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Adapting Cereal Grain Crops to Drought Stress: 2020 and Beyond

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Abstract

Among other environmental instabilities, drought stress is the primary limitation to cereal crops growth, development and productivity. In the context of continuing global climate change, breeding of drought resistant crop cultivars is the most economical, effective and sustainable strategy for adapting the crop production system and ensuring food security for the growing human population. Additionally, there is need for improving management practices. Whereas conventional breeding has sustained crop productivity gains in the past century, modern technological advancements have revolutionized our identification of important drought tolerance genes and underlying mechanisms, and accelerated new cultivar development. Large-scale high throughput sequencing, phenotyping, 'omics' and systems biology, as well as marker assisted and quantitative trait loci mapping based breeding approaches have offered significant insights into crop drought stress tolerance and provided some new tools for crop improvement. Despite this significant progress in elucidating the mechanisms underlying drought tolerance, considerable challenges remain and our understanding of the crop drought tolerance mechanisms is still abstract. In this chapter, therefore, we highlight current progress in the identification of drought tolerance genes and underlying mechanisms, as well as their practical applications. We then offer a holistic approach for cereal crops adaptation to future climate change exacerbated drought stress.

Keywords: drought stress, drought tolerance, cereal crops, omics approaches, phenotyping, genetic engineering, climate change, conservation agriculture

1. Introduction

Drought stress is the primary environmental factor influencing the growth, development and productivity of crops and its significance is expected to increase in the wake of global climate change [1–4]. This presents a serious challenge to the food and nutrition security of an ever-rising world human population. Moreover, the current transition from carbon/fossil intensive fuel driven economies to modern climate-smart low-carbon economies further strains our crop production systems [5]. Adapting field crops to drought stress therefore becomes critical for sustainable agricultural production under such climate change scenario [6]. To achieve that goal, breeding drought resilient crop cultivars that maintain yield stability under such conditions befits the most economical, effective and sustainable strategy. This is particularly relevant for cereal grain crops.

Cereal grain crops, chiefly rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), sorghum [*Sorghum bicolor* (L.) Moench], barley (*Hordeum*

vulgare L.), and pearl millet (*Pennisetum glaucum* L.) provides above 50% of the total food calorie requirements of billions of people in developing countries across the Sub-Saharan Africa, South Asia and Latin America [7–9]. For instance, the top three cereals; maize, rice, and wheat jointly provide 48% of the total calories and 42% of total protein consumed in developing countries. Additionally, as staple foods, maize and wheat contribute approximately two thirds of the global food energy intake [8]. Further, these cereal crops are important raw materials in the animal feed and bio-fuel manufacturing industries [10]. However, most of these crops are grown across arid and semi-arid regions of the world, where they often endure exposure to recurrent drought episodes throughout their growth cycles. Therefore, understanding how cereal crop plants respond to drought stress is critical for guiding drought tolerance breeding.

In the last century, conventional breeding approach has proven itself capable of sustaining productivity growth in various crops [11]. Meanwhile, modern technological advancements have accelerated the pace and impact of new cultivar development. Such technologies include high throughput omics approaches, identification of quantitative trait loci (QTL) underlying abiotic and biotic stress resistances, marker assisted selection (MAS) and gene cloning [12–15]. Despite this significant progress in elucidating the mechanisms underlying drought tolerance, considerable challenges remain and our understanding of the crop drought tolerance mechanisms is still abstract.

In this chapter, therefore, we look at various aspects of drought stress in major cereal grain crops such as maize, sorghum, wheat, rice and finger millet. We also discuss the current approaches in identifying drought tolerance genes and metabolic pathways. Further, we highlight the progress made to date on elucidation of key drought stress responses, phenotyping and QTL mapping for drought tolerance, genetic engineering of drought tolerant crops and management of crops. We conclude by offering an integrated strategy for adapting cereal grain crops to drought stress in the context of climate change.

2. Drought stress effects in cereal grain crops

A decrease in water inputs into an agro/ecosystem over time that is sufficient to cause soil water deficit (SWD) is often termed drought, and this encompasses various forms such as rainfall anomalies, irrigation failure, seasonal or annual dry spells [16]. In agricultural context, drought signifies a period of below-average precipitation when the available soil water in the plant rhizosphere drops beyond the thresholds for efficient growth and biomass production [17]. The resultant oxidative stress emanating from such SWD is dubbed drought stress.

Numerous research reports have reflected on the effects of drought stress on cereal crops. Drought stress effects span from morphological to molecular levels, and are exhibited at all phenological growth stages at whatever stage the water deficit takes place. Generally, drought stress impairs seed germination resulting in poor crop stand establishment [1, 18]. Drought stress reduces the plant cellular water potential and turgor pressure, thereby increasing the cytosolic and extracellular matrices solute concentrations. Resultantly, cell growth is diminished due to the reduction in turgor pressure [19]. Additionally, abscisic acid (ABA) and compatible osmolytes such as proline are excessively accumulated, causing plant wilting. Simultaneously, reactive oxygen species (ROS) such as H₂O₂ are overly produced. Although they function as signal transduction molecules, over-accumulation of ROS could result in extensive cellular oxidative damage and inhibition of photosynthesis [20].

Moreover, when moisture deficit becomes severe, cell elongation becomes inhibited by the interruption of water flow from the xylem vessels to the surrounding elongating cells [21]. Consequently, vegetative growth, dry matter partitioning,

reproductive organ development and reproductive processes, grain filling and grain quality are disrupted [22]. In cereal grain crops, reproductive processes and grain filling are more susceptible to water deficit stress, with optimum and ceiling temperatures that are relatively lower than those for seedling and vegetative growth stages [21, 23–25]. Moisture deficit stress reduces yield by delaying silking, thus increasing the anthesis-to-silking interval [11]. Drought stress at flowering period is critical as it can increase pollen sterility resulting in hampered grain set [26].

