



# Drought Tolerance Strategies in Plants: A Mechanistic Approach

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## Abstract

Anthropogenic activities in the past and present eras have created global warming and consequently a storm of drought stress, affecting both plants and animals. Being sessile, plants are more vulnerable to drought stress and consequently reduce plant growth and yield. To mitigate the effects of drought stress on plants, it is very crucial to determine the plant response mechanisms against drought stress. Drought response mechanism includes morph-physiological, biochemical, cellular and molecular processes takes place in plants underlying drought stress. These processes include improvement in root system, leaf structure, osmotic adjustment, relative water content and stomata regulation. In addition, calcium and phytohormone (Absciscic acid, Jasmonic acid, Salicylic acid, Auxins, Gibberellins, Ethylene etc.) signaling pathways and scavenging of reactive oxygen species are the key mechanisms to cope with drought stress. Moreover, microorganisms such as bacteria and fungi also have an important role in drought tolerance enhancement. To further elucidate and improve drought tolerance in plants, quantitative trait loci, transgenic approach and application of exogenous substances (nitric oxide, 24-epibrassinolide, glycine betaine and proline) are very crucial. Hereby, the present study integrates various mechanisms of drought tolerance in plants.

**Keywords** Bacteria · Drought · Fungi · Phytohormones · Signaling pathways

## Introduction

Water scarcity is the universal problem both in developing and developed countries (Hanna et al. 2016). Anthropogenic activities affect the balance between incoming solar radiation and outgoing radiation as a result the Earth's energy in the form of heat increases and finally leading to global warming (IPCC Climate Change 2014). Global warming

increases water evaporation and consequently leads to drought stress. It is predicted with reasonable belief that at the end of twenty-first century, the wave of heat will be frequent and more intense (Field 2014). Due to increase in temperature, some crucial changes in atmospheric condition could happen, including high summer temperature and drought (Stocker 2014; IPCC Climate change 2013). These climate changes affect trophic interaction, species distribution and ecosystem function. With rapid growth of population, drought and high temperature stresses are expected to be increased in the future. High temperature and water scarcity are two important interconnected stresses affecting crop growth and productivity and ultimately the safety of food (Zandalinas et al. 2017). Hereby, to cope with the drought stress in the future, it is crucial to determine the morph-physiological mechanisms and molecular signaling pathways responsible for increased drought tolerance.

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## Effects of Drought Stress on Plant Growth and Yield

Drought stress generally affect seed germination, plant growth and yield, while specifically it affect transpiration rate, net photosynthetic rate, stomatal conductance, leaf relative water content and water potential (Ullah et al. 2017a). It is one of the most important stresses in arid and semi-arid areas (Anjum et al. 2016, 2017a). About 67% plants yield were reduced due to high temperature and drought stress in past 50 years in the United States (Comas et al. 2013). Drought stress is an uncontrolled stress which damages almost all stages of plants directly or indirectly (Golldack et al. 2014; Anjum et al. 2017b). Seed needs humidity in the soil to be germinate which is affected due to the less amount of water present in the soil (Cardoso 2012). Drought is also responsible for late/less emergence and seedling establishment (Yan 2015; Steiner et al. 2017). Drought stress causes various undesirable effects on productivity due to abnormal physiological process like loss of turgidity, rate of carbon assimilation, gaseous exchange and oxidative damage (Hussain et al. 2018; Ullah et al. 2018a). In addition, it causes decline in leaf development, suffer various enzymatic activities, and absorption of ions which result in loss of crop yield (Anjum et al. 2017a; Todaka et al. 2017). Reactive oxygen species (ROS) are highly reactive and toxic, therefore it may be harmful or beneficial to cell depending upon the concentration (Miller et al. 2010). Over production of ROS damage the cell and may lead to plant necrosis (Petrov et al. 2015). ROS have been discussed in detail in the Sect. 3.4 (Reactive oxygen species). Nutrients are very important for growth and production of crops, specifically macronutrients, and

