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Water Stress in Crop Plants: Challenges and its Management–A Review

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ABSTRACT

In 21st century, shrinkage of land resources, heavy population pressure and degradation of soil has declined the fertility and productivity of soil. Water stress is the main factor that decreases growth, development and photosynthesis of plants because water is the central molecule for transporting metabolites and nutrients, forms biomass of 80-90% in plants. Water stress disturbs organization of proteins with lipids, transportation, activities of enzymes and also decreases biosynthesis of mRNAs, proteins and overall yield up to 80 %. During stress conditions, abscisic acid, diacylglycerol (DAG), inositol triphosphate and inositol hexaphosphate acts as signal molecules and controls gene expression. Therefore, plant has developed defensive mechanisms at morphological, physiological, molecular and biochemical level such as: lower CO_2 concentration, impairment in carbon and nitrogen metabolism, decrease in stomatal conductance, CO_2 assimilation, etc. Moreover, there are two component of antioxidant defence system in cell of plants: non-enzymatic and enzymatic). The various components of enzymatic system are as follows; glutathione reductase, superoxide dismutase, ascorbate peroxidise, catalase and peroxidise. The components of non-enzymatic systems are ascorbic acid, cysteine and reduced glutathione. The other enzymes are glutathione reductase, monodehydroascorbate reductase, ascorbate peroxidise and dehydro-ascorbate reductase. The antioxidative defence system is considered as the important adaptive mechanism The most critical hormone is ABA which helps in conducting resistance to abiotic and biotic stress. The catabolism and synthesis of many PGRs such as gibberellins, auxins, cytokinins, jasmonic acid, ethylene, brassinosteroids, etc. are the main consequent of osmotic damage of plants. But it can be improved by exogenous application of substances, fertilizers, bio fertilizers, plant growth regulators, hydrogels, genomic editing and agronomic approaches, etc. Apart from these, resistant varieties can be used for better yields and returns.

Keywords: Photosynthesis; morphological; physiological; molecular

1. INTRODUCTION

Water is the major factor which determines how the plants are distributed throughout world.[1] The limiting water availability and coming time demand of food for growing population may exacerbate impacts of adverse environmental conditions.[2] Water stress decreases turgor and water potential of plant to that much level that it cannot perform complete physiological activities. Therefore, water stress found to be more complex problem for food security of world. The end of this century will reportedly expect to mark by increasing water stress.[3]

The major aspect may decrease productivity of crops from water deficiency of soil are absorption of canopy from photo-synthetically active radiation (PAR), decreased efficiency of radiation and decline in index of harvesting. Water use efficiency has become a vital selection feature and an attribute of performance of plants. Though, several adaptations have been done by plants at various levels for changing the utilization of water and adapt themselves against unfavourable abiotic conditions.[4] Approximately, 34 million hectares of land is salinized globally, which costs about US $11 billion annually.[5]

In moisture stress conditions, the plant ware affected at various levels and several adaptive mechanism were also developed. During morphological changes, reduction in stomatal density, decrease in growth and leaf thickness was observed. In physiological responses the stomatal closure and osmotic balance was studied. Moreover the evolution of drought sensitive and drought tolerant was also found.[6] These resistance mechanism in plants varied according to different plant genotypes. Plant regulates their growth by adjusting and stabilising their utilization of resources in adverse climatic.[7,8] Accordingly, these mechanism also stimulated the responses of plant at the molecular level such as signal transduction, enhances.[9] The molecular mechanism involves the induction of transcriptional factors, enhanced ion transport, and formation of stress hormones.[10,11] At molecular levels, several stress related genes are upregulated or downregulated in moisture scare condition, such as dehydrin-type genes (LEA) as reported by Sivamani, *et al.*[12] which were highly enhanced in roots of barley and rice. Moreover, water scare situation also

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enhanced the genes for dehydrin responses[13], molecular chaperone[14,15], expression of H1-S[15,16] and expression of homeodomain leucine zipper proteins.[17]

Moreover, in higher plants, lack of moisture causes production of reactive oxygen species (ROS) which leads to inhibition of growth and decrease in functions of photosynthesis.[18] In many plants, the role of osmolytes are played by proline and soluble sugars which helps in stabilization of membrane protein and consequently, increases resistance of plants to limited water supply.[19] The antioxidants like peroxidase (POD), superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase (GR) get activated to detoxify ROS.[20] Recently, it becomes vital to develop mechanisms for tolerance to water stress in varying climatic conditions.

2. TYPES OF WATER STRESS

2.1 Drought

Simply, drought is an event of shortages of water supply whether it is at atmospheric, ground and surface levels. The types of physical drought are as follows: hydrological, metrological and agricultural drought. These droughts have a consequent occurrence of incidence because deficiency in precipitation leads to meteorological drought (Fig. 1) which consequently leads to agricultural drought (Fig. 3) as meteorological drought affects moisture availability of soil. Hydrological drought (Fig. 2) leads to diminished amount of water in streams and lakes due to lack of recharge of water from soil.

2.2 Water Logging

It is a phenomena where surplus quantity of water is present than normal optimal requirements. Water logging leads induces anaerobic condition within rhizosphere. In this condition, creation of anaerobic environment in the surrounding area of roots is the first and foremost effect of water logging from which roots of plants cannot obtain oxygen. In the field capacity, soil has 10 to 30 % volume of air filled spaces. However, decrease in percentage occurs along with decrease in content of water. So, the oxygen supply is greatly reduced, causes death of the plant. The water logged roots could export some substances that cause closure of stomata. It causes yellowing of leaves from base to top of plants, drooping of petioles, leaf epinasty, hypertrophy, wilting etc.

3. WATER STRESS ON PLANTS

Impact of water stress can be seen morphological to physiological attributes, mostly marked in many reproductive phases of plant. The various responses of plant are presented below

3.1 Photosynthesis

Photosynthesis is generally water stress sensitive but structural and functional rearrangement of photosynthetic machinery confers resistance of crop plants. As leaf water potential and relative water content decreases, then photosynthesis in higher plants decreases. Water stress decreases photosynthetic capacity of plants and generally associated with closure of stomata and metabolic impairment.

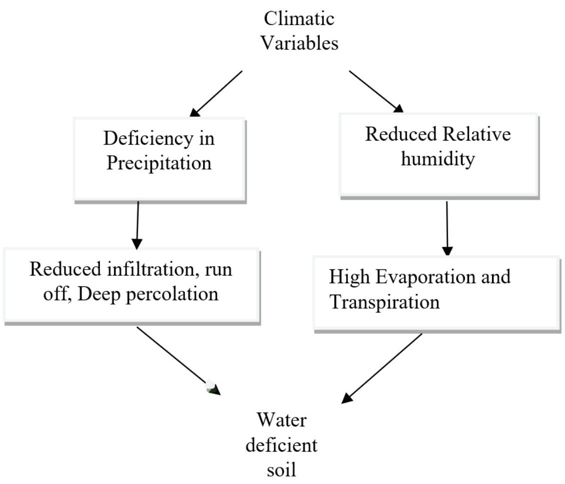

Figure 1. Meteorological drought.

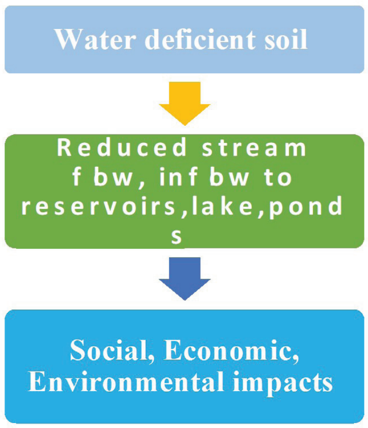

Figure 2. Hydrological Drought.

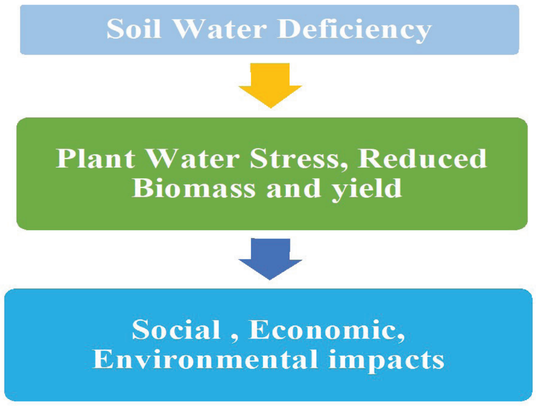

Figure 3. Agricultural drought.

Studies claimed that stomatal closure inhibits photosynthesis in C4 plants during stress conditions but some reported that several other factors also had a vital play. Photosynthetic capacity of C3 and C4 plants decreases during stress condition. This is evident that photosynthetic capacity of C4 plants is found more susceptible as compared to C3 plants and C4 plant, like Zea mays L. has more sensitivity to stress than wheat which is a C3 plant. The photosynthesis decreases due to changes in quality and quantity of photosynthetic pigments, low assimilation of photosynthesizing leaves, low CO_2 uptake.[21]

A disruption of chlorophyll biosynthesis occurs in following phases:

- Development of (ALA) 5-aminolevuliniuc acid.
- Condensation of ALA in primary tetrapyrrol, porphobilinogen and protochlorophyllide.
- Protochlorophyllide conversion to chlorophyllide in the presence of light.
- Chlorophyll a, b and photosynthetic machinery are formed.