Drought stress induced yield reduction in cereal crops depends upon the severity and duration of the stress period. The reduction in photosynthesis, emanating from the decrease in leaf expansion, impaired photosynthesis machinery, premature leaf senescence and related food production decreases, is the major contributing factor on yield reduction [21, 23]. Drought stress induced yield reductions have been reported and reviewed in maize [1, 21, 26–29], wheat [26, 27, 30, 31], rice [1], sorghum [32–33] and pearl millet [25].

3. Plants drought stress responses and resistance mechanisms

Plants have evolved numerous dynamic acclimation and adaptive ways of responding to and surviving short-term and long-term drought stresses [34]. The physiology of plants' drought response at the whole plant level is complicated as it encompasses lethal and adaptive alterations. Moreover, how plants respond to drought stress differ significantly at various organizational levels, and this is generally dependent on plant species; the nature, duration and intensity of the drought stress; plant growth and phenological state at the time of stress exposure [19].

Drought stress triggers a wide range of plant structural changes which are essential for plants to respond to such drought stress conditions. These adjustments include morphological adaptations such as reduced growth rate, deepened rooting system, and root-to-shoot ratio modifications. The increased root-to-shoot ratio under drought stress conditions enables water and nutrient uptake and maintenance of osmotic pressure [19, 26, 35]. Additionally, in their response to moisture fluctuations in the soil rhizosphere, plants alter their physiology, modify their root growth and architecture, and regulate the closure of stomata on their aboveground structures. Such tissue-specific responses adjust the cell signals flux, consequently inducing stunted growth or premature flowering, and generally reduced yield [36]. Thus, drought stress is associated with alterations in leaf anatomy and ultrastructure. Reduced leaf size, decreased number of stomata; thickened leaf cell walls and induced premature senescence are some of those morphological changes [19].

Plants resist drought stress through a combination of strategies, which have been widely classified as drought escape, drought avoidance and drought tolerance [18, 21, 37, 38]. Drought escape is achieved by matching the duration of the crop cycle to water supply through genetic variation in phenology [39]. Plants prioritize early flowering and completing their life cycles before the effects of drought cause harm [21].

Drought avoidance denotes plant's ability to maintain high tissue water potential under drought conditions. Usually, plants achieve drought avoidance through morphological and physiological alterations, including reduced stomatal conductance, decreased leaf area, promotion of extensive rooting systems and increased root to shoot ratios [38]. Drought avoidance mechanisms help in maintaining favorable cellular water balance, by enhancing water absorption, decreasing water loss, or allowing desiccation tolerance at low leaf water potential [34]. Stomatal closure, reduction of leaf growth and increased root length and density all contribute to increased water use efficiency under drought stress conditions. Further, water flux into the plant is reduced or water uptake enhanced to achieve drought avoidance [19].

On the other hand, plants attain a state of drought tolerance by cell and tissue specific physiological, biochemical, and molecular mechanisms. Drought tolerance is a complex trait which refers to the capacity of the plant to be more productive under drought stress [40]. In other words, it denotes the potential of crop plants to maintain their growth and development under drought stress [21]. The main aspects of plant drought tolerance mechanism include homeostasis maintenance, via ionic balance and osmotic adjustment; ROS scavenging and antioxidant enzyme activation; growth regulation and recovery by way of phytohormones; specific gene expression; and accumulation of specific stress responsive proteins [1, 2, 19, 21, 26].

To protect themselves against ROS induced oxidative stress and photo inhibition, plants activate an efficient antioxidant (enzymatic and non-enzymatic) defense system [17, 18, 21, 41]. Enzymatic antioxidant enzymes include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione peroxidase (GPX) and glutathione S-transferase (GST) among others. SOD acts as the first line of defense by converting singlet oxygen into H_2O_2 . APX and GSTs then detoxify H_2O_2 [42]. Non-enzymatic antioxidants including glutathione (GSH), ascorbic acid (AsA), carotenoids, tocopherols and flavonoids are also crucial for ROS homeostasis in plants [43].

At the molecular level, our current knowledge thus far regarding drought stress response pathway suggest that, sequentially, the stress is relayed through the following chain: signal perception, signal transduction, transcriptional control by way of transcription factors (TFs), stress responsive genes activation, and in-turn activation of physiological and metabolic responses [1, 19, 37, 44].

Stress signal perception in plants has revealed the role of plasma membrane in perceiving and transmitting signals to the cell interior, where molecules such as receptor-like kinases and G-proteins function as primary receptor molecules [45]. The roles of Ca^{+} and ROS as secondary messengers in stress perception and signaling have also been well acknowledged [4]. These secondary messengers adjust the calcium levels and activate protein phosphorylation. Then, phosphorylation of inactive proteins may be directly involved in cellular protection by protein folding or activation of stress specific genes. The dominant plant signal transduction pathways involve the mitogen activated protein kinase (MAPK) and calcium dependent protein kinases (CDPK) cascades, and their role in abiotic stress response have been well reviewed [38, 42, 46].

