

DROUGHT STRESS IN CROP PLANTS: PHYSIOLOGICAL ASPECTS

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ABSTRACT

Drought is the most serious stress which limits agricultural growth and its development and further leads to a great risk to the world food-security. Drought related stress mainly occurs in arid and semiarid regions, in the conditions of shortage of rainfall, intense temperature fluctuation, salinity, high intense light. The dry spell of weather over a certain period may lead to the conditions of drought stress in plants which adversely distress the plant-development and total yield of the plants. Plants have developed different morphological, biochemical and physiological response mechanisms to cope with these environmental stresses but are different in different species of the plants. Plants response to drought stress by a various mechanism like an escape, avoidance, tolerance, use of growth regulators and some molecules which helps them to survive under high and low temperature. In this review, we study the effect, mechanism and management of drought stress in plants. Here, we discuss various morphological, physiological and biochemical mechanisms which help to tolerate the drought stress in plants and promote them to grow and perform functions in drought stress conditions.

Keywords: Agriculture, Biochemical, Drought, Environment, Growth regulators, Tolerance.

INTRODUCTION

Plants are generally bare to different environmental adversities during varying weather and different climatic conditions under natural and agricultural influences. Various environmental stresses such as heat, cold, drought, high and low temperature, salinity, chilling, freezing, molecular stress affect the plants from seed germination to seed maturity. It plays a very essential part in most phases of plant growth, development, metabolism, biochemical activities etc. (Hirt and Shinozaki, 2004). In the present scenario, water stress is the main environmental stress for the plants. Drought stress is most damaging among all environmental stresses which affect the plant growth, inhibits crop production and distribution worldwide especially in arid and semiarid areas (Madhava *et.al.*2006). In the next decades, as a continuous increase in the dry periods or high temperature is going on, it is predicted that there is a drastically great increase in the drought conditions (IPCC, 2007). Drought stress adversely affects plant growth and limits its total yield potential. It inhibits the growth of the plant, decrease photosynthetic activity, damage organelle structure and function, degrade chlorophyll

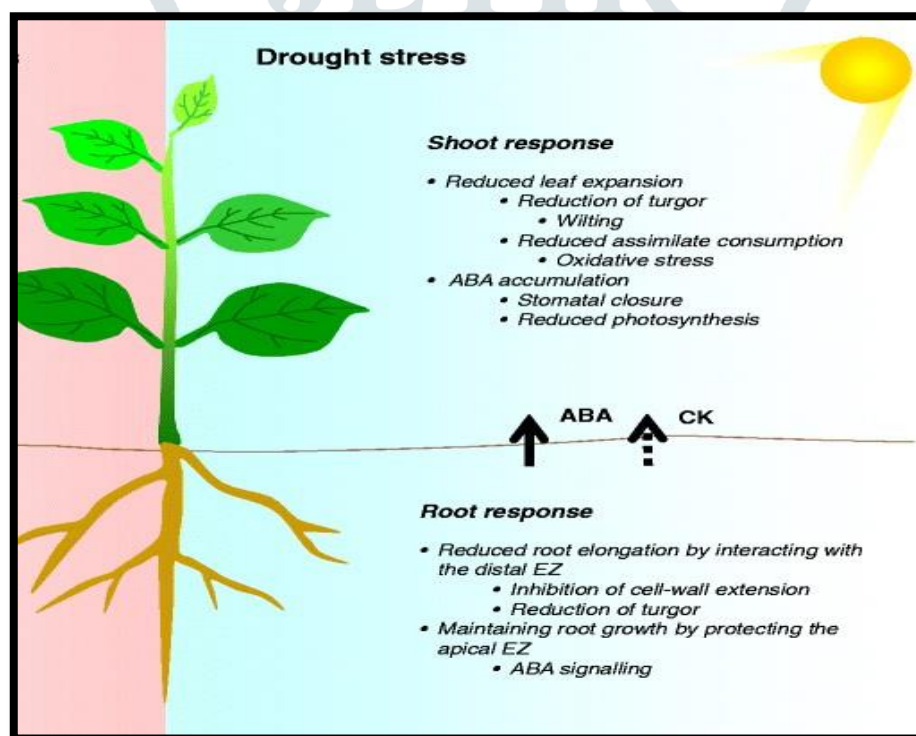
content, include water loss in the leaves and accelerate the ageing process in the early stages of the plant (Munne-Bosch et al., 2001; Lei et al., 2006; Xiao et al., 2009). Drought factor induces oxidative stresses which is the direct results of the accumulation of reactive-oxygen species (ROS) in the plant cells (Munne-Bosch et al., 2001; Xiao et al., 2009; Lipiec et al., 2013). The main target of reactive oxygen species (ROS) is membrane phospholipids which prevent membrane damage and increase its permeability also influence the peroxidation of lipids (Sharma et al., 2012). However, almost all the plants have a drought stress tolerance in various capability depending on species type. The drought stress in plants can be mitigated by different strategies. Plants use various mechanism to tolerate drought stress. The ability to withstand drought up to a certain extent. Certain molecules, proteins and growth regulators serve as osmolytes to protect the structure and functioning of cellular components inside the cell membrane. Molecules like Melatonin regulates different biochemical, physiological, and molecular processes in the plants and further aid the plant to deal with the drought-stress or to survive under drought-stress situation. Drought stress is obtained to be an ordinary decline in water, which causes stomatal closure and limits the gaseous exchange in the plant species. Dehydration is much more which can promote the degradation of metabolism and cell structure. To develop or make a new variety of crops having a good productivity under water-stress conditions needs a better understanding of plant physiological and v changes is required. To understand the plant response towards drought is one of the most important and fundamental parts to make the plants stress-tolerant. Plants can perform various mechanism like drought escape and drought-avoidance and drought-tolerance in response to drought-stress (Levitt, 1980; Price et al., 2002). Drought escape is defined as the ability of the plants to complete their life cycle before the entrance of severe stress. Drought avoidance is described as maintaining high water potential in the tissue instead of soil water deficit. Drought tolerance is the ability of the plant to perform functions in tolerating the drought-stress.