3.2 Photosynthetic Enzymes

The activity of photosynthesis along with photosynthetic enzymes decreases. Lack of moisture causes shrinkage of cell and increases interactions between proteins and disturbs the protein structures. The rate of synthesis and degradation controls the level of Rubisco in leaves. Rubisco activity declined in severe water stress conditions.[21] Loreto,[22] *et al.* reported the changes in photosystem II and CO_2 availability in chloroplast which was tuned with the functioning of photosynthesising ETS (electron transport chain).

In many species, the formation of 2-carboxyarabinitol-1-phosphate occurs at night which binds with Rubisco to inhibit catalytical site activity. It is noticed that in light, the inhibitors binds tightly may decrease the activity of Rubisco. Parry, [23] *et al.* studied Nicotiana tabacum and revealed that the activity of Rubisco decreases not due to activation of Mg^{2+} and CO_2 but due to inhibitors of tight bindings. It is evident that photosynthesis is also limited by synthesis of (ATP) adenosine triphosphate in mild water stress conditions. Tezara,[24] *et al.* showed that impairment in ATP biosynthesis and photophosphorylation may be major components to limit photosynthesis.

3.3 Protein Biosynthesis

Expression of genes, biosynthesis of mRNAs and protein are disrupted by water stress conditions. Water stress results in biosynthesis of different proteins like; cold regulation proteins, ABA, desiccation stress proteins, heat shock proteins and enzymes which are needed for biosynthesis of osmoprotectants and various enzymes for detoxification. Further, the synthesis of protein kinases and transcription factors are also occurs to regulate gene expression and signal transduction. Dehydrin proteins have a conserved domain and hydrophobic interactions for stabilization of macromolecules. These proteins are accumulated during maturation of embryo and seed production. These stress proteins acts as defence mechanism for macromolecules like mRNAs, lipids and enzymes from dehydration. Generally, HSPs are considered molecular chaperones and perform functions like targeting, protein synthesis, degradation and maturation, protein refolding membranes and protein stabilization under water stress.[22]

3.4 Lipid Biosynthesis

Water stress causes a disturbance in organization of proteins with lipids, transportation ability and activities of membrane enzymes. In chloroplasts, it changes the number of carbon atoms of fatty acids having carbon number more than 16. Increased levels of intercellular ROS may induce oxidative destruction to nucleic acids, lipids and proteins. An antioxidant defence system is activated in higher plants to this response.[25]

There are various stages of lipid peroxidation; initiation, propagation and termination. In lipid peroxidation, fatty acid radicals are produced and react with poly unsaturated fatty acid (PUFA) methylene group and produces hydroperoxides, conjugated dienes and lipid peroxy radicals . These peroxy radicals are highly reactive and may start a chain of propagation. After decomposition of lipid peroxidation, various types of aldehydes such as crotonaldehyde, malondialdehyde and acrolein, lipid epoxides alcohols and lipid alkoxyl radicals alkanes are produced[26] and help plant to withstand water stress.

3.5 Nutrients

The impact of water stress can be seen in mineral nutrition of plants and homeostasis balance. The functional and structural organisation of membrane of plants is done by calcium. Potassium has a major role in osmotic adjustment, water relation, plant resistance and stomatal movement. After investigation of chickpea genotypes H-208 and H-82-2 under water stress it has been noticed an increase in fixation of nitrogen along with an increase in potassium concentration. It was found more in case of H-208.[27] Now, it is clear that metabolism of nitrogen is vital component influencing growth and development of plant.

Various studies found a reduction in uptake of nutrient and nitrate reductase activity. It increases nitrogen level, decreases phosphorus level but has no effect on potassium concentration. This interference of nutrient uptake results in lower absorption of transpirational flow and inorganic nutrients.[28] However, in water stress situation, mineral uptake varies according to the genotypes and species of plants. But application of potassium increases nitrite content in chickpea under water deficit condition.[27] Supplementation of potassium improved the nodulation, nitrogen fixation and enzymes of nitrogen assimilation in mungbean[29].

3.6 Attributes of Water

Canopy temperature, leaf water potential, relative water content, leaf temperature, stomatal resistance and rate of transpiration are considered as essential parameters which hamper different attributes related to water. In case of wheat, during development of leaves, the relative water content was prominent but reduced in dry matter of matured leaf. It clearly shows that there was a low level of relative water content in rice and wheat in stress conditions as compared to plants in non- stress conditions. In some plants, water potential, relative water content, transpiration rate etc. was diminished in sufficient supply of water but leaf temperature was increased.[30]

The content of water of cladode of Opuntia ficus-indica was reduced approx. 57% in stress conditions. The turgor potential of cladode of Opuntia shows that the parenchymatous cells vanished a larger quantity of water as compared to chlorenchymatous cells.[31] In Hibiscus rosa-sinensis, turgor potential, stomatal conductance, water-use efficiency, relative water content and transpiration has been reduced in limited water conditions.[32] The ratio of dry matter and consumable water in a plant is termed as water use efficiency (WUE).[33] These studies clearly shows link between WUE and stomatal closure during water stress.

3.7 Abscisic acid Accumulation (ABA)

During dehydration, ABA accumulated and has a vital play in water stress. It stimulates stomatal closure of stomata and expression of many genes which helps in developing defence mechanisms in plants. In limited availability of water, ABA concentration increased in xylem sap which in turn increases ABA concentration in several parts of plants. In plants, decrease in plasma membrane-ATPase activity is also seen which increases pH of cell wall and results in accumulation of ABA-transition structure. After this, ABA translocated in leaf apoplasm through water stream because it has not the ability to enter plasma membrane. The concentration of ABA increased in guard cell which results in stomatal closure and helps in conservation of water for plants.[18]

3.8 Crop Growth

In cowpea of Africa, the decline in yield ranges from 34-68% as yield is dependent upon timing of development throughout stress period[34]. Kaya,[35] *et al.* reported that water stress decreases seedling and germination of seed. Drought results a decline in yield by 40% in Zea mays but 21% in Triticum aestivum at 40% reduction in water.[36] However, Zeid and Shedeed,[37] reported a decrease in hypocotyl length, germination potential, fresh and dry weight of shoot and root in stress condition created by polyethylene glycol, but increase of length of root was seen in Medicago sativa. Reduction of yield of crops is shown in Table 1.

Table 1. Reduction in yield during water stress

Crops	Stages	Yield Loss
Wheat	Vegetative[38]	80%
Barley	Filling of seed[39]	49-57%
Maize	Reproductive[40]	47-70%
Wheat	Filling of grains[41]	50%
Rice	Reproductive[42]	53-92%
Soybean	Reproductive[43]	35%
Chickpea	Reproductive[44]	45-69%
Rice	Grain filling[45]	24-84%
Agrostis palustris	Reproductive[46]	50%
Common bean	Reproductive[47]	58-87%
Canola	Reproductive[48]	30%
Sunflower	Reproductive[49]	60%
Cowpea	Reproductive[50]	60-11%

3.9 Partitioning of Assimilates

Reproductive sink requires assimilation and translocation for seed development. Asch,[51] *et al.* reported that limited availability of moisture hampers seed set and filling. In fact, water uptake is also enhanced by distribution of dry biomass in roots. It was revealed that water stress increases root to shoot ratio in perennial variety of cotton due to increase in dry matter and starch in roots. Komor,[52] reported that the translocation of sucrose depends upon sucrose concentration and rate of photosynthesis in leaves of plants. Metabolism of carbohydrates, sucrose concentration and photosynthetic rate is also influenced by water stress. Moreover, Kim,[5] *et al*. reported that these effects are due to increased activity of acid invertase. Accumulation of sucrose and photosynthesis can obstruct the export rate of sucrose from source to sink which consequently inhibits development of reproductive organs of plants.

3.10 Respiration

During water stress, membrane components were damaged because of excessive generation of ROS[54]. In water stress, the physiological activities of metabolites are maintained by activity of alternative oxidase activity. The cytochrome oxidase terminated in potassium cyanide and inhibits respiration up to 80%. Shugaeva,[55] *et al.* during early water stress, found the reduction in cytochrome-mediated oxidation pathway which was managed by mitochondrial alternative oxidase, but in longer period of water stress, some other oxidative systems were also activated which were not sensitive to salicylhydroxamate and potassium cyanide.

Moisture deficiency increases root respiration in rhizosphere and creates an unevenness in carbon resources utilization, increases generation of ROS, reduces generation of adenosine triphosphate (ATP) etc. In mitochondria, Möller[56], Noticed that O2 interacts with electron transport chain components and results in formation of ROS but hydrogen peroxide (H2O2) are produced by peroxisomes. Both non-enzymatic and enzymatic reactions are responsible for reactive oxygen species formation.

4. WHAT CHANGES TAKES PLACE IN PLANTS DURING WATER STRESS

Limited water availability decreases growth, development and photosynthetic rate of plants. Further, the findings showed increased water stress increases plant responses to water stress as chlorophyll responds to stress conditions. It clearly reveals sensitivity of chlorophyll to water scarcity. A diversity of changes like morphological, biochemical and physiological occurs in plants in adverse conditions[57]. The changes are shown in (Fig. 4)

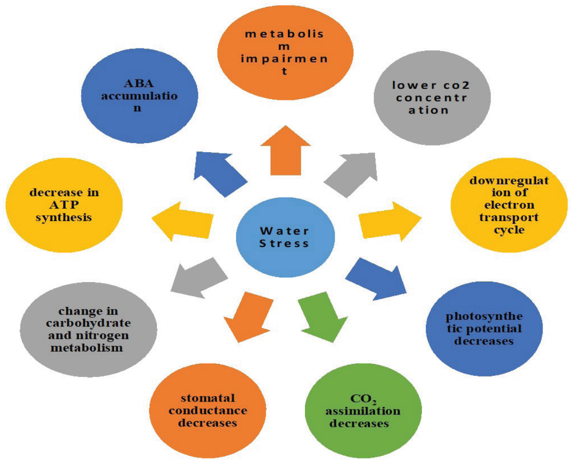

Figure 4. Responses of plants against water stress.