Upon drought exposure, the resulting signal transduction triggers the production of several biochemicals, including phytohormones, to respond and adapt to the ensuing drought stress [47]. Phytohormones are molecules produced in low concentrations but are critical in regulating plant growth, development, response to biotic and abiotic stresses, and other physiological processes [48]. These phytohormones include ABA, salicylic acid (SA), ethylene (ET), cytokinins (CKs), gibberellin acid (GA), jasmonic acid (JA) and brassinosteroids (BRs) among others. Among these, ABA is the key and most extensively studied hormone that regulates drought resistance in plants [38, 49]. ABA acts as the second messenger coordinating hormonal cross-talk between several stresses signaling cascades, thereby leading to adaptations to changing physiological and environmental conditions [50]. Additionally, SA, ET, JA, CKs, GA, and BRs play vital roles in regulating various phenomena in plants acclimatization to drought stress [51].

At the molecular level, plants institute stress responsive proteins, TFs and signaling pathways among other strategies. Several studies [52, 53] have identified conserved and species-specific drought responsive genes, including membrane stabilizing proteins and late embryogenic abundant (LEA) proteins, which increase cells' water binding capacity [1, 14]. Several heat shock proteins (HSPs), which play a major role in stabilizing protein structure, were also identified [54, 55]. The HSPs are chiefly

involved in unwinding some folded proteins and averting protein denaturation under abiotic stress conditions. The membrane stabilizing proteins, LEA proteins, detoxification enzymes, water channel proteins and ion transporter genes all constitute a group of functional proteins, that is, a group of important enzymes and metabolic proteins which directly function to protect cells from stress [37, 56]. Besides functional genes, regulatory genes are also critical for drought tolerance. These encode various regulatory proteins such as transcriptional factors (TFs), protein kinases and protein phosphatases – involved in regulating signal transduction and gene expression in response to stress [57, 58]. Several TFs that regulate a large spectrum of downstream stress-responsive genes and provide adaptive response under drought stress have been identified and reviewed, including myeloblastosis (MYB), abscisic acid responsive element binding factor (ABF), ABRE binding (AREB), dehydration responsive element binding (DREB), C-repeat binding factor (CBF), [NAM, ATAF1/2, and CUC2 containing proteins] (NAC) and WRKYs [59–63].

Additionally, protein kinases and protein phosphatases mediate phosphorylation and dephosphorylation of proteins, respectively. In several signal transduction pathways; they are vital and an effective mechanism for stress signal relaying [19, 56, 63]. At the phosphorylation cascade terminals, protein kinases or phosphatases activate or suppress TFs, respectively. The TFs further specifically bind to cis-elements in the promoters of stress responsive genes, thereby modulating their transcription [64]. The TFs are further subjected to post translational modifications (PTMs), including ubiquitination and sumoylation, thereby forming an intricate regulatory network to modulate stress responsive genes, which consequently trigger the activation of appropriate physiological and metabolic responses [62, 65].

4. Approaches for deciphering drought stress responsive genes, proteins and metabolic pathways: where are we?

The recent convergence of crop physiology, next generation sequencing and molecular biology approaches has offered us convenience in deciphering mechanisms underlying plants' response to various abiotic stresses [13, 15, 66]. Whereas plant physiology enhances our understanding of the complex network of traits related to drought tolerance and improving selection efficiency, genomics and molecular biology methods identify the candidate genes and quantitative trait loci (QTLs) underlying these traits [11, 13]. The classical cDNA and oligonucleotide microarrays have been widely employed to identify candidate genes for drought tolerance in several cereal grain crops including maize [67, 68], rice [69, 70] and barley [71]. Additionally, the use of tiling microarrays has allowed for the identification of differentially expressed DNA sequences at the whole genome level [72]. Other techniques such as differential display; cDNA amplified fragment length polymorphism (cDNA-AFLP); and serial analysis of gene expression (SAGE) have been essential in analyzing global gene expression profiles in functional genomics studies [56, 73–74].

Analysis of large scale, high throughput sequencing data is now facilitating the identification and cloning of important genes at target QTLs. Additionally, the 'omics' analysis approaches are showing monumental capacity to quicken and broaden our understanding of the molecular, genetic and functional basis of crop drought stress tolerance [12, 75]. Encouragingly, some novel insights meant to help us develop new drought tolerant cultivars are being generated [76]. Due to its low cost, high-throughput, and high sensitivity, RNA sequencing (RNA-seq) has offered us breakthrough in performing transcriptome analysis of plants' drought stress responses [77]. Resultantly, we have obtained transcripts from RNA in a tissue- or cell-specific manner, and transcribed at a different developmental stage

or functional state; this has been fundamental to fishing out functional genes [78]. Therefore, our knowledge pertaining to gene expression networks modulating drought stress tolerance has been significantly improved. RNA-seq technology has been used in several drought stress response studies in cereal crops and numerous genes have been identified [79–81].

Recently, large scale, high-throughput proteomics has become a very powerful tool for performing comprehensive analysis of crop proteins and identification of stress responsive proteins in comparative abiotic stress studies [82, 83]. Proteomic approaches, particularly gel free methods, that is, those involving digestion of intact proteins into peptides prior to separation, have now become very popular in proteome profiling, comparative expression analysis of two or more protein samples, localization and identification of post translational modifications (PTMs) [14]. For instance, isobaric tags for relative and absolute quantitation (iTRAQ) and isotope-coded affinity tags (ICAT) based methods have become widely used in descriptive and comparative drought stress proteomic studies in cereals [84–87]. The iTRAQ-based method allows for the time-dependent analysis of plant stress responses or biological replicates in a single experiment [88]. Besides, proteomics offers complementarity to genomics; providing clues on the molecular mechanisms underlying plant growth and stress responses, as well as being a crucial link between transcriptomics and metabolomics [82]. Moreover, genomics based methods offer access to agronomically desirable alleles localized at QTLs that affect particular physiological responses. This helps us to effectively improve the drought resilience and yield of crops. Additionally, MAS has aided us in improving drought-related traits [12, 89].

