



## Consequences and mitigation of water deficit stress in pulses

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### Abstract

Impacts of drought on morphophysiological, biochemical and molecular changes in crops limit the performance and their yield. Its impacts include growth and development, water relations, membrane integrity, pigment content, osmotic adjustment, photosynthetic activity and harvest index. The different acclimation factors such as changes in plant structure, wax deposition, reduced growth rate, tissue osmotic potential and antioxidant defenses. Oxidative stress is common detrimental factors in drought which produce reactive oxygen species (ROS) viz. superoxide ( $O_2^-$ ) radicals, singlet oxygen ( $1O_2^-$ ), hydroxyl ( $\cdot OH$ ), alkoxyl ( $RO\cdot$ ), peroxy ( $ROO\cdot$ ), lipid peroxy ( $LOO\cdot$ ), hydrogen peroxide ( $H_2O_2$ ), etc. that causes sequential damage of membranous structure in the cell and eventually lead to dry and decay of whole plant. The metabolites that have different types of role in metabolism play a major role in suppression of these ROS in plants. The Ascorbic acid, Glutathione, Carotenoids, Phenolics, flavonoids, alkaloids, Tocopherols, Tocotrienols, Proline, taurine, nano-silicon etc. are the major metabolite that scavenge the ROS in different metabolic pathway. The enzymatic antioxidants viz. superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX) and glutathione reductase produced under drought and scavenge ROS and minimize the drought. Molecular changes during drought produce the several enzymes that catalyze the production of ROS scavenger and drought responsive metabolites. Thus internal mechanism and structural changes during drought save the crops from diurnal and long term drought.

**Keywords:** Drought, pulses, antioxidants, ROS, stress, plants

### Introduction

Pulses keep important place in our food due to cost effective sources of protein and considered as food grain for balance diets. They have ability to fix atmospheric nitrogen in the root nodules and provide nutritious green fodder and feed for livestock as well as enhance soil nitrogen status. Hence soil requires fewer amounts of inorganic fertilizers and keeps its fertility for next crops. Soil fertility also maintained by crop cultivation practices like intercropping, crop rotation and mixed cropping (Kumawat *et al.*, 2020) [44]. Pulses are cultivated almost all over the world due to their wide range of soil and climatic conditions adaptation. The rainfed cultivation suffers from water stress mainly which lead to decrease of yield and production (Kamachi *et al.*, 2024) [35]. India is the largest producer of pulses despite imports pulses and trying to achieve self-sufficiency due to lack of agronomic and management practices (Mishra *et al.*, 2023) [52].

They are typically cultivated in rainfed areas where the water deficit stress occurs frequently. However, their highly susceptibility towards abiotic stress especially water deficit stress their production is not so much to fulfill the demand (Khatun *et al.* 2021) [40]. The reproductive stages are more susceptible to water stress especially during flowering and anthesis lead to disruption of ovule and pollen development and pollen sterility and eventually failure of fertilization (Devi *et al.*, 2022) [15]. The 90% fresh mass of growing region of plants occupied by the water hence its deficiency at any growth stage significantly affecting the flowering, grain filling and yield (Nayyar and Gupta, 2006) [59]. The extent of decrease in yield depends on the developmental stages of plants drought intensity, duration and genetic factors (Nadeem *et al.*, 2019) [58]. Plants cope up the short term water stress by stomatal closure, leaf rolling and

reduced metabolism (Ding *et al.*, 2020) [16]. They produce reactive oxygen species, antioxidants, phytohormone ethylene and abscisic acid as well as adapting their root and shoot structures (Ahluwalia *et al.*, 2021) [1]. Chickpea and lentil grown as a rainfed crop in northern India during the winter months from November to April after the harvest of paddy. Their grain filling stage falls in spring (February to April) when temperatures ranges 32-35 °C and very less precipitation those environmental effects lead to dramatic decrease in yield if the scarcity of water persist for prolong time (Awasthi *et al.* 2014) [4].

Drought is the common environmental factor which adversely affects the growth, development and yield of the crops. Prolonged period of abnormally low precipitation that occurs at a specific location when the amount of rainfall consistently falls below the average is known as drought (Ahmad *et al.* 2018) [2]. The drought is divided into three categories viz. hydrological, agricultural, and meteorological drought. Sporadic precipitation and excessive evaporation, or inadequate rainfall results in agricultural drought while lower than normal precipitation coupled with warmer temperatures considered as meteorological drought (Lima *et al.*, 2019) [45]. When there is a prolonged decrease in water availability that impacts water reservoirs and water table is known as a hydrological drought. It occurs frequently in rainfed condition where pulses are generally grown after or during the kharif crop season. The world's farmed land approximately 1474 million hectares are falls under rain fed agriculture makes up a substantial majority of the agriculture (Yohannes *et al.*, 2024) [70]. They suffer from water stress either the field is not saturated with field capacity for a long time or the balance between water supply to roots becomes less than the transpiration rate (Jongdee *et al.*, 2002) [34]. The water table of available water