Moreover, plants of different categories showed evolution at various levels to cope up the drastic changes caused due to water stress situations. The changes of plants varied and particularly dependent on the genotype and the extent of water deficit situations. Accordingly various adaptations were done in plants[7,8].

5. WATER STRESS ADAPTATIONS IN PLANTS

The ability of plants to develop, grow and show a better productivity in limited water is termed as water stress adaptability. Root anatomy, salts and water availability in soil have a critical role in transportation of water in plant roots.[58] Several water stress tolerance mechanisms are as follows.

5.1 Responses at Morphological Level

There are several internal strategies of plants which help in increasing capability for limited water availability in different plants as shown in Fig. 5

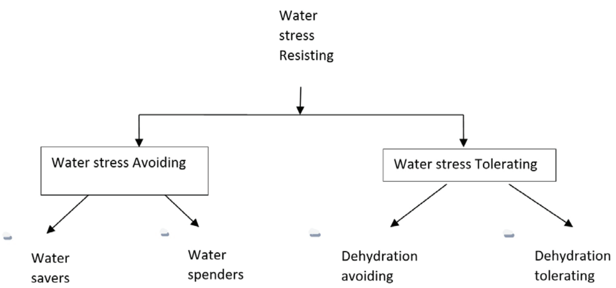

Figure 5. Types of plants on the basis of stress resistance.

5.1.1 Escape

Araus,[59] *et al.* stated that the plants shorten their life cycle in a growing period before the conditions become unfavourable. The occurrence of flowering stage is very critical in plant life cycle. The genotypic variety of plant and environment determines the crop duration and capability of plants to adapt unfavourable environmental conditions. DaMatta[60,] noticed the leaf shedding pattern in Robusta coffee and found that during water stress the leaf shedding takes place from mature leaves to younger leaves which indicates that leaf shedding increases with increasing water stress intensity. The development of reproductive organs is accompanied with availability of moisture of soil and it leads to drought escape when season of growth become short.[59]Abbo and Kumar,[61] stated that the major trait of a crop adaptation is the time of flowering during high temperatures and water stress. The efficient mechanism to minimize the loss of productivity in water stress is developing short-duration varieties because the availability of soil moisture and growth duration of plant is very crucial for better yield of seeds.

5.1.2 Avoidance

Reduced conductance, increased root system, increased leaf thickness, decreased leaf area, leaf rolling and reduced stomatal number are some physiological mechanisms which decreases evapo-transpiration and provide an avoidance to plants from water stress.[62] Several components of roots also help plant to avoid water stress as: root length, root biomass, root depth and root density etc. Drought avoidance mechanisms reduce loss of water in plants, due to stomatal control of transpiration which in turn regulate uptake of water by an extensive and deep root system.[63] Thick and extensive roots may help in extraction of water from a substantial depth of soil. The waxy coating on the surface of leaves also assist in maintaining elevated water potential in tissue, that's why it is known to be favourable and desirable characteristics against water stress.[64]

5.1.3 Tolerance

A tolerance strategy and some xeromorphic traits are also used by plants for water stress tolerance like trichomes production on both surfaces of leaves and presence of hairs on leaves. The root density, proliferation, root size and growth rate considered as the important attributes. Osmotic adaptation and accumulation of compatible solutes, antioxidant system, alteration in metabolic pathways, closure of stomata and an increase in root/shoot ratio are some other strategies used against water stress. Hydrostatic pressure is maintained by biochemical and cellular modifications, mainly through osmotic adjustments in tolerance strategy.[65]

5.2 Responses at Physiological Level

Osmoprotection, osmotic adjustment, scavenging defence system and many complex mechanisms are suggested by the researchers. However, some other mechanisms are as follows;

5.2.1 Cuticular Wax Synthesis

Lee and Suh,[66] found that the cuticle of some aerial plants synthesises waxes on their surface. This makes surface of plants highly oily which reduces transpiration form plants. It is considered as an adaptive behaviour. In case of six cultivars of Avena sativa (L.) the cuticular transpiration rate was higher in water stress tolerant variety i.e. Stormogul II of non-stressed seedlings. Plant also modifies their leaf thickness, leaf tissue density and leaf areas in water stress.[67]

5.2.2 Conservation of Water in Tissue and Cell

Osmotic potential decreases during osmotic adjustment of cell in plant which enhances the turgor pressure and water influx gradient. Cell wall elasticity and osmotic adjustment improves the water level in tissues of plant and helps plants to combat prolonged water stress.68 Water stress is determined by leaf water potential in case of Faba beans but did not appropriate for differentiating resistant varieties from susceptible varieties. Further studies noticed the drought toleration in chickpea is screened after calculating the water potential of leaf at dawn and content of water in afternoon.[69] During water scare conditions, the plant initially reduces transpiration by storing water in their leaves and stems and thus conserves water. The susceptible genotype of pea was found to be greatly influenced from decreased relative water content as compared to resistant genotypes under water stress conditions.[70]

5.2.3 Antioxidant Defence System

There are two component of antioxidant defence system in cell of plants: non-enzymatic and enzymatic. During adverse environmental conditions, the activities of components of non-enzymatic system and antioxidant enzymes were increased. Several water and lipid soluble substances and antioxidant enzymes detoxifies the ROS.[71] The various components of enzymatic system are as follows; glutathione reductase, superoxide dismutase, ascorbate peroxidase, catalase and peroxidase. The components of non-enzymatic systems are ascorbic acid, cystein and reduced glutathione. The other enzymes are glutathione reductase, monodehydroascorbate reductase, ascorbate peroxidise and dehydro-ascorbate reductase.[72] Besides these systems, a pathway called as ascorbate-glutathione cycle also helps in detoxification of H2O2 and superoxide radicals.

5.2.4 Stability of Cell Membrane

Water stress damages the selective permeability of plasma membrane and it is used for screening of tolerant and sensitive genotypes. The stability of cell membrane is an important quantitative trait which is reasonably inheritable, having an elevated genetic relationship with grain yield in wheat. Water stress resistant plants maintain the stability and integrity of their membranes during limited water availability[73]. However, application of potassium on sweet corn increases membrane stability index in stress conditions.[74] Dhanda,[75] *et al.* reported that the screening of germplasms of water resistant varieties can be done by determining the stability of membranes of leaves.

5.3 Biochemical Responses to Water Stress

In plants, the Receptor-Like Kinase (RLK), considered the first kinase,[76] was discovered in 1990s. The findings reported that aquaporin proteins are the important proteins helps in maintaining the hydraulic conductivity and are regulated by environmental stimuli along with several changes in calcium and cytoplasmic pH level, phosphoryaltion and intracellular compartments re-localisation.[77] The WAKs (Wall-Associated Kinases), a subfamily of RLKs in vascular plants, signal is perceived from adjacent cell and outside to stimulate complete signalling pathway.[76]

Hydraulic conductivity and long distance signalling of shoot and root of plants are mainly regulated by plants growth regulators (PGRs). The most critical harmone is ABA which helps in conducting resistance to abiotic and biotic stress.[78] The catabolism and synthesis of many PGRs such as cytokinins, auxins, gibberellins, jasmonic acid, brassinosteroids, ethylene, etc. are the main consequent of osmotic damage of plants.[79] During stress conditions, diacylglycerol (DAG), inositol triphosphate, ROS and inositol hexaphosphate acts as signal molecules and induces a higher level of intracellular calcium ions. The stimulated phosphatases and kinases may dephosphorylate and phosphorylate some specific TFs which in turn control levels of expression of specific genes.[80]

Overproduction of ROS is caused by abiotic stress (Fig. 6) and causes oxidative damage via destructing the lipids, DNA, carbohydrates and protein.[81] Under abiotic stress, production of ROS is accompanied by formation of methylglyoxal via various non-enzymatic and enzymatic systems. Plant cell functions are damaged by methylglyoxyl and leads to destruction of DNA.[82] The detoxification of methylglyoxalis is done by the glyoxalase system which catalyzes D-lactate from methylglyoxal through using cofactor, reduced glutathion Transcriptional factors such as WRKY, DREB, bZIP, bHLH, ERF, NAC and MYB83 also have a critical play. In case of Arabidopsis the Cycling Dof Factor 3 is over expressed to improve tolerance to salt, cold and drought stress[84].

