International Journal of Bio-resource and Stress Management https://ojs.pphouse.org/index.php/IJBSM

Crossref

IJBSM March 2024, 15(3): 01-10

Article AR5124

Review Article

Natural Resource Management

DOI: HTTPS://DOI.ORG/10.23910/1.2024.5124

Developing Drought Tolerance in Field Crops towards Current Century: An Integrated Bio-molecular Approach

Sanjoy Shil[1], Ankam Shashank[2], Bhukya Rambabu[3], Ponaganti Shiva Kishore[3] and Sujaya Dewanjee[4]

[1]Bidhan Chandra Krishi Viswavidyalaya (Bankura Campus), Susunia, Bankura, West Bengal (722 132), India
[2]Dept. of Plant Physiology, [3]Dept. of Genetics and Plant Breeding, Bidhan Chandra Krishi Viswavidyalaya, F/Ag. Mohanpur, Nadia, West Bengal (741 252), India
[4]Dept. of Genetics and Plant Breeding, Regional Research Sub-Station, red and Laterite Zone, Bidhan Chandra Krishi Viswavidyalaya, Raghunathpur, Purulia, West Bengal (723 133), India

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Corresponding sreejashil2010@gmail.com

0000-0002-6580-0434

ABSTRACT

Drought stresses are foremost threat to plant growth, productivity as well as sustainability towards agriculture through worldwide. Some of the classical breeding approaches have been attempted to develop crop performance towards stress without significant success and so therefore, recently genetic engineering in crop plants is recognized as an alternative strategy to generate drought tolerant crop plants. Various integrated biological approaches have been undertaken to overcome such drought hurdles in achieving the full potentiality of the plant growth and production as well as improving the drought tolerance in different field crops. Some approaches are commonly used to identify genes related to drought tolerance and genes to be identified which are involved in processes known to be critical for drought tolerance; whose expression is regulated by drought stress and that consists in the identification of drought tolerance determinants based on functionality. Plant researchers have developed several spurts of biological novel 'Omics' technologies viz. genomics, transcriptomics, proteomics and metabolomics etc to engineer plant stress tolerance. In this review, an attempt has been made to summarize the current information based on recent literature towards recent understanding as well as latest advancement related to the adverse effect of plant under drought and their adaptations or tolerance towards such abiotic stress with a focus on the identification of drought tolerance mechanisms by soil management practices, crop establishment and exogenous application of growth regulators by regulating an appropriate level of water due to osmotic adjustment and stomatal performance etc at an integrated biological level of approach.

KEYWORDS: Drought stress, omics techniques, tolerance mechanisms, transgenic approach

Citation* (VANCOUVER)*: Shil et al., Developing Drought Tolerance in Field Crops towards Current Century: An Integrated Bio-molecular Approach. *International Journal of Bio-resource and Stress Management,* 2024; 15(3), 01-10. HTTPS://DOI.ORG/10.23910/1.2024.5124.

Data Availability Statement: Legal restrictions are imposed on the public sharing of raw data. However, authors have full right to transfer or share the data in raw form upon request subject to either meeting the conditions of the original consents and the original research study. Further, access of data needs to meet whether the user complies with the ethical and legal obligations as data controllers to allow for secondary use of the data outside of the original study.

Conflict of interests: The authors have declared that no conflict of interest exists.

RECEIVED on 11th January 2024 RECEIVED in revised form on 28th February 2024 ACCEPTED in final form on 14th March 2024 PUBLISHED on 25th March 2024