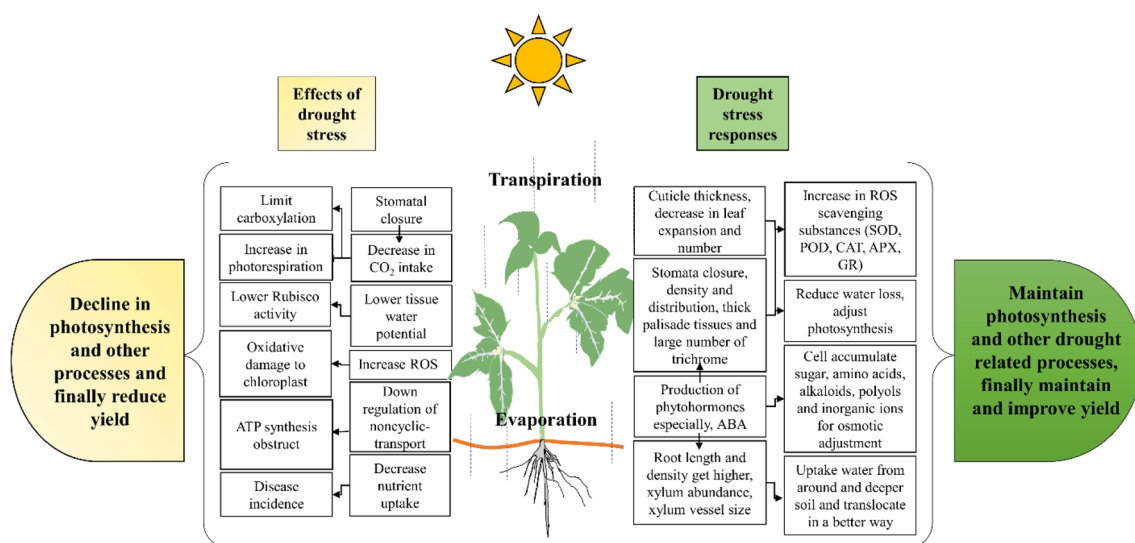
the translocation of nutrients are affected in drought stress condition (Aroca 2012). Drought stress also affects the composition of minerals, antioxidant and proteins (Singh et al. 2012). The accumulative effects of drought stress on plants have been shown in the Fig. 1.

## Plant Response to Drought Stress

Plants underlying drought stress, shows various response mechanisms in the form of morph-physiological and molecular changes.

### Morph-Physiological Response Mechanisms

Plants generally show four kinds of response mechanisms to drought stress i.e., drought avoidance, drought escape, drought tolerance, and drought recovery (Fang and Xiong 2015). Drought tolerance and drought avoidance are the major strategies of plants against water deficit stress. Drought tolerance is the ability of plant to resist dehydration through various physiological activities, such as osmotic adjustment via osmoprotectants (Luo 2010). Drought avoidance is the continuity of physiological processes for example stomata regulation, root system development and other processes during water deficit. Drought escape is the capacity to adjust their life cycle (short life cycle to avoid drought stress). Drought recovery is the ability of plant to restart growth after the exposure to extreme drought stress (Manavalan et al. 2009). Morph-physiological responses of plants to escape, avoid, recover or tolerate drought stress, has been listed below and summarized in the Fig. 1.



**Fig. 1** Effects of drought stress and morpho-physiological responses in plants

## Leaf Structure and Shape

Reduction in transpiration is very important for plants under water deficit condition, dropping and reduction in leaf size reduce transpiration, respectively (Fang and Xiong 2015b). Under water scarcity, the leaves become wilt, margin get yellow, suppress the shoot and leaf development, consequently affect the growth and productivity of plant (Fanizza and Ricciardi 2015). For adaptation to drought stress, plants reduce transpiration via development of waxy and thick leaf cuticle layer (Ullah et al. 2017a). Plant leaves develop some xeromorphic characters, and change their structure to increase drought tolerance, such as smaller and less number of stomata, thick palisade tissues, large number of trichomes, thicker and tiny leaves and developed vascular tissues (Iqbal et al. 2013). For example, overexpressing *MtCAS31* enhanced drought tolerance in transgenic *Arabidopsis* by reducing stomatal density (Xie et al. 2012).