Several metabolites like amino acids, glucose, sugars, sugar alcohols, fructose etc. re-establish homeostatic balance. These compounds are responsible for tolerance to abiotic stress, maintenance of protein structures, cellular membranes stabilisation and cell turgor balance.[85] The amino acid, proline is associated with osmotic balance during water stress conditions.[86] A sufficient amount of proline was also accumulated in capsicum during polyethylene glycol induced water stress condition. In some plants, the water stress tolerance is also done by glycine betaine. Secondary metabolites like lignin,

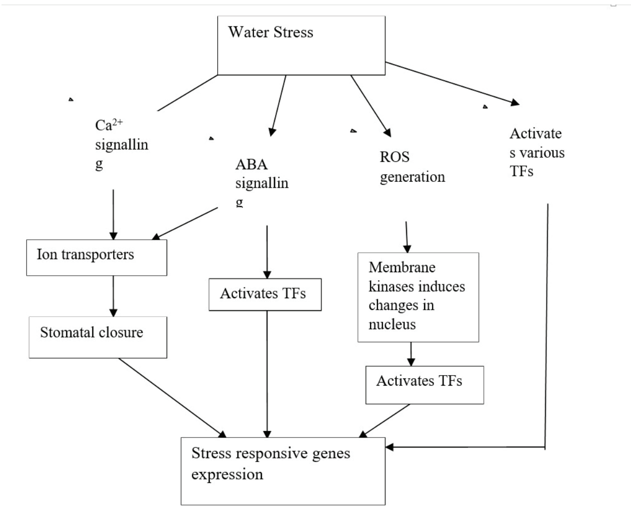

Figure 6. Role of signalling molecules in stomatal closure.

coumarins, tannins, anthocyanins and flavonoids have also been considered as essential compounds of plant acclimation in fluctuating climatic changes.[87]

5.4 Molecular Response to Water Stress

The exogenous application of ABA is responded by some water-stress-inducible genes and some do not. Recent analysis shows that these genes sometimes not needed the application of ABA in water stress and cold stress.[88] In case of Arabidopsis thaliana, 27 genes are induced and 3 genes are repressed under water stress. The induced genes are associated with metabolism, hydrophilic proteins, signalling, transcription etc.

The external stimulus for drought is perceived by sensors which activates water stress responsive genes and various pathways of signal transduction and results in drought tolerance. Calcium, ABA, ROS, transcriptional regulators, diacylglycerol and phosphoglycerol has a major role in many signal transmitting pathways. Drought stimulates synthesis of ABA in roots and moves in shoots which in turn inhibits growth via closure of stomata. The control of stomatal aperture is done by ABA through the biochemical regulation of ion and water transport processes. According to ABA dependency, water stress genes are of two type; ABA-independent and ABA dependent.89 Dehydration stimulates time variation, the expression patterns of genes and different response behaviour of plants for elevated ABA. ABA dependent transcriptional components are members of zinc finger proteins in Arabidopsis genome. Drought stress tolerance is also done by ABA-responsive elements-binding protein which increases at transcriptional and post-transcriptional level of gene expression. Several other genes in Arabidopsis are ANAC072, ANAC019 and ANAC055 synthesised during drought stress.[90]

5.5 Role of Chromatin Combating Water Stress

A few findings reveal the role of chromatin in responses to water stress. It is noticed that direct targets of signalling pathways are remodelling of chromatin and modification of enzymes. Chromatin regulator modulation activity in signalling pathways are significant in decreasing possible trade-offs flanked by growth and stress responses. Stress memory may be furthermore added by the organization of chromatin, remodelling of chromatin and modification of enzymes.[91]

5.6 Agronomic Strategies for Improving Tolerance to Water Stress

The detrimental effects in waters stress can be alleviated by means of crop management practices such as: collection of correct variety, culture practice and soil management, mulching, crop residues and irrigation. Reddy,[92] *et al.* reported that increase in soil moisture storage by soil profile management may help in quick recovery from water stress. This study was done in Arachis hypogea (L.). When silicon was applied, their photosynthetic pigments content and antioxidant activities were enhanced at par and results in increased level of gene expression which is associated with antioxidant response, biosynthesis of flavanoids and activation of ascorbate-reduced glutathione cycle.[93] The alkaline stress of maize plantlets is overcome by the priming of seed with Si.[94]

During water stress soybean yield was increased by ABA supplementation. Currently, for commercial growers, noval formulation of ABA is offered for water stress resistance and to avoid wilting symptoms.[95] Exogenous application of ABA induces the transcripts of ABFs, including ABF2/AREB1, ABF1, ABF4/AREB2 and ABF3,[96] ABA analogs and concentrated formulations of ABA are used in horticultural crops to maintain its marketability so that it can decrease symptoms of water stress. In case of miniature rose (Rose hybrida L.), the application of ABA decreases transpiration and increases longevity of flowers during spring or summer season.[97]

5.7 Exogenous Application of Substances

5.7.1 Hydrogels Supplementation

Hydrogels are considered the polymers of super absorbent capacity which can absorb significant amount of water. In agriculture, hydrogels can increase water retention capacity of soil. The naturally occurring hydrogels are chitin, pectin, carboxymethyl cellulose and cellulose. In water, hydrogels enlarge to retain water and increases the uptake of water, regulate infiltration rates, soil permeability, decreasing soil erosion, reducing irrigation frequency and decreases loss of water loss.

The hydrogel increases the plants circumference and enhances availability of water in roots of plants which infer the longer duration of irrigation. However, hydrogel application creates a reservoir of water near the plant root zone, increase the capacity of soil available water, decrease osmotic moisture of soil and increases growth, yield and production of crops.[98] Under arid and semi-arid conditions, hydrogel also increases plant viability, ventilation, root development and seed germination. It can be used as an additive with seed, plant growth regulators, biocides, herbicides, seedling root and protecting agents.[99] Hydrogel can also absorb water solubilised fertilizers and discharge at an appropriate phase of development.

5.7.2 Selection of Fertilizers

Potassium, phosphorus and Nitrogen (NPK) are considered as most important mineral elements enhancing growth and development in plants. The role of nutrients is given in Table 2.

It has also been seen that the fresh weight, dry weight, height and leaf area were all higher in treatments of higher K_2SO_4 in Brassica juncea L. under low water stress.[105] The same enhancement was seen in relative water content, membrane stability index and photosynthetic pigments with highest concentration of potassium chloride in water deficit conditions.[106]

5.7.3 Plant Growth Regulators (PGRs)

During water stress the internal level of cytokinin, auxins and gibberellins generally decreases and the content of ethylene and abscisic acid increases which results in production of endogenous auxin.[107] However, stomatal conductance and net photosynthetic rate of cotton is generally enhanced by supply of auxin in drought stress. The synthesis of Indole-3-butyric acid is enhanced by application of abscisic acid and water stress in maize. Currently, it was reported that water stress also induces indole-3-butyric acid synthetase in Arabidopsis.[108] Development of hairless, short and tuberised root is reported from brassicaceae family and related families when adaptive strategy of drought rhizogenesis was studied under progressive drought stress.

Decreased cytokinin and increased ABA favours stomatal closure in plants which in turn limits loss of water in the course of transpiration during limited water availability.[109] Increased synthesis of ABA results in wilting of plants. ABA also hampers the comparative rates of growth in plant such as formation of deeper and intensive root system, leaf area development and root-to-shoot dry weight ratio.[110]

Table 2. Role of Nutrients

Nutrients	Effect
Phosphorus	In wheat and pearl millet, shoot biomass and dry matter increased after phosphorus application under water stress conditions. It also increased shoot biomass and grain yield in sunflower.[100]
Calcium	It helps in novel cell wall synthesis in mitotic spindle during cell division and it also binds with a protein i.e. calmodulin and forms a complex which in turn activates several target proteins.[101]
Magnesium	It is a central molecule of chlorophyll and helps in energy conservation, protein synthesis, phosphor- rylation, dephosphorylation and hydrolysis of compounds.[102]
Sulphur	S is an essential component of amino acids and helps in development of vitamins, aromatic oils, enzymes and chlorophyll in various plants such as mustard.[103]
Silicon	Silicon application decreases shoot to root ratio in sorghum during water stress. Si Application improves uptake of Ba, Cr, Rb, Sr, Al, V, Cl, Mn, Cu, Fe, etc., in sunflower under water stress conditions.[104]

5.7.4 Use of Biofertilizers

In agriculture, Nikitas,[111] *et al.* investigated the exogenous application of compost and stated that it acts as conditioner for soil and can enhance yield, tolerance and resilience of crops. Generally, composts are eco-friendly and helps in increasing water retention capacity of soil, mineral nutrition and soil suppressiveness.[112] In the recent research scenario, use of strains of PGPR (Plant growth promoting rhizobacteria), exotic and native AMF along with combination of composts have been found more effective in improving crop yield under water deficit conditions. PGPR are essential bacteria required for breakage of product of plants which in turn made plants capable to withstand water scare conditions.

PGPR also produces various compounds like siderophores, deaminase enzymes and indole acetic acid[113], salicylic acid microbiocidal/biostatic enzyme and PO^{42-} solubilizing enzyme. A variety of microbes such as Rhizobium, Azotobactor, Anabaena, Acetobactor, Bradyrhizobium, Psedomonas etc. helps in nitrogen fixation.[114] These microbes infiltrates and associates with the plant body to enhance the nutrition, survival rate of plant against adverse environmental stress.

5.8 Genetic and Genomic Approaches

Genomics and genetic transformation stimulates plants to produce proteins, enzymes, biochemical compounds etc. in response to water stress. The mitigation effect of abiotic stress on plant productivity by conventional breeding has had a limited success. Generally, this complexity is connected to traits which are regulated through different genes present on different quantitative trait loci (QTL) in genome of plant.[115] But still, conventional breeding found effective in developing traits for water stress resistance in some cases. Recently, the development of 61 ILs was seen by introgressing the QTL-hotspot genomic region which contains QTLs for several water stress resistant traits.[116] Haley,[117] *et al.* found a wheat variety, Ripper which is a drought tolerant variety. This variety performed better with superior grain yields, bread-baking quality and milling capacity in non-irrigated situation. Badu-Apraku and Yallou,[118] also found maize varieties of superior yield than the varieties of control conditions which were developed in water stress.