1. INTRODUCTION

Water stress is an alarming threat in both developing and developed countries (Hanna et al., 2016). Drought and salinity covers approximately 22% of the world's agricultural land and such land area are already expanding (Ahmed and Sarwat, 2009) and cause of more than 50% losses in crop productivity. Drought is one of the major stresses in arid and semi-arid areas (Anjum et al., 2016, 2017a) and causes drastic changes at physio-morphological, biochemical and molecular level. Some of the biological responses that occurs under drought tolerance in plants include at physiological level (osmotic adjustment, carbon fixation rate, hormonal regulation, osmoprotection, antioxidation and a scavenging defense system), morphological, biochemical (Changes and induction of stress proteins and enzymatic activities) and molecular levels (Changes in gene expression at the transcriptional level, intensive action of several genes). Enzymatic and non-enzymatic defense mechanisms have important role in detoxification and scavenging of the ROS [hydroxyl radicle (HO•), hydrogen peroxide (H_2O_2), singlet oxygen ($_1O^2$) and super oxide anion radical (O^{2-}) (Ullah et al., 2018a)] and increase drought stress tolerance (Choudhury et al., 2017). Regulation of various stress response genes is the important factors that cope the plant with such abiotic stresses and increase stress tolerance (Hozain et al., 2012; Ullah et al., 2020). Very recently, a large number of genes have been reported in plants that are involved in drought stress tolerance. Transformation of gene, ScALDH21 from *Syntrichia carninervis* enhanced drought tolerance in cultivar cotton (Yang et al., 2016) and genome editing technologies like, transcription activator-like effectors nucleases (TALENs), zinc fingers nucleases (ZFNs), homing meganucleases and clustered regularly interspaced short palindromic repeats (CRISPR) have enabled to produce targeted genetic modification in organisms of choice (Martignago et al., 2019). Drought is a complex mechanism that uses a broad spectrum of 'Omics' techniques viz. proteomics, metabolomics, transcriptomics, functional genomics and molecular genetics combined with advanced phenotyping techniques.

Molecular responses are considered as a complex process based on the modulation of transcriptional activity of stress-related genes. Recent advancement in various biological systematic approaches of plant responses to drought stress includes genomics, transcriptomics, metabolomics, proteomics and different transgenic-based approaches etc (Figure 1) have amplified our concept regarding plant signal transduction and gene regulation towards the better understanding of the plant responses against drought stress. Various plants signal transduction pathways that activate ion channels produce ROS and accumulate salicylic acid, abscisic acid and jasmonic acid etc leads to transcriptional changes that cause development of drought tolerant in the plant.

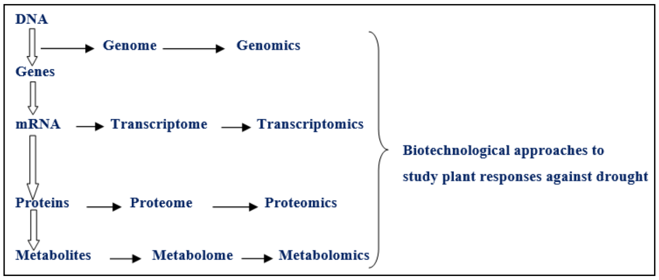

Figure 1: Various novel omics technique is emerged to study the plant responses towards drought stress

Several strategies to engineer field crops for drought stress tolerance have been undertaken that mainly focused on gene expression involving osmolyte (glycine, proline, mannitol, betaine, sucrose, trehalose, raffinose family oligosaccharides (RFOs) and fructans etc) accumulation and osmotic adjustment; genes encoding ROS scavenging enzymes [Super Oxide Dismutase (SOD), catalase, guaiacol peroxidase (GPX), Glutathione Reductase (GR), Glutathione peroxidase (GPX), Ascorbate peroxidase (APX) etc]; genes encoding transcription factors like DREB (dehydration responsive element binding protein), genes encoding LEA (Late Embryogenesis protein) protein and genes for molecular chaperons (Heat Shock Protein (HSPs)) etc. The decreased rate of transpiration, thick cuticle and small stomatal aperture enhance drought tolerance in plants (Ullah et al., 2018b) and dense root system absorbs larger quantity of water than thinner roots because of higher number of roots may contact with more water vapors present in the soil (Abdelraheem et al., 2019). All these strategies are responsible to produce a transgenic with better drought tolerance in plants. For increasing drought tolerance in plants, genetic modification is therefore utmost essential and required the expression of some stress-related genes to engineer such crops and these genes have to be identified that cause better drought tolerance and improve growth and survival of transgenic crops.