DROUGHT STRESS PLANT PHYSIOLOGY

Under drought stress, plants face many challenges in the physiochemical and molecular functioning of the plants which can eventually upset the growth, development and yield quality of the plants (Hussain et al., 2018; Ahmad et al., 2018). During drought stress, by light-harvesting mechanization, there is an efficient decline in the photosynthetic activity of the plants which ultimately decreases the functioning of the enzyme Rubisco (Foyer, C. et. al. 2000, Bota, J. et. al. 2004 and Fu, J. et. al. 2001). The photosynthetic performance also declined by the malfunctioning of the chloroplast structure. Drought condition also influences the carbon dioxide level in the plants which takes part in the photosynthetic electron transport generation. This results in the enhance degeneration of ROS activity which directly affects the photosynthetic apparatus and damages the apparatus so that decreases the level of photosynthesis (Basu, S. et. al. 2016). Due to dysfunctioning of photosynthetic apparatus in drought stress, there is a decline in photosynthetic rate, stomatal conductance,

transpiration rate, photochemical efficiency of PSII and photosynthetic electron transport rate (Meng, J.F. et. al. 2014, Campos, C.N. et. Al. 2019, Ye, J. et. al. 2016). During drought or water deficit conditions, the closing of stomata is regulated by the increase in the level of abscisic acid (ABA). This act as a molecule of signalling which regulates the functioning of various physiological and molecular processes. Due to drought, there is a decline in water potential and also a decrease in the relative water content of the plants (de Campos, M.K.F et. al. 2011, Nayyar, H. et. al. 2006, Liu, F. et. al. 2004). With the decrease in the water potential, there is a reduction in the uptake of the many different macro and microelements, nitrogen transports and its metabolism, reduction in compounds like ammonium transporter, nitrate reductase, nitrite reductase and glutamine synthetase (Ahmad, Z. et. al. 2018 and Gunes, A. et. al. 2007). During water stress at the root zone, there is a great decline in the growth of the root tissues which affect the nutrient uptake by the roots and their translocation to the target sites.

Figure 1: Schematic representation of factors responsible for root and shoot-growth inhibition by drought stress



(Source: <https://media.springernature.com/original/springer-static/image/art>)

EFFECT OF DROUGHT STRESS ON PLANTS

The drought stress affects the range of plant species from their morphological to molecular levels and inhibits growth and development of the plants. The various effects of drought stress on the plants are described as:

