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Recent advances in understanding the morpho-physiological and biochemical mechanisms in crop plants towards drought stress

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Abstract
Global warming and consequently a storm of drought stress due to anthropogenic activities in recent past and present greatly affect the growth and development of sessile plants. Drought is one of the most adverse factors and severe threat for sustainable crop production and productivity. It triggers a wide variety of plant responses at various morpho-physiological, biochemicals or even at molecular levels. However, plants have developed several mechanisms at different levels to cope up with and adapt against such abiotic stress that imposed frequently. Understanding the complex interactions or crosstalk of morpho-physiologiacl and biochemical responses to drought is therefore utmost essential for a holistic perception of plant tolerance towards moisture-limited conditions. In this context, an attempt has been made to focus on their responses, ability and strategies of crop plants to resist and adapt towards drought stress.

Keywords: Drought stress, global warming, morpho-physiological and biochemical mechanisms, adaptations/tolerance

1. Introduction

Drought an adverse situation resulting from plant exposure to sub or supra- optimal levels of water that generally leads to reduction on CO_2 assimilation rate due to decrease in stomatal conductance, membrane damage, disturbance in various enzymatic activities (especially involved in ATP synthesis) and ultimately reduced in crop growth and yield. It is considered as one of the single most devastating abiotic stresses that reduce crop production much more than any other stresses (Lambers *et al*. 2008). Stress is an altered physiological condition caused by biotic and abiotic factors that tend to disrupt the equilibrium. Strain is the resultant of stress at physical or chemical level (Gaspar *et al*., 2002) [17]. Drought impairs normal growth by reducing normal rate of cell division and expansion; reducing leaf size, stem elongation/extension and root proliferation; disturbing stomatal oscillations, plant water relations and nutrient assimilation, disrupts photosynthetic pigments and reducing gas exchange; reducing water use efficiency in plants and ultimately diminished crop growth and productivity (Li *et al*., 2009; Farooq *et al*., 2009a) [15]. Drought tolerance is the ability of a crop plants to grow and reproduce satisfactorily under limited water supply and tolerance mechanism involved with strategies like resistance mechanism (ability to survive under dehydrated conditions) and avoidance mechanism (growth that prevent plant exposure towards osmotic stress like development of deep rooting or complete crop cycle within a short period).Hereby, to withstand or cope with the drought stress it is crucial to determine as well as understanding the morpho-physiological, biochemical plant and molecular signaling pathways responsible for developing drought tolerance in plants. As a whole, plants displays a wide range of physio-biochemical mechanisms that leads to adaptive changes like changes in plant structure, growth rate, tissue osmotic potential and antioxidative defenses mechanism leads to acclimatize them to water deficit stress (Dual *et al*., 2007). In general, plants can develop mechanisms like reduce water loss by increasing diffusive resistance, increased water uptake by developing with a prolific and deep root system, reduce leaf size and succulent leaves to minimize transpirational water loss, improve relative water content and stomatal regulation, accumulation of low molecular osmolytes (glycine betaine, proline and other amino acids, organic acids and polyols etc) for sustaining cellular functions, accumulation of hormones such as abscisic acid, salicylic acid, ethylene, jasmonic acid etc and generation of active oxygen species for developing antioxidative defense systems. The sensing of such stresses induces multiple pathways of cellular signaling cascades that activate ion channels, kinase cascades, production of ROS (Reactive Oxygen Species) have complex interactions or crosstalk ultimately induce expression of sub-sets of defense genes leads to the assembly of the overall defense reaction.

Therefore, proper-understanding the effects of drought on plants and their mopho-physiological as well as biochemical adaptations are crucial (Yamaguchi-Shinozaki and Shinozaki 2006) [49]. This article attempted to provide a current understanding of morpho-physiological and biochemical strategies build up for improving drought tolerance in field crops.