2. IMPROVING DROUGHT STRESS TOLERANCE THROUGH FUNCTIONAL GENOMICS APPROACH

Recently, genetics and functional genomics (Mapping, sequencing and functional analysis of genome) approach play an imperative role in gathering massive knowledge in genetic improvement of drought tolerance in several field crops. Though such molecular mechanistic tools of drought tolerance have been most widely studied in well known model plant, *Arabidopsis* spp but yet more as well as better understanding at molecular level for improvement of drought tolerance is utmost required as such information is underlying limited in most of the field crops. Genetics and genomics approach provide foundation tools for research on the molecular improvement of drought tolerance in field crops based on their phenomics/phenotyping.

Now-a-days, genomic resources, molecular markers and Quantitative Trait Loci (QTL) mapping approaches have been successfully implicated in improving drought tolerance in crops. For an instance, QTL for osmotic potential (Tschaplinski et al., 2006) and QTL for Water Use Efficiency (Monclus et al., 2012) have been successfully identified for improving drought tolerance. Genomic improvement in drought tolerance is involved in the development of genetic tools manipulated by drought induced up and down regulation of gene expression that results transcription as well as accumulation of stress proteins. Such stress proteins functions in stress tolerance and different genes that encode the enzymes of osmolyte biosynthesis permit the synthesis of osmotic compounds in response to drought stress.

On the other hand, high throughput single nucleotide polymorphism (SNP) and whole genome sequencing are involved in characterizing polymorphism (Slavov et al., 2012). Marker assisted selection (MAS) are used as a substitute for or assist in phenomics and such marker assisted breeding are used to improve the crop varieties with better drought tolerance. Gene pyramiding is another genetic approach for achieving desired characteristics in plants and in future such approach may helpful in improving drought tolerance also. Some of the genomic resources are involved in drought tolerance represented in Table 1.

Table 1: Genomic resources involved in drought tolerance in some plants.

Crop species	Genomic resources	Descriptions	References
Zea mays L.	MaizeGDB	QTL/SNP	(Lawrence et al., 2004; Lawrence et al., 2005)
Zea mays L.	MaizePLEXdb	Transcriptome/drought	(Zheng et al., 2010) http://www.plexdb.org/plex.php?database=maize
Glycine max L.	SoyBase	Genome/Transcriptome	http://soybase.org/(Grant et al., 2010)
Sorghum bicolor L.	CSGR	Genome/EST	http://csgr.pgml.uga.edu/Data/SorgSig.asp

3. IMPROVING DROUGHT STRESS TOLERANCE THROUGH TRANSCRIPTOMICS APPROACH

Transcriptomic analysis is another most widely used biological approach to develop drought tolerance in plants. Transcriptomic analysis measures plenty of transcripts in parallel and such techniques include microarrays (e.g. At Gen Express; Kilian et al., 2007) and next-generation sequencing-based profiling methods (e.g. RNA-Seq). Transcriptome sequencing has been used to develop gene expression profiling in drought response plants. Transcriptional profiling also has been extensively used to identify drought tolerant genes in maize (Lu et al., 2010). Transcriptome analysis have been extensively conducted in different crops (Potato, Arabidopsis, rice, wheat, sugarcane) that exhibited different level of drought tolerance and reported that such analysis is potential strategies for improving drought tolerance in crops (Wong et al., 2006; Mohammadi et al., 2007, 2008; Mane et al., 2008; Rabello et al., 2008; Aprile et al., 2009; Ergen et al., 2009; Rodrigues et al., 2009).

A number of genome wide transcriptional changes during drought stress have been identified and over expression of a number of droughts responsive down regulated transcription gene seems to be hopeful approach to develop drought tolerance in plants by transgenic tools. This approach concludes third generation of stress response that initiates with the perception of drought signals by various membrane receptors (GPCRs, RLKs, histidine kinases and ion channels etc) that generate signaling molecules like ROS [Superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), hydroxyl radical (HO•)], ABA, cytokinins, ethylene, inositol phosphate etc. These signaling molecules initiate a protein phosphorylation cascade by various kinases (CDPKs, CIPKs, protein kinase, protein phosphatases etc) and activate several transcription factors (DREB/CBF, AREB/ABF, bZIP, MYC/MYB, WRKY etc) through phosphorylation and dephosphorylation reactions. Such activated transcription factors may results the activation of stress responsive genes that includes genes coding HSPs, LEA (late embryogenesis abundant) proteins, LTPs (lipid transfer protein), ion transporters, osmolytes and antioxidants etc and develops drought stress tolerance in plants. Some expression of regulatory genes used as transcription factors for improving drought tolerance in plants are represented in Table 2.