1. Crop growth and yield

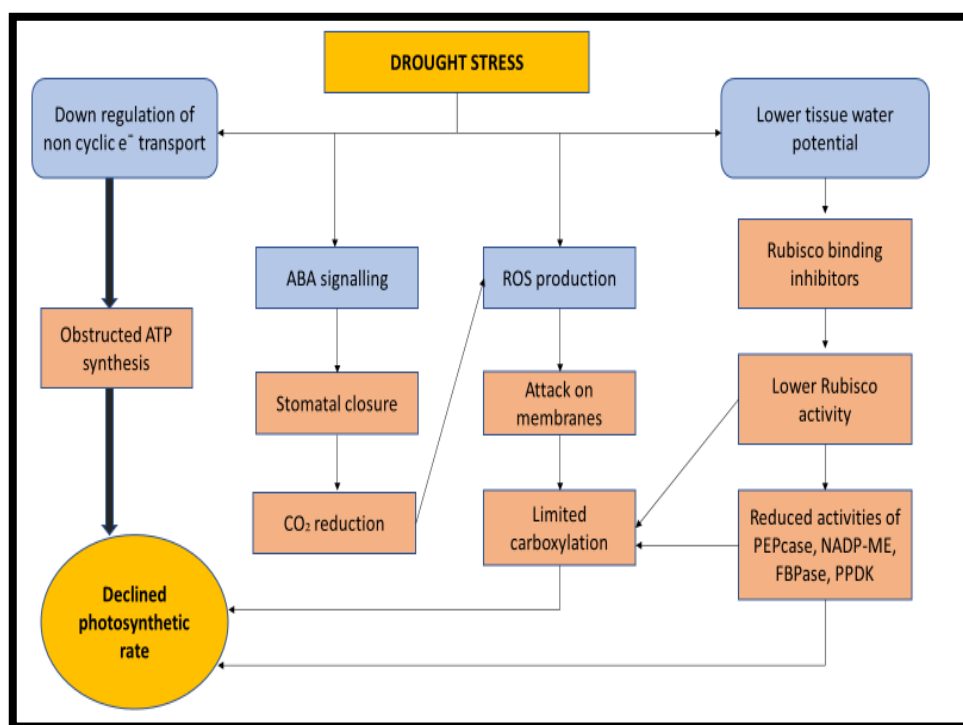
Drought influences the crop-growth and its enlargement in a great way and limits its quality yield or yield potential. The first effect of drought is that it imparts poor germination and poor plant stand establishment (Harris et al., 2002). Drought stress severely decreases germination rate and seedling stand of various crops. Cell division, elongation and maturation are the processes of the overall growth of the plant. It also includes physical, chemical, genetic and molecular growth functions. The water deficit conditions i.e. drought stress affect these growth functions and leads to a great loss in both qualities as well as the quantity of the produce. Under severe drought condition, cell elongation of higher plants can be reduced and there is a decline in the growth rate when the level of water-flow is decreased from the xylem to the elongating cells, (Nonami, 1998). During the grain filling stage, there is the formation of starch and carbohydrates. Due to water deficiency in grain filling stage, there is a reduction in the synthesis of sucrose and carbohydrate and a decrease in quality yield.

2. Nutrient relations

Drought stress limits the availability of total nutrient uptake in the plants and there is a limited concentration of the mineral and nutrients in the crop plants. Cellular tissues get shrunk or ultimately damaged due to severe water deficit conditions. There is a limitation in the accumulation and absorption of the nutrients in the root zone and their translocation from root to shoot becomes difficult during drought stress. Limited absorption of mineral and nutrients can lead to a decline in other nutrient uptake and can reduce transpiration flow (Garg, 2003; McWilliams, 2003). During water deficit, transpiration occurs at a high rate initially and dehydrate the cellular tissues and its components. In severe water stress condition, there is a decline in transpiration rate so that lower absorption of nutrients from root to shoot.

3. Photosynthesis

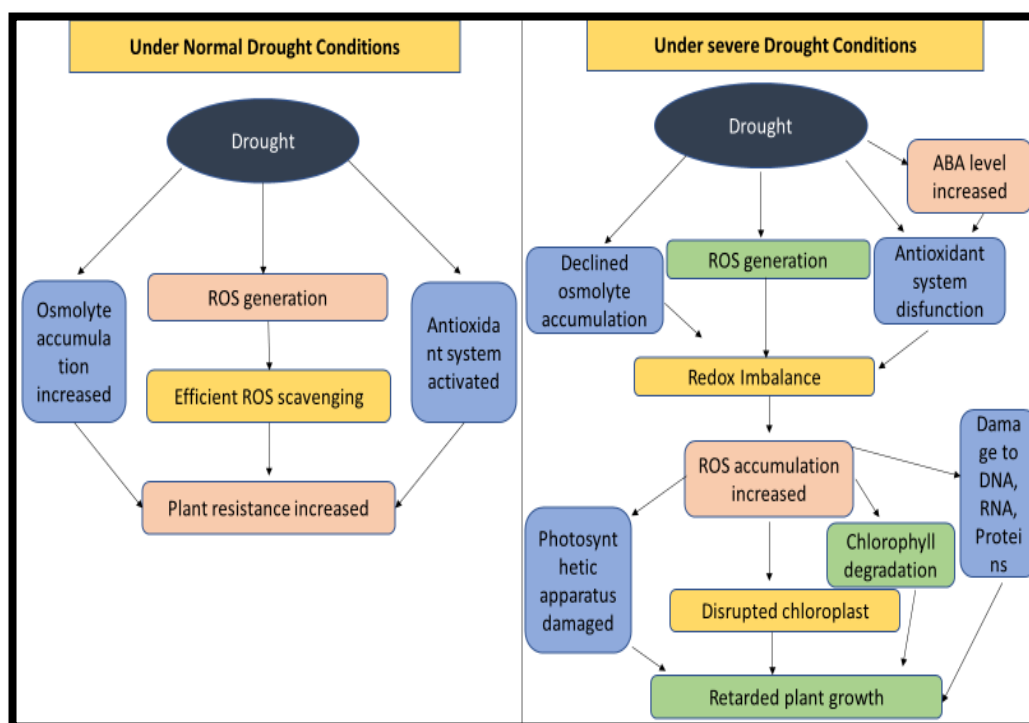
Drought stress mainly reduces the photosynthetic rate due to a decrease in the leaf area expansion, improper photosynthesis apparatus, senescence of the leaves prematurely (Wahid and Rasul, 2005). CO₂ uptake can be reduced with the degradation in the opening and closing of stomata. In very severe drought conditions, photosynthetic activity is reduced by a decrease in Rubisco enzyme activity (Bota et al., 2004). Cellular tissues shrinkage and decrease in their structure and volume occur due to high water stress. Drought stress causes changes in the photosynthetic functions which damages the biochemical structure and functioning of Calvin cycle enzymes which are directly related to the yield reduction (Monakhova and Chernyadèv, 2002). Rubisco enzyme performs various functions, underwater deficit or drought stress conditions it acts as oxygenase and therefore fixation of CO₂ is reduced.

