

## Trehalose induced drought tolerance in plants: physiological and molecular responses

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### Abstract

Drought stress is significant abiotic stress that limits crop growth and productivity across the globe. The intensity of drought stress continuously rises due to rapid climate change. Drought-induced alterations in physiological and bio-chemical processes by generating membrane dis-stability, oxidative stress, nutritional imbalance and leading to substantial reduction in growth and productivity. Plants accumulate various osmolytes that protect themselves from abiotic stresses' harmful effects. Trehalose (Tre) is a non-reducing sugar found in multiple microbes ranging from bacteria to yeast and in plants and it possesses an excellent ability to improve drought tolerance. Trehalose appreciably enhanced the plant growth, and counter the drought induced damages by maintaining cellular membranes, plant water relations, stomatal regulation, photosynthetic activities, nutrient uptake, osmolyte accumulation, activating stress proteins and detoxifying the reactive oxygen species (ROS) by strengthening the anti-oxidant system. Therefore, it is essential to understand the mechanism of exogenous and endogenous Tre in mitigating the drought-induced damages and to identify the potential research questions that must be answered in the future. Therefore, to better appraise the potential benefits of Tre in drought tolerance in this review, we discussed the diverse physiological and molecular mechanisms regulated by Tre under drought stress. We have a complete and updated picture on this topic to orientate future research directions on this topic.

**Keywords:** drought; osmolytes accumulation; oxidative stress photosynthesis; stress proteins; trehalose

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**Abbreviations:** ABA: abscisic acid, FC: field capacity, GB: glycine-betaine, H<sub>2</sub>O<sub>2</sub>: hydrogen per-oxide, IAA: Indole acetic acid, LOX: lipoxygenase, MDA: malondialdehyde, mM: milli molar, ROS: reactive oxygen species, RWC: relative water contents, Tre: trehalose, T6P: trehalose-6-phosphate, WUE: water use efficiency.

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## Introduction

Drought is significant abiotic stress that significantly limits crop productivity across the globe (Rollins *et al.*, 2013; Rasheed *et al.*, 2017; Rasheed *et al.*, 2018; Rasheed *et al.*, 2019). The recent climate change has increased the intensity of drought stress, posing a serious threat to crop production and good global security (Hassan *et al.*, 2021; Neha *et al.*, 2021). Thus, it is imperious to understand the mechanisms of drought stress in plants to improve crop productivity (Singh and Laxmi, 2015). Water deficiency is a significant challenge of the 21<sup>st</sup> century because agriculture is the cause and victim of this deficiency because 70% of available water is used in the agriculture section (Akram *et al.*, 2015). The world's population is continuously soaring up; therefore, it is urgent to develop the appropriate to improve crop production to ensure global food security.

Drought stress induces severe alterations in plant physiological and biochemical processes; however, these drought-induced alterations largely depend on the stage of plant growth, frequency, and duration of drought stress (Hassan *et al.*, 2017; Ahmad *et al.*, 2018; Hassan *et al.*, 2019; Hassan *et al.*, 2021). Drought stress also significantly reduced plant growth development (Xiong *et al.*, 2019), photosynthetic efficiency (Dias *et al.*, 2021), nutrient absorption, carbohydrate, and chlorophyll synthesis (Akram *et al.*, 2017; Fahad *et al.*, 2017). Reactive oxygen species (ROS) are produced due to abiotic stresses (Rasheed *et al.*, 2020b; Rasheed *et al.*, 2021c) which damage lipids, enzymes configuration and resultantly cause cell death (Waszczak *et al.*, 2018; Khan *et al.*, 2020). Moreover, plants have an anti-oxidant defense system that protects them from ROS's adverse impacts (Sewelam *et al.*, 2016; Hasanuzzaman *et al.*, 2019). Nonetheless, severe drought stress disrupted this anti-oxidant system and cause imbalance in redox homeostasis in plant cells (Talaat *et al.*, 2015).

To cope with abiotic stresses plants have developed different mechanisms (Rasheed *et al.*, 2020a; Rasheed *et al.*, 2020; Rasheed *et al.*, 2021a; Rasheed *et al.*, 2021b), including the accumulation of different osmolytes to mitigate the deleterious impacts of drought stress (Ashraf, 2009). Plants grown under drought stress possess an excellent ability to accumulate various osmolytes; however, the accumulation of these osmolytes varies from species to species. Nonetheless, the accumulation of osmolytes substantially improved the plant tolerance against drought stress (Khan *et al.*, 2010). Moreover, exogenous application of different osmolytes is also considered as an effective, eco-friendly, and economical approach to reducing deleterious impacts of abiotic stresses (Ahmad *et al.*, 2018; Hassan *et al.*, 2019; Mehmood *et al.*, 2021; Seleiman *et al.*, 2021a). Trehalose is a non-reducing sugar (Fichtner and Lunn, 2021), and it acts as an essential protective agent under adverse environmental conditions (Acosta-Pérez *et al.*, 2020). Trehalose is chemically non-reactive and it has higher solubility, which allows him to accumulation at higher concentrations without affecting the normal metabolism (Lin *et al.*, 2020; Wang *et al.*, 2020a). Trehalose also improves drought tolerance in plants, and beneficial impacts of Tre in enhancing drought tolerance are linked with its ability to enhance the anti-oxidant activities, cellular redox balance, and photosynthetic efficiency (Lin *et al.*, 2020; Kosar *et al.*, 2021). Trehalose stabilizes plant biological structures by crystallizing into a glassy state that resists drought tolerance (Acosta-Pérez *et al.*, 2020). Additionally, Tre is in-expensive and widely available and its exogenous application appreciably improved the plant tolerance against drought stress (Lin *et al.*, 2020; Kosar *et al.*, 2021).

In recent years considerable research has been performed to explore the role of Tre in mitigating drought stress. However, the role of Tre in mitigating the drought stress is not fully explored, and there is a dire need to have comprehensive knowledge about the exact mechanisms of Tre-induced drought tolerance in plants. Therefore, this review has discussed the recent advances linked with Tre-mediated drought tolerance in plants.

We also shed light on future research direction for making him an essential osmo-protectant for drought tolerance.