4. IMPROVING DROUGHT STRESS TOLERANCE THROUGH PROTEOMICS APPROACH

Proteomics is another biological omics tool that involved a large number of proteins and their mechanism

Table 2: Over expression of regulatory genes used as transcription factors for improving drought tolerance in plants

Crop species	Gene	Gene action	References
Rice	OCPI1	Transcription factor	Huang et al., 2007
Rice	DREB1 or OsDREB1	Transcription factor	Ito et al., 2006
Rice	ABF3	Transcription factor	Oh et al., 2005
Rice	HvCBF4	Transcription factor	Oh et al., 2007
Wheat	DREB1A	Transcription factor	Pellegrineschi et al., 2004
Wheat and barley	DREB2/DREB3	Transcription factor	Morran et al., 2010
Tobacco	DREB1A	Transcription factor	Kasuga et al., 2004
Arabidopsis	DREB2A	Transcription factor	Sakuma et al., 2006
Arabidopsis	DREB	Transcription factor	Kasuga et al., 1999
Arabidopsis	CBF4	Transcription factor	Haake et al., 2002
Arabidopsis	OsDREB1A	Transcription factor	Dubouzet et al., 2003
Tobacco	CAP2	Transcription factor	Shukla et al., 2006
Glycine max L.	GmDREB2	Transcription factor (drought and cold inducible)	Chen et al., 2007
Maize	ZmDREB1A	Transcription factor (drought and cold inducible)	Qin et al., 2004
Maize	ZmDREB2A	Transcription factor (drought and cold inducible)	Qin et al., 2007
Arabidopsis	ABF3	Transcription factor	Abdeen et al., 2010
Arabidopsis	OsWRKY45	Transcription factor	Qiu and Yu, 2009
Populus euphratica L.	PeSCL7	Transcription factor (drought inducible)	Ma et al., 2010
Glycine max L.	GmWRKY54	Transcription factor (drought and cold inducible)	Zhou et al., 2008
Sorghum bicolor	SbDREB2	Transcription factor (drought and cold inducible)	Bihani et al., 2011

towards the development of drought tolerance in plants. Such proteins viz. Late Embryogenesis Abundant (LEA) proteins, anti-freeze proteins, phosphoproteins, protective detoxification as well as oxidation-reduction reactions proteins, heat shock protein, aquaporins, chaperons and other stress-related proteins etc. This type of protein analysis directly linked to genome-sequence in functional genomics and in a single proteome study a large number of differentially expressed proteins can be identified. For an example, Ford et al., 2011 has been conducted first shotgun proteomics to gain insights into protein response to drought in wheat results identification of 1299 wheat proteins that are differentially expressed. Peng et al., 2009 has reported different expression of 114 drought-responsive proteins in bread wheat by proteomics study and in alfalfa leaf, drought causing damage to the photosynthetic activity was impaired by down-regulation of Rubisco and proteins involved in Rubisco assembly (Aranjuelo et al., 2011). Larrainzar et al., 2007 has identified subsets of plant and bacterial proteins involved in drought stress under proteomic analysis in Medicago roots nodules.

Based on proteomics profiling in rice seedlings, Shu et. al., 2011 and Mirzaei et al. (2012) established that primary drought related up-regulated protein components (protective detoxification and oxidation-reduction reactions proteins etc) involved in protein processing, anabolic enzymatic activities, metabolic processing, protein re-folding and amino acid synthesis and membrane transport, pathogen–related metabolism, protein chaperons.