Fig.2: photosynthesis under drought stress

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4. Respiration

Instead of germination and plant development, drought also influences the respiration-rate. During water-deficit conditions, there might be a change in carbon metabolism which can result in decreases the photosynthesis and respiration (Arbona et al., 2013). Plants begin to produce ROS in the mitochondria when they come in contact with severe drought stress. Drought stress enhances the accumulation of brassinosteroid (BR) in the plants which increases the water uptake and cell membrane stability due to water deficit conditions (Bhargava S and Sawant K, 2013).

Fig.3: Various responses of plants under drought conditions

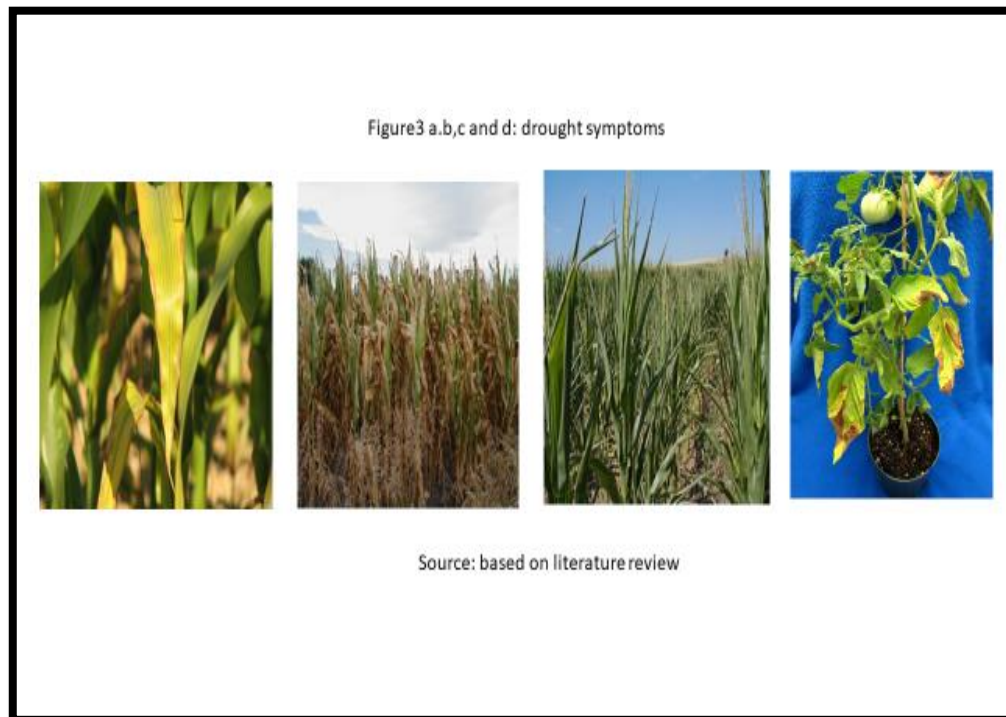
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5. Oxidative damage

When there are any stress conditions to the plants, the activation of reactive oxygen species can lead to an increase in the levels of superoxide anion radicals, hydroxyl ions, hydrogen peroxide (Munne-Bosch and Penuelas, 2003). Reactive oxygen species (ROS) cause great damage to the normal functioning of the cells and cellular tissues and causes oxidative damage to the plants by reacting with the proteins, lipids and deoxyribonucleic acid (DNA) (Foyer and Fletcher, 2001).

SYMPTOMS OF DROUGHT

Drought stress affects plant growth and development is a great way and creates a heavy loss of quality produce and yield. Its symptoms on plants varying from plant to plant and species to species. Drought stress affects the germination stage, developmental stage, anthesis, and seed filling stage under different environmental factors (Arbona *et.al.*2013). Severe drought conditions, length of the drought period, physiological and chemical conditions of the soil and plant, plant ability to cope with stress are the factors comes under enhancing symptoms of drought in plants. Usually, drought stress exerts various symptoms in the plants such as loss of turgidity, unavailability of the mineral and nutrients, wilting of the standing plant, yellowing of the leaves and stem, and early maturing leaf fall. Drought symptoms also involved cracking and breaking of bark and branches, dieback of the plant, thinning tree and shrub canopy, necrosis of the tip tissues, declined or stunted growth. During severe drought conditions, death of the plant may occur.