## Root Structure

Roots are possibly the first organ that perceive drought stress, root system have a critical role in response to drought stress. Longer roots are more favorable for drought tolerance as compared to shorter roots. A considerable decrease in number of roots is noted in drought stress, which is demonstrated in *Helichrysum petiolare* (Caser et al. 2016). Drought tolerant adaptive characters of plant roots including long roots, high density, and intense root system. To maintain the productivity under water scarcity, plant needs long roots with high density particularly when water is deeper (Comas et al. 2013). Denser root system also absorbs larger quantity of water than thinner roots because of higher number of roots may contact with more water vapors present in the soil (Abdelraheem et al. 2019). In a case, overexpression of *AtHDG11* enhanced drought tolerance in transgenic cotton by longer and denser root system in addition to other drought tolerance characteristics such as, reduced stomatal content, higher accumulation of malondialdehyde (MDA), proline content and ROS scavenging enzymes (Yu et al. 2016).

## Stomata

In response to drought stress, stomata closure is the first step to reduce transpiration, stomata conductance indicate the drought tolerance. There is an opposite relation between drought tolerance and stomata conductance, i.e., closing of stomata reduce transpiration which enhance drought tolerance, while it's opening increase transpiration and subsequently reduce plant drought tolerance (Ullah et al. 2017a; Clauw et al. 2015). However, there is a direct proportion of stomata conductance with photosynthesis, because stomata regulation is involve in maintenance of photosynthetic

capability of plants under drought stress (Martin et al. 2014). Opening of stomata led CO<sub>2</sub> to the mesophyll tissues and continue photosynthesis process; however, closing of stomata reduce photosynthesis, respectively (Urban et al. 2017). Decrease in number of stomata is another physiological response to drought stress. Moderate drought has an additive impact on the stomata number, while the number of stomata decreases under drastic drought condition. The lower transpiration rate, thick cuticle and small stomatal aperture enhance drought tolerance in plants (Ullah et al. 2018b).

## Biochemical and Molecular Adaptations

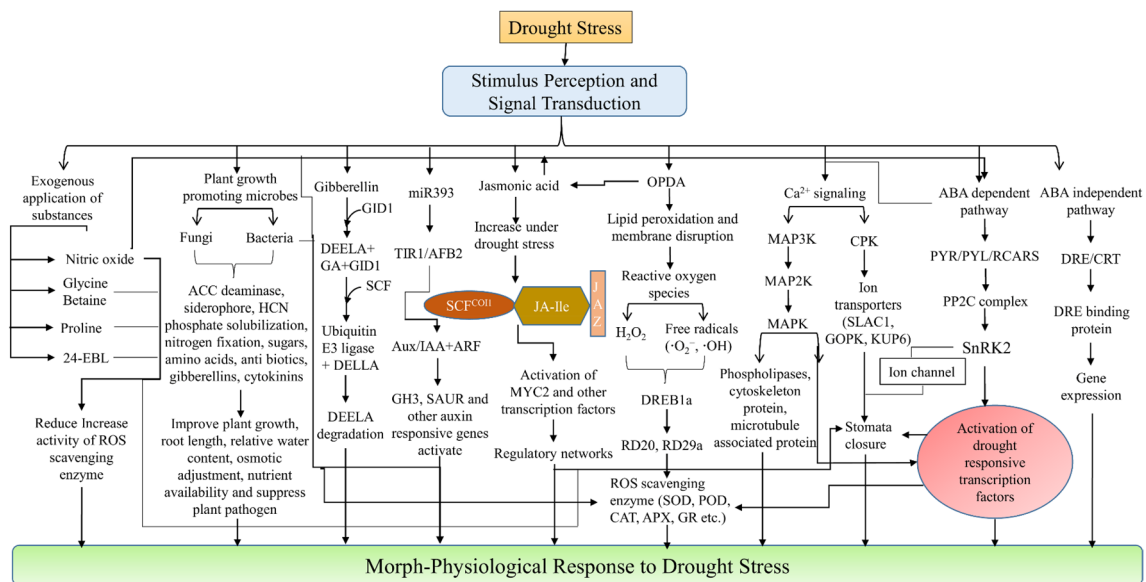
Plants show multiple response mechanisms to drought stress, like production of specific proteins, high level of metabolites and gene expression. In stress condition, the production of ROS increases, as a result damage plant cells (Ullah et al. 2017a). For the adaptation to stress conditions, plants have numerous mechanisms including the accumulation of solutes (like sugar and proline), enzyme activation (Peroxidase (POD), Superoxide dismutase (SOD), Ascorbate (ASC) and catalase (CAT)), and non-enzymatic (reduced glutathione (GSH)) substances (Anjum et al. 2016). In addition, phytohormones have key role in response to abiotic and biotic stresses (Table 1). Drought stress also affect the production of endogenous level of hormones, like Absciscic acid (ABA), Jasmonic acid (JA), Ethylene (Eth), Gibberillins (GA), Auxins (Aux), Salicylic acid (SA) and Cytokinins (CK) (Ullah et al. 2018b). These phytohormones have important role in regulating the plant growth development and responses to water deficit conditions. In stress, these phytohormones trigger various signaling pathways, consequently enhance antioxidant enzyme production, secondary metabolites and heat shock protein. To increase drought tolerance in plants, it is needed to study and develop numerous phytohormones related strategies to decrease economic losses (Ullah et al. 2017a). These numerous biochemical and molecular response mechanisms have been discussed below and elaborated in the Fig. 2.