Activities of several protective proteins are up-regulated along with altering physio-biochemical strategies towards stress when the plants are subject to drought that leads them first line of defense. Proteomics study revealed that a plant builds their amelioration either by re-watering or by increasing the levels of heat shock proteins (HSPs), molecular chaperons, aquaporins and other stress related proteins. Amudha and Balasububramani, 2011 and Rohila et al., 2002 has been reported that high molecular weight LEA proteins may accumulate in barley and wheat respectively under drought and salinity stress. Over expression of a group 3 LEA protein (HVA1) from barley exhibits tolerance to drought and salinity in transgenic rice and expression of a group of 2 LEA proteins (PMA80) gene in wheat or wheat LEA group 1 protein (PMA1959) gene results tolerance to drought and salinity.

MYB15 an over-expressive line in *Arabidopsis* exhibit their mechanism of drought tolerance that results a higher sensitivity towards ABA-induced stomatal closure due to positive downstream effect on the synthesis of stress-tolerant proteins (Ding et al., 2009). Proteomic study in *Brassica napus* reported by Bazargani et al., 2011 that BnD22 (a 22 kD stress protein) causes an increase in nitrogen recycling and utilization for protection of younger leaf from nitrogen starvation caused by drought.

Proteomic studies in different tissues and cell organelles of rice plants like in leave (Salekdeh et al., 2002), roots (Yan et al., 2005; Lee et al., 2009), anthers (Liu et al., 2011), cell-suspension culture (Rao et al., 2010), embryo (Fukuda et al., 2003), mitochondria (Chen et al., 2009) etc leads to the identification of several stress-induced protein and their physiological functions. Proteomics profiling involves a large network of proteins that act as a biological tool to illuminate various bio-molecular mechanisms towards drought stress in crop plants (Ashan et al., 2009). Different stress-inducible genes responsible for synthesis of osmoprotectants (LEA proteins, detoxification enzymes, anti-freeze proteins and chaperons etc) are directly related to protect the plants from drought stress. Table 3 enlisted the proteomics profiling in some rice varieties focused on the identification of polypeptides towards drought stress.

Table 3: Proteomics profiling in some rice varieties focused on the identification of polypeptides towards drought stress

Varieties	Major findings	References
Nipponbare and Zhonghua 8	(i) Signal transduction: actin depolymerizing factor (ii) Stress defense: Salt-induced protein (SALT) and Super oxide dismutase (SOD) (iii) Energy and metabolism: Oxygen-evolving complex (OEC)protein in PS II, RUBISCO-small and large subunits, Chloroplast ATPase, LHC-II (Light Harvesting complex)	Ali and Komatsu, 2006
CT9993 and IR62266	(iv) Stress defense and antioxidant enzymes: GSH-dependent dehyro-ascorbate reductase and Super oxide dismutase (SOD) (v) Energy and metabolism: Triose phosphate isomerase, RUBISCO-activase (vi) Signal transduction: actin depolymerizing factor and translation elongation factor	Salekdeh et al., 2002

5. IMPROVING DROUGHT STRESS TOLERANCE THROUGH METABOLOMICS APPROACH

Metabolomics is another omics tools for functional genomics and system biology that generates large amounts of data for further development in the area of analytical science and bioinformatics. Processing, handling and analyzing of such data are needed for specialized analytical, statistical and bioinformatic tools (Shulaev, 2006). It is an emerging field in molecular biology that includes comprehensive measurements (identification, extraction and quantification) of key metabolites (alanine, glutamine, aspartate, tyrosine, isoleucine, glucose 6-phosphate, GDP-fucose, cysteine and cystine etc) in a plant sample that are specific to a drought stress. Metabolome represents the downstream gene expression that closer to phenotype or genotype differences between plant species than transcript expression or proteins. Several analytical technologies are available for metabolomics study on drought stress includes high throughput approaches like NMR (Nuclear Magnetic Resonance) (Kim et al., 2010); GC-MS (Gas-Chromatography-Mass Spectrophotometry) (Kaplan et al., 2004); FT-IR (Fourier transform infrared) (Johnson et al., 2003); Ultra high-resolution Fourier transform-ion cyclotron MS (Hirai et al., 2004).