Fig.4: Drought symptoms

PLANT RESPONSE TO DROUGHT STRESS

Plants response to environmental stress is no so diverse for plants are multicellular-organisms and their response is very complex or complicated against biotic and abiotic stress (Bhargava and Sawant. 2013). The tolerance of plants to different biotic and abiotic-stress may be divided into three main categories: escape, avoidance and tolerance.

1. Escape

Environmental conditions play an important role in the growth and development of the plant throughout their whole life cycle. When there is fluctuation in the environment and it becomes adverse, the plant has to develop various mechanisms to overcome this problem or to survive under adverse climatic conditions. Plants are seasonal in nature and have a short life cycle. To survive under drought conditions or when the environment becomes dry, they allow themselves to reproduce before the excessive dryness in the environment takes place or increase in temperature starts to begin, it becomes necessary to escape from the drought for the plant (Akhtar I. and Nazir N.2013). A short life cycle helps them to escape from the drought due to early flowering, which can be described as a form of adaptation by the plant to survive under drought stress or to avoid drought stress.

2. Avoidance

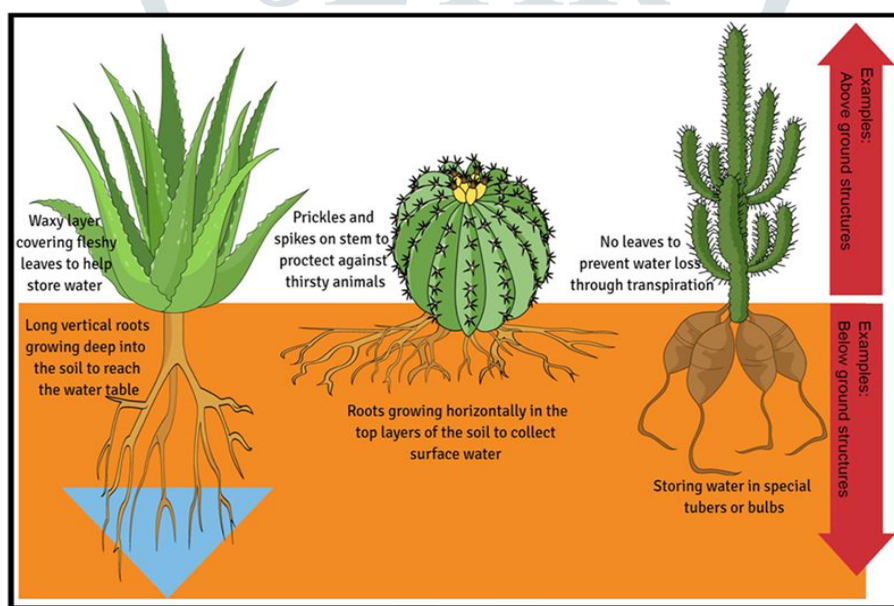
This mechanism help plant to evade drought-stress by collecting and storing the high amount of water level in plants. The main characteristic of this mechanism is to reduce water loss by transpiration from stomatal opening and closing and maintaining water absorption by an efficient and prolific root system from the soil (Bray EA, 2001). To absorb water from a considerable soil depth a deep, thick and prolific root system will

help the plant to do so and help them to survive under severe drought stress. Usually, The small size of plants uses this avoidance mechanism to deal with the drought stress or to maintain the relative water content in the plants (Farooq M and Wahid A, 2009).

3. Tolerance

For drought resistance, plants use a tolerance mechanism which helps them to reduce the number of leaves from the plants and also the area of the leaves to tolerate the water stress-conditions. The presence of unique structural features containing the outside membrane of plants that defends them against water-loss as well as certain parts of plants e.g. thorns, which aid the plants absorb and store water, for example, desert-plants. Plant hairs decrease the leaf-temperature, however, transpiration enhances light-reflectance and decreases water-loss by increasing the cell membrane resistance against the loss of water vapours from the leaf surface (Bray EA.2001).

Figure 5: Extreme structural-adaptations existed in plants to cope with water-loss and storing extra water



(Source: <https://kids.frontiersin.org/article/10.3389/frym.2017.00058>)

4. Cell water conservation

Osmotic potential or relative water content in the cells can be increased by the adjustments in the osmotic sequence. Due to adjustments in the osmotic potential, there is an increase in the influx of water and maintenance of turgor pressure inside the cells which can improve the tissue water status in the plants. This activity is very important for maintaining phytochemical and physiological activity for a longer period of drought stress (Kramer and Boyer, 1995). Delay in damage done by dehydration in severe drought conditions can be occupied by only osmotic adjustments and is very essential to maintain cell turgor pressure or other physiological processes (Taiz and Zeiger, 2006). During grain filling, the osmotic adjustment helps in better

translocation of carbohydrate are-flowering stage. On the other hand, high turgor pressure enhances the photosynthetic rate of the plant to a great extent (Ludlow and Muchow, 1990; Subbarao et al., 2000).