resources for rainfed crop production has been decreasing in many regions of our country (Anjum *et al.*, 2017) <sup>[3]</sup>. The sensitivity of different pulses to water stress depends on the developmental stages, different accompanying stress factors and level of stress. The morphological traits viz. leaf area, root growth, shoot growth decreased while adaptive changes viz. smaller plant size, early maturation, increased leaf thickness and restricted leaf expansion appeared in drought stress (Bengough *et al.*, 2011) <sup>[8]</sup>. Plant also minimize rate of transpiration, regulating stomatal conductance, curling leaves and formation of trichomes which reflect sunlight and help to lower leaf temperature (Kumar *et al.*, 2014) <sup>[42]</sup>. Pulses access moisture from deeper soil layers by development of longer and deep root systems and avoid water deficit in rhizosphere. The sensitivities of drought in different pulses first occurs in rhizosphere where germination, hypocotyls elongation, seedling vigor mostly affected (Raina *et al.*, 2016) <sup>[61]</sup>. Green gram, Pigeon pea, Lentil, Black gram, Cowpea, Faba bean and Moth bean showed early maturation and reduced plant heights in drought stress. The increased root length results in increase of root-to-shoot ratio in chickpea and cowpea while due to arid zone moth bean showed reduced root length (Kumari *et al.*, 2021) <sup>[43]</sup>. The reduced shoot length led to lower shoot biomass in Chickpeas, Green gram, Pigeon pea, Lentil, Cowpea, Faba bean and Moth bean under drought affecting both biological and economical yield (Jha *et al.*, 2022) <sup>[15]</sup>. Flowering behavior mostly regulated by photoperiod and temperature but the acceleration of flowering occurs in different pulses viz. Lentil, Chickpeas, Green gram, Pigeon pea, Cowpea, Faba bean and Moth bean due to adverse effects of drought (Kaushal *et al.* 2013) <sup>[37]</sup>. Pollen tube growth and pollen germination inhibited led to inhibition of fertilization and embryogenesis in black gram and Faba beans. Pod formation and pod filling were found to shorten in chickpeas and green gram due to adverse effects of drought and high temperature (Liu *et al.*, 2011) <sup>[46]</sup>.

#### Effects on morpho-physiological parameters:

Water deficit in plant disrupt the flow of water from the xylem to growing region results in decrease of turgidity of the cells and plant loss its stature. They causes several abnormalities such as burning and flaccidity, brittleness or curling, leaf chlorosis, senescence and abscission of leaves, etiolation, wilting, eventually dry and decay (Rehshuh and Ruehr, 2022) <sup>[63]</sup>. The leaves are the primary site of metabolism in plants hence leaves affected adversely in deficiency of water (Jongdee *et al.*, 2002) <sup>[34]</sup>. Their size and length reduces gradually results in reduction in dry matter in shoots as well as crop growth rate. Morphological alteration in leaves reduce their leaf area, leaf area index and leaf-specific activity consequently the chlorophyll content and photosynthetic rate (Bashir *et al.*, 2021) <sup>[6]</sup>. The Soybean plant under water-stress decreases their photosynthetic rate due to reduced carbon fixation per unit leaf area due to reduced number of active stomata per unit leaf area (Salgotra and Chauhan, 2023) <sup>[65]</sup>. Roots are the primary sense organ those receive signal of water deficit and transmit them to leaves for synthesis of abscisic acid, closure of stomata and slow down the transpiration. The root architecture such as root length, surface area, volume, elongation rate and spatial structure modified under the influence of water stress (Boguszewska-Mankowska *et al.*, 2020) <sup>[16]</sup>. The elongated root facilitate plant access to deeper

layer of soil for water; thereby minimize the water scarcity in plants. Increase in the elongation of primary roots and quantity of lateral root system and root hairs withstand short term drought while in long term drought the decrease in number of mitochondria and other cytoplasmic organelles leads to deficiency of ATP and in root activity, ultimately causing deceleration or complete cessation of growth and development of the plant (Kim *et al.*, 2020) <sup>[41]</sup>. Hence, the water uptake and transportation in plants effectively managed by the modification in the root architecture. The decrease in the number of tillers per plant and flowering time were affected in faba beans and cowpeas due to water stress (Guerfel *et al.*, 2009) <sup>[24]</sup>. The flowering time adversely affected in lentil due to water deficit and it was accelerated in flowering and premature seed set in lentil. Photosynthetic process depends on availability of water, its deficiency induce the synthesis of abscisic acid (ABA) which trigger the closure of stomata (Basu *et al.*, 2022) <sup>[7]</sup>. The decreased stomatal conductance obstructs the entry of CO<sub>2</sub> and exit of water vapour. Deficiency of CO<sub>2</sub> in the cell particularly in stroma reduces the Calvin cycle as well as activity of rubisco in soybean chickpeas (Mafakheri *et al.*, 2010) <sup>[47]</sup>. Canopy temperature depression and the transpiration rate reduced during water deficit in soybean and chickpeas (Tiwari *et al.*, 2023) <sup>[69]</sup>. The unavailability of CO<sub>2</sub> during drought and intense sunlight promote the oxygenase activity of rubisco and facilitate the process of photorespiration which is a carbon diversion process from the Calvin cycle, leads to overall reduction in photosynthetic efficiency and loss of ATP. The chlorophyll fluorescence (Fv/Fm ratio) indicates the conversion of light energy into flow of electron in electron transport chain. The overall process of light reaction reduced due to decrease of chlorophyll fluorescence (Fv/Fm ratio) under drought results in decreased quantum yield and photophosphorylation in chick pea and mung bean (Kumar *et al.*, 2014) <sup>[42]</sup>. The relative water content, chlorophyll content and membrane stability index decreased during water stress in chickpea, soybean, mung bean, moth bean and cowpea (Jayawardhane *et al.*, 2022) <sup>[30]</sup>.