### **Effect of drought stress on plants**

Plants face many abiotic stresses during their life cycle, which negatively affect their growth and productivity. Drought stress negatively affects plant growth, productivity, and quality (Zlatev and Lidon, 2012; Jaleel *et al.*, 2009; Mafakheri *et al.*, 2010). Drought stress also negatively affects cell division, cell elongation and causes a reduction in turgor pressure (Figure 1), photosynthetic efficiency, and enzymatic activities (Osakabe *et al.*, 2014). The turgor and water potential of plants is significantly decreased under drought stress (Figure 1). Plants cannot perform well under these conditions (Zlatev and Lidon, 2012; Osakabe *et al.*, 2014). Drought also induced a reduction in relative water contents (RWC) (Farooq *et al.*, 2009) and lower RWC leads to a reduction in leaf water potential and causes stomata closing. Drought-induced increase in stomatal resistance decreases the transpiration rate and increases leaf temperature, reducing membrane stability and affecting plant metabolism (Ahmad *et al.*, 2018). All these alterations are the main reasons for disturbed photosynthetic efficiency, mineral uptake, and synthesis of proteins and amino acids (Tiwari and Yadav, 2020). The less water availability also reduced the nutrient uptake (Elemike *et al.*, 2019), which is a significant reason for the drought-induced reduction in growth and productivity (Hafez and Seleiman, 2017).

Drought stress negatively affects the inter-cellular CO<sub>2</sub> concentration, reducing the photosynthetic electron transport and leading to ROS production of ROS which cause damages to photosynthetic apparatus (Basu *et al.*, 2016). The disruption in photosynthetic apparatus due to ROS causes reduction in photosynthetic and transpiration rate and efficiency of PS-II (Meng *et al.*, 2014; Campos *et al.*, 2019;). The stomata closing during drought stress is regulated by increased ABA level, which works as a signaling molecule to modulate diverse physiological and molecular processes. ABA also works as a primary messenger for cell signaling, which increases ROS production followed by increased Ca<sup>2+</sup> accumulation in the cytosol, which acts as a secondary messenger to stimulate other signaling cascades to regulate plants processes at the molecular level (Osakabe *et al.*, 2014).

Drought stress also induced ROS production (Hussain *et al.*, 2018), which causes damages to membranes, proteins, and lipids (Apel and Hirt, 2004). Moreover, increased ROS also causes a reduction in CO<sub>2</sub> fixation along with increased photo-respiration (Cruz and Milach, 2004). Plants possess an excellent defense system (enzymatic and non-enzymatic) to cope with drought-induced ROS production (Gill and Tuteja, 2010; Hassan *et al.*, 2021; Seleiman *et al.*, 2021b). However, severe drought stress also causes an imbalance in redox homeostasis resulting in a reduction in anti-oxidant activities (Sharma and Dubey, 2005). The intensity, duration, and frequency of drought stress and plant growth stage strongly influence the drought-induced damages (Zoghi *et al.*, 2019). Drought stress increased leaf senescence and dropping cause leaf rolling and the brittleness (Ruehr *et al.*, 2019). Moreover, drought stress also causes flower sagging etiolation, wilting, and leaf yellowing, resulting in a reduction in final productivity (Ruehr *et al.*, 2019). In many cases drought stress also cause branches dieback, leaf necrosis, stunted growth and cracking of plant bark and shrubs (Toscano *et al.*, 2019). Additionally, plants are also dying under drought stress (Zargar *et al.*, 2017). In conclusion, drought stress negatively affects the growth, physiology, metabolic processes, biochemical functioning resulting in substantial reduction in final productivity. Plants cannot move from their place; therefore, they must have to tolerate the drought stress. Plants have developed a different mechanism to confer drought tolerance. The response of plants to drought stress is very complex. Plants generally rely on three other tools: drought escape, avoidance, and tolerance, to cope with the harsh conditions of drought stress (Hassan *et al.*, 2020).

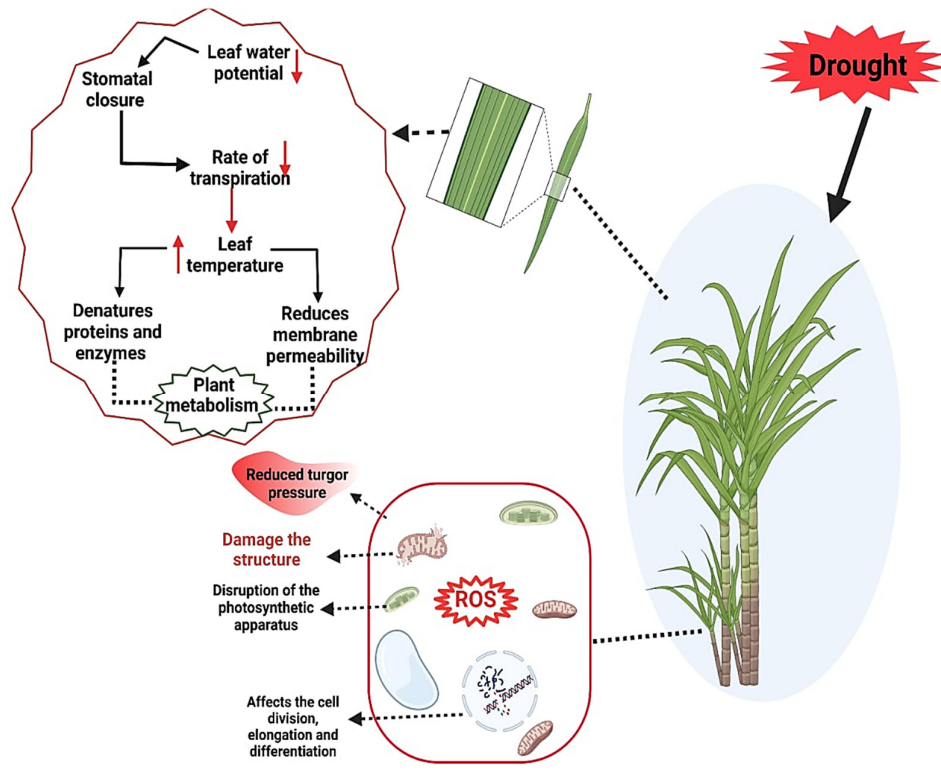
**Table 1.** Effect of drought stress on crop growth, yield, and quality