2. Morpho-physiological aspects and mechanisms of drought stress: When plant is subjected to drought, it goes through a cascade of metabolic alterations started with progressive decrease in photosynthetic pigmentation and thereby decline in photosynthesis rate. Progressive increase in water stress cause several responses *viz*. decrease in leaf expansion and leaf number, decrease in root-shoot ration, decrease chlorophyll a/b and carotenoids, decrease in leaf internal CO2 and CO2 assimilation in leaves, lower tissue water potential, increased photorespiration, obstructed ATP synthesis, lower RUBISCO activity, incidence of disease, pests, disturbs the plant water relations, limits the mineral uptake and assimilation, oxidative damage to chloroplast and limited carboxylation, reduce transpiration, develop the epinasty/hyponasty effects (O'Toole and Cruz, 1980), and ultimately decrease in photosynthetic rates and biomass production (Sangtarash *et al*., 2009, Leach *et al*., 2011 and Maes *et al*., 2009) [38, 23, 28].

Different morpho-physiological traits *viz*. osmolytes accumulation and osmotic adjustment, phenotypic plasticity and turgor maintenance, cell membrane stability, stomatal conductance, production of phytohormone especially ABA etc have so far been identified and exhibited a positive correlation with drought tolerance in plants. Though crop plants have four kinds of strategies against water deficit stress such as drought avoidance, drought escape, drought tolerance and drought recovery (Fang and Xiong, 2015) [13], but drought tolerance is the major strategies towards drought stress.

Such drought tolerance is a complex phenomenon involved with cuticle thickness, stomatal regulation, well-developed deep rooted system, hormonal balance and regulation, maintenance of tissue water potential, osmotic adjustment and antioxidant defense system etc. When a genotype has the ability to produce higher biomass and grain yield as compared to others against drought stress is denoted as truly drought resistant (Fukai and Cooper 1995; Kilic and Yag˘basanlar 2010) [16, 21].

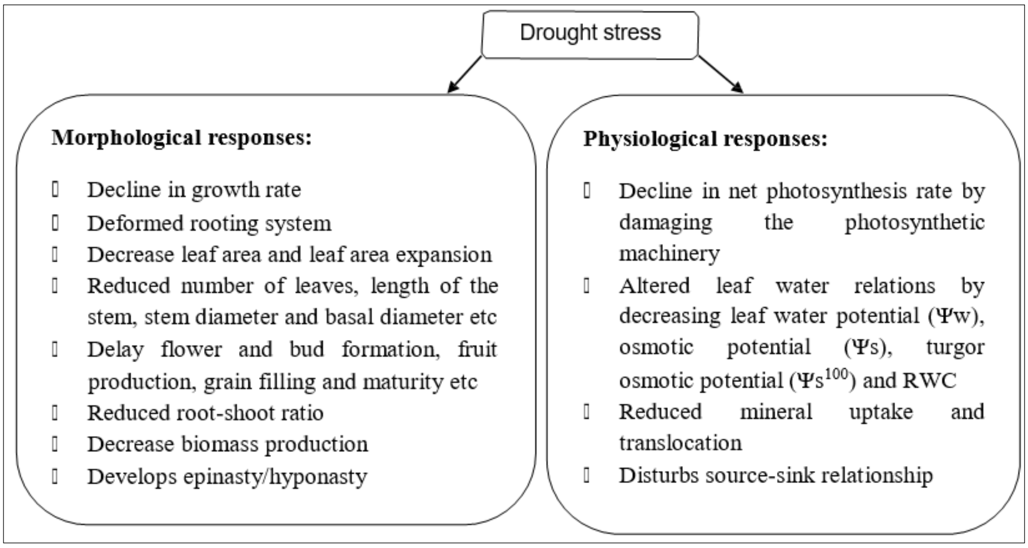

Fig 1: Some morphological, physiological responses in plants exposed to drought stress.

2.1 Plant water relations and Water Use Efficiency (WUE): Majors aspects of plant water relations includes leaf water potential, Relative Water Content (RWC), osmotic potential, pressure potential and transpiration loss/ transpiration efficiency etc are significantly affects the plant growth under moisture stress (Kirkham, 2005) [22]. Leaf water potential interacts with stomatal conductance and maintains a positive correlation between leaf water status and stomatal conductance under drought stress. There is a positive correlation between higher WUE and total biomass under drought results superior yield performance.