In epigenetic, DNA structure modification can change expression of gene. Different modifications of DNA are; histones modification, non-coding RNA modification, alteration at methylation site etc. In plant breeding the variation in traits can be done by epigenetics. The modifications in epigenetics can occur at the time of prolonged stress and results in modification of expression of genes and may remain for a number of generations.[119] All experiments observed that abiotic stress and ABA results in modification of developmental programmes and profiles of expression of genes which can improve plant resistance to water stress.[120]

5.9 Transgenic and Genome editing tool

To develop resistant plant varieties and genotypes, the transgenic approaches are used to inoculate desirable and favourable characters. In water stress tolerant crops, the genetic manipulation is done by phytohormones which are potential targets. ABA hypersensitive response is caused by over expression of ABA-pathway-related TFs which helps in the water stress resistance in modified crops.108 In canola, over expression of farnesyltransferase protein was much higher during flowering period under moderate drought stress.[121] Different TFs enhances WUE, root growth and root architecture which helps in improving water stress resistance in transgenic plants of Arabidopsis and rice.[122]

Abiotic stress tolerance can be enhanced by the proper utilisation of the glyoxalase system in various plants. The over expression and upgradation of glyoxalase system may improve potential of plants to various environmental conditions.[123] In technologies of gene editing, the sequence specific nucleases are used to modify the targeted DNA sequence. In rice, some drought resistant varieties are identified by molecular mapping and breeding programmes for gaining high yield potential, a good grain quality and reducing water consumption by 50%. Major technologies in gene editing are; clustered, regularly interspaced, short palindromic repeats (CRISPR), zinc finger nucleases and transcription activator–like effector nucleases.[124]

CONCLUSION

The climatic conditions in world showing unpredictable weather pattern such as water logging, water deficit, drought, salinity, heat stress etc. During evolution, plants have evolved complex innate adaptive mechanisms to withstand diversity of environmental stresses. But all plants are not capable to combat water scare conditions. However, it has been seen that water stress resisting varieties of plants changes their response to change their molecular, physiological and biochemical mechanisms. But a single parameter may not provide the complete picture of behaviour of different varieties so minimum two or three parameters must be considered.

Therefore, it can be suggested that focus on research of target environment, genetics and physiology of plants may presents clear base for enhancing the efficacy of breeding methods to improve water stress resistant varieties. Genomics and genetic transformation has made a significant transformation in understanding the complex traits in crop plants. However, it is also important to consider models of climate change in breeding programmes. This type of outcome will help in various applications which can be used in enhancing tolerating effect of adverse environmental conditions and it will improve to the crop yield and food security. Still, there are some hidden areas in the field of water stress and there is a need of more efforts for this.

REFERENCES

1. Bradford, K. J. & Hsiao, T. C. Physiological responses to moderate water stress. *Part of the Encyclopedia of Plant Physiology book series.* 1982, (920, **12**/B). https://link.springer.com/book/10.1007/978-3-642-68150-9 (Accessed on 12 Jan 2022).
2. Briscoe, J. & Somerville, C. Genetic Engineering and Water. *Science*, 2001, **292**(5525):2217 doi: 10.1126/science.292.5525.2217.
3. Choat, B.; Jansen, S.; Brodribb, T. J.; Cochard, H.; Delzon, S. & Bhaskar, R. Global convergence in the vulnerability of forests to drought. *Nature,* 2012, **491**, 752–755. doi: 10.1038/nature11688
4. Yamaguchi-Shinozaki, K. & Shinozaki, K. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annu. Rev. Plant Biol.,* 2006, **57**, 781–803. doi: 10.1146/annurev.arplant.57.032905.105444.
5. FAO. Management of irrigated-induced salt-affected soils FAO: Rome. 2005.
6. Giordano, M.; Petropoulos, S.; Cirillo, C.; Rouphael, Y. Biochemical, Physiological, and Molecular Aspects of Ornamental Plants Adaptation to Deficit Irrigation. *Horticulturae,* **2021**, **7**, 107.
7. Osakabe, Y.; Osakabe, K.; Shinozaki, K.; Tran, L.S.P. Response of plants to water stress. *Front. Plant Sci.* 2014, **5,** 86. doi: 10.3389/fpls.2014.00086
8. Bielach, A.; Hrtyan, M.; Tognetti, V.B. Plants under stress: Involvement of auxin and cytokinin. *Int. J. Mol. Sci.* 2017, **18**, 1427. doi: 10.3390/ijms18071427.
9. Zandalinas, S.I., Fritschi, F.B., Mittler, R. Signal transduction networks during stress combination. *J. Exp. Bot.* 2020, **71**, 1734–1741. doi: 10.1093/jxb/erz486.
10. Prakash, V.; Singh, V.P.; Tripathi, D.K.; Sharma, S.; Corpas, F.J. Crosstalk between nitric oxide (NO) and abscisic acid (ABA) signalling molecules in higher plants. *Environ. Exp. Bot.*2019, **161**, 41–49. doi: 10.1016/j.envexpbot.2018.10.033.
11. Kumar, M.; Kesawat, M.S.; Ali, A.; Lee, S.C.; Gill S.S.; Kim, H.U. Integration of abscisic acid signaling with other signaling pathways in plant stress responses and development. *Plants.* 2019, **8**, 592. doi: 10.3390/plants8120592.
12. Sivamani, E.; Bahieldin, A.; Wraith, J.M. Improved biomass productivity and water use efficiency under water deficit conditions in transgenic wheat constitutively

expressing the barley *HVA1* gene. Plant Sci. **155**: 1-9, 2000.

13. Seki, M.; Narusaka M.; Abe, H. Monitoring the expression pattern of 1300 Arabidopsis genes under drought and cold stresses by using a full-length cDNA microarray. *Plant Cell* **13**, 61-72, 2001.
14. Close, T.J. Dehydrins: A commonalty in the response of plants to dehydration and low temperature. *Physiol. Plantarum* **100**, 291-296, 1997.
15. Bhargava, S., Sawant, K.: Drought stress adaptation: metabolic adjustment and regulation of gene expression. *Plant Breeding* **132**: 21-32, 2013.
16. Scippa, G.S., Di Michele, M., Onelli, E. The histone-like protein H1-S and the response of tomato leaves to water deficit. *J. Exp. Bot*. **55**: 99-109, 2004.
17. Mahajan, S., Tuteja N. Cold, salinity and drought stresses: an overview. *Arch. Biochem. Biophys.* **444**: 139-158, 2005.
18. Deeba, F.; Pandey, A.K.; Ranjan, S.; Mishra, A.; Singh, R.; Sharma, Y.K.; Shirke, P.A. & Pandey, V. Physiological and proteomic responses of cotton (*Gossypium herbaceum L.*) to drought stress. Plant Physiology and Biochemistry, 2012, **53**, 6–18. doi:10.1016/j.plaphy.2012.01.002
19. Gomes, F.P.; Oliva, M.A.; Mielke. M.S.; Almeida, A.A.F.and Aquino, L.A. Osmotic adjustment, proline accumulation and cell membrane stability in leaves of Cocos nucifera submitted to drought stress. *Scientia Horticulturae*, 2010, **126**, 379–384. doi:10.1016/j.scienta.2010.07.036
20. Gill, S.S. & Tuteja, N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry,* 2010, **48**, 909–930. doi: 10.1016/j.plaphy.2010.08.016
21. Bota, J.; Flexas J. & Medrano H. Is photosynthesis limited by decreased Rubisco activity and RuBP content under progressive waterstress*? New Phytol*, 2004, **162**, 671–681. doi: 10.1111/j1469-8137,2004.01056.x.
22. Loreto, F.; Tricoli D. & Di Marco, G. On the relationship betweenelectron transport rate and photosynthesis in leaves of the C_4 plant Sorghum bicolor exposed to water stress, temperature changes andcarbon metabolism inhibition. *Aust. J. Plant Physiol,* 1995, **22**, 885–892. doi: 10.1023/A:1006910823378
23. Parry, M.A.J.; Andralojc, P.J.; Khan, S.; Lea, P.J. & Keys, A.J. Rubisco activity: effects of drought stress. *Ann. Bot.,* 2002, **89**, 833–839. doi:10.1093/aob/mcf103.
24. Tezara, W.; Mitchell, V.J.; Driscoll S.D. & Lawlor D.W. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature*, 1999, **401,** 914–917. www.nature.com. Accessed on 12 Jan 2022.
25. Sharma, P., Jha, A. B. & Dubey, R. S. "Oxidative stress and antioxidative defense system in plants growing under abiotic Stresses," in *Handbook of Plant and Crop Stress*. M. Pessarakli, Ed., 2012, 89–138, CRC Press. doi:10.1155/2012/217037
26. Stadtman, E. R. "Oxidation of proteins by mixed-function oxidation systems: implication in protein turnover, ageing and neutrophil function,"*Trends in Biochemical Sciences*, 1986, **11**(1), 11–12. doi:10.1016/0968-0004(86)90221-5
27. Singh, N. & Kataria, N. Role of potassium fertilizer on nitrogen fixation in chickpea (*Cicer arietinum L.*) under quantified water stress. *Journal of agricultural technology*, 2012, **8**(1), 377-392. http://www.ijat-aatsea.com
28. Garg, B.K. Nutrient uptake and management under drought:nutrient-moisture interaction. Curr. *Agric., 2003*, **27**, 1–8. doi:10.1007/978-3-642-32653-0_7
29. Kataria, N. & Singh, N. Role of Potassium on Growth, Nitrogen Fixation and Biochemical Traits in [*Vigna radiata* (L.) Wilczek] under Water Stress. *Legume Research- An International Journal,* 2020. doi: 10.18805/LR-4295
30. Siddique, M.R.B.; Hamid, A. & Islam, M.S. Drought stress effects on water relations of wheat. *Bot. Bull. Acad. Sinica*, 2001, **41**, 35–3. https://www.cabdirect.org/cabdirect//20000706361
31. Nerd, A. & Nobel, P.S. Effects of drought on water relations and nonstructural carbohydrates in cladodes of *Opuntia ficus-indica*. *Physiol. Plant*., 1991, **81**, 495–500. doi:10.1111/j.1399-3054.1991.tb05090.x
32. Egilla, J.N.; Davies, Jr. F.T. & Boutton, T.W. Drought stress in-fluences leaf water content, photosynthesis, and water-use effi-ciency of *Hibiscus rosa-sinensis* at three potassium concentrations. *Photosynthetica*, 2005, **43**, 135–140 doi:10.1007/s11099-005-5140-2
33. Monclus, R.; Dreyer, E.; Villar, M.; Delmotte, F. M.; Delay, D. & Petit, J. M. Impact of drought on productivity and water use efficiency in 29 genotypes of *Populus deltoides* × *Populus nigra*. *New Phytol.,* 2006, **169,** 765–777. doi: 10.1111/j.1469-8137.2005.01630.x
34. Farooq, M.; Gogoi, N.; Barthakur, S.; Baroowa, B.; Bharadwaj, N. & Alghamdi, S. S. Drought stress in grain legumes during reproduction and grain filling. *Journal of Agronomy and Crop Science,* 2017, **203,** 81-102. doi: 10.1111/jac.12169
35. Kaya, M.D.; Okçub, G.; Ataka, M.; Çıkılı,c Y. & K o l s a r ıcıa Ö. Seed treatments to overcome salt and drought stress during germination in sunflower (*Helianthus annuus* L.). *Eur. J. Agron*., 2006**, 24**, 291–295. doi:10.1016/j.eja.2005.08.001
36. Daryanto**,** S.; Wang, L. & Jacinthe, P.A. Global Synthesis of Drought Effects on Maize and Wheat Production. *PLoS ONE,* 2016, **11**(5):e0156362. doi: 10.1371/journal.pone.0156362
37. Zeid, I.M. & Shedeed, Z.A.Response of alfalfa to putrescine treatment under drought stress. *Biol.*