On the contrary, glucose and proline were found regulated in rice plant but not in other plant species under stress conditions. Both glucose and proline are two metabolites that are well known as compatible osmolyte for osmotic adjustment under stress condition. Accumulation of Osmolytes like sucrose, mannitol, arabinitol, pinitol, inositol, ononitol, glycerol, sorbitol and other polyols (carbohydrate); malic acid, oxalic acid (Organic acid) and proline, glycine betaine, glutamate, aspartate, choline, polyamines (Putrecine, spermidine, spermine) and ABA etc plays an important role in the cell growth and keeps the ion concentrations at low levels.

Under drought stress condition, the accumulation of proline is caused by inducing the biosynthesis of proline (act as osmoticum) and by inactivation of the degradation of proline. At the transcriptional level, the L-proline synthesis in plants from L-glutamic acid via pyrroline-S-carboxylate (P5C) is regulated by two enzymes viz. P5C synthetase (P5CS) and P5C reductase (P5CR) during dehydration and rehydration. Overproduction of proline under stresses like drought and salinity causes tolerance towards osmotic stress in genetically engineered crops (Yoshiba et al., 1997) and production of such osmoprotectant regulated by glutamine synthetase (Lee et al., 2010).

Transcription factors in ABA signaling pathway is a mechanistic approach of genetic improvement towards stress tolerance. bZIP and MYB are the two families that involved in ABA signaling and its gene activation. Yamaguchi-Shinozaki and Shinozaki, 2006 has been reported that constitutive expression of ABF3 or ABF4 results drought tolerance in *Arabidopsis* with altered expression of ABA/Stress-responsive genes, for example rd29B, rab18, ABI1and ABI2. Ito et al., 2006 also has been reported that over expression of OsDREB1 or Arabidopsis DREB1 in rice made 96 transgenic plants more tolerance towards drought.

Generally, concentration of different secondary metabolites increases under drought and metabolite profiling as well as metabolic fingerprinting of those metabolites and hormones along with genomics tool may be used to identify some up or down regulated genes for improving drought tolerance in crops. Targeted analysis is one of the recently developed analytical approaches in metabolomics (Djoukeng et al., 2008) that measure few metabolites either by MS (Mass spectrometry) or NMR (Nuclear magnetic resonance spactrophotometry) or Liquid chromatography (LC) or GC (Gas chromatography).

Metabolite profiling is another approach that attempts to identify and quantify a class of chemically related metabolites (Seger and Sturm, 2007) and metabolic fingerprinting uses signals from hundreds to thousands metabolites for rapid sample classification via statistical analysis (Chatterjee et al., 2010). Hummel et al., 2010 have found under metabolite profiling that 30 different enzyme activities in *Arabidopsis* drought adaptation did not involved to carbon metabolism and organic acids mainly contributed to osmotic adjustment. Table 4 represents some metabolites and hormones associated with stresses.

Table 4: Some metabolites and hormones associated with various stresses

Metabolites/hormones	Type of stress	References
ROS, Malondialdehyde	Biotic and abiotic stresses	Jaspers and Kangasjarvi, 2010; Arbona and Gómez-Cadenas, 2008; Hossain et al., 2009
Polyamines, Abscisic acid, Jasmonic acid and Salicylic acid	Drought and Salinity	Jaspers and Kangasjärvi, 2010; Arbona and Gómez-Cadenas, 2008; Liu and Moriguchi, 2007; Wang et al., 2011; Liu et al., 2011
Proline, glycine-betaine and compatible osmolytes (sucrose, mannitol, arabinitol, pinitol, inositol, ononitol, glycerol, sorbitol etc)	Drought, salinity and osmotic stresses	Ashraf and Foolad, 2007; Hmida-Sayari et al., 2005; Umezawa, 2006

6. CONCLUSION

Research for improving drought tolerance has been underway for long time but recently an explosion of molecular tools, omics techniques and their integration, second generation and emerging third generation DNA sequencing technology, genomic scale investigation, understanding of transcriptional regulators behind co-expressed genes and QTL identification, protein and metabolite profiling, high-throughput phenotyping platforms, improved bioinformatics resources etc that provides a basis for identification of more functional genes and novel possibilities for precise development of stress-tolerant crop varieties at cellular level Thus, to unravel the drought intricacy, a proper understanding of stress signaling pathways are require through an integrated biomolecular approaches.

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