## Absciscic Acid

Absciscic acid regulate different developmental and physiological processes including, seed dormancy, plant development, stomata opening, embryo morphogenesis and the synthesis of storage lipids and proteins. This is a principal phytohormone that is involved in response to abiotic stresses specifically in osmotic stress (Sah et al. 2016; Ullah et al. 2017a). ABA is a crucial plant stress regulator, which controls different biochemical and morpho-physiological processes that help plant to adapt to abiotic stresses (Seo and Koshiba 2011; Kalladan et al. 2017). Abiotic stresses such

**Table 1** Case studies of phytohormones enhanced drought tolerance in plants

Phytohormones	Phytohormones level	Plant	Environmental condition	Beneficial feature	References
Absciscic acid	400 mol·(m <sup>2</sup> s) <sup>-1</sup>	<i>Triticum aestivum</i>	Greenhouse	Increased root elongation, root shoot ratio, expression of stress related genes	(Zhou et al. 2019)
Absciscic acid	100 µL	<i>Fragaria ananassa</i> (Octoploid strawberry)	Greenhouse	Accelerated fruit ripening, higher diameter of roots	(Li et al. 2019a, b, c)
Auxin	10 <sup>-5</sup> M	<i>Oryza sativa</i> (Rice)	Nursery	Less lipid peroxidation, H <sub>2</sub> O <sub>2</sub> and O <sub>2</sub> <sup>-</sup> levels were significantly reduced	(Sharma et al. 2018)
Auxin	0.4 mg L <sup>-1</sup>	<i>Malus domestica</i>	Lab	Upregulation of antioxidant enzymes genes, promoted superoxide enzyme activities and decreased the H <sub>2</sub> O <sub>2</sub> concentration	(Torres et al. 2017)
Cytokinin	[pmol/10 mL]	<i>Lens culinaris</i> (Lentil)	Lab	Reduced transpiration, higher chlorophyll content	(Lemes et al. 2019)
Cytokinin	100 µM	<i>Agrostis stolonifera</i> (Creeping Bentgrass)	Growth chamber	Enhanced the activities of superoxide dismutase (SOD), APX, CAT, and POD	(Chang et al. 2016)
Salicylic acid	0.5 mM	<i>Brassica juncea</i> (Mustard)	Greenhouse	Increased the proline production, decreased proline oxidase activity, improved ethylene formation	(Nazar et al. 2015)
Ethylene	0.1 µM	<i>Triticum aestivum</i> (Wheat)	Glasshouse	Increased shoot relative growth rate, higher galactose, lower maltose in the shoot	(Valluru et al. 2016)
Jasmonic acid (Jasmonate)	0.5 mM	<i>Mentha spicata</i> (Spearmint)	Field	Concentration of beta-caryophyllene increased	(Zheljazkov et al. 2013)
Jasmonic acid (Jasmonate)	0.2, 0.5, and 1.0 mmol L <sup>-1</sup>	<i>Nicotiana tobaccum</i> (Tobacco)	Lab	Mitigated the effects of drought stress i.e., photochemical efficiency, potential activities of PSII, electron transport rate, photochemical quenching and non-photochemical quenching	(Wei-Wei et al. 2011)
Brassinosteroids	In various treatment of 0, 10–6, 10–9, 10–12 M	<i>Brassica juncea</i> (brown mustard)	Lab	Activity of SOD, CAT, APOX, GR, DHAR, MDHAR increased	(Kaur et al. 2018)