5. Membrane stability

During any environmental stress conditions, the cell membrane is the primary component to face the damage very first. The cell membrane is the outer layer of the cell to protect the plants and if it gets damaged then there are further great losses in terms of plant growth and production of stratified yield. Therefore, it is the main important thing to protect the cell membrane or increase its stability due to any environmental stresses. The stability of the membrane of leaf tissues was the most important aspect to check the germplasm under drought resistance (Dhanda et al. (2004). Moderate hardening of the seeds can lead to enhance cell membrane stability up to some extent. To decrease the membrane injury index of the plants, various compounds found such as glycine betaine, proline, carnitine, glutamate mannitol, etc. and oligosaccharides which can protect the cell membrane under severe stress conditions.

6. Growth regulators

Phytohormones enhance the physiological processes of the plants at much decreased concentrations when used on the plants (Morgan, 1990). Plant growth regulators play a wide and very important role in plants against drought tolerance. For drought tolerance, efficient root induction or proliferation plays a very important role. Growth hormone auxin enhances new root-formation by flouting the dormancy induced by cytokinins. When there is an increase in abscisic acid and ethylene content under drought stress it decreases the induction of auxin in the plants (Nilsen and Orcutte, 1996). The naturally occur in auxin is Indole-3-butyric acid which helps in root proliferation under drought stress conditions. Absciscic acid increases in the plant when it starts wilting under drought stress and helps in photosynthesis (Taylor, 1991).

7. Aquaporins

Plasma membrane widely contains aquaporins and vascular bundle cell membranes of the plants (Tyerman et al., 2002). Aquaporins play a major role in regulating osmotic potential and water relations in cellular tissues of the roots.

8. Melatonin

Melatonin is a molecule or growth regulator which performs various functions in the plants to protect them from adverse environment conditions directly from drought stress. Melatonin helps to increases the level of ROS scavenging and protect the photosynthetic apparatus during drought stress. During drought stress, Melatonin prevents the chlorophyll from degradation and enhance the physiological processes like photosynthesis, transpiration and stomatal conductance (Liang, B. et. al. 2018 and Karaca, P 2019). due to its nature of growth regulate or molecule it regulates all the processes at the molecular level and helps the plants to tolerate the drought stress. Melatonin enhances ROS scavenging to protect the plant from drought induce

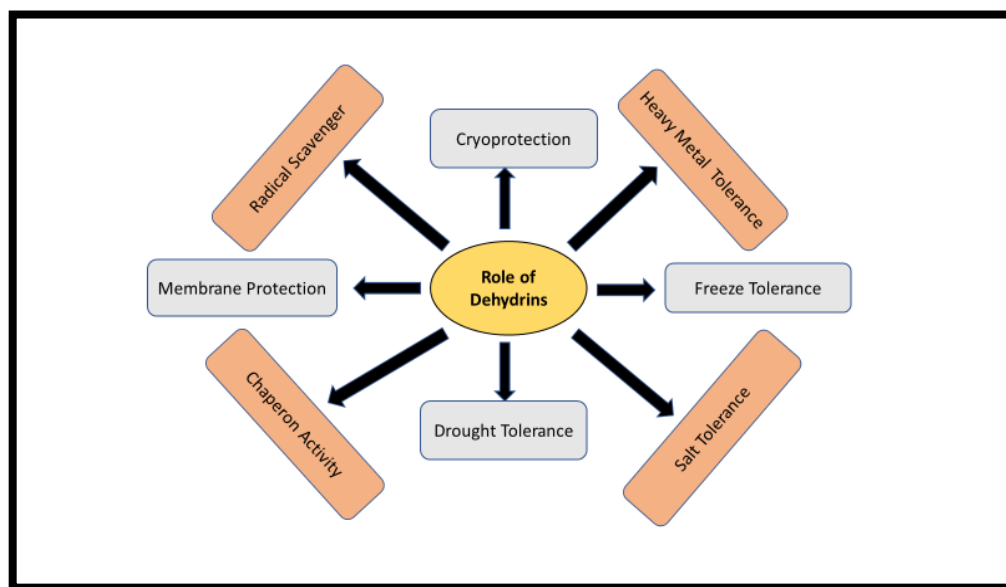
oxidative stress. It also increases the accumulation and biosynthesis of abscisic acid (ABA) in plant cells in drought stress conditions. Melatonin regulates various functions under drought stress conditions when applied externally on the anti-oxidative enzymes.

9. Seed priming

Seed-priming is one of the greatest effective method to survive the plant under drought stress conditions. In this process, seeds are brought to contact with water or hydrated up to a point at which it starts germination (Farooq et al., 2006). Seed priming helps the seed to germinate even under drought stress conditions and protect the cell membrane from getting damaged due to high temperature. Seed priming influences the germination rate and percentage of the seeds (Kaya et al., 2006; Farooq et al., 2007). With the enhancement in seed germination, it induces the faster growth of seedlings and induces early flowering which ultimately enhances the crop growth and yield. From seed priming, the seed will grow better in minimum moisture and does not require much water for its development. It also helps in protecting outermost cellular tissues from the high temperature due to the presence of hard seed coat around the seeds.