#### Effects on Biochemical parameters:

Antioxidants are the biomolecules in the cell which produced during stress to protect the cell from damage of organelles and membrane. They have the capacity to reduce the reactive oxygen/nitrogen species produced during water stress in cellular compartments and consequently the integrity of the entire plant (Hasanuzzaman *et al.*, 2019) <sup>[25]</sup>. The metabolites which are capable of scavenging the ROS non-specifically are most important in the system for minimizing the adverse effects of free radicals produced during the stress (Khan *et al.* 2019) <sup>[39]</sup>. These metabolites are known as non-enzymatic antioxidants and they have the ability to neutralize a variety of reactive oxygen species (Ghosh *et al.*, 2021) <sup>[22]</sup>. Hence, in the living system particularly plants which suffers from different type of stress day by day it is necessary to maintain sufficient antioxidant production to suppress the production of reactive oxygen species (Tiwari *et al.*, 2023) <sup>[69]</sup>. Excess ROS in the system causes several disorders and eventually in uncontrolled state led to great loss of structure of the plants. The biomolecules which act specifically in scavenging of ROS are come under enzymatic antioxidants defense system; they act specifically in a catalytic reaction

and convert the ROS into different products. Hence, non enzymatic and enzymatic antioxidants defense system tools can manage and minimize the effects of oxidative stress and save the system from unwanted disorder and damage (Mishra *et al.*, 2023) <sup>[52]</sup>

### Oxidative stress

The excess production of ROS damage the system through lipid peroxidation, protein oxidation, DNA fragmentation, and enzyme inactivation, eventually affecting crop growth, development and yield. Excess production of ROS generally occurs in mitochondria, peroxysome, chloroplast etc. but during the drought, chloroplast affected first and degraded

hence mitochondrial and peroxisomal ROS affect the metabolism of the plants (Hodges *et al.*, 2004) <sup>[27]</sup>. The free radicals having the one or more unpaired electrons, produced due to lack of consumption and utilization of O<sub>2</sub> in the system especially during abiotic and biotic stress. These ROS molecules viz. O<sup>2-</sup>, IO<sup>2-</sup>, OH<sup>-</sup>, and H<sub>2</sub>O<sub>2</sub>. begin the series of chain reactions and regenerated repeatedly, and they form the free radicals include alkoxy (RO•), peroxy (ROO•), lipid peroxy (LOO•) etc. in the system (Gill and Tuteja, 2010) <sup>[23]</sup>. During the progression of severe stress the electron transport chain disrupted and whole metabolism of respiration blocked due to blockage of sink of electron (Dietz and Geilfus, 2021) <sup>[14]</sup>.

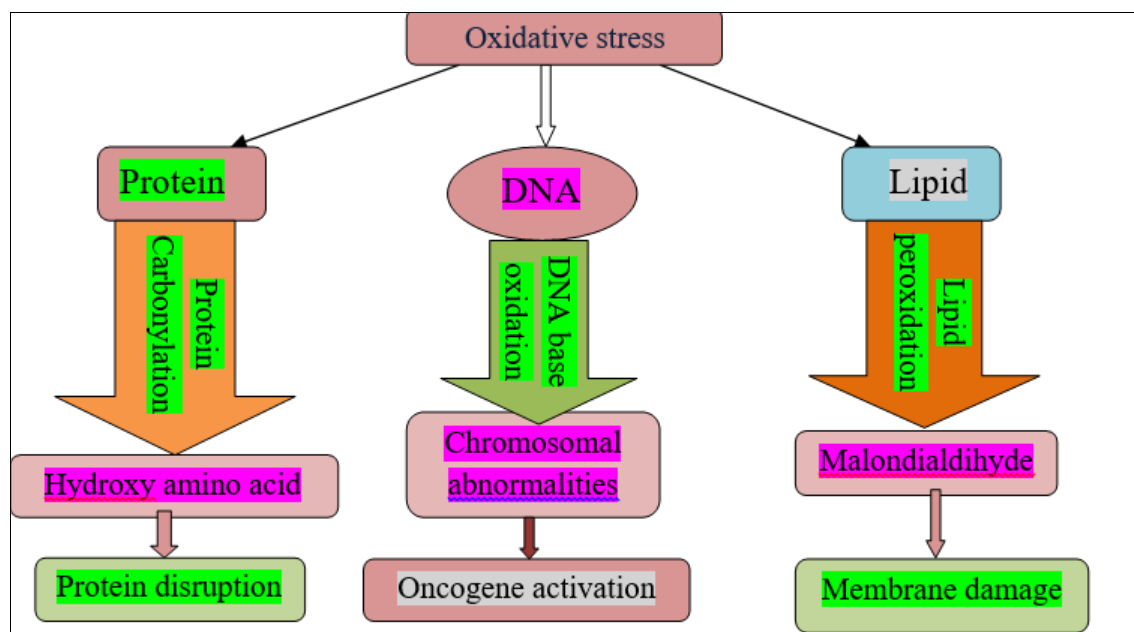


**Fig 1:** Effects of oxidative stress on three biomolecules in the cell

Thus, mitochondria get excess O<sub>2</sub> having the unpaired electron resulting in production of excess ROS. The antioxidants defense system developed as the ROS production increases during progression of water stress, but under the severe water stress the plants have not such capacity to manage excess ROS and they need special care for their protection (Du *et al.*, 2018). The formation of O<sub>2</sub>- during the progression of water stress induce the formation of other ROS viz. <sup>1</sup>O<sub>2</sub><sup>-</sup>, OH•, H<sub>2</sub>O<sub>2</sub>, etc. resulting in lipid peroxidation and a chain of reaction which led to leakage in the membrane (Jimenez *et al.*, 2002) <sup>[32]</sup>.

### Non enzymatic and enzymatic antioxidants

The ascorbic acid (AsA) and glutathione (GSH) are the water soluble while Carotenoids, Phenolics, Tocopherols and Tocotrienols are the lipid soluble non-enzymatic antioxidants produced during stress in the cell. These biomolecules act in different ways at different location/organelles in the cell and scavenge the excess ROS (Hasanuzzaman *et al.*, 2020) <sup>[26]</sup>. Ascorbic acid, carotenoids and phenolics abundantly found in most of the cell while tocopherols and tocotrienols are relatively in low amount as compared with nuts and grains. They are the molecules having the capacity to donate electron and reduced the oxidized state due to their electron-rich structure in the form of oxidizable double bonds and hydroxyl groups (Foyer *et al.*, 2020) <sup>[20]</sup>. The metal ions which are potent pro-oxidants

viz. Cu, Fe etc. can be chelated by vicinal hydroxyl groups on certain phenolic antioxidants (Shahidi *et al.*, 2009).