WUE is often equated with drought resistance and thus improved crop production under stress (Blum, 2005) [4] and it is essential to maximize WUE under extreme shortage of water i.e. grow more crops per drop (Vadez *et al*., 2011) [45]. It can be improved significantly by reduced soil evaporation by using relevant genotypes and agronomic practices during winter and minimize in spring that observed in Australia (Siddique *et al*., 2001) [41]. Thus, understanding on the physiological basis for stomatal regulation and improved WUE in drought-stressed plants is required (Liu *et al*. 2005a). Drought effect also depends on the different genotypes, duration and intensity of drought and drought- tolerant genotypes maintained a higher leaf water potential for longer and wilted later than sensitive genotypes under drought (Ouvrard *et al*. 1996) [32].

2.2 Phenotypic plasticity and drought avoidance
Morphological traits like leaf size, shape and length of the stem etc shows variation when grow in varied environment conditions and this type of variation is known as phenotypic plasticity. It denotes the range of phenotypes that an organism

can express its phenotypic characters as well as function of its environment (Schlichting, 1986) and such varied environment is the resultant component of the genotypes by environment interaction. Avoidance towards drought is the ability of a plant to sustain high water potential or cellular hydration where the plant shows the mechanism either by absorbing more water or by minimizing transpirational water loss (Blum, 2005) [4] or by maintaining higher root-shoot ratios with fewer and smaller leaves or reduced leaf size and reduced biomass.

Root plasticity is one of the drought avoidance mechanisms that is the ability of a genotype to regulate its root growth pattern (Yamauchi *et al*. 1996) [50] and root proliferation, root length or more rooting depth causes etc are considered as drought avoidance traits to fetch more water (Matsui and Singh 2003; Wang and Yamauchi 2006).

2.3 Phenological and anatomical changes under drought

Several phonological *viz*. days to flowering, pod formation, days to maturity, growth of primary and secondary branches per plant, plant height etc and anatomical or architectural changes both at tissue or cellular level as well as at the sub-cellular level *viz*. reduced cell size and damaged cells, larger xylem vessels, increased stomatal and trichomatous densities, closure stomata and curtailed water loss, deformation of chloroplast and stromal lamellae shape etc occurs when exposed to mild or severe drought.

Zhang *et al.*, 2005 [51] observed the main anatomical modifications at the sub-cellular level are in the shape of the chloroplasts, swelling of stromal lamellae, clumy vacuoles that change the structural organization of thylakoids and form antenna depleted PS II and thus results in reduced photosynthetic and respiratory activities. Drought adaptation in crop is a complex interaction of phenology with the pattern of water use efficiency (Sekhon *et al*., 2010; Wahid *et al*., 2007) [40, 46] and limited shoot growth followed by a decreased number of tillers under moisture stress is consider as a strategy to reduce water use (El Soda *et al*., 2010) [11].

As a whole, short-duration crop generally shows better performance than long-duration crops grown under drought stress due to their well-developed root system (Singh *et.al.*, 2010) [42] and reduced plant size and decreased stomatal conductance may be responsible for reduced crop yields and productivity (Deikman *et al*., 2012) [9].

2.4 Phytohormone-mediated stimulus perception and signal transduction mechanisms of drought tolerance: Drought stress alters the endogenous synthesis of phytohormones and their balance that includes increased ABA, a small decline in IAA and GA, decrease in cytokinin contents. Drought stress results signal transduction induced by the generation of different constituents including phytohormones to adapt under stress. The concentration of growth retardants increases at the expanse of growth promoters to regulate limited water budget in plants (Farooq *et al*. 2009a) [15].

Among these, ABA plays an important role in drought tolerance by triggering diverse signaling mechanisms (Bücker-Neto *et al*., 2017) [5] and elevated ABA concentrations in plant organs leads to several physiological changes like stimulation of stomatal movement, develops root architecture and regulate photosynthesis etc to modulate plant growth under water stress conditions. In roots, high accumulations of ABA under stress send the signals to the leaves for inducing stomatal closure and avoid transpiratory water loss (Davies and Zhang 1991) [7]. Furthermore, a high accumulation of ABA in guard cells induces a signals that results K+ outflow in the guard cells and reduced turgor pressure that ultimately cause stomatal closure (Lim *et al*., 2015 and Salazar *et al*., 2015) [26, 37]. Some of the ABA-induced genes that encodes dehydrins protein and phospholipids signaling enzymes, ROS-detoxifying enzymes etc for improving drought tolerance in plants (Fahad t. al., 2019). Such higher level of ABA under drought can able to build up drought tolerance in wheat by improving stem lengths, increasing plant biomass and declining the level of H2O2 and malondialdehyde (MDA) as suggested by Wei *et al*., 2015 [48].