Crop	Drought stress	Effects	References
Maize ( <i>Zea mays</i> )	50% FC	Drought stress decreased root and shoot biomass, photosynthetic pigments and increased the accumulation of MDA and H <sub>2</sub> O <sub>2</sub> .	(Shemi <i>et al.</i> , 2021)
Soybean ( <i>Glycine max</i> )	30% FC	Drought reduced biomass production, RWC, and soluble sugars.	(Imran <i>et al.</i> , 2021b).
Safflower ( <i>Carthamus tinctorius</i> )	25% FC	Drought stress reduced the leaf area, plant biomass production and increased the accumulation of secondary metabolites.	(Chavoushi <i>et al.</i> , 2020)
Sunflower ( <i>Helianthus annuus</i> )	Drought was imposed by withholding water for ten days.	Drought stress decreased the root and shoot growth, leaf nutrient, protein, and phenolic contents	(Khan <i>et al.</i> , 2018)
Coffee ( <i>Coffea arabica</i> )	40% FC	Drought stress reduced the chlorophyll contents and increased the anti-oxidant activities.	(Cherono <i>et al.</i> , 2021)
Rice ( <i>Oryza sativa</i> )	Drought was imposed by withholding water for 60 days.	Drought stress decreased the yield and increased the brown rice rate, kernel chalkiness, and kernel protein and amylase contents.	(Yang <i>et al.</i> , 2019)

FC: field capacity

### Trehalose biosynthesis and structural properties

Trehalose biosynthesis in plants involving the production of trehalose-6-phosphate (T6P) from glucose-6-phosphate and UDP-glucose by trehalose-6-phosphate synthase (TPS), and the subsequent dephosphorylation of T6P to trehalose by trehalose-6-phosphate phosphatase (TPP) (Cabib and Leloir, 1958). Trehalose is a non-reducing sugar that contains two sub-units of glucose linked by alpha-1 glycosidic bond. Moreover, Tre is also considered a special disaccharide sugar because both reducing sub-units are involved in making the glycosidic bond (Jain and Roy, 2009). Tre also remains resistant against hydrolysis and elevated temperature (Teramoto *et al.*, 2008). Moreover,  $\alpha$ - $\alpha$  linkage of Tre is also very stable (Richards *et al.*, 2002), and it also has higher hydrophilicity owing to its inability for internal hydrogen bonding (Paul and Paul, 2014). Trehalose also possesses an excellent vitrification and dehydration ability (Shafiq *et al.*, 2015). In the dehydration case, Tre makes a hydrogen bond with surrounding membranes and molecules by replacing water molecules (Crowe, 2007). In severe water deficiency Tre also crystallized into glassy appearance that is its particular characteristic (Cesaro *et al.*, 2008; Einfalt *et al.*, 2013). The formation of the glassy appearance of Tre under water deficiency preserves the bio-molecules and recovers their functional activities (Fernandez *et al.*, 2010). Trehalose acts as inert sugar, and it has deficient bonding energy (1 kcal mol<sup>-1</sup>) (Schwarz and Van Dijck, 2017), all these characteristics make Tre is an important osmoprotectant to be used under stress conditions.



**Figure 1.** Drought stress-induced stomata closure decreases the rate of transpiration, membrane permeability, denatures proteins and enzymes, damages cellular structures and photosynthetic apparatus, therefore, causes a significant reduction in final productivity

### Effect of trehalose on growth and development under drought stress

Drought stress significantly reduced seed germination owing to reduced water availability. The reduced seed germination due to drought reduces planting density and final productivity (Hassan *et al.*, 2019; Joshi *et al.*, 2020). Trehalose appreciably improved the seed germination and resulting in significant improvement in growth and productivity (Table 2). Likewise, Horita and Saruyama (2006) noted that seed treatment with Tre (400 mM) appreciably improved the seed germination and subsequent seedling growth of onion. Trehalose application also overcame the stress response and improved germination due to better carbon assimilation and protection from stress-induced oxidative stress (Farooq *et al.*, 2017). Trehalose supply appreciably improved the plant growth and development in water deficit conditions (Table 2).

The improved growth under drought stress with Tre is attributed to the maintenance of membrane integrity, better photosynthetic efficiency, and chlorophyll synthesis. Tre mediated the protection of membranes and PS-II from over-excitation and oxidative stress (Kosar *et al.*, 2018; Zulfiqar *et al.*, 2021). Trehalose application enhanced the photosynthetic performance by interacting with sugar signaling (Ibrahim and Abdellatif, 2016). Improved photosynthetic efficiency with Tre leads to an appreciable increase in plant height, yield traits, grain weight and grain productivity.

**Table 2.** Effect of trehalose application on growth, yield, and quality under drought stress

Crop	Drought stress	Tre application	Effects	References
Sunflower ( <i>Helianthus annuus</i> )	In drought stress, 6 irrigations were applied while in control eight irrigations were applied	30 mM	Tre application improved the root and shoot growth, achene yield, oil contents, and total protein contents	(Kosar <i>et al.</i> , 2021)
Sweet Basil ( <i>Ocimum basilicum</i> )	60% FC	30 mM	Tre supplementation improved the root and shoot growth, biomass production	(Zulfiqar <i>et al.</i> , 2021)
Wheat ( <i>Triticum aestivum</i> )	Drought stress was imposed by applying irrigation with 20 days interval	10 mM	Tre supply improved the root and shoot growth, biomass production, yield traits, grain weight, accumulation of protein, amino acids, and phenolic	(Ibrahim and Abdellatif, 2016)
Radish ( <i>Raphanus sativus</i> )	60% FC	25 mM	Tre supply plant growth, biomass production, and nutrient contents (phosphorus and calcium) in plant parts	(Akram <i>et al.</i> , 2016)
Radish ( <i>Raphanus sativus</i> )	60% FC	50 mM	Exogenous applied Tre improved the root and shoot growth, biomass production, and total phenolic contents	(Shafiq <i>et al.</i> , 2015)

FC: Field capacity, mM: milli molar

Trehalose supplementation also up-regulated the oxidant defense system and maintained the turgor potential and nutritional balance under drought stress, leading to an appreciable increase in growth (Alam *et al.*, 2014). The onset drought stress damaged the PS-I and PS-II, which negatively reduced the synthesis of chlorophyll contents (Athari and Talebi, 2014). However, Tre supply markedly improved the chlorophyll contents by protecting the photosynthetic apparatus from oxidative stress and increasing growth under drought stress (Akram *et al.*, 2016; Sadak, 2016). Additionally, Tre increased tolerance against drought by improving water retention and osmoregulation and closing stomata at drought stress (Gómez *et al.*, 2010). In conclusion, Tre improved the plant water relationships, photosynthetic performance, anti-oxidant activities and maintained the membrane integrity, resulting in marked improvement in growth under drought stress.