Ascorbic acid (AsA) is a naturally occurring organic compound and first discovered antioxidant, usually acts as a co-factor in many enzymatic reactions and detoxifies the excess ROS particularly H<sub>2</sub>O<sub>2</sub> through ascorbate peroxidase (Forni *et al.*, 2019) <sup>[19]</sup> known as Haliwall-Asada pathway. The content of AsA in growing cell depends on the strict regulation of metabolic recycling and degradation. The recycling of AsA under water stress occurs in association with glutathione/glutathione reductase and NADH/NADPH that recycle the AsA for further scavenging of other free radicals (Mittler, R., 2002) <sup>[55]</sup>. Higher AsA levels improve both biotic and abiotic stress tolerance in plants and enhance survival capacity. Ascorbic acid can also interact with the plasma membrane by donating electrons to the α-tocopheroxyl radical and regenerating α-tocopherol. Recycling of α-tocopherol by ascorbate helps to protect membrane lipids from peroxidation (Mishra and Panda, 2017) <sup>[53]</sup>.

Carotenoids are the biomolecules which acts as a pigment in the photosystem II and also quench the singlet oxygen and peroxy radicals due to the presence of conjugated double bonds in its structure (Moller *et al.*, 2007) <sup>[56]</sup>. They get excited after quenching these free radicals and dissipate newly acquired energy through a series of rotational and vibrational interactions with the solvent. The original

unexcited carotenoid again regenerated for further reuse in the cycles (Gill and Tuteja, 2010) <sup>[23]</sup>. Among the carotenoids family lycopene is the most efficient singlet oxygen quenchers of the natural carotenoids while  $\beta$ -Carotene yellow carotenoids scavenge peroxy radicals via an unstable  $\beta$ -carotene radical adduct (Demmig-Adams *et al.*, 2006) <sup>[13]</sup>. They terminate radical reactions by binding to the attacking free radicals and further undergo decay to generate non radical products (Fieder, J. and Burda, K. 2014) <sup>[18]</sup>. The lipid soluble biomolecule antioxidants reside predominantly in biomembranes, quench  $^1\text{O}_2$  and protect the cell from oxidative stress. The tocopherol considered as one

of the lipid soluble potential scavengers of ROS and lipid radicals in biomembranes, where they have the role in both antioxidant and non-antioxidant functions (Hollander-Czytko *et al.*, 2005) <sup>[28]</sup>. The antioxidant activity depends on the presence of phenolics compounds which are responsible for suppressing free radicals production with donation of electron or transferring hydrogen atom by flavonoids. The flavonoids also scavenge the transition metal-catalyzed production of reactive species through metal chelation and acts cooperatively with other antioxidants (Stewart *et al.*, 2000) <sup>[67]</sup>.

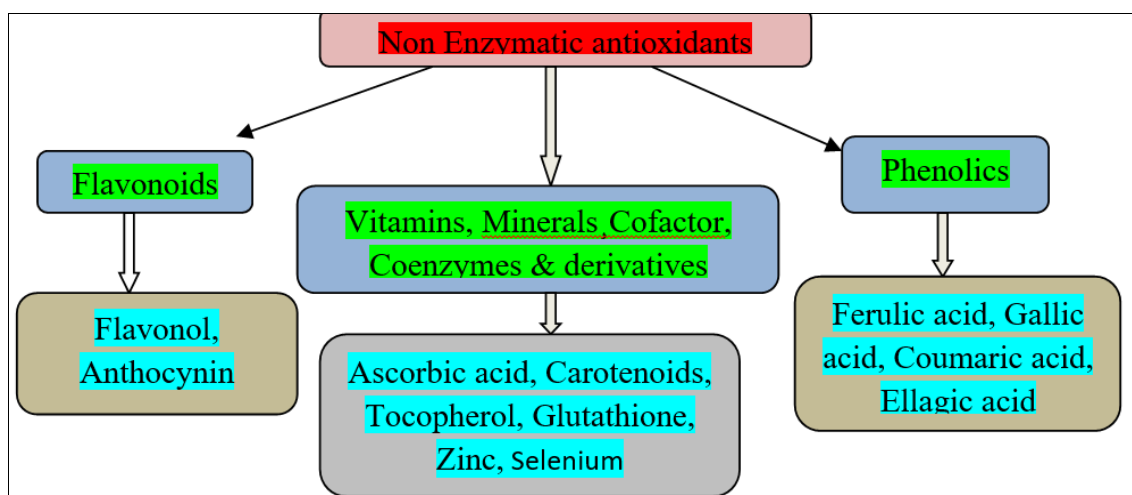


Fig 2: ROS scavenger non enzymatic antioxidants in the cell

#### Enzymatic antioxidants

**Superoxide dismutase (SOD), Catalase (CAT), Guaiacol peroxidase (GPOX), Ascorbate peroxidase (APX), Glutathione reductase (GR)**