Plant, 2006, **50,** 635–640. https://link.springer.com/article/10.1007/s10535-006-0099-9.

38. Gutiérrez-boem, F.H. & Thomas, G.W. Phosphorus nutrition effects in wheat response to water deficit. *Agronomy Journal*. 1998, **90**, 166-171, doi:10.1016/j.agwat.2021.106765
39. Samarah, N.H. Effects of drought stress on growth and yield of barley. *Agron. Sustain. Dev*., 2005, **25**, 145–149. doi:10.1051/agro:2004064
40. Chapman, S.C. & Edmeades, G.O. Selection improves drought tolerance in tropical maize populations II. Direct and correlated responses among secondary traits. *Crop Sci.,* 1999, **39,** 1315–1 doi:10.2135/cropsci1999.3951315x.
41. Epule, E. T.; Peng, C.; Lepage, L.; & Chen, Z. The causes, effects and challenges of Sahelian droughts: a critical review. *Reg. Environ. Change.,* 2013, **14,** 145–156. doi: 10.1007/s10113-013-0473-z44.
42. Lafitte, H.R.; Yongsheng, G.; Yan, S. & Li1, Z.K. Whole plant responses, key processes, and adaptation to drought stress: The case of rice. *J. Exp. Bot*., 2007, **58,** 169–175. doi: 10.1093/jxb/erl101
43. Jin, J.; Wang, G.; Liu, X.; Pan, X.; Herbert, S.J. & Tang, C. Interaction between phosphorus nutrition and drought on grain yield, and assimilation of phosphorus and nitrogen in two soybean ultivars differing in protein concentration in grains. *Journal of Plant Nutrition*., 2006, **9**, 1433-1449. doi: 10.1080/01904160600837089
44. Nayyar, H.; Kaur, S.; Singh, S. & Upadhyaya, H.D. Differential sensitivity of Desi (small-seeded) and Kabuli (large-seeded) chickpea genotypes to water stress during seed filling: effects on accumulation of seed reserves and yield. *J. Sci. Food Agr*., 2006**, 86**, 2076–2082. doi:10.1002/jsfa.2574
45. Venuprasad, R.; Lafitte, H.R. & Atlin, G.N. Response to direct selection for grain yield under drought stress in rice. *Crop Sci*., 2007, **47**, 285–293. doi:10.2135/cropsci2006.03.0181
46. Saneoka, H.; Moghaieb, R.E. A.; Premachandra, G.S. & Fujita, K. Nitrogen nutrition and water stress effects on cell membrane stability and leaf water relations in Agrostis palustris Huds. *Environmental and Experimental Botany*., 2004, **52**, 131-138. doi:10.1016/j.envexpbot.2004.01.011
47. Martínez, J.P.; Silva, H.; Ledent, J.F. & Pinto, M. Effect of drought stress on the osmotic adjustment, cell wall elasticity and cell volume of six cultivars of common beans (*Phaseolus vulgaris* L.). *Eur. J. Agron*., 2007**, 26**, 30–38. doi:10.1016/j.eja.2006.08.003
48. Sinaki, J.M.; Heravan, E.M.; Rad, A.H.S.; Noormohammadi, G. & Zarei, G. The effects of water deficit during growth stages of canola (*Brassica napus* L.). Am.-Euras. *J. Agri. Environ. Sci.,* 2007, **2**, 417–422. https://www.idosi.org/aejaes/jaes2(4)/17.pdf
49. Mazahery-Laghab, H.; Nouri, F. & Abianeh, H.Z. Effects of the reduction of drought stress using supplementary irrigation for sunflower (*Helianthus annuus)* in dry farming conditions. Pajouheshva-Sazandegi. *Agron. Hort*., 2003**, 59**, 81–86. http://aims.fao.org/aos/agrovoc/c_8679
50. Ogbonnaya, C.I.; Sarr, B.; Brou, C.; Diouf, O.; Diop, N.N. & Roy-Macauley, H. Selection of cowpea genotypes in hydroponics, pots, and field for drought tolerance. *Crop Sci*., 2003, **43**, 1114–1120. doi: 10.2135/cropsci2003.1114
51. Asch, F.; Dingkuhnb, M.; Sow, A. & Audebert, A. Drought-induced changes in rooting patterns and assimilate partitioning between root and shoot in upland rice, Field. *Crop. Res*., 2005, **93**, 223–236 203. doi: 10.1016/j.fcr.2004.10.002
52. Komor, E. Source physiology and assimilate transport: the interaction of sucrose metabolism, starch storage and phloem export in source leaves and the effect on sugar status in phloem. *Aust. J.Plant Physiol*., 2000, **27**, 497–505. doi:10.1071/pp99127
53. Kim, J.Y.; Mahé, A.; Brangeon, J. & Prioul, J.L. A maize vacuolur invertase, IVR2, is induced by water stress. Organ/tissue specificity and diurnal modulation of expression. *Plant Physiol.,* 2000**, 124**, 71–84 doi: 10.1104/pp.124.1.71.
54. Blokhina, O.; Virolainen, E. & Fagerstedt, K.V. Antioxidants, oxidative damage and oxygen deprivation stress: a review. *Ann. Bot*., 2003, **91**,179–194. doi: 10.1093/aob/mcf118
55. Shugaeva, N.; Vyskrebentseva, E.; Orekhova, S. & Shugaev, A. Effect of water deficit on respiration of conducting bundles in leaf petoles of sugar beet. *Russ. J. Plant Physiol*., 2007, **54,** 329–335. doi:10.1134/S1021443707030065
56. Möller, I.M. Plant mitochondria and oxidative stress: electron transport, NADPH turnover, and metabolism of reactive oxygen species. *Annu. Rev. Plant Phys*., 2001, **52**, 561–591. doi: 10.1146/annurev.arplant.52.1.561
57. Huber, A.E. & Bauerle, T.L. Long-distance plant signaling pathways in response multiple stressors: the gap in knowledge. *J. Exp. Bot*., 2016, **67**, 2063–2079. doi: 10.1093/jxb/erw099
58. Boursiac, Y.; Chen, S.; Luu, D.T.; Sorieul, M., Van den Dries, N. & Maurel, C. Early effects of salinity on water transport in Arabidopsis roots. Molecular and cellular features of aquaporin expression. *Plant Physiol*., 2005, **139**, 790–805. doi: 10.1104/pp.105.065029
59. Araus, J.L.; Slafer, G.A.; Reynolds, M.P. & Royo, C. Plant breeding and drought in C_3 cereals: what should we breed for? *Ann. Bot*., 2002, **89**, 925–940. doi: 10.1093/aob/mcf049
60. DaMatta, F.M. Exploring drought tolerance in coffee: a physiological approach with some insights for plant breeding. *Braz. J. Plant Physiol*., 2004, **16**, 1–6. doi:10.1590/S1677-04202004000100001