10. LEA proteins

Group II LEA proteins (Dehydrins) is the most commonly described group which is thermostable and help the plant in a stressful environment. Dehydrins acts a key role in protecting the plants against drought-stress. The interaction of Dehydrin – protein is regulated by the amphipathic (hydrophilic & hydrophobic) helices structure by which dehydrins attached to the dehydrated surfaces and protect the cells from further desiccation or water deficit conditions (Ganguly et al. 2012). Therefore, Dehydrins act as "molecular sponges" leads to water retention in the desiccated cells in case of drought and high salt stress. Due to their hydrophilic nature, they can perform the function like hydration buffers and can reduce the rate of water loss from the cellular zone under severe drought conditions. By inducing preferential hydration, they may stabilize membranes or promote water exchange at the different sites with other macromolecules (Roychoudhury and Nayek 2014).

Fig.6: Dehydrins in response to abiotic stress

Source: <https://www.semanticscholar.org/paper/>

LEA proteins perform various functions to protect the plants under water deficit conditions

Protein protector: LEA proteins can protect other proteins. During water stress conditions or drought, they accumulate and inactivate in the plants to carry on the function of another protein. Group 2 LEA prevent aggregation of protein during heat stress (Kovacs, D. et.al. 2008). With the increasing population and stress to the environment, there is a threat of global warming and great fluctuation in the temperature which affect the normal growth of the plant. In this, the LEA proteins can act as a molecular shield to protect the plants from environmental stresses. This shield of LEA plays a role of space filler during water deficit to prevent cell collapse.

Membrane protector: water plays an important role in the functioning of cellular components within the cell membrane. During desiccation, to protect the cell membrane is very important to carry out cellular functions smoothly. During a dry spell, LEA proteins accumulate with sugars to form a network of H- bond to protect cell membrane (Hoekstra, F.A., 2001). In drought-conditions, these polypeptides fold to form amphipathic α -helices to protect membranous tissues.

Antioxidant: During dehydration or water deficit, there is an increase in intracellular ion concentration which affect the structure and functioning of macromolecules. LEA proteins have different amino acid residues which can act as sequester ions (Dure, L. (1993). Metal ions accumulation with group 2 LEA can serve as an antioxidant for the plant species. LEA proteins scavenge ROS and reduce oxidative stress in water deficit cells.

CONCLUSION

Drought stress affects the plants physiological, biochemical and molecular functions. It causes a reduction in growth and quality yield by affecting flowering and seed filling phase. It is the most serious stress which limits agricultural growth and its development and further leads to a great threat to world food security. It affects the plant water relation and damages the structure and functioning of various cellular tissues of the root and shoot cells. The plant itself has some molecular or physiological mechanisms by which they can survive under environmental stress conditions. These mechanisms help the plants to tolerate biotic and abiotic stresses and perform their regular functions to enhance the growth and quality yield. Drought stress damages the photosynthetic apparatus and decreases the chlorophyll content so that the plant cannot synthesis its food for better development. Molecular structures like melatonin and LEA group II proteins helps to enhance the structure and functioning of cellular tissue and induce the relative water content in the cells which makes the cells hydrated and helps in better development and quality yield of the produce.

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AUTHOR CONTRIBUTION

The study was planned and written by M.S., P.K., and T.K.,

CONFLICT OF INTEREST STATEMENT

The authors state that they have no interest in conflicts.

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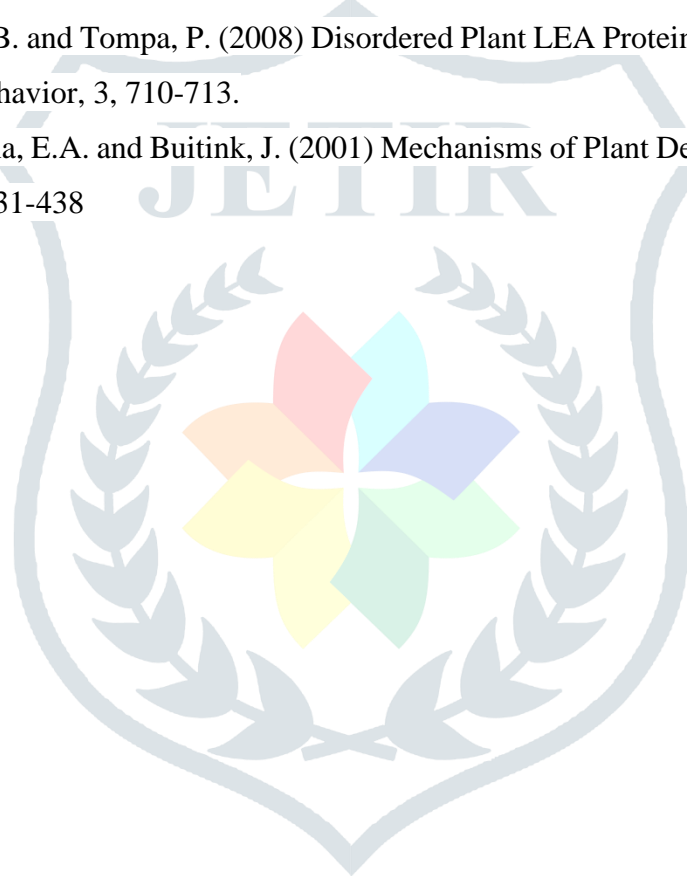