**Fig. 2** Biochemical and molecular signaling pathways in response to drought stress. ABA is the principal phytohormones in drought response with the regulation of other signaling pathways i.e.,  $\text{Ca}^{2+}$ , JA, IAA and Gibberellin

as salinity, drought, heat, and cold increase the ABA level in plants (Lata and Prasad 2011). Absciscic acid synthesis increases under drought stress and consequently activates drought response signaling pathways in plants (Cutler et al. 2010). It triggers various drought related genes lead to closing of stomata, improve root architecture, increase synthesis of drought tolerance substances and other drought tolerant mechanisms (Lim et al. 2015). The accumulation of ABA regulates the closure of stomata to reduce transpiration (Munemasa et al. 2015; Man et al. 2011). Stomata closure reduces exchange of gases, as a result decrease in rate of photosynthesis and transpiration (Mittler and Blumwald 2015). Normally, light activate stomata opening, while ABA and raised  $\text{CO}_2$  level stimulate incomplete or complete closing down of stomata (Kim et al. 2010). ABA change transport of ions in guard cell, that stimulate stomata closing, and prevent it from opening, to decrease transpiration (Kim et al. 2010; Dong et al. 2015). For instance, Zhang et al. (2015) observed that plant performed better under drought stress, when the ABA either activated endogenously or added exogenously than non-treated plants. Upon the perception of stimulus, ABA dependent signaling pathways are initiated to respond to drought stress. ABA dependent signaling pathways respond to drought stress via various morpho-physiological and biochemical processes. Under normal condition, ABA level is low, the activity of SnRK2 protein is inhibited by PP2C (protein phosphatase 2C) phosphatases which causes dephosphorylation (Ullah et al. 2018a). Under drought stress, the ABA level increases, which lead ABA bind to PYR/PYL/RCARs, which in turn bind to and deactivate PP2Cs (Ullah et al. 2017a). SnRK2s

proteins are auto activated, when they separate from PP2Cs. The activated SnRK2s phosphorylate downstream target and activate ABA, which leading to molecular and physiological responses against drought stress (Dong et al. 2015; Mehrotra et al. 2014) as shown in the Fig. 2.

### Jasmonic Acid

Jasmonic acid (JA) is an  $\alpha$ -linolenic acid derived phytohormone involved in plant growth, tendril coiling, and pollen production. The active derivative of Jasmonic acid also known as Jasmonates which have important role in controlling response to various biotic and abiotic stresses (Ullah et al. 2017a). JAs have important role in stress responses, including signal development and various gene expression, which is responsible for stresses (Ahmad et al. 2016). Jasmonate synthesis occurs in plastids, cytosol and peroxisomes. JAZ (Jasmonate Zim Domain) proteins have a principal role in JA signaling pathway because JAZ function as a switch for the JA signaling. In normal condition, when JA is absent or in a very low concentration, JAZ or JAI3 proteins attach to numerous transcription factors, such as Myelocytomatosis (MYC2) to minimize their activity (Ullah et al. 2017a). However, in stress conditions, the Jasmonic acid and its derivatives are present in large quantity, the JAZ protein are degraded and various stress responsive transcription factors are activated which further regulate numerous genes that involve in stress response (Wager 2012). JA enhance drought tolerance by different procedures, including closing of stomata, root development and scavenging of ROS. The JA precursor, 12-oxo phytodienoic acid (12-OPDA) closed the



stomata in treated *Arabidopsis*. When the 12-OPDA level upraised in *Arabidopsis*, the number of stomata decreased, hence increased drought tolerance (Ullah et al. 2018a). JAs have also role in hydraulic conductivity to uptake water from soil in slight humid condition (Sánchez-Romera et al. 2014). de Ollas et al. (2013) observed that the JA accumulation in roots for short term, the ABA level increased under water scarcity. It suggests that JA also regulate ABA in plants under drought stress condition.