#### **Effect of Trehalose on membrane stability and plant water relationships under drought stress**

Drought stress negatively affects plant water relationships, causes oxidative stress, and reduces cell division and plant growth. Moreover, drought stress also increased the electrolyte leakage (EL) owing to the increased accumulation of H<sub>2</sub>O<sub>2</sub> and MDA (Bijanazadeh *et al.*, 2019). However, Tre supplementation maintains the plant water contents and improved plants growth and biomass productivity (Ali and Ashraf, 2011). Trehalose supply reduced the drought-induced oxidative damages on the plant by improving the tissue water status and relative water contents (RWC) and stomatal closing on the occurrence of drought stress (González *et al.*, 2009). Drought stress significantly increased membrane permeability (Hammad and Ali, 2014; Akram *et al.*, 2015). Nonetheless, the Tre supply decreased the membrane permeability and stabilized the membrane integrity under drought stress conditions (Akram *et al.*, 2015; Hammad and Ali, 2014).

The water deficiency alters plant water relations and inhibits photosynthesis and plant growth (Hasanuzzaman *et al.*, 2018) Trehalose, supply maintains the water balance, which was evidenced in terms of better seedling growth, plant height, and biomass production (Alam *et al.*, 2014). Exogenous Tre maintained the osmotic balance, which inhibited the water loss, maintained the RWC and subsequently improved plant growth under drought stress (Alam *et al.*, 2014; Akram *et al.*, 2016). Thus, all these findings suggested that Tre supply maintain the membrane stability and plant water relationships for ensuring better growth under drought stress (Nounjan *et al.*, 2012; Abdallah *et al.*, 2016). In conclusion, Tre improves the anti-oxidant activities, maintain membrane integrity, reducing the MDA and H<sub>2</sub>O<sub>2</sub> accumulation, and improving plant water relationships.

### **Effect of Trehalose on water use efficiency and nutrient uptake under drought stress**

Stomata closing is considered the first line of defense against drought stress. Water use efficiency (WUE) is considerably decreased in drought conditions due to a reduction in the conductance of stomata (Kosar *et al.*, 2018). Stomata movement modification affects the plant photosynthetic efficiency due to protein denaturation linked with the photo-system (Kosar *et al.*, 2018). Drought stress negatively affects the photosynthetic rate (A), stomatal conductance (gs), transpiration rate (E), sub-stomatal CO<sub>2</sub> concentration (C<sub>i</sub>) and WUE, however, foliar spray of Tre appreciably improved the WUE and other traits under drought stress (Angioni *et al.*, 2006; Ali and Ashraf, 2011; Kosar *et al.*, 2018). Likewise, Akram *et al.* (2016) noted that Tre seed priming appreciably improved the WUE of radish plants under drought stress. The onset drought stress decreased the photosynthetic pigments and disrupted the stomatal plant activity (Zulfiqar *et al.*, 2021). However, Tre supply maintains stomata movement by maintaining the membrane integrity (Zulfiqar *et al.*, 2021). Drought stress reduced the K<sup>+</sup> contents in guard cells, which increased the K<sup>+</sup> leakage owing to membrane damage (Hassan *et al.*, 2021). Tre supply maintains K<sup>+</sup> influx and improves the stomatal conductance and osmolyte accumulation, which improves the plant WUE (Zulfiqar *et al.*, 2020). Moreover, the Tre application also lowered the cell osmotic potential, increasing the plants' ability to absorb water from soil, increasing plant water contents (Kaya *et al.*, 2007; Parida *et al.*, 2008). A balance between organic and inorganic nutrients is essential for getting maximum growth and yield (Ashraf, 2009). Drought stress significantly disturbs the nutritional balance and induces a significant reduction in production and final quality (Maksimović *et al.*, 2003; Hu and Schmidhalter, 2005). Drought stress significantly reduced the Ca<sup>2+</sup>, K<sup>+</sup>, and P uptake and accumulation in plants (Kosar *et al.*, 2015; Akram *et al.*, 2016;). However, Tre application improved the uptake and accumulation of Ca<sup>2+</sup>, K<sup>+</sup>, N, and P under drought stress (Kosar *et al.*, 2015; Akram *et al.*, 2016; Dawood, 2017). Moreover, impact Tre application on nutrient uptake under drought stress is poorly studied therefore; more research is direly needed to underpin the role of Tre on nutrient uptake under drought stress. Thus, Tre supply maintains K<sup>+</sup> influx, which improves the stomata conductance and leads to significant improvement in WUE.

### **Effect of trehalose on photosynthesis under drought stress**

Drought stress causes a notable reduction in photosynthetic efficiency, mainly due to dehydration that induces stomata closing and limits CO<sub>2</sub> diffusion. Moreover, drought stress also inhibits the RuBisco activity (Perdomo *et al.*, 2017) and reduces the chlorophyll contents which is also major reasons of drought-induced reduction in photosynthetic efficiency (Sadak, 2016; Dawood, 2017). In contrast, Tre application appreciably overcomes the deficit caused damages and improves the photosynthetic efficiency by increasing the chlorophyll contents (Table 3) (Akram *et al.*, 2016) and carotenoid ranges, which is attributed to preserving the chlorophyll envelope stability and maintenance of chloroplast osmotic potential (Duman *et al.*, 2011; Sadak, 2016).

