al., 2016). Relatively small investments in cultivar development and seed multiplication now can save substantial costs later (Cacho et al., 2016), while the cost may be enormous if investment is delayed in maize breeding and seed systems (Challinor et al., 2016). It seems considerable work remains to be done with respect to the kinds of enabling policies and informational environment needed in different contexts, if adoption of bred cultivars by smallholder farmers at the scales required is to occur in the coming decades.

CONCLUSION AND RECOMMENDATIONS

Today’s agriculture is faced with increasing intensity of drought and heat stress worldwide. Greenhouse gases are the major source of global warming. The positive impact of eCO$_2$ on crop productivity may be nullified or even overwhelmed by increased drought and heat stress. Developing crops that are tolerant to stress and responsive to eCO$_2$ is a considerable challenge. While research on drought has long been the focus, genetic and physiological research on plant responses to eCO$_2$ and heat stress has gained momentum. Tolerance to drought and heat stress is under distinct genetic control. Accessions and traits responsive to eCO$_2$ (increased photosynthesis) or stress tolerance have been found in germplasm collections. The knowledge gained about the physiological and molecular bases of stress tolerance has facilitated greater access and intake of stress-tolerant germplasm by cross breeding. Advances in high-throughput genotyping and precision-based phenotyping platforms as well as the parallel development of bioinformatic resources and tools to handle large datasets are enabling crop genetic enhancements to accelerate introgression of candidate genes associated with stress tolerance into improved genetic backgrounds. Many breeding programs are routinely using these resources, which increase the speed and efficiency of selection. A few drought or heat stress-tolerant cultivars of cereals and legumes, developed by crossbreeding, are becoming popular among farmers in stress-prone environments. How are stress-tolerant crops making an impact on food and nutritional security across the globe? DTM cultivars out-yielded commercial controls on farmers’ fields, with significant gains under stress, showing the huge potential for uptake of DTM seed in Africa. However, barriers to adoption exist, such as lack of seed availability, inadequate information, resource crunch, high seed cost, and consumer preference, that must be overcome for greater uptake of seed-embedded technology to enhance food and nutritional security in the developing world.

Today, agricultural production worldwide is affected by climate change. Landraces and crop wild relatives are unique genetic resources to meet current and new challenges for farming in stressful environments. However, plant breeders are reluctant to use these unique genetic resources in breeding largely due to fear of loss of co-adapted gene complexes, linkage drag, and the protracted time needed to develop cultivars. Considerable knowledge gap also exists about crop response to eCO$_2$, for example, the variance in results between controlled environment and FACE experiments, discovering plant traits most responsive to eCO$_2$, or selection criterion to be adapted in breeding for the development of crop cultivars responsive to eCO$_2$. Future research should focus on (i) capturing and harnessing variation in landraces and crop wild relatives, (ii) cost-effective precision-based high-throughput phenotyping platforms amenable to small-scale breeding programs, (iii) use of image-based traits (i-trait) to measure response to stress, (iv) traits and methodology to access response to selection under eCO$_2$ conditions, (v) the molecular basis of plant response to selection under eCO$_2$ conditions, (vi) traits, genetics, and methods to select for enhanced photosynthesis, (vii) genes and networks to unravel crosstalk involving drought × heat, genotype × eCO$_2$, drought × heat × eCO$_2$, and genotype × drought × heat × eCO$_2$, (viii) haplotype-specific associations and protein–protein interactions to delineate natural alleles and superior haplotypes, and (ix) phenotyping and sequencing wild and weedy relative genomes of crop species to identify and relate differences with sequence variation. A focus on these issues can be expected to increase breeding efficiency to develop crops responsive to eCO$_2$, stress tolerance and productivity.

AUTHOR CONTRIBUTIONS

All co-authors participated in planning, outlining, and writing sections of the manuscript under the lead of SD, while RO took care of the overall editing of various drafts of the manuscript after interacting with all co-authors.

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The reviewer SW and the handling Editor declared their shared aﬃliation.

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