SOD is the first line of defense against ROS among the enzymatic antioxidants. It is the metalloenzyme scavenges  $\text{O}_2^{\cdot -}$  and converts it into  $\text{H}_2\text{O}_2$  and  $\text{O}_2$ . This prevents the production of hydroxyl ( $\cdot\text{OH}$ ) and peroxyxynitrite ( $\text{OONO}\cdot$ ) in the cell (Choudhury *et al.*, 2013) <sup>[11]</sup>. There are three types of SOD: i) Fe-SOD -located in chloroplast ii) Mn-SOD - located in Mitochondria and Cu/Zn SOD -located in chloroplast and cytosol. They are produced in the cell when free radicals usually produced due to metabolic reactions (Tiwari *et al.*, 2023) <sup>[69]</sup>. Catalase is the second enzymatic antioxidants after SOD which directly dismutates  $\text{H}_2\text{O}_2$  into  $\text{H}_2\text{O}$  and  $\text{O}_2$ . It is a haeme containing enzyme mostly found in peroxisome, mitochondria and cytosol (Jincy *et al.*, 2019) <sup>[33]</sup>. It has three isoforms Cat1, Cat2 and Cat3 they become more active when stress induced ROS especially  $\text{H}_2\text{O}_2$  accumulate in the cell. Cat 1 activity is mostly observed in leaves while Cat2 activity mostly found in phloem. Catalase has lower affinity for  $\text{H}_2\text{O}_2$  than APX and GPOX due to high  $V_{\text{max}}$  value and it does not consume reducing power during scavenging of  $\text{H}_2\text{O}_2$  (Keerthi *et al.*, 2023) <sup>[38]</sup>. Guaiacol peroxidase (GPOX) acts on the reducing substrate guaiacol a phenolic compound (o-methoxyphenol) that donate electron by oxidizing itself during scavenging of  $\text{H}_2\text{O}_2$ . GPOX is an important enzyme among different peroxidases and scavenges  $\text{H}_2\text{O}_2$  in cytosol, vacuole as well as apoplastic region (Meriga *et al.*, 2004) <sup>[50]</sup>. Lignin in cell wall can be biosynthesize with the catalytic activity of GPOX and decomposes to produce indole-3-acetic acid that helps in defense against the pathogen (Jain, A K., 2014) <sup>[29]</sup>.

**Monodehydroascorbate reductase (MDHAR), Dehydroascorbate reductase (DHAR), Glutathione reductase (GR) and Glutathione peroxidase (GPX)**

APX is the efficient enzymatic antioxidants having the low  $V_{\text{max}}$  value and it saturate at micro- molar range of  $\text{H}_2\text{O}_2$  concentration. It acts as the main detoxifier of  $\text{H}_2\text{O}_2$  in plant via ascorbate-glutathione cycle. It is a haeme containing enzyme using ascorbate (AsA) as electron donor capable and convert  $\text{H}_2\text{O}_2$  to water (Suzuki *et al.*, 2012) <sup>[68]</sup>. AsA is the main inducer of APX, in absence AsA the enzyme is labile hence for maintaining the antioxidant system in the cell high level of endogenous AsA is required for activation of APX (Mundiyara *et al.*, 2017) <sup>[57]</sup>. The enzymatic activity is quickly lost below the 20  $\mu\text{M}$  concentration of AsA. The enzyme present in different number of isoforms varies its number in different crops. There are eight isoforms reported in rice which are mainly present in cytosol, chloroplast, peroxisome and mitochondria (Shigeoka *et al.*, 2002) <sup>[66]</sup>. APX activity during drought and salinity protect the plant from adverse effects of oxidative stress (Pandey *et al.*, 2021) <sup>[60]</sup>. MDHAR generally found in cytosol, chloroplast, peroxisome and mitochondria It is is a flavin adenine dinucleotide and the pyridine nucleotide-binding domain of flavoenzymes. It reduces monodehydroascorbate (MDHA) to Dehydroascorbate and Ascorbate by oxidizing NADH/NADPH (Millar *et al.*, 2008). It is similar to the iron-sulphur protein reductase of bacteria not ferredoxin-NADP reductase of plant and acts together with APX during the dismutation of  $\text{H}_2\text{O}_2$ . As compared to DHAR it is more efficient enzyme in converting monodehydroascorbate to ascorbate (Tiwari *et al.* 2023) <sup>[69]</sup>.

Dehydroascorbate reductase (DHAR) oxidized the glutathione and regenerates the ascorbic acid (AsA) for its recycle in the scavenging of H<sub>2</sub>O<sub>2</sub>. The cellular ascorbic acid concentration again maintained by this pathway. Cysteine residue in the enzyme involves in the regeneration of AsA from reduction of dehydroascorbate and reduces dehydroascorbate to AsA (Kaur *et al.*, 2019) <sup>[36]</sup>. The oxidized catalytic cysteine residue is reduced again from sulphenic to sulphinic acid using glutaredoxin and again regenerates the DHAR for next cycle of the Halliwal-Asada pathway (Castro *et al.*, 2021) <sup>[10]</sup>.

Glutathione reductase (GR) mainly presents in a chloroplast but also present in cytosol and mitochondria. It plays essential role in ascorbate-glutathione cycle and defense against ROS (Menconi *et al.*, 1995) <sup>[49]</sup>. Glutathione (GSH) in its reduced state acts as antioxidants and glutathione reductase keep the reduced state of Glutathione and maintains the GSH pool in the cell. Hence, GR and GSH help in suppression of oxidative stress in pulses during the drought stress (Rani *et al.*, 2020) <sup>[62]</sup>.

### Glutathione peroxidase (GPX)

H<sub>2</sub>O<sub>2</sub> dismutated to H<sub>2</sub>O by using reduced glutathione catalyzed by glutathione peroxidase. The oxidized glutathione again reduced by glutathione reductase using reducing molecule NADPH (Chowdhury *et al.*, 2024) <sup>[12]</sup>. Glutathione peroxidase mediated ROS scavenging generally occurs in chloroplast and cytosol (Long He *et al.*, 2017).