Further, a systems biology approach, premised on the advancement and integration of omics (genomics, transcriptomics, metabolomics, phenomics and proteomics) methods to establish a meaningful relationship between the genotype, phenotype and subsequent abiotic stress tolerance, has also become prominent [76]. Integrated knowledge of the morphological, physiological, biochemical, genetic and molecular events in plants allows for in depth understanding of the complex physiological and cellular processes involved in drought stress adaptation. Thus, meaningful interpretations from complex networks and component integrations can be developed from voluminous omics data, which helps us better decipher the mechanisms underlying cereal crops drought tolerance [63].

Meanwhile, the physiological analysis on contrasting genotypes provides information on the mechanisms underlying drought tolerance and aids as a useful screening strategy for drought tolerance [41]. Therefore, it is important to realize that physiological analysis remains essential in corroborating the molecular analyses in abiotic stress response studies. Thus, it would be essential that, going forward, we build on the progress made to date by harnessing the full potential of genomics-assisted breeding, and integrating our knowledge on the physiological and molecular basis of drought tolerance. This calls for crop physiologists, molecular geneticists, breeders and cytogeneticists to collaborate in a multidisciplinary manner [12].

5. Some identified key drought tolerance mechanisms, genes and metabolic pathways

By applying genetic, biochemical and molecular approaches, we have identified essential genes central in plant responses to drought stress. For instance, several physiological responses contributing to drought tolerance in cereal crops have been identified including thermal dissipation of light energy, stomatal closure, decreased hydraulic conductance, altered source-sink relations and carbon partitioning, ABA biosynthesis, among others (**Table 1**).

No.	Physiological response	Purpose	Reference
1	Thermal dissipation of light energy	Uncoupling of photophosphorylation and electron transport	[41, 90]
2	Activation of photosynthesis (PSII) proteins	Preventing photoinhibition of the PSII and improving leaf photosynthetic capacity	[81, 91]
3	Altered source–sink relations and carbon partitioning	Induction of root growth	[92]
4	Prioritized supply of CHOs to rapidly growing or metabolically hyperactive cells or tissues	Promotion of early seedling/hypocotyle growth	[80]
5	Cell wall biosynthesis	Enhancing cellular contents preservation	[81, 93, 94]
6	Cell wall remodeling	Increasing cell wall elasticity to maintain tissue turgidity	[80]
7	Amino acid biosynthesis	Enhanced protein biogenesis	[80]
8	Osmotic adjustment through increased synthesis of soluble solutes (proline, soluble sugars, etc.)	Increased cellular homeostasis maintenance	[11, 40, 95, 96]
9	Changes in ROS scavenging and enzyme activities	Prevention of cellular oxidative damage	[18, 81]
10	ABA biosynthesis	Stomatal closure regulation and improved stress signaling	[11, 40]
11	Stomatal closure and reduced hydraulic conductance	Prevention of water loss through transpiration	[97]
12	Alteration in root morphology and physiology	Increased water and nutrient absorption under drought conditions	[98, 99]
13	Reduced stomatal density and enhanced control of stomatal opening and closure	Improved cellular water conservation	[100]
14	Alternative oxidase pathway, uncoupling proteins, NADPH dehydrogenases down-regulated	Uncoupling of oxidative phosphorylation and electron transport	[101]

Table 1.
Some key drought stress tolerance mechanisms identified in cereals.

Besides the mechanisms highlighted in **Table 1**, several drought responsive genes have been identified and validated in different crop species. For instance, recent excellent reviews [4, 26, 102–106] provide highly informative details about some crop drought tolerance conferring genes that have been functionally validated to date. Some of these genes are listed in **Table 2**.

Further, several metabolic pathways implicated in drought stress tolerance in cereal grain crops have been identified through comparative physiological and omic analysis approaches. Chief among these pathways are those related to photosynthesis, secondary metabolites biosynthesis, plant hormone signaling, starch and sucrose metabolism, and nitrogen metabolism. Chloroplasts, particularly the thylakoid membranes—PSII reaction centers, are one of the organelles most influenced by drought stress [123, 124]. Photosynthesis (antenna protein) pathway related genes *lhcb5-1* and *lhcb5-2* are part of the light harvesting complexes (LHCs) and the electron transport components of the PSII of the plant photosynthesis machinery, where they participate

No.	Gene name	Donor	Host	Physiological change	References
1	<i>ZmVPP1</i>	<i>Arabidopsis thaliana</i> L. (Arabidopsis)	Maize	Enhanced photosynthetic efficiency and root development	[81, 107]
2	<i>ZmPP2C-A10</i>	Arabidopsis	Maize	ABA signaling	[108]
3	<i>Zeaxanthin epoxidase (ZEP)</i>	Arabidopsis	Maize	Improved ABA biosynthesis	[104, 109]
4	Mannitol-1-phosphate dehydrogenase (<i>mtlD</i>)	<i>Escherichia coli</i>	Wheat	Improved fresh and dry weights, plant height, and flag leaf length	[110]
5	<i>AtNF-YB1</i>	Arabidopsis	Maize	Higher photosynthesis capacity	[102, 111]
6	<i>AtABF3</i>	Arabidopsis	Rice	Higher Fv/fm	[112]
7	<i>OsDREB1A</i>	Arabidopsis	Rice, wheat	Shoot growth retardation at the expense of root growth	[102]
8	<i>AtHARDY</i>	Arabidopsis	Rice	Enhanced WUE and photosynthesis efficiency	[113]
9	<i>OsWRKY11</i>	Rice	Rice	Sluggish water loss and lessened leaf wilting	[114]
10	<i>AtLOS5 (LOS5/ABA3)</i>	Arabidopsis	Maize	Increased ABA biosynthesis	[115]
11	<i>HVA1</i>	Barley	Rice	Higher WUE	[116]
12	<i>HVA1</i>	Barley	Wheat	Enhanced biomass accumulation and WUE	[26, 117]
13	<i>Beta</i>	<i>Escherichia coli</i>	Wheat	Accumulation of glycine betaine	[118]
14	<i>Nicotiana protein kinase (NPK1)</i>	Tobacco	Maize	Preventing dehydration damage to the photosynthesis machinery	[119]
15	<i>AtSNAC1</i>	Arabidopsis	Rice	ABA-hypersensitive, stomatal shutdown	[120, 121]
16	<i>SbER2-1</i>	Sorghum	Maize	Increased Pn rate and higher WUE	[122]
17	Light harvest complex related genes (<i>LHCA1, LHCB, LHCA3, LHCA2</i>)	Maize	Maize	Balancing light capture in the PSII	[91, 93]