Auxin play an important role in improving drought tolerance as it is the main classical hormone that involved in the development of plant roots (Saini *et al*. 2013) and thus under moisture stress, the level of auxin increases to defend against drought (Llanes *et al*. 2016) [27]. In *Arabidopsis*, drought stress promoted *YUC7* gene in roots and increased free auxin level causes development of root architecture. Such *YUC7-1D* gene in plant exhibits drought resistant and regulate drought responsive genes (Lee *et al*. 2012) [24]. Ethylene also contributes in drought tolerance by altering several mechanisms and in association with ABA and JA through a member of Ethylene Response Factors (ERFs) [Müller and Munné-Bosch 2015] [30].

Cytokinin contributes several drought tolerance mechanisms by protecting chloroplasts from oxidative damage, regulate water balance and growth, induce antioxidative substances and regulate stress related hormones especially in association with ABA. Cytokinins also modulate plant response towards drought via root-shoot signals in plants (Rivero *et al*. 2007) [33] and Salicylic acid (SA) is involved in plant drought tolerance by regulating several physiological processes through signaling that regulate drought-induced leaf senescence in perennials (Abreu and Munne-Bosch 2008) [2]. Cytokinins also regulated the genes that involved in CO2 assimilation, photosynthetic rate and electron transport and chlorophyll levels (Sahebi *et al*. 2018) [35]. Jasmonic acid (JA) and its methyl esters are seems to play role in the biosynthesis of ABA and also induces drought tolerance by stimulating root growth, decreasing ROS level and promoting stomatal closure (Ullah *et al*., 2018) [44]. Drought stress causes an increase in JA concentration with the subsequent increase in ABA concentration and this is possibly due to that JA act as the signal transduction cascade during drought stress (De Ollas *et al*., 2012) [8].

2.5 Osmotic adjustment and membrane stability: Plant accumulates different types of organic and inorganic solutes in the cytosol to maintain cell turgidity and such accumulation of osmolytes is a prerequisite for osmotic adjustment under stress (Zhang *et al*., 2009) [52]. Osmotic adjustment is one of the adaptive strategies of the plants under stress that attains by accumulation of proline, sucrose, soluble carbohydrate, glycine betaine, free amino acids and organic acids, other solutes and inorganic ions of sodium, potassium, calcium and chloride etc in the cytoplasm by improving the water uptake from dry soils for maintaining the cell turgor (essential for cell viability as well as for elongating cells and stomata). This type of adjustment assists the plant to get rid of ion toxicity

and water uptake for turgor maintenance under stress (Abdelmalek and Khaled, 2011; Chen and Jiang, 2010) [1, 6].
Stability of cell membrane is another strategy that used as indicator of drought tolerance and the rate of injury to the cell membrane can be assessed by measuring electrolytic leakages from the cell (Blum and Ebercon, 1981) [3]. Shafeeq and Zafar, 2006 observed that some wheat genotypes have been maintained higher cell membrane stability (CMS) at about 70-80% that performed better adaptation under drought.