### Effect of water stress on yield

Water stress at critical stages of growth viz. flowering, pod formation, grain filling etc. cause significant reduction in yield and it has been reported that 50% to 60% of loss in yield of pulses occurs in drought stress. The yield determining factors such as leaf area index, photosynthetic activity and harvest index reduced in pulses under water deficit (Dietz *et al.*, 2021) <sup>[14]</sup>. The water stress at maturity stage reduce the time of flowering while water stress after flowering stage reduce the grain-filling period which eventually reduce the grain size and yield (Garcia-Leon *et al.*, 2021) <sup>[21]</sup>. Moreover, water is the platform of metabolic reaction hence any stages of growth affected by deficiency of water (Khatun *et al.*, 2021) <sup>[40]</sup>.

### Conclusion

When plants suffer from either biotic or abiotic stress or developmental stress such as ripening and senescence, the production of ROS increased in the cell. The production and removal of ROS in cell balanced when the antioxidants activity and content of antioxidants sufficient in the cell. Secondly, the morphophysiological behavior of plants which are regulated either by intrinsic or extrinsic factors that concentration must be maintained during the stress.

### References

1. Ahluwalia O, Singh PC, Bhatia R. A review on drought stress in plants: Implications, mitigation and the role of plant growth promoting rhizobacteria. *Resources, Environment and Sustainability*, 2021;5:100032.
2. Ahmad Z, Waraich EA, Akhtar S, Anjum S, Ahmad T, Mahboob W, *et al.* Physiological responses of wheat to drought stress and its mitigation approaches. *Acta Physiol. Plant.*, 2018;40:1–13.
3. Anjum SA, Ashraf U, Tanveer M, Khan I, Hussain S, Shahzad B, *et al.* Drought induced changes in growth, osmolyte accumulation and antioxidant metabolism of three maize hybrids. *Front. Plant Sci.*, 2017;8:69.
4. Awasthi R, Kaushal N, Vadez V, Turner NC, Berger J, Siddique KHM, *et al.* Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. *Funct. Plant Biol.*, 2014;41:1148.
5. Bangar P, Chaudhury A, Tiwari B, Kumar S, Kumari R, Bhat KV. Morphophysiological and biochemical response of mung bean (*Vigna radiata* (L.) Wilczek) varieties at different developmental stages under drought stress. *Turk J Biol.*, 2019;43(1):58–69.
6. Bashir SS, Hussain A, Hussain SJ, Wani OA, Zahid Nabi S, Dar NA, *et al.* Plant drought stress tolerance: Understanding its physiological, biochemical and molecular mechanisms. *Biotechnol. Biotechnol. Equip.*, 2021;35:1912–1925.
7. Basu S, Sarkar S, Prasad R, Kumar G. Current approaches for alleviating abiotic stress tolerance in crops: Role of beneficial microorganisms. *Beneficial Microorg. Agric.*, 2022, 231–248.
8. Bengough AG, Mckenzie B, Hallett P, Valentine T. Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. *J. Exp. Bot.*, 2011;62:59–68.
9. Boguszewska-Mańkowska D, Zarzyńska K, Nosalewicz A. Drought differentially affects root system size and architecture of potato cultivars with differing drought tolerance. *Am. J. Potato Res.*, 2020;97:54–62.
10. Castro B, Citterico M, Kimura S, Stevens DM, Wrzaczek M, Coaker G. Stress-induced reactive oxygen species compartmentalization, perception and signaling. *Nat. Plants.*, 2021;7:403–412.
11. Choudhury S, Panda P, Sahoo L, Panda SK. Reactive oxygen species signaling in plants under abiotic stress. *Plant Signal Behav.*, 2013, 8(4).
12. Chowdhury MSN, Sani MNH, Siddique AB, Hossain MS, Yong JWH. Synergistic effects of biochar and potassium co-application on growth, physiological attributes, and antioxidant defense mechanisms of wheat under water deficit conditions. *Plant Stress.*, 2024;12:100452.
13. Demmig-Adams B, Adams III WW. Photoprotection in an ecological context: the remarkable complexity of thermal energy dissipation. *New Phytol.*, 2006;172(1):11–21.
14. Dietz KJ, Zörb C, Geilfus CM. Drought and crop yield. *Plant Biol.*, 2021;23:881–893.
15. Devi P, Jha UC, Prakash V, Kumar S, Parida SK, Paul PJ, *et al.* Response of physiological, reproductive function and yield traits in cultivated chickpea (*Cicer arietinum* L.) under heat stress. *Front. Plant Sci.*, 2022;13:1–19.
16. Ding Y, Wang W, Zhuang Q, Luo Y. Adaptation of paddy rice in China to climate change: The effects of shifting sowing date on yield and irrigation water requirement. *Agric. Water Manage.*, 2020;228:105890.
17. Du H, Huang F, Wu N, Li X, Hu H, Xiong L. Integrative regulation of drought escape through ABA-dependent and independent pathways in rice. *Mol. Plant.*, 2018;11:584–597.