Table 2. Examples of drought tolerance conferring genes that have been functionally validated in cereal crops.

as peripheral antenna systems enabling more efficient absorption of light energy [125, 126]. Further, Lhch5-1 is involved in the intracellular non-photochemical quenching and the cysteine biosynthesis processes [91]. Previously, the photosynthesis pathway

has been significantly enriched in drought stress response in maize, with chlorophyll a-b binding proteins being up-regulated in an ABA-dependent manner [87, 91], and pearl millet [127]. This photosynthesis related pathway plays a critical role in balancing light capture and utilization to avoid photoinhibition of the PSII [87].

Phenylpropanoid metabolism is the first step of the secondary metabolites (flavonoids, phenylpropanoids, phenolic compounds and lignin) biosynthesis and phenylpropanoids act as antioxidants to protect plants against oxidative damage [128, 129]. Flavonoids play different molecular functions in plants, including stress protection. All these compounds are widely synthesized in response to several abiotic stresses, including drought [130]. In wheat leaves, an increase in flavonoid and phenolic acids content was shown together with stimulation of genes involved in flavonoid biosynthesis pathway in response to drought stress [131]. Moreover, secondary metabolites biosynthesis related pathways were found to be significantly enriched in response to drought stress in maize [80] and sorghum [37], suggesting their involvement in plant protection. A coordinated reaction of the genes and pathways involved in secondary metabolite biosynthesis is therefore vital for improved drought stress tolerance in plants [80]. Plant hormone signaling pathway participates in drought stress response via either ubiquitin-mediated proteolysis or ABA-mediated response [132], and was observed to be significantly enriched in pearl millet response to drought stress [127].

Sucrose is widely acknowledged to play a crucial role as a key molecule in energy transduction and as a regulator of cellular metabolism [130]. Additionally, sucrose and other sugars are energy and carbon sources required for defense response and are necessary for plant survival under drought stress conditions [133]. Further, sucrose can act as primary messenger controlling the expression of several sugar metabolism related genes [134]. Nitrogen metabolism pathway, being the most basic and central physiological metabolic process during plants' growth period, directly influences the formation of cellular components and regulation of cellular activities, as well as the transformation of photosynthetic products, mineral nutrient absorption and protein synthesis. It therefore follows that the nitrogen pathway is directly affected by drought, hence its significant enrichment under such conditions [80, 127]. These key identified drought responsive pathways should be used as targets for future genetic engineering of drought stress tolerant genotypes.

6. QTL mapping for drought tolerance in cereals

Most yield-related traits in cereal crops are quantitative. Therefore, cloning of the causal genes and deciphering the underlying mechanisms influencing these traits remains critical for continuous genetic improvement [135]. Precisely, drought tolerance is a complex quantitative trait that is multi-genic in its expression and one of the most challenging traits to study and characterize [11]. In comparison to conventional approaches, genomics offers unparalleled opportunities for dissecting quantitative traits into their single genetic determinants, known as QTL, thereby facilitating MAS, gene cloning and their direct manipulation via genetic engineering [12]. Through advances in next generation sequencing, identification of major QTLs regulating specific drought responses has been made possible, via the development of large numbers of genetic markers such as single nucleotide polymorphisms (SNPs) and insertion-deletions (InDels), thereby opening the doors for an efficient way to improving drought tolerance in cereal crops [89]. Additionally, large-scale genome-wide association studies (GWAS) have been conducted to detect genomic regions and candidate genes for various agronomic traits, including drought tolerance in cereals [13, 136, 137]. Resultantly, hundreds of studies reporting thousands of major drought-responsive genes and QTLs in cereal grain crops

can be found in the literature, including those for maize [13, 138–140], rice [12, 13, 105, 138, 141, 142], wheat [13, 31, 137, 138, 143], sorghum [138, 144, 145], barley [138, 146], and pearl millet [136, 147, 148]. The high number of studies on QTL mapping suggests that for the past decade, QTL has been the focal target of research to identify the genetic loci regulating the adaptive response of crops to drought stress. Although several QTLs for drought tolerance have already been mapped in these cereal crops, there has been little success in introgression of those QTLs and the number of causal genes that have been confirmed within these QTL regions remains relatively small as compared to *Arabidopsis* and rice [11, 106].

Going forward, MAS remains a useful tool for major QTL, whereas QTL cloning is increasingly becoming a more routine activity. This has been necessitated by increased use of high-throughput sequencing, precise phenotyping and identification of appropriate candidate genes through omics approaches [89, 136, 137]. Cloned QTL facilitate a more targeted search for novel alleles and will offer novel insights for genetic engineering of drought resilient cereal crops [13]. Moreover, compared to other crops, research in millets is still lagging behind. However, with millets considered predominantly climate resilient crops, millets could serve as valuable source of novel genes, alleles and QTLs for drought tolerance. Therefore, the identification and functional characterization of these genes, alleles and QTLs in millets is critical for their introgression and drought tolerance improvement in cereal grain crops [89].