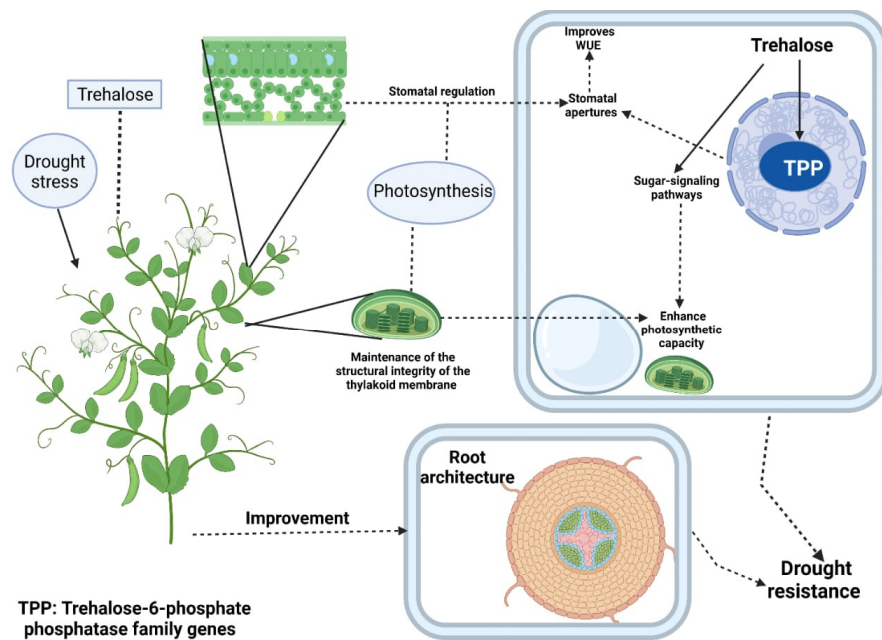
**Table 3.** Effect of trehalose application on photosynthetic parameters and anti-oxidant activities under drought stress

Crop	Drought stress	Tre application	Effects	References
Ginger ( <i>Zingiber officinale</i> )	65% FC	25 mM	Tre application improved the chlorophyll contents, proline, and glycine- betaine and activities of POD and SOD.	(Zulfiqar <i>et al.</i> , 2021)
Sunflower ( <i>Helianthus annuus</i> )	60% FC	30 mM	Tre supplementation improved photosynthetic rate, transpiration rate, stomatal conductance, WUE, anti-oxidant activities, and accumulation of proline and glycine-betaine	(Kosar <i>et al.</i> , 2018)
Wheat ( <i>Triticum aestivum</i> )	Drought stress was imposed by withholding water for 15 days at the plant reproductive stage	1.5 mM	Exogenous applied Tre improved transpiration rate, WUE, and RWC	(Aldesuquy <i>et al.</i> , 2018)
Cowpea ( <i>Vigna unguiculata</i> )	50% FC	500 $\mu$ M	Tre application improved the chlorophyll contents, accumulation of soluble sugars, Tre, proline, and activities of APX, CAT, POD, and SOD	(Khater <i>et al.</i> , 2018)
Fenugreek ( <i>Trigonella foenum-graecum</i> )	60% FC	500 $\mu$ M	Tre application increased the chlorophyll contents, carotenoid contents, carbohydrate, protein, phenolic, and flavonoid contents	(Sadak, 2016)
<i>Brassica napus</i>	Plants were grown in 15% PEG solution	5 mM	Tre application improved the RWC, chlorophyll contents, proline accumulation, reduced the MDA, H <sub>2</sub> O <sub>2</sub> , and LOX contents, and increased AsA, GSH, APX, MDHAR, DHAR, GR, GST, APX and POD activities.	(Alam <i>et al.</i> , 2014)
Maize ( <i>Zea mays</i> )	Drought stress was imposed by applying irrigation after three weeks interval	30 mM	Trehalose improved photosynthetic, transpiration, stomatal conductance, RWC, ascorbic acid, CAT, POD, and SOD activities.	(Ali and Ashraf, 2011)

FC: Field capacity, mM: milli molar, WUE: water use efficiency.



Trehalose supply improved the plant photosynthetic pigments (Figure 2) under drought stress by up-regulating plant water relations and increasing the anti-oxidant activities (Sadak, 2016). Moreover, improved photosynthetic performance under drought stress by Tre application can be due to the interaction of Tre with sugar signaling pathways and increase in endogenous Tre accumulation under drought stress (Zeid, 2009; Paul and Paul, 2014). Trehalose supply also improved the stomatal conductance, which improved the photosynthetic efficiency under drought stress (Ali and Ashraf, 2011). Additionally, the positive effect of Tre on photosynthetic pigments can also be attributed to its role in stabilizing the membranes, protein, and lipids (Lunn *et al.*, 2014; Khater *et al.*, 2018). To summarize, Tre supplementation induces positive effects on photosynthetic attributes. It protects plants from drought, causes oxidative damage, and leads to an appreciable increase in plant photosynthetic performance grown under drought stress.



**Figure 2.** Trehalose mediated improvement in photosynthesis under drought stress  
Trehalose application maintains the membrane integrity, stomatal regulation and triggers the signaling pathways and water uptake, thereby improving photosynthetic efficiency and WUE under drought stress.