18. Fieder J, Burda K. Potential role of Carotenoids as antioxidants in Human health and disease. *Nutrients*,2014;6:466-488.
19. Forni C, Facchiano F, Bartoli M, Pieretti S, Facchiano A, Arcangelo D, *et al.* Beneficial role of Phytochemicals on Oxidative stress and age-related diseases. *Bio Med Research International*, 2019, 1-17.
20. Foyer CH, Haynes PA, Noctor G. Redox signaling and stress memory in plants. *Plant Physiol. Biochem*,2020;155:81-93.
21. Garcia-Leon D, Standardi G, Staccione A. An integrated approach for the estimation of agricultural drought costs. *Land Use Policy*,2021;100:104923.
22. Ghosh UK, Islam MN, Siddiqui MN, Cao X, Khan MAR. Proline, a Multifaceted Signalling Molecule in Plant Responses to Abiotic Stress: Understanding the Physiological Mechanisms. *Plant Biol*,2021;23:1-14.
23. Gill SS, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*,2010;48:909-930.
24. Guerfel M, Baccouri O, Boujnah D, Chaibi W, Zarrouk M. Impacts of water stress on gas exchange, water relations, chlorophyll content and leaf structure in the two main Tunisian olive (*Olea europaea* L.) cultivars. *Sci. Horticult*,2009;119:257-263.
25. Hasanuzzaman M, Alam MM, Rahman A, Hasanuzzaman M, Nahar K, Fujita M. Exogenous glutathione mitigates salt stress in mung bean by regulating the antioxidant defense and methylglyoxal detoxification systems. *Plants*,2019;8:575.
26. Hasanuzzaman M, Bhuyan MHMB, Zulfiqar F, Raza A, Mohsin SM, Mahmud JA, *et al.* Reactive oxygen species and antioxidant defense in plants under abiotic stress: Revisiting the crucial role of a universal defense regulator. *Antioxidants*,2020;9:681.
27. Hodges DM, Lester GE, Munro DK, Toivonen PMA. Oxidative stress: Importance for postharvest quality. *Hort Science*,2004;39:924-929.
28. Hollander-Czytko H, Grabowski J, Sandorf I, Weckermann K, Weiler EW. Tocopherol content and activities of tyrosine aminotransferase and cystine lyase in *Arabidopsis* under stress conditions. *Journal of Plant Physiology*,2005;162:767-770.
29. Jain AK. Heat sensitivity on physiological and biochemical traits in chickpea (*Cicer arietinum* L.). *Adv. Environ. Res*,2014;3(4):307-19.
30. Jayawardhane J, Goyali JC, Zafari S, Igamberdiev AU. The response of cowpea (*Vigna unguiculata*) plants to three abiotic stresses applied with increasing intensity: Hypoxia, salinity and water deficit. *Metabolites*,2022;12(1):38.
31. Jha UC, Devi P, Prakash V, Kumar S, Parida SK, Paul PJ, *et al.* Response of physiological, reproductive function and yield traits in cultivated chickpea (*Cicer arietinum* L.) under heat stress. *Front Plant Sci*, 2022, 13.
32. Jimenez A, Creissen G, Kular B, Firmin J, Robinson S, Verhoeven M, *et al.* Changes in oxidative processes and components of the antioxidant system during tomato fruit ripening. *Planta*,2002;214:751-758.
33. Jincy M, Jeyakumar P, Boominathan P, Manivannan N, Varanavasiappan S, Prasad VBR. Impact of drought and high temperature stress on oxidants and antioxidants in greengram (*Vigna radiata* (L.) Wilczek). *J. Pharmacogn Phytochem*,2019;8(3):1809-13.
34. Jongdee B, Fukai S, Cooper M. Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. *Field Crop. Res*,2002;76:153-163.
35. Kamatchi KM, Anitha K, Kumar KA, Senthil A, Kalarani MK, Djanaguiraman M. Impacts of combined drought and high temperature stress on growth, physiology and yield of crops. *Plant Physiology Reports*,2024;29(1):28-36.
36. Kaur N, Kaur J, Grewal SK, Singh I. Effect of heat stress on antioxidative defense system and its amelioration by heat acclimation and salicylic acid pre-treatments in three pigeon pea genotypes. *Indian J Agric Biochem*,2019;32(1):106-10.
37. Kaushal N, Awasthi R, Gupta K, Gaur P, Siddique KHM, Nayyar H. Heatstress-induced reproductive failures in chickpea (*Cicer arietinum*) are associated with impaired sucrose metabolism in leaves and anthers. *Funct. Plant Biol*,2013;40:1-16.
38. Keerthi Sree Y, Lakra N, Manorama K, Ahlawat Y, Zaid A, Elansary HO, *et al.* Drought-induced morpho-physiological, biochemical, metabolite responses and protein profiling of chickpea (*Cicer arietinum* L.). *Agronomy*,2023;13(7):1814.
39. Khan N, Bano A, Rahman MA, Rathinasabapathi B, Babar MA. UPLC-HRMS-based untargeted metabolic profiling reveals changes in chickpea (*Cicer arietinum*) metabolome following long-term drought stress. *Plant Cell Environ*,2019;42(1):115-32.
40. Khatun M, Sarkar S, Era FM, Islam AKMM, Anwar MP, Fahad S, *et al.* Drought Stress in Grain Legumes: Effects, Tolerance Mechanisms and Management. *Agronomy*,2021;11:2374.
41. Kim I, Chae HM, Choi B. Effects of experimental through fall exclusion on soil respiration in a continental coniferous stand, South Korea. *Forests*,2020;11:972.
42. Kumar AN, Vijayalakshmi C, Vijayalakshmi D. Chlorophyll and chlorophyll fluorescence as influenced by combined heat and drought stress in rice. *Trends Biosci*,2014;7:1461-1465.
43. Kumari VV, Roy A, Vijayan R, Banerjee P, Verma VC, Nalia A, *et al.* Drought and heat stress in cool-season food legumes in sub-tropical regions: consequences, adaptation, and mitigation strategies. *Plants*,2021;10:1-21.
44. Kumawat A, Yadav D, Samadharmam K, Rashmi I. Soil and water conservation measures for agricultural sustainability. In *Soil Moisture Importance*; IntechOpen: London, UK., 2020.
45. Lima RP, Silva DD, Moreira MC, Passos JB, Coelho CD, Elesbon AA. Development of an annual drought classification system based on drought severity indexes. *Anais da Academia Bras. Ciências*,2019;91:e20180188.
46. Liu P, Guo W, Jiang Z, Pu H, Feng C, Zhu X, *et al.* Effects of high temperature after anthesis on starch granules in grains of wheat (*Triticum aestivum* L.). *J. Agric. Sci*,2011;149:159-169.
47. Mafakheri A, Siosemardeh AF, Bahramnejad B, Struik PC, Sohrabi Y. Effect of drought stress on yield, proline