### Auxins

Auxin is another crucial plant hormone that control growth of plant and respond to unfavorable environmental conditions, such as drought (Kazan 2013). Biosynthesis of auxin mainly take place in leaf primordial, juvenile leaves and developing seed (Ullah et al. 2018a). Some pathways are proposed for the biosynthesis of auxin, which include tryptophan (Trp) dependent, and Trp-independent pathway (Mano and Nemoto 2012). The pathway is extensively self-regulated through positive and negative feedback (Kieffer et al. 2010). Auxin normally moves from the tip of the shoot towards the tip of the root, these moves long distances through the phloem, or through cell to cell transport. Auxin also moves via auxin transport proteins. Auxin transport is facilitated by auxin efflux carriers including PIN proteins, which can have a polar distribution on the cell membrane. Under water scarcity, the auxin levels in plants are increased to cope with drought stress (Llanes et al. 2016). In a case, 31 *Aux/IAA* genes were found in rice induced by drought stress and one of these genes, *OsIAA6* was confirmed to be involved in drought stress (Jung et al. 2015). In another study, overexpression of *AtYUC6*, gene in transgenic potato showed auxin overproduction phenotypes and as a result increased drought tolerance (Kim et al. 2010). Auxin hormones are mainly recognized as key regulator in the development of plant roots (Saini et al. 2013) while roots have crucial role in improving drought tolerance. For instance, primarily drought promote *YUC7* gene in roots and increased the free auxin level in *Arabidopsis*, the *YUC7-1D* stimulate root growth, and increase root architecture. Consequently, plants having *YUC7-1D* gene showed resistant to drought stress and also controlled drought responsive genes (Lee et al. 2012).

### Ethylene

Ethylene is a gaseous hormone, involve in multiple action, such as seed germination, plant growth, flowering, fruit ripening and response to different stresses (Arraes et al. 2015). Ethylene is produced from methionine (Met) via S-adenosyl-methionine (AdoMet) by the action of ACC synthase (ACS) and ACC oxidase (ACO). It has been studied that ethylene

regulate many biological mechanisms to response various biotic and abiotic stresses (Muller and Munné-Bosch 2015). In a study, a member of Ethylene response factor (ERF) i.e., *GmERF3* was induced by ABA, JA, ET, SA, salt and drought stress. The overexpressing *GmERF3* tobacco exhibited higher tolerance to drought stress due to higher proline content and soluble sugars as compared to wild type plants (Zhang et al. 2009). Similarly, overexpression of another ERF gene, *AtERF019* delayed flowering time, senescence and importantly drought stress via lower transpiration rate. Ethylene also interacts with other plant hormones like ABA and Jasmonic acid through ERFs in various abiotic stresses (Müller and Munné-Bosch 2015).

### Cytokinin

Cytokinin (CK) is a plant hormone which promotes cell division, root nodule development, delay leaf senescence, regulate nutrient allocation, and plant response to pathogen interactions. In addition, it also regulates drought stress responses (Li et al. 2016; Zwack and Rashotte 2015). In a case, CK related genes i.e., *CKX1*, *CKX2*, *CKX3* and *CKX4* were overexpressed in *Arabidopsis* which consequently decreased Cytokinin level and subsequently increased drought tolerance (Nishiyama et al. 2011). There are five mechanisms of Cytokinin in contribution to enhance drought tolerance; protection of photosynthetic apparatus, increase of antioxidant substances, regulate water balance, control plant growth, and regulate stress related hormones. Under drought stress, Cytokinin regulates the genes that involved in CO<sub>2</sub> assimilation, electron transport rate, increase photosynthesis rate, and chlorophyll level (Sahebi et al. 2018). CK works in association with ABA to adapt the plant under drought stress. For drought stress, it has been reported that CK have both negative and positive effects on plants (Zwack and Rashotte 2015).

### Brassinosteroids

Brassinosteroids (BRs) contribute in plant growth, cell division, differentiation and elongation, development of reproductive parts and stress tolerance. It is reported that BRs involved in tolerance to various environmental stresses, including drought stress (Ciura and Kruk 2018). Overexpression of brassinosteroids biosynthetic gene *AtDWF4* in *Brassica napus*, resulted in increased growth, yield and drought stress tolerance (Sahni et al. 2016). BRs also reported for their negative role in drought tolerance, for example knock-down of *BRI1* in *Brachypodium distachyon* via RNA interference increased drought tolerance (Feng et al. 2015). In addition, *WRKY46*, *WRKY54* and *WRKY70* are transcription factors involved in the brassinosteroids-regulated plant growth and responses to water scarcity. These transcription

factors were negatively involved in drought tolerance because the triple mutants had defect in brassinosteroid-regulated growth and had more tolerant to drought stress (Chen et al. 2017).