### Effect of trehalose on osmolytes and hormones accumulation under drought stress

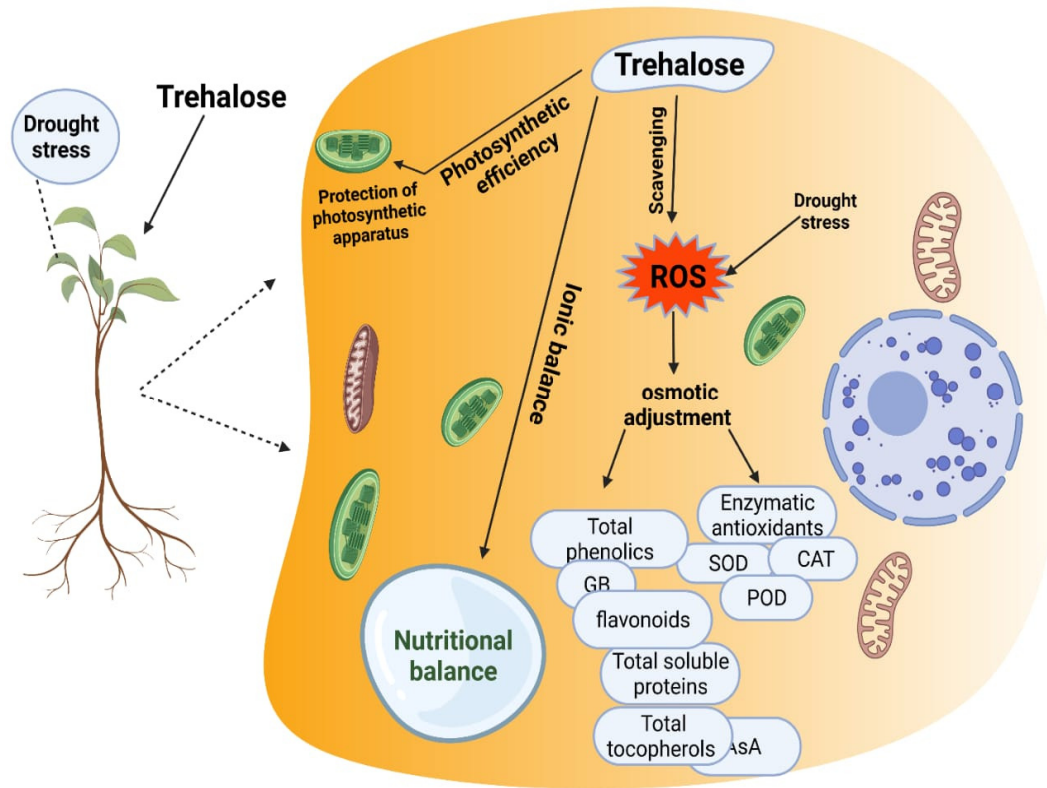
The compatible osmolytes play a significant role in protecting the plants from the deleterious impacts of drought stress (Hassan *et al.*, 2021). These osmolytes up-regulate plant physiological processes and improve the plant's acclimatization under stress conditions (Nounjan *et al.*, 2012). The accumulation of various osmolytes, including proline, glycine-betaine (GB), significantly improved under drought stress tolerance (Kosar *et al.*, 2018). Trehalose application increases the accumulation of GB and proline under drought stress (Alam *et al.*, 2014). Besides foliar supplementation, Tre seed treatment also significantly increased the proline accumulation under water deficit conditions (Akram *et al.*, 2016). Moreover, other authors also reported significant improvements in drought tolerance due to GB accumulation following the exogenous application of Tre (Akram *et al.*, 2012; Shafiq *et al.*, 2015). Trehalose application also improved the accumulation of GB, total soluble sugars, and endogenous Tre, which also confer drought tolerance (Akram *et al.*, 2016). The over-expression of the *OsTPS1* gene improved the Tre biosynthesis, which increased the GB and proline accumulation and conferred the drought tolerance in rice plants (Li *et al.*, 2011).

Plant roots readily take up and transport Tre into above-ground parts, strengthening the plant capacity to withstand the adverse impacts of drought stress (Nounjan *et al.*, 2012; Ma *et al.*, 2013). Trehalose application significantly increased the endogenous Tre under drought stress (Chen and Murata, 2002; Ahmed *et al.*, 2016), and this increase in Tre level maintained the plant turgor pressure and improved the plant performance under drought stress (Khater *et al.*, 2018). Similarly, Zeid (2009) also noted that seed treatment of maize seeds with Tre (10 mM) increased the metabolic activities, photosynthetic pigments, and accumulation of soluble sugars, soluble proteins, and proline under stress conditions. Moreover, Ibrahim and Abdellatif (2016) reported that Tre (10 mM) treatment increased the accumulation of soluble sugars, proline, and free amino acids and confer drought tolerance. Drought-induced significant changes in the accumulation of various hormones. It has been reported that drought stress decreased the IAA accumulation (Dawood, 2017) owing to IAA destruction by increasing the activity of IAA oxidase (Bae *et al.*, 2005). However, Tre, improves drought tolerance by manipulating the accumulation of phytohormones (Ahmed *et al.*, 2016). Likewise, Delorge *et al.* (2014) noted that Tre of T6P participates in a complex network with other hormones to improve plants' growth under stress conditions. To summarize, the Tre supply improved the accumulation of osmolytes and hormones which improved the plant performance by increasing the synthesis of photosynthetic pigments, anti-oxidant activities, and maintaining the membrane integrity.

### **Effect of trehalose on polyamines under drought stress**

Flavonoids are one of the largest classes of plant phenolics that perform various functions in plants ranging from pigmentation to defense (Harborne and Williams, 2000). Drought stress increased the flavonoids accumulation in plants (Haghighi *et al.*, 2012). This increase in flavonoid contents can be due to induction of enzymatic activities that favor flavonoid production under stress conditions (Aldesuquy and Ghanem, 2015). Trehalose application appreciably increased the total phenols and flavonoid contents under drought stress, which is an important practice to reduce the deleterious impacts of drought stress on plant phenols and flavonoids (Aldesuquy and Ghanem, 2015). Trehalose being a signaling molecule, speed up the rate of ROS production which sends signals to activate the anti-oxidant defense system for encountering stress-induced oxidative damages (Aldesuquy and Ghanem, 2015).

The exogenously applied Tre effectively reduce the impacts of oxidative stress (Nounjan *et al.*, 2012; Ma *et al.*, 2013). The foliar spraying of Tre (30 mM) increased the anti-oxidant activities as evidenced by higher flavonoid accumulation under drought stress (Ali and Ashraf, 2011). The increase in phenolics and flavonoid concentration by Tre application can be attributed to the role of Tre as a signaling molecule that induces the plants to activate non-enzymatic anti-oxidants for scavenging of ROS under drought stress (Ibrahim and Abdellatif, 2016). The exogenous Tre application also significantly increased the starch accumulation in *Arabidopsis* seedlings under drought stress (Bae *et al.*, 2005). Exogenously applied Tre induced the starch accumulation by increasing ADP-glucose pyrophosphorylase activity which is considered a major enzyme responsible for starch synthesis (Wingler *et al.*, 2000; Ramon *et al.*, 2007). Ahmed *et al.* (2013) noted that Tre accumulation in the wheat plant has appreciable potential to raise the starch and sucrose contents in wheat shoots. Trehalose also regulates allocation of carbohydrates in plant development under water deficit conditions (Eastmond and Graham, 2003). Trehalose supplementation increases the phenolic plant contents, leading to a substantial increase in anti-oxidant activities and conferring plant stress tolerance (Aldesuquy and Ghanem, 2015; Sadak, 2016). A strong correlation between phenolic contents and anti-oxidant species has been reported in cereals and soybean (Dykes and Rooney, 2007; Kumar *et al.*, 2009). Similarly, a positive correlation between anti-oxidant activities and phenolic contents with Tre application has also been reported in maize (Ali and Ashraf, 2011; Sadak, 2016; Dawood, 2017). Thus, erogenous Tre polyamines confer drought tolerance by regulating the anti-oxidant activities.