Table 1: Yield losses (%) in important crops under drought stress

Crop	Growth Stages	Yield Reduction	References
<i>Hordeum vulgare</i>	Seed filling stage	49-57%	Samarah (2005)
<i>Zea mays</i>	Grain filling stage	79-81%	Monneveux et al. (2005)
<i>Zea mays</i>	Reproductive stage	63-87%	Kamara et al. (2003)
<i>Zea mays</i>	Reproductive stage	70-47%	Chapman and Edmeades (1999)
<i>Zea mays</i>	Vegetative stage	25-60%	Atteya et al. (2003)
<i>Zea mays</i>	Reproductive stage	32-92%	Atteya et al. (2003)
<i>Oryza sativa</i>	Reproductive stage (mild stress)	53-92%	Lafitte et al. (2007)
<i>Oryza sativa</i>	Reproductive stage (severe stress)	48-94%	Lafitte et al. (2007)
<i>Oryza sativa</i>	Grain filling stage (mild stress)	30-55%	Basnayake et al. (2006)
<i>Oryza sativa</i>	Grain filling stage (severe stress)	60%	Basnayake et al. (2006)
<i>Oryza sativa</i>	Reproductive stage	24-84%	Venuprasad et al. (2007)
Chickpea	Reproductive stage	45-69%	Nayyar et al. (2006)
Pigeon Pea	Reproductive stage	40-55%	Nam et al. (2001)
Common Beans	Reproductive stage	58-87%	Martinez et al. (2007)
Soybean	Reproductive stage	46-71%	Samarah et al. (2006)
Cowpea	Reproductive stage	60-11%	Ogbonnaya et al. (2003)
Sunflower	Reproductive stage	60%	Mazahery-Laghab et al. (2003)
Canola	Reproductive stage	30%	Sinaki et al. (2007)

Potato	Flowering stage	13%	Kawakami et al. (2006)
Soybean	Pod set stage	73-82%	Wei, Y. et.al (2018)
Soybean	Reproductive phase	46-71%	Samarah, N.H.et. al. (2006)
Soybean	Grain filling stage	42%	Maleki, A.et. al. (2013)
Chickpea	Reproductive stage	45-69%	Nayyar, H.et. al. (2006)
Chickpea	Ripening stage	49-54%	Samarah, N.H. et. al. (2009)
Chickpea	Anthesis stage	27-40%	Mafakheri, A. et. al. (2010)
Chickpea	Ripening stage	50%	Varshney, R.K. et. al. (2014)
Cowpea	Reproductive phase	60%	Ogbonnaya, C.I. et. al. (2003)
Cowpea	Reproductive phase	34-66%	Ahmed, F.E. et. al. (2010)
Cowpea	Pod filling stage	29%	Kyei-boahen, S. et. al. (2017)
Common bean	Reproductive stage	58-87%	Martinez, J.P. et. al. (2007)
Common bean	Pod filling stage	40%	Ghanbari, A.A. et. al. (2013)
Common bean	Flowering stage	49%	Rosales-Serna, R. et. al. (2004)
Pigeon pea	Reproductive stage	40-55%	Nam, N.H. et. al. (2012)
Moong bean	Reproductive stage	26%	Al, R. et.al. (2012)
Moong bean	Flowering stage	31-57%	Ahmad, A.et. al. (2015)
Fava bean	Grain filling stage	68%	Ghassemi-Golezani, K.et. al. (2009)
Lentil	Pod development	70%	Shrestha, R.A. et. al. (2006)
Lentil	Reproductive phase	24%	Allahmoradi, P. et. al. (2013)

Table 2: Effect of application of melatonin on different anti-oxidative enzymes under drought stress

Crops	Concentration	Impact on antioxidant enzyme activity	Reference
<i>Brassica napus</i>	50µM	Enhanced activities of APX, CAT, POD and SOD	Li, J. et. al. 2018
<i>Coffea arabica</i>	300 µM	Enhanced activities of APX and CAT	Campos, C.N. et. al. 2019
<i>Cucumis sativus</i>	100 µM	Enhanced activities of CAT, POD and SOD	Zhang, N. et al 2013
<i>Malus domestica</i>	100 µM	Enhanced activities of APX, CAT, POD, DHAR, MDHAR and GR	Wang, P. et. al 2013
<i>Solanumlycopersicum</i>	200 µM	Enhanced GR activity	Karaca, P. et. al 2019
<i>Triticum aestivum</i>	100 µM	Enhanced activities of APX, GPX, DHAR, MDHAR, GST and GR	Cui, G. et. al. 2017
<i>Zea mays</i>	100 µM	Enhanced activities of APX, CAT,POD and SOD	Ye, J. et. al. 2016