7. Phenotyping for drought tolerance in cereal grain crops

Phenotyping has become an integral component of the crop improvement programme by contributing towards understanding of the genetics behind crop drought tolerance [105, 149]. Since many component traits of drought tolerance are controlled quantitatively, improving the accuracy of phenotyping has become more important to improve the heritability of the traits, and the target traits would require rapid and precise measurement [106]. High throughput phenotyping now provides an essential link in translating laboratory research to the field. This is vital in developing novel genotypes that incorporate gene(s) expressing promising trait (s) into breeding lines adapted to target field environments [150].

Auspiciously, the recent advances in phenotyping technology and robotics for measuring large number of plants means that large numbers of genotypes could be readily phenotyped [34, 151–153]. More promising approaches that target complex traits tailored to specific requirements at the different main crop growth stages are now available [150]. Precise phenotyping of drought-related physiological traits often requires the utilization of sophisticated and expensive techniques. These include magnetic resonance imaging (MRI) and positron emission tomography (PET), near-infrared (NIR) spectroscopy on agricultural harvesters, canopy spectral reflectance (SR) and infrared thermography (IRT), nuclear magnetic resonance, hyperspectral imaging, laser imaging, 3D imaging and geographical information systems (GIS), among others [34, 138, 154, 155]. For example, 3D visual modeling can be used to determine the plasticity of the canopy architecture, and to evaluate the architectural and physiological characteristics that contribute to the higher productivity of the super rice varieties under drought stress conditions [156]. Though currently expensive, up scaling the use of these phenotyping platforms will eventually enhance our understanding of crop growth kinetics and aid us improve crop models for systems biology and drought tolerance breeding programs.

Selection of primary (grain yield and yield contributing traits) and secondary agronomically important traits (ASI, root architecture, stay green, etc.) is the way to achieve drought tolerance in cereal grain crops [31, 35, 106, 152]. Yield and yield

attributing factors are targeted for direct selection whilst secondary traits are vital in conferring drought tolerance and contributing to final yield indirectly [157]. Crucially, considering that under drought stress conditions, the genetic correlation between grain yield and some secondary traits increases meaningfully, and the heritability of some secondary traits remains high, identification and selection of those highly heritable secondary traits that are positively correlated with yield related traits in the target environment, and responsive to high throughput phenotyping, will be critical in achieving the desired drought tolerance goals [11, 152, 158]. Managed stress screening approaches through the utilization of phenomics offers an opportunity to keep heritability high and phenotyping under controlled environments can be helpful in large-scale characterization studies such as trait mapping experiments [13]. However, great caution needs to be taken when phenotyping for drought stress tolerance since controlled environments may fail to mimic the real field conditions, thereby becoming less useful to study the genotype \times environment interactions which are very essential to dissect the drought tolerance mechanisms [106].

8. Genetic engineering of drought tolerant cereal crops

The development of tolerant crops by genetic engineering requires the identification of key genetic determinants underlying stress tolerance in plants, and introducing these genes into crops [159, 160]. The momentous progress garnered in abiotic stress response research in the model plant *Arabidopsis* has created an avenue for the identification of drought tolerance conferring genes and the development of transgenics carrying these genes in other crop species. Therefore, genetic engineering approach has opened the door to the development of new crop genotypes with improved drought tolerance [103]. Over the past decade, numerous articles and reviews on drought stress tolerant transgenic crop species have been gathered [4, 26, 102–106, 160]. A selected list of transgenic cereal grain crops, which includes information on transgenes used for the transformations and the resultant drought stress tolerance mechanisms, has already been provided above in **Table 2**. Despite the availability of numerous reports in the scientific literature of transgenic approaches to improving drought tolerance, restrictions on the establishment of transgenic plants in the field presents a bottleneck in true testing of the effectiveness of transgenic approaches to improve crop drought tolerance [161].

In recent years, transgenesis has taken center stage in our crop improvement efforts. Advances in genome engineering has made it possible to precisely alter DNA sequences in living cells, providing unprecedented control over a plant's genetic material [162]. The genome engineering approaches, also known as gene editing or genome editing techniques, involve the use of programmable site-directed nucleases (SDNs) engineered to modify target genes at desirable locations on the genome [163]. These SDNs cleave the double-stranded DNA at a particular location by means of clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9 (CRISPR/Cas9), zinc finger nucleases (ZFNs), or transcriptional activator-like effector nucleases (TALENs). The double-stranded DNA break then undergoes natural reparation either via homologous recombination or non-homologous end joining [105, 164]. The restoration of the DNA break can be directed to create a variety of targeted DNA sequence modifications such as DNA deletions or insertions of large arrays of transgenes [162].

Among the several genome editing methods developed to date, CRISPR-Cas9 is the most advanced and has received much attention because of its great accuracy, quickness, adaptability and simplicity [165, 166]. This technique has been successfully used in major food crops [167–169]. Whereas conventional genomics and breeding

approaches alone cannot resolve the global food security challenge [170], genetic engineering approaches have great potential to improve crops that feed the burgeoning populations of developing countries [162, 166, 171]. However, the extent of regulation imposed upon crop cultivars generated through genetic engineering will have a huge impact on the cost of their development itself and how rapidly they will be deployed into the food supply chain. Linked to that, the readiness with which the public will accept food products made from genetically engineered crops will also play a role in the extent to which this new technology will be fully utilized for crop improvement, particularly in the developing countries where cereal grain crops are staple diets [162].