**Figure 3.** Effect of trehalose under drought stress

Trehalose application scavenged the by increasing the anti-oxidant activities and accumulation of osmolytes and maintaining the nutritional balance and photosynthetic activities, which improved the drought tolerance.

### Effect of Trehalose on detoxification of ROS and anti-oxidant activities under drought stress

Drought stress induces the production of ROS, which causes damages to major molecules and cellular organelles (Hassan *et al.*, 2017; Hassan *et al.*, 2020). The ROS produced as a result of water deficiency disrupt the membranous fatty acids, which increase lipid per-oxidation and MDA accumulation (Farooq *et al.*, 2013; Shafiq *et al.*, 2015). However, Tre possesses an excellent potential to scavenge the ROS (Figure 3). Many authors noted that Tre supplementation substantially reduced the MDA accumulation in rice, wheat, brassica, and radish crop under drought stress (Theerakulpisut and Phongngarm, 2013; Alam *et al.*, 2014; Shafiq *et al.*, 2015). Lipoxygenase (LOX) activity considerably increased under drought stress with a corresponding increase in MDA accumulation (Sadak *et al.*, 2019). The increased LOX activity contributes to lipid per-oxidation of membrane lipids and thus participates in drought-induced oxidative damages (Sadak *et al.*, 2019). However, Tre significantly reduced the LOX activity and H<sub>2</sub>O<sub>2</sub> and MDA accumulation in plants grown under drought stress (Nounjan *et al.*, 2012; Ma *et al.*, 2013; Sadak *et al.*, 2019).

Anti-oxidant enzymes including SOD, CAT and POD substantially suppress the effects of ROS produced by drought stress (Akram *et al.*, 2017). The activities of these anti-oxidant increased under drought stress; however, server water deficiency significantly reduced activities of these anti-oxidants under drought stress (Selote and Khanna-Chopra, 2010; Darvishan *et al.*, 2013). The exogenous Tre supply increased APX, CAT, POD, and SOD activities and conferred drought tolerance (Aldesuquy and Ghanem, 2015). Trehalose supplementation effectively counters water deficiency impacts because Tre works as direct and indirect

scavengers of ROS under drought stress (Fernandez *et al.*, 2010). Trehalose also works as a signaling molecule under drought, which induces the plants to increase the rate of ROS production and then sends signal to activate the anti-oxidant system for scavenging to ROS to counter the deficit caused by oxidative stress (Fernandez *et al.*, 2010). The exogenous Tre application increased the SOD activity to counter the impacts of ROS (Ali and Ashraf, 2011; Duman *et al.*, 2011; Nounjan *et al.*, 2012). CAT is also an imperative anti-oxidant enzyme with a higher turnover than other enzymes (Garg and Manchanda, 2009). The exogenous Tre application increased the endogenous Tre contents, which increased the CAT activity in maize plants grown in drought stress (Ali and Ashraf, 2011). The exogenous Tre supplementation also improved the APX activities to counter oxidative damages (Yang *et al.*, 2014). Trehalose supplementation appeared to mitigate the drought induced damages with diverse magnitudes by stimulating the enzymatic and non-enzymatic anti-oxidants (Ali and Ashraf, 2011; Aldesuquy and Ghanem, 2015).

In another study Shafiq *et al.* (2015) noted that Tre foliar spray and seed treatment effectively improved the plant growth and reduced the MDA contents by increasing the phenolic contents and activities of CAT, POD, and SOD. The over-expression of OtsA in tobacco increased T6P levels, which increased the photosynthetic efficiency and growth due to improved efficiency of PS-II and anti-oxidant activities (Pellny *et al.*, 2004). Trehalose foliar treatment increased the SOD, scavenging the ROS and protecting the plants from oxidative stress (Nounjan *et al.*, 2012; Abdallah *et al.*, 2016). CAT is also an essential anti-oxidant enzyme (Garg and Manchanda, 2009), and increases CAT activity following Tre supplementation, considered an efficient H<sub>2</sub>O<sub>2</sub> scavenging mechanism under drought stress (Mostofa *et al.*, 2015). Thus, Tre appeared as an effective osmoprotectant to improve the anti-oxidant activities to protect the plants from drought-induced oxidative damage.

### **Effect of Trehalose stress proteins and transcription factors under drought stress**

The stress proteins are water soluble and protect against drought stress by hydrating the cellular structures (Wahid *et al.*, 2007). The over-expression of Tre genes increases the plant tolerance to stress conditions. For instance, over-expression of Tre genes in *Arabidopsis* appreciably increased the plant tolerance to drought, salinity, heat and cold stresses (Miranda *et al.*, 2007; Lin *et al.*, 2019). The over-expression of Tre biosynthetic genes [otsA (TPS) and otsB (TPP)] in rice improved growth and reduced oxidative damages (Garg *et al.*, 2002). Moreover, increase in expression of Tre mediated genes (ZxTPP) appreciably enhanced the drought tolerance in tobacco crop (Pilon-Smits *et al.*, 1998). Additionally, increased Tre levels followed by transformation of *ostA* and *ostB* genes in rice also improved the plant performance under drought and salinity stresses (Garg *et al.*, 2002).

The exogenous Tre supply triggered the calcium and ROS signaling transduction, including and increased the expression of OsTPP1 or OsTPP3 in rice and maize, increasing the drought tolerance (Jiang *et al.*, 2019; Shi *et al.*, 2019). Drought stress also lowered the expression of *ZmTPP1* genes; however, Tre supplementation increased the expression of this gene to confer drought stress (Acosta-Pérez *et al.*, 2020). Likewise, TPP promoters Cis-regulatory element (CREs) and triggers Tre metabolism in plants and improves drought tolerance. For instance, in *Arabidopsis*, ABF1, ABF2, and ABF4 directly affect the expression of AtTPPI to induce drought tolerance by changing the stomatal movements (Lin *et al.*, 2020). The transcriptional factor that responds to ABA in the presence of ABA and ABF2 binds the AtTPPE promoter and triggers its expression for increasing the root length and stomatal movements by producing ROS in water deficiency (Wang *et al.*, 2020b). *DREB1A* is another essential gene that also up-regulated the *AtTPPF* transcription and improved the drought tolerance in plants (Lin *et al.*, 2019). In conclusion, the Tre supply enhances stress expression, which enhances the drought tolerance by increasing the anti-oxidant activities, stomata movements, and ABA accumulation.