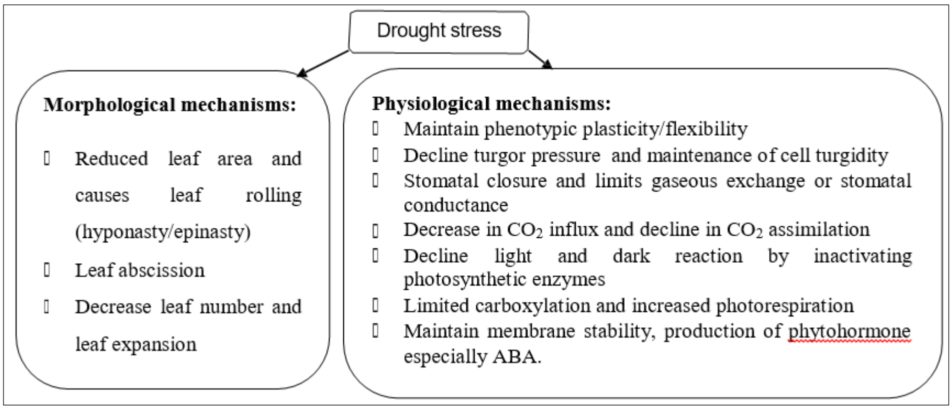

Fig 2: Possible physiological and morphological strategies for drought tolerance in plants.

3. Biochemical strategies for drought adaptations/tolerance: Plant exhibits several adaptive mechanisms including long-term evolutionary morpho-physiological adaptations and short-term adaptations mechanisms includes changing leaf orientation, transpirational cooling, and or alteration of membrane compositions etc under drought stress (Hasanuzzaman *et al*., 2011) [19]. Drought avoidance and tolerance are the two main strategies of the plants for their survival under drought and plants have also adopted several strategies for developing drought tolerance by mobilizing various defense mechanisms as well as altering their physio-biochemical metabolism and growth pattern (Mittler, 2002) [29].
Some major tolerance mechanisms includes ion transporters, late embryogenesis abundant (LEA) proteins, osmoprotectants, antioxidative defensive system and different factors involves in signaling cascades and transcriptional control etc significantly counteract with stress (Rodríguez *et al*., 2005; Wang *et al*., 2004) [34, 47].
Phytohormones and their regulations, synthesis of secondary metabolites and primary metabolites like carbohydrates, amino acid and polyamines play important roles in developing stress tolerance towards drought by improving osmoregulation, stabilize cell membrane, scavenging ROS etc at the biochemical level (El Shabag *et al*., 2019).

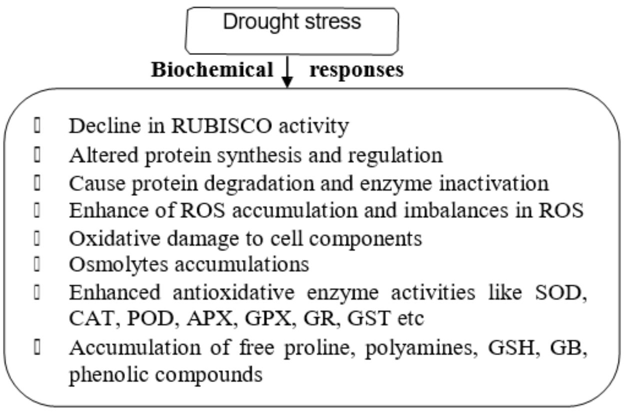

Fig 3: Biochemical responses in plants under drought stress.

3.1 ROS (Reactive Oxygen Species): When plants are exposed to drought, there is generation of ROS (Reactive Oxygen Species) or Reactive Oxygen Intermediate (ROI) or Active Oxygen Species (AOS) *viz*. hydroxyl radical (HO•), hydrogen peroxide (H2O2), singlet oxygen (1O2), super oxide anion radical (O2-) and alkoxy radical (RO) due to incomplete reduction of atmospheric oxygen and such ROS causes oxidative damage to various cell components like protein (degradation), lipids (peroxidation) and nucleic acids (fragmentation) etc (Ullah *et al*. 2018a) [43] and impairs normal metabolic functions of the cell or ultimately leads to death.
Drought stress leads to spontaneous generation of ROS in the cell enzymatically through the action of soluble membrane-bound enzymes and non-enzymatically by auto-oxidation reactions. ROS generation (oxidative collapse) is an earliest biochemical defense response occurs under drought that acts as secondary messenger to trigger subsequent defense reactions in plants. Some of the ROS are physiologically useful like SOD (Super oxide dismutase) but they may dreadful when presence in excess or inappropriate amounts.