9. Field management of crops in the context of climate change

Genetic and management strategies that are aimed at improving grain yields under water constrained environments target three variables, which are the amount of water captured by the plant (W), the efficiency with which that water is converted to biomass (water use efficiency, WUE), and the harvest index (HI) or the proportion of biomass forming grain. Interestingly, each of these variables can be altered [172]. For instance, WUE can be maximized by early planting of crops, and by maintaining healthy leaves with high levels of nutrients [173]. Additionally, extending leaves' longevity through selection for delayed leaf senescence is commonly regarded important for maintaining WUE and root health, as well as increasing the kernel filling duration [172]. Supplementation of irrigation, where available, would be the major means for combating drought stress condition, besides being a prime approach to the intensification of agriculture and the generation of stable income for farmers [174]. However, its uptake will depend on various environmental, economic and social factors on both micro and macro levels [175].

Additionally, agronomic interventions, that is, improved crop management methods can complement the use of drought tolerant cultivars, contributing meaningfully to enhanced and stabilized yields under water constrained environments. Conservation agriculture (CA), a collection of practices embodying the use of reduced tillage and mulch to reduce evaporation of soil water, is an obvious means of increasing water available to the plants [172, 176]. Scaling up CA, which has recently gained wider acceptance in developing countries, offers a great potential of increasing drought resilience and sustainability of cropping systems and ensuring food security. The use of plastic mulch in semi-arid cooler areas on the Loess Plateau of China has significantly increased WUE in maize [177]. Moreover, CA has become the cornerstone of dryland systems in some regions of USA, Canada and Australia [174]. Recently, the application of melatonin with date (*Phoenix dactylifera* L.) residue and wheat straw biochars has enhanced biochar efficiency for drought tolerance in maize cultivars [178]. This can be a game changer in CA farming systems where biochar is a key component for ground cover. Therefore, the management of a sustainable dryland farming system would require that farmers apply good agronomic practices (GAPs) such as improved soil and water conservation and the associated reduced tillage practices, holistic weed and pathogen control, soil fertility management with respect to water regimes, optimized plant population densities and effective control of soil biotic stress factors that may inhibit root development, as well as practicing crop diversification in order to reduce the risks associated with farming in unpredictable environments. Further, governments should increase investments in weather forecasting and cloud seeding.

All these approaches and decision support systems, when integrated, would birth a more holistic strategy for adapting cereal grain crops to future climate change induced drought stress as summarized in **Figure 1**.

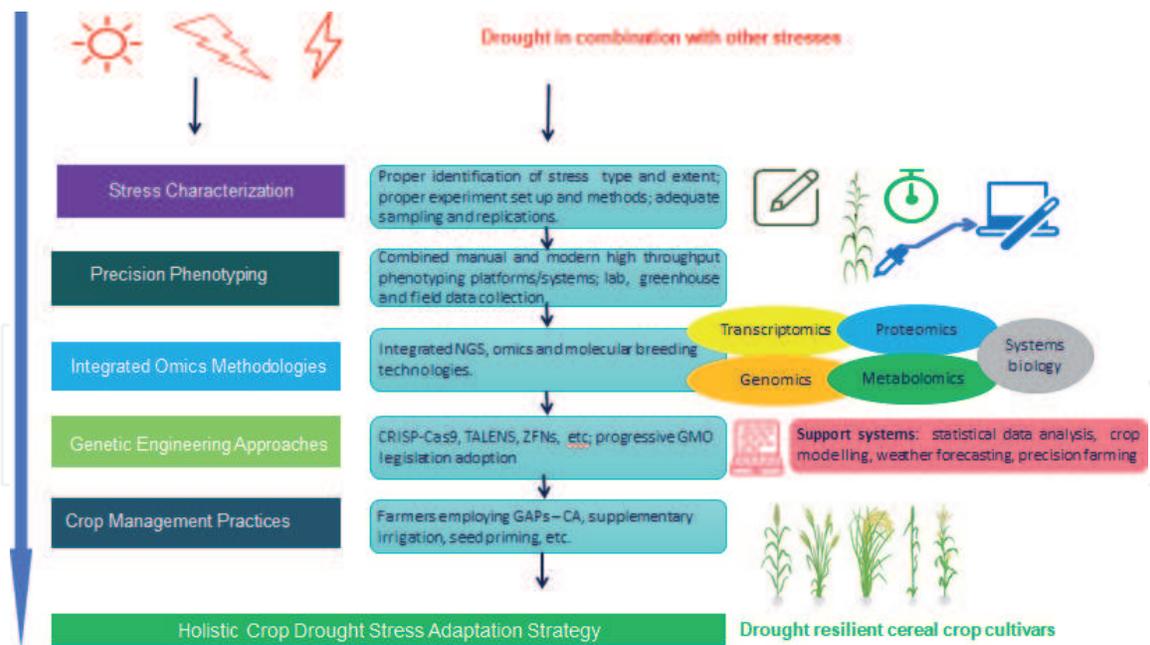


Figure 1.
 Proposed holistic approach to cereal crop drought stress adaptation.