61. Kumar, J. & Abbo, S. Genetics of flowering time in chickpea and its bearing on productivity in the semi-arid environments. *Adv. Agron*., 2001, **72**, 107–138. URL http://oar.icrisat.org/id/eprint/5696
62. Sicher, R.C.; Timlin, D. & Bailey, B. Responses of growth and primary metabolism of water-stressed barley roots to rehydration. *J. Plant Physiol.,* 2012, **169**, 686–695. doi: 10.1016/j.jplph.2012.01.002.
63. Kavar, T.; Maras, M.; Kidric, M.; Sustar-Vozlic, J. & Meglic, V. Identification of genes involved in the response of leaves of Phaseolus vulgaris to drought stress. *Mol. Breed*., 2007, **21**, 159–172. doi:10.1007/s11032-007-9116-8
64. Richard, R.A.; Rawson, H.M. & Johnson, D.A. Glaucousness in wheat: its development, and effect on water-use efficiency, gas exchange and photosynthetic tissue temperatures. *Functional plant biology*, 1986, **13**(2), 465-473. doi:10.1071/PP9860465
65. Khan, M.S.; Kanwal, B. & Nazir, S. Metabolic engineering of the chloroplast genome reveals that the yeast ArDH gene confers enhanced tolerance to salinity and drought in plants. *Front. Plant Sci*., 2015, **6**, 725. doi: 10.3389/fpls.2015.00725
66. Lee, S.B. & Suh, M.C. Recent advances in cuticular wax biosynthesis and its regulation in Arabidopsis. *Mol. Plant*., 2013, **6**, 246–249. doi: 10.1093/mp/sss159
67. Werner, C.; Correia, O. & Beyschlag, W. Two different strategies of Mediterranean macchia plants to avoid photoinhibitory damage by excessive radiation levels during summer drought. *Acta Oecologica,* 1999, **20**, 15–23 doi:10.1016/S1146-609X(99)80011-3
68. Kramer P.J. & Boyer J.S. Water relations of Plants and Soils. Academic Press, San Diego, London, 1995. 50pp. doi:10.1016/s0176-1617(97)80106-x
69. Pannu, R.K.; Singh, D.P.; Singh, P.; Chaudhary, B.D. & Singh, V.P. Evaluation of various plant water indices for screening the genotypes of chickpea under limited water environment. *Haryana J. Agron*., 1993, **9**, 16–22. doi: doi:10.54386/jam.v9i1.1076
70. Upreti, K.K.; Murti, G.S.R. & Bhatt, R.M. Response of pea cultivars to water stress: changes in morpho-physiological characters, endogenous hormones and yield. *Veg. Sci*., 2000, **27**, 57–61. https://www.cabdirect.org/cabdirect/2001310171
71. Hasegawa, P.M.; Bressan, R.A.; Zhu, J.K. & Bohnert, H.J. Plant cellular and molecular responses to high salinity. *Annu. Rev. Plant Phys*., 2000, **51**, 463–499. doi: 10.1146/annurev.arplant.51.1.463
72. Fazeli F.; Ghorbanli M. & Niknam, V. Effect of drought on biomass,protein content, lipid peroxidation and antioxidant enzymes in two sesame cultivars. *Biol. Plant*., 2007, **51**, 98–103 doi:10.1007/s10535-007-0020-1
73. Bajji, M.; Kinet, J. & Lutts, S. The use of the electrolyte leakage method for assessing cell membrane stability as a water stress tol-erance test in durum wheat. *Plant Growth Regul*., 2002, **36,** 61–70. doi:10.1023/A:1014732714549
74. Rao, S.; Groach, R.; Singh, S. & Singh, N. Efficacy of polyethylene glycol(PEG) induced drought on germination indices and photosynthetic pigments of sweet coen va. NSC-901B. *Asian Journal of Bioscience.,* 2017**. 12**(2), 185-188. doi:10.15740/HAS/AJABS/12.2/185-188
75. Dhanda, S.S.; Sethi, G.S. & Behl, R.K. Indices of drought tolerance in wheat genotypes at early stages of plant growth. *J. Agron. Crop Sci.,* 2004, **190,** 6–12. doi:10.1111/j.1439-037X.2004.00592.x
76. Walker, J. C. & Zhang, R. Relationship of a putative receptor protein kinase from maize to the S-locus glycoproteins of Brassica. *Nature,* 1990, **345**, 743–746. doi: 10.1038/345743a0
77. Boursiac, Y.; Boudet, J.; Postaire, O.; Luu, D.T.; Tournaire-Roux, C. & Maurel, C. Stimulus-induced downregulation of root water transport involves reactive oxygen species-activated cell signalling and plasma membrane intrinsic protein internalization. *Plant J.,* 2008, **56**, 207–218. doi: 10.1111/j.1365-313X.2008.03594.x
78. Zhang, J.; Jia W.; Yang, J. & Ismail, A.M. Role of ABA in integrating plant responses to drought and salt stresses. *Field Crop Res.,* 2006, **97**, 111–119. doi:10.1016/j.fcr.2005.08.018
79. Nakashima, K. & Yamaguchi-Shinozaki, K. ABA signaling in stress-response and seed development. *Plant Cell Rep*., 2013, **32**, 959–970**.** doi: 10.1007/s00299-013-1418-1
80. Reddy, A. S.; Ali, G. S.; Celesnik, H. & Day, I. S. Coping with stresses: roles of calciumand calcium/calmodulin-regulated gene expression. *Plant Cell.,* 2011**, 23**, 2010–2032. doi: 10.1105/tpc.111.084988
81. Zlatev, Z. & Lidon, F. C. An overview on drought induced changes in plant growth, water relations and photosynthesis. *Emir. J. Food Agric*., 2012, **24**, 57–72. doi **:** doi:10.9755/ejfa.v24i1.10599
82. Hasanuzzaman, M.; Nahar, K.; Hossain, M.S.; Mahmud, J.A.; Rahman, A. & Inafuku, M. Coordinated actions of glyoxalase and antioxidant defense systems in conferring abiotic stress tolerance in plants. *Int. J. Mol. Sci*., 2017, **18**, 200. doi: 10.3390/ijms18010200
83. Shinozaki, K.; Yamaguchi-Shinozaki, K. & Seki, M. Regulatory network of gene expression in the drought and cold stress responses. *Curr. Opin. Plant Biol*., 2003, **6**, 410–417. doi: 10.1016/s1369-5266(03)00092-x
84. Corrales, A.R.; Nebauer, S.G.; Carrillo, L.; Fernández-Nohales, P.; Marqués, J. & Renau Morata, B. Characterization of tomato Cycling Dof

Factors reveals conserved and new functions in the control of flowering time and abiotic stress responses. *J. Exp. Bot*., 2014, **65**, 995–1012. doi: 10.1093/jxb/ert451