3.2 Antioxidative defense mechanisms

As the ROS is extremely reactive and its excess amounts may leads to oxidative damage in plants and prolonged stress increases the ROS in the cell components like cell wall, membrane, chloroplast, mitochondria, peroxisomes and nucleus (Gill and Tuteja 2010) [18]. When such situation arises, an efficient, prompt antioxidant defense system is developed in plants to provide drought tolerance (Hussain *et al*., 2019) [10]. This mechanistic system of defense involves both enzymatic [superoxide dismutase (SOD), peroxidase (POD/POX), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX), guaicol peroxidase (GOPX), glutathione-S-transferase (GST)] and non-enzymatic [ascorbic acid, glutathione (GSH), phenolic compounds, alkaloids, non-protein amino acids, carotenoid, tocopherols, thioredoxin, poly amines (PAs), salicylates (SAs), vitamin E, compatible solutes such as proline, GB and zeaxanthin etc] detoxification moieties that lessen or repair the injuries triggered by ROS and develop the drought tolerance in plants.

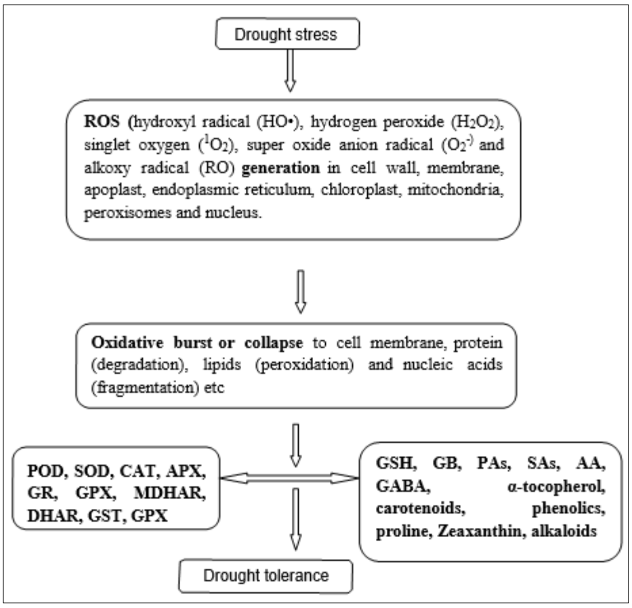

Fig 4: ROS generation and their scavenging through antioxidative defense mechanism in plants.

4. Conclusions and future projections

Drought is globally an adverse growth limiting factors that alters morphology, physiology and metabolism in plants. However, duration, severity, pattern of growth, crop species and environments etc are undoubtedly important factors in determining how a plant responds to water deficit and may improve their level of tolerance at cell, organs and entire plant level. Protective mechanisms at the leaf level, prevent photosynthetic machinery, scavenging ROS by enzymatic and non-enzymatic processes, maintenance of cell membrane stability and integrity, usage of precise plant genotypes, exogenous application of growth regulators, stimulus perception and signal transduction, production of key osmolytes or osmoprotectants (proline GB, amino acids and sugars etc) and other compatible solutes and secondary metabolites, expression of aquaporins and stress-related proteins (LEA) are vital to improve the level of drought tolerance in plants.

Level of phytohormone and their regulation in plants are generally increase upon drought stimulus that leads to activation of several signal transduction pathways and other biochemical pathways includes MAPK signaling pathway, calcium signaling pathway, regulation of transcription factors in plants to mitigate the drought stress. Recently plant scientists are trying to improve the level of drought tolerance mechanisms via exogenous application of compounds (NO, 2,4-epibrassinolide, proline, GB), plant breeding and crop improvement, transgenic approaches to generate transgenic plants.

Thus, the aim of the current understanding was to aggregate the morp-physiological (leaf structure, root development and stomatal regulation) metabolic processes (phytotohormone regulation, osmotic regulation, ROS scavenging and developing antioxidative defense system etc) to further improve drought tolerance level. The combined knowledge of traditional breeding along with marker assisted selections as well as application of various modern omics tools like genomics, proteomics, metabolomics, ionomics, transcriptomics, bioinformatics etc to engineer plant stress tolerance and makes the plants to induce drought tolerance in crop plants to enhance and sustain the crop productivity in drought-prone environments.

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