- and chlorophyll contents in three chickpea cultivars. *Aust. J. Crop Sci.*,2010;4:580-585.
48. Malacrida CR, Kimura M, Jorge N. Phytochemicals and antioxidant activity of citrus seed oils. *Food Science Technology Research.*,2012;18:399-404.
  49. Menconi M, Sgherri CLM, Pinzino C, Navari-Izzo F. Activated oxygen production and detoxification in wheat plants subjected to a water deficit programme. *J. Exp. Bot.*,1995;46:1123-1130.
  50. Meriga B, Reddy BK, Rao KR, Reddy LA, Kishor PK. Aluminium-induced production of oxygen radicals, lipid peroxidation and DNA damage in seedlings of rice (*Oryza sativa*). *J Plant Physiol.*,2004;161(1):63-68.
  51. Miller G, Shulaev V, Mittler R. Reactive oxygen signaling and abiotic stress. *Physiol Plant.*,2008;133(3):481-89.
  52. Mishra P, Al Khatib AM, Lal P, Anwar A, Nganvongpanit K, Abotaleb M, *et al.* An overview of pulses production in India: retrospect and prospects of the future food with an application of hybrid models. *National Academy Science Letters.*,2023;46(5):367-74.
  53. Mishra SS, Panda D. Leaf traits and antioxidant defense for drought tolerance during early growth stage in some popular traditional rice landraces from Koraput, India. *Rice Sci.*,2017;24:207-217.
  54. Mishra N, Jiang C, Chen L, Paul A, Chatterjee A, Shen G. Achieving abiotic stress tolerance in plants through antioxidative defense mechanisms: A Comprehensive Review. *Front. Plant Sci.*,2023;14:1110622.
  55. Mittler R. Oxidative stress, antioxidants and stress tolerance. *Trends Plant Sci.*,2002;7:405-410.
  56. Moller IM, Jensen PE, Hansson A. Oxidative modifications to cellular components in plants. *Annu. Rev. Plant Biol.*,2007;58:459-481.
  57. Mundiyyara R, Kumar P, Jitarwal RK, Bajya M, Bhat L. Different antioxidants in fruits and vegetables for human health. *International Journal of Pure and Applied Bioscience.*,2017;5:340-346.
  58. Nadeem M, Li J, Yahya M, Sher A, Ma C, Wang X, *et al.* Research Progress and Perspective on Drought Stress in Legumes: A Review. *Int. J. Mol. Sci.*,2019;20:2541.
  59. Nayyar H, Gupta D. Differential sensitivity of C3 and C4 plants to water deficit stress: association with oxidative stress and antioxidants. *Environ. Exp. Bot.*,2006;58:106-113.
  60. Pandey BB, Ratnakumar P, Usha Kiran B, Dudhe MY, Lakshmi GS, Ramesh K, *et al.* Identifying traits associated with terminal drought tolerance in sesame (*Sesamum indicum* L.) genotypes. *Front. Plant Sci.*,2021;12:739896.
  61. Raina SK, Govindasamy V, Kumar M, Singh AK, Rane J, Minhas PS. Genetic variation in physiological responses of mung beans (*Vigna radiata* (L.) Wilczek) to drought. *Acta Physiol Plant.*,2016;38:1-12.
  62. Rani A, Devi P, Jha UC, Sharma KD, Siddique KH, Nayyar H. Developing climate-resilient chickpea involving physiological and molecular approaches with a focus on temperature and drought stresses. *Front Plant Sci.*,2020;10:1759.
  63. Rehschuh R, Ruehr NK. Diverging responses of water and carbon relations during and after heat and hot drought stress in *Pinus sylvestris*. *Tree Physiol.*,2022;42:1532-1548.
  64. Shahidi F, Janitha PK, Wanasundara PD. Phenolic antioxidants. *Critical Review in Food Science and Nutrition.*,1992;32:67-103.
  65. Salgotra RK, Chauhan BS. Ecophysiological responses of rice (*Oryza sativa* L.) to drought and high temperature. *Agronomy.*,2023;13:1877.
  66. Shigeoka S, Ishikawa T, Tamoi M, Miyagawa Y, Takeda T, Yabuta Y, *et al.* Regulation and function of ascorbate peroxidase isoenzymes. *J. Exp. Bot.*,2002;53:1305-1319.
  67. Stewart AJ, Bozonnet S, Mullen W, Jenkins GI, Lean MEJ, Crozier A. Occurrence of flavonols in tomatoes and tomato-based products. *Journal of Agricultural Food Chemistry.*,2000;48:2663-2669.
  68. Suzuki N, Koussevitzky S, Mittler R, Miller G. ROS and redox signalling in the response of plants to abiotic stress. *Plant Cell Environ.*,2012;35(2):259-70.
  69. Tiwari PN, Tiwari S, Sapre S, Tripathi N, Payasi DK, Singh M, *et al.* Prioritization of physio-biochemical selection indices and yield-attributing traits toward the acquisition of drought tolerance in chickpea (*Cicer arietinum* L.). *Plants.*,2023;12(18):3175.
  70. Yohannes H, Argaw M, Seifu W. Impact of land use/land cover change on surface water hydrology in Akaki river catchment, A wash basin, Ethiopia. *Phys. Chem. Earth Parts A/B/C.*,2024;135:103690.