### Engineered Trehalose for inducing drought tolerance in plants

The accumulation of different osmolytes, hormones and soluble sugars improves growth and development under stress conditions. Because of the promising characteristics of Tre, efforts are being made to develop transgenic plants with increased Tre levels to confer stress tolerance. The introduction of diverse genes in rice, tomato, and Arabidopsis from the bacteria and yeast has increased their tolerance to stress conditions (Karim *et al.*, 2007). The over-expression Tre biosynthetic genes are imperative for improving plant tolerance against stress conditions. Therefore, TPP and TPS genes got significant attention across the globe owing to their roles in the biosynthesis of Tre (Van Dijk *et al.*, 2002; Delorge *et al.*, 2015). These genes work as imperative growth regulators during stress conditions and improve crop performance in terms of better yield. For instance, AtTPS1 expression in Arabidopsis conferred the drought tolerance by increasing the Tre and T6P levels (Avonce *et al.*, 2004).

*AtTPPF* also regulates the Tre levels and improves plant performance under drought stress (Lin *et al.*, 2019). Similarly, in transgenic tobacco plants, the diverse genes, including *ScTPS1* and *ScTPS2* increased Tre's over-expression and the drought tolerance (Lin *et al.*, 2019). Moreover, *BvMTSH* increases the over-expression of Tre, which in turn improves the plant growth under water deficit conditions (Joo *et al.*, 2014). Another study reported that over-expression of TPP genes improved the yield and yield traits under drought stress (Nuccio *et al.*, 2015). Likewise, OsTPS1 over-expression increased the endogenous Tre and proline levels which conferred the drought, cold, and salinity tolerance (Li *et al.*, 2011). The OsTPS1 over-expression increased the drought tolerance by increasing the accumulation of proline and Tre (Li *et al.*, 2011). Moreover, Jiang *et al.* (2019) noted that OsTPP3 over-expressing plants showed an appreciable improvement in growth and drought tolerance compared to typical plants. In soybean plants, over-expression of *AtDREB1D* genes improved the RWC, and reduced the water loss and improved the drought tolerance by increasing endogenous Tre (Guttikonda *et al.*, 2014). The over-expression of *AtTPPI* genes in transgenic plants enhanced drought tolerance. Abscisic acid (ABA) induced the closing of stomata in genotypes with less expression of *AtTPPI*. In contrast, the over-expression of *AtTPPI* improves the stomata movements, root growth, and WUE compared to genotypes with more minor manifestations of *AtTPPI* in drought stress (Lin *et al.*, 2020). Therefore, engineering Tre is considered an imperative approach to improving the plants' performance grown under drought stress.

### Effect of Trehalose on yield and quality under drought stress

Water deficiency adversely affects the yield contributing traits, final productivity, and quality (Shahbaz *et al.*, 2008; Akram and Ashraf, 2011). Trehalose possesses an excellent ability to improve the plants' growth and production in water deficit conditions. Many authors noted that Tre supplementation improved the growth and productivity of cotton, sunflower, and *Moringa oleifera* (Aamer *et al.*, 2018; Akram and Ashraf, 2011). Trehalose application improved the growth and quality which can be attributed to improved photosynthetic performance, stomatal movement, nutrients uptake, and reduced ROS production (Akram *et al.*, 2017). Moreover, Tre also improved the dry matter production resulting in a significant increase in yield production under stress conditions (Khater *et al.*, 2018). Water deficiency adversely affects the final quality and chemical composition of the final product ((Akram and Ashraf, 2011; Angioni *et al.*, 2006). However, Tre application appreciably improved grain nutrient and protein concentration under drought stress conditions (Kosar *et al.*, 2021). In conclusion, Tre-mediated improvement in yield and quality is linked with ROS scavenging, stomatal movements, and photosynthetic performance.

## Conclusions

Trehalose possesses an excellent potential to improve plant performance under adverse conditions, and it got appreciable attention across the globe to be used as an osmoprotectant. Trehalose supplementation improves plant tolerance against drought stress by scavenging ROS. This increase in ROS scavenging by trehalose protects the plant cells and photosynthetic apparatus from oxidative damages resulting in significant improvement in photosynthetic efficiency and subsequent growth and productivity. Trehalose application also maintains the membrane permeability, plant water relationship, and nutrient uptake, improving the overall plant performance and drought tolerance. Trehalose also triggers the signaling pathways, increases the expression of stress-responsive genes, and accumulates various osmolytes which confers drought tolerance. Drought stress directly reduced the crop yield and final quality; however, the application of Trehalose at the field level can be promising from an agronomic point of view. Recently, genes manipulation linked with enhanced Tre bio-synthesis also produced better results in growth, productivity, and drought tolerance.

Despite all these exciting facts about Tre many questions still need to be answered in future studies. The role of trehalose on plant mineral nutrition under drought stress is poorly studied. Therefore, future studies should determine trehalose's impact on the nutrient accumulation in plants under drought stress. Similarly, role of trehalose on osmolytes and hormones accumulation under drought stress is also poorly studied. Therefore, it would be fascinating to underpin the complexity of trehalose signaling in drought stress to determine if trehalose would increase the endogenous osmol-lytes and hormonal levels to counter the effects of drought stress. Aquaporins are channel proteins that play an impervious role in drought tolerance; however, no single study is available on the impact of trehalose on activity of aquaporins under drought stress. Therefore, future studies must be performed to underpin the role of trehalose on aquaporins activity under drought stress. Moreover, future studies are also direly needed to understand the role of trehalose on the expression of heat shock and late embryogenesis proteins under drought stress. Additionally, functions of TPS and TPP genes are unknown in signaling pathways involved in growth, development, and stress tolerance. Thus, the characterization of TPP and TSS is critical to investigate molecular mechanisms to increase our knowledge and understanding about trehalose for improving drought tolerance by gene manipulation.

## Authors' Contributions

JS conceptualized and prepared the original draft. WW, FR, HM, KH, MIA, TSA, MA, QU, GH, MUH, MA and SHQ reviewed and improved the manuscript. All authors read and approved the final manuscript.

## Ethical approval (for researches involving animals or humans)

Not applicable.

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### Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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