85. Arbona, V.; Manzi, M.; Ollas, Cd. & Gómez-Cadenas, A. Metabolomics as a tool to investigate abiotic stress tolerance in plants. *Int. J. Mol. Sci*., 2013, **14,** 4885–4811. doi: 10.3390/ijms1403488
86. Kaplan, F. & Guy, C.L. β-Amylase induction and the protective role of maltose during temperature shock. *Plant Physiol*., 2004, **135,** 1674–1684. doi:10.1104/pp.104.040808
87. Fraser, C. M. & Chapple, C. The phenylpropanoid pathway in Arabidopsis. *Arab. Book*., 2011, **9:**e0152. doi: 10.1199/tab.0152
88. Ingram, J. & Bartels, D. The molecular basis of dehydration tolerance in plants. *AMU Rev Plant Physiol Plant Mo1 Biol*. 1996**, 47**, 377403. doi: 10.1146/annurev.arplant.47.1.37789.
89. Kim, T.H.; Bohmer, M.; Hu, H.; Nishimura, N. & Schroeder, JI. Guard cell signal transduction network: advances in understanding abscisic acid, CO2, and Ca2+ signaling. *Annu Rev Plant Biol*., 2010, **61**, 561–591. doi: 10.1146/annurev-arplant-042809-112226
90. Tran, L.S.; Nakashima, K.; Sakuma, Y.; Simpson, S.D.; Fijita, Y.; Maruyama, K.; Fujita, M.; Seki, M.; Shinozaki, K. & Yamaguchi-Shinozaki, K. Isolation and functional analysis of Arabidosis stress inducible NAC transcriptional factors that bind to a drought responsive cis element in the early responsive to dehydration stress 1 promoter. *The plant cell*., 2004, **16**, 2481-2498. doi: 10.1105/tpc.104.022699
91. Han, S.K. & Doris, W. Role of chromatin in water stress responses in plants. *Journal of Experimental Botany*., 2014, **65**, 10, Pages 2785–2799, doi:10.1093/jxb/ert403
92. Reddy, T.Y.; Reddy, V.R. & Anbumozhi, V. Physiological responses of groundnut (*Arachis hypogeal* L.) to drought stress and its amelioration: a critical review. *Plant growth regulation.,* 2003, **41**(1), 75-88. doi:10.1023/A:1027353430164
93. Ma, D.; Sun, D.; Wang, C.; Qin, H.; Ding, H. & Li, Y. Silicon application alleviates drought stress in wheat through transcriptional regulation of multiple antioxidant defense pathways. *J. Plant Growth Regul.,* 2016, **35**, 1–10. doi:10.1007/s00344-015-9500-2
94. Latef, A.A. & Tran, L-S.P. Impacts of priming with silicon on the growth and tolerance of maize plants to alkaline stress. *Front Plant Sci.,* 2016, **7,** 243. doi:10.3389/fpls.2016.00243
95. Barrett, J. & Campbell, C. S-ABA: Developing a new tool for the big grower. *Big Grower.,* 2006, **1**, 26–29. doi:
doi:10.21273/HORTSCI.45.3.409
96. Choi, H.; Hong, J.; Ha, J.; Kang, J. & Kim, S.Y. ABFs, a family of ABA-responsive element binding factors. *J. Biol. Chem.,* 2000, **275**, 1723– 1730. doi: 10.1074/jbc.275.3.1723
97. Monteiro, J. A.; Nell, T.A. & Barrett, J.E. Postproduction of potted miniature rose: flower respiration and single flower longevity. *J. Amer. Soc. Hort. Sci.,* 2001, **126**, 134–139. doi:10.21273/JASHS.126.1.134
98. Helalia, A.M. & Letey, J. Effects of different polymer on seedling emergence, aggregate stability and crust hardiness. *Soil Science*, 1989, **148**(3), 199– 203. https://eurekamag.com/research/007/272/007272847.php
99. Abd EI-Rehirn, H.A.; Hegazy, E.S.A. & Abd El-Mohdy, H.L. Radiation synthesis of hydrogels to enhance sandy soils water retention and increase performance. *J Appl. Polym. Sci*., 2004, **93**(3), 1360–1371. doi:10.1002/app.20571
100. Faye, I.; Diouf, O.; Guissé, A.; Sène, M. & Diallo, N. Characterizing root responses to low phosphorus in pearl millet [Pennisetum glaucum (L.) R. Br.]. *Agronomy Journal*, 2006, **98,** 1187-1194. doi:10.2134/agronj2005.0197
101. Shao, H.B.; Song, W.Y. & Chu, L.Y. Advances of calcium signals involved in plant anti-drought. *Comptes Rendus Biologies*, 2008, **331**, 587-596. doi:10.1016/j.crvi.2008.03.012
102. Amtmann, A. & Blatt, M.R. Regulation of macronutrient transport. *New Phytologist*, 2009, **181**, 35-52. doi: 10.1111/j.1469-8137.2008.02666.x
103. Itanna, F. Sulfur distribution in five Ethiopian Rift Valley soils under humid and semi-arid climate. *J Arid Environ*., 2005, **62**, 597–612. doi:10.1016/j.jaridenv.2005.01.010
104. Hattori, T.; Inanaga, S.; Araki, H.; An P.; Morita, S.; Luxová, M. & Lux, A. Application of Silicon Enhanced Drought Tolerance in Sorghum bicolor. *Physiologia Plantarum*, 2005**, 123**, 459-466. doi:10.1111/j.1399-3054.2005.00481.x
105. Rani, P.; Saini, I.; Singh, N.; Kaushik, P.; Wijaya, L.; Al-Barty, A. & Darwish, H. Effect of potassium fertilizer on the growth, physiological parameters, and water status of *Brassica juncea* cultivars under different irrigation regimes. *Plos One,* 2021, **16**(9): e0257023. doi:10.1371/journal.pone.0257023
106. Meenakshi, Rani, P & Singh N. Growth, Water Relations And Chlorophyll Enhancement By Potassium Application In Intercropping System Of Gossypium Hirsutum L. And Cajanus Cajan (L.) Millsp. Under Different Irrigation Regimes. Journal of Pharmaceutical Negative Results, 2022, **13**, 9, 3329-3336. doi: 10.47750/pnr.2022,13.S09.415.
107. Nilsen, E.T. & Orcutte, D.M. Physiology of Plant under Stress: Abiotic Factors. John Wiley and Sons, New York. 1996, 183–198p.
108. Ludwig-Müller J. Indole-3-butyric acid synthesis in ecotypes and mutants of *Arabidopsis thaliana* under different growth conditions. *J. Plant Physiol*., 2007, **164**, 47–59.

doi: 10.1016/j.jplph.2005.10.008

109. Morgan, P.W. Effects of abiotic stresses on plant hormone systems, in: Stress Responses in plants: adaptation and acclimation mechanisms. *Wiley-Liss., Inc*. 1990, 113–146. doi: 10.1186/1471-2229-11-163
110. Sharp, R.E.; Wu, Y.; Voetberg, G.S.; Soab, I.N. & LeNoble, M.E. Confirmation that abscisic acid accumulation is required for maize primary root elongation at low water potentials. *J. Exp. Bot.,* 1994, **45,** 1743–1751. doi:10.1093/jxb/45.Special_Issue.1743
111. Nikitas, C.; Pocock, R.; Toleman, I. and Gilbert, E. J. *The State of Composting and Biological Waste Treatment in the UK 2005/06. Wellingborough: The composting Association for organic cycling.* 2008. doi:10.3389/fpls.2020.516818
112. Luciens, N.K.; Yannick, U.S.; Yambayamba, K.; Michel, M.M. & Louis, B. Amélioration des propriétés physiques et chimiques du sol sous l'apport combiné des biodéchets et des engrais minéraux et influence sur le comportement du maïs (*Zea mays* L. variété Unilu). *J. Appl. Biosci.,* 2014, 6121–6130. doi:10.4314/JAB.V74I1.7
113. Saleem, A.R.; Bangash, N.; Mahmood, T.; Khalid, A.; Centritto, M. & Siddique, M.T. Rhizobacteria capable of producing ACC deaminase promote growth of velvet bean (*Mucuna pruriens*) under water stress condition. *Int. J. Agric. Biol.,* 2015, **17,** 663–667 doi: 10.17957/IJAB/17.3.14.788
114. Attitalla, I.H. Traits biologically interacting *Azospirillum lipoferum* strain R_{23}. *Adv Biol Res*., **6**(2), 87–94. doi: 10.1007/s00253-018-9214-z
115. Parmar, N.; Singh, K.H.; Sharma, D.; Singh, L.; Kumar, P. & Nanjundan, J. Genetic engineering strategies for biotic and abiotic stress tolerance and quality enhancement in horticultural crops: a comprehensive review. *3 Biotech*., 2017, **7**, 239. doi: 10.1007/s13205-017-0870-y
116. Bhardwaj, C.; Tripathi, S.; Sorean, K.R.; Thudi, M.; Singh, R.K.; Sheoran, S.; Roorkiwal, M.; Patil, B.S.; Chitikineni, A.; Palakurti, R.; Vemula, A.; Rathore, A.; Kumar, Y.; Chaturvedi, S.K.; Mondal, B.; P.S., Srivastava, A.K.; Dixit, G. P.; Singh, N. P. & Varshney, R.K. Introgression of "*QTL-hotspot*" region enhances drought tolerance and grain yield in three elite chickpea cultivars. *The plant genome,* 2021, **14**(1). doi:10.1002/tpg2.20076
117. Haley, S.D.; Johnson, J.J.; Peairs, F.B.; Quick, J.S.; Stromberger, J. A. & Clayshulte, S. R. Registration of "Ripper" wheat. *J. Plant Reg*., 2007, **1,** 1–6. doi: 10.3198/jpr2006.10.0689crc
118. Badu-Apraku, B. & Yallou, C.G. Registration of-resistant and drought-tolerant tropical early maize populations TZE-W Pop DT STR C and TZE-Y Pop DT STR C. *J. Plant Registr.,* 2009**, 3**, 86–90. doi: 10.3198/jpr2008.06.0356crg
119. Boyko, A. & Kovalchuk, I. Epigenetic control of plant stress response. *Environ. Mol. Mutagen,* 2008, **49**, 61–72. doi: 10.1002/em.20347
120. Abe, H.; Urao, T.; Ito, T.; Seki, M.; Shinozaki, K. & Yamaguchi-Shinozaki, K. Arabidopsis AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. *Plant Cell,* 2003, **15**, 63–78. doi: 10.1105/tpc.006130
121. Wang, Y.; Ying, J.; Kuzma, M.; Chalifoux, M.; Sample, A. & McArthur, C. Molecular tailoring of farnesylation for plant drought tolerance and yield protection. *Plant J.,* 2005, **43**, 413–424. doi: 10.1111/j.1365-313X.2005.02463.x
122. Redillas, M. C.; Jeong, J. S.; Kim, Y. S.; Jung, H.; Bang, S. W. & Choi, Y. D. The overexpression of OsNAC9 alters the root architecture of rice plants enhancing drought resistance and grain yield under field conditions. *Plant Biotechnol. J*., 2012, **10**, 792–805. doi:10.1111/j.1467-7652.2012.00697.x
123. Alvarez-Gerding, X.; Cortes-Bullemore, R.; Medina, C. & Romero-Romero, J.L. Inostroza-Blancheteau, C. & Aquea, F. Improved salinity tolerance in Carrizo citrange rootstock through overexpression of glyoxalase system genes. *BioMed Research International,* 2015, 1-7. doi: 10.1155/2015/827951
124. Voytas, D.F. Plant genome engineering with sequence-specific nucleases. *Annu. Rev. Plant Biol*., 2013, **64**, 327–350. doi: 10.1146/annurev-arplant-042811-105552

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