10. Future outlook

Currently, crop improvement efforts are shifting focus from solely yield, quality, or abiotic stress resistance to a holistic approach integrating breeding for a combination of these factors. For example, targeting breeding for combined drought and heat stress tolerance [179, 180], drought tolerance and nutritional quality [161] or drought tolerance and disease resistance [3, 181] are being underlined. Drought-tolerant micro-nutrient dense cereal crop cultivars have been developed [8]. In that regard, future-proofing of global food security would call for double-pronged transformation aimed at developing high yielding cultivars possessing both adaptability to abiotic or biotic stresses and higher nutritional quality. Thus, going forward, it is necessary that more breeding programs use high-priority abiotic stresses in their portfolios [11]. In the wake of addressing malnutrition challenges in developing countries, breeding for bio-fortified drought tolerant cultivars should be strengthened [8, 182]. In addition, promising genotypes in trials for fall armyworm (*Spodoptera frugiperda* L.) resistance, once approved, should be screened for drought tolerance and improved cultivars harboring both traits be developed. Though seemingly a daunting task, combined efforts from crop physiologists, molecular geneticists, breeders and pathologists would make this a reality.

In our 'omics research', future proteomics studies should intensify the identification, quantification and analysis of stress-responsive proteins PTMs, since PTMs can affect protein functions, interactions, subcellular targeting and stability [183]. Moreover, breeding for resource use efficiency, for instance, nitrogen use efficiency (NUE) should be integrated in future drought tolerance breeding programs. Previously, researchers have revealed that improving NUE in crops such as paddy rice and cotton will be critical in greenhouse gas emission management [184–188]. Additionally, application of biochar, either singly [189] or in combination with P [190] has been shown to alleviate heat-induced oxidative stress damage on the cellular physiological processes in rice plants. Thus, as we navigate the future, breeding for NUE and its proper management in the field remains essential in helping adapting crop plants to abiotic stresses such as drought.

Another area of focus will be crop physiology. Since photosynthesis is the basis of plant growth, improving photosynthesis can significantly contribute towards greater food security in the future. Multiple targets for manipulation of crop photosynthesis have been extensively reviewed. These include improving Rubisco kinetic properties and improving canopy architecture to enhance light penetration [191]. Therefore, harnessing the benefits of improved photosynthesis for greater yield potential will require that we intensify manipulation of these targets.

Furthermore, the microbes resident in the rhizosphere can potentially improve plant growth and enhance crop resilience to abiotic stresses [192]. For instance, phosphate-solubilizing bacteria can nullify the antagonistic effect of soil calcification on bioavailable phosphorus in alkaline soils, and thus, can be one of the best options for improving soil P nutrition [193]. It would be crucial to investigate, understand and quantify the complex feedback mechanisms occurring between root and microbial responses to drought stress, particularly in cereal crops. Integrating crop ecology, physiology and molecular methodologies in a multi-disciplinary approach would be central [194].

In the short to medium term, exogenous application of plant growth regulators at different crop growth phases would be an important strategy in inducing drought resistance. In a very short term, seed priming will be of value [3]. The crucial roles of plant phytohormones and growth-promoting rhizobacteria in abiotic stress responses have been extensively reviewed [195–197]. Particularly, the exogenously applied plant growth regulators can enhance morpho-physiological, growth and abiotic stress responses of crops such as rice [198–203]. Recently, Saleem et al. [204] have shown that exogenously applied gibberellic acid (GA3) can reduce metal toxicity induced oxidative stress in jute (*C. capsularis* L.) seedlings. Moreover, exogenous application of salicylic acid (SA) has been shown to ameliorate the adverse effects of salinity on maize plants [205]. Further, silicon (Si) application improved plant water relations, photosynthesis and drought tolerance in Kentucky bluegrass [206, 207], and Si enhanced germination, growth, P and arsenic uptake in rice [208]. Therefore, targeting the modification of hormone biosynthetic pathways may be a gateway to the development of drought tolerant transgenic plants.

Meanwhile, the potential of transgenic technologies across developing countries, particularly in Sub-Saharan Africa, is being hampered by uncoordinated over-regulation by authorities. Unfortunately, the biosafety framework leading to ordered testing and deregulation in such countries is being developed on individual countries basis, instead of a more efficient resource-use regional approach. Moreover, present systems are modeled on overestimated, not science-evidence-based risks [172]. There is need for policy makers to revisit their stance on genetically modified organisms (GMOs) with science guaranteed evidence, not political grand-standing, guiding formulation, adoption and utilization of GMO related policies for food and nutritional security.

11. Conclusion

Though a daunting task, breeding for drought tolerance in cereal crops remains the most economical, effective and sustainable strategy for ensuring food security for the ever increasing human population. While a significant progress has been made to date towards achieving that goal, our understanding of the mechanisms underpinning plant drought stress tolerance remains fragmentary. In the face of global climate change, a multi-disciplinary research strategy becomes obligatory to integrate physiological, genotypic, omics and epigenetics data essential to dissect the complex networks regulating plant drought tolerance, which can then be manipulated through genetic engineering to develop drought resilient

crops. Additionally, cereal crop breeding programs should integrate high-priority abiotic stresses, particularly drought and heat, with other goals such as resource use efficiency, biotic resistance, and nutritional improvement. Further, formulation and effective deployment of efficient screening and precise phenotyping approaches at both laboratory and field levels to identify drought tolerant genotypes or mutants remains critical. Promisingly, our new cultivar development thrusts are now endowed with some innovative methodologies that include high-throughput phenotyping, doubled haploidy, mutation and speed breeding, as well as CRISP-Cas 9 technologies. Going forward, we should harness the potential of these technologies. Eventually, our understanding of the crop drought tolerance mechanisms will be quickened and broadened, greatly assisting our development of new drought-resilient cereal crop cultivars. This should be supported by robust, science-evidence-based and progressive policy frameworks that recognize the centrality of GMOs and modern biotechnology in increasing food production. Consequently, this would lead to improved sustainable crop productivity and global food security.

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Conflict of interest

Authors declare that they have no conflict of interests.

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