### Mitogen Activated Protein Kinase

Mitogen activated protein kinase (MAPK) involved in signaling transduction to response various stresses such as pathogen, cold, salinity, ozone, wounding and drought (Berriri et al. 2012). MAPK are involved in many ABA responses including guard cell signaling, seed germination and antioxidant defense system (Zhang et al. 2010). A transcriptomic study revealed that MAPK are activated by multiple abiotic stresses, like cold, drought, ABA, and pH (Zhu et al. 2013). Xu and Chua (2012) reported that in *Arabidopsis*, MAP kinase, *MPK6* enhanced the plant tolerance to drought stress. In *Oryza sativa* Ning et al. (2010), identified raf-like MAPKKK protein, DSM1 (drought sensitive mutant1) functioning as potential scavenging of ROS, and increased stress tolerance to water deficit stress. *GhMPK2* as cotton MAPK role to adjust osmotic pressure and reduce water loss under water stress condition (Zhang et al. 2011). *GhMPK6* have important role in  $H_2O_2$  production and ABA-induced catalase expression (Luo et al. 2011). Two MAPKs, *GhMPK16* and *GhMPK7* are involved in resistance to various stresses and regulation of stress signaling pathways (Zhang et al. 2011).

### Reactive Oxygen Species

Reactive oxygen species (ROS) come from the incomplete reduction of atmospheric oxygen, it is also known as reactive oxygen intermediate (ROI) or active oxygen species (AOS). Basically there are four forms of ROS; hydroxyl radicle ( $HO\bullet$ ), hydrogen peroxide ( $H_2O_2$ ), singlet oxygen ( $^1O_2$ ) and super oxide anion radical ( $O_2^-$ ) (Ullah et al. 2018a), these ROS are harmful to cellular components, such as nucleic acid, lipids and proteins. To survive in drought stress, plants have developed multiple and interrelated signaling pathways to regulate variety of stress responsive genes for the production of different classes of protein, like protein kinases, enzymes, transcriptional factors and other functional proteins, that leads to diverse metabolic and physiological responses and enhance tolerance to drought stress. Plants keep ROS in balance, but abiotic stresses imbalance it and increase the production of ROS at subcellular and cellular level. There are two important sources of reactive oxygen species i.e., metabolic ROS and signaling ROS. Metabolic ROS directly change redox status of rate limiting enzymes and also control the metabolic fluxes in cell, thereby it alter the metabolic reactions to decrease the effects of stresses (Miller et al. 2010). It can affect transcription and translation

by changing the function of regulatory protein, via ROS derived redox moderation (Foyer and Noctor 2016). When stress sensor response to stress, the signaling ROS are generated. Signaling ROS also alters redox status of regulatory proteins and alters the transcription and translation resulting in activation of acclimation response that reduces the effects of stress by decreasing the metabolically produced ROS. However, prolonged drought stress increases the production of ROS in the cell components, such as cell wall, plasma membrane, chloroplast, mitochondria, peroxisomes and nucleus (Gill and Tuteja 2010). Increased production of ROS is harmful to the cells and affect other developmental processes. If the oxidation of these components is not controlled, it may lead to cell death (Fang et al. 2015). Hereby, enzymatic and non-enzymatic defense mechanisms have important role in detoxification and scavenging of the ROS and increase drought stress tolerance (Choudhury et al. 2017). Various enzymes, sugars and amino acids present in different parts of the plant cells involved in scavenging of ROS, such as glutathione reductase (GR), ascorbate peroxidase (APX), SOD, POD, glutathione peroxidase (GPX), CAT, monodehydroascorbate reductase (MDHAR), ascorbic acid (AA), reduced glutathione (GSH),  $\alpha$  tocopherol, carotenoids, osmolyte proline and flavonoids (Wang et al. 2016). The enzyme, SOD convert the  $O^{2*}$  into hydrogen peroxide ( $H_2O_2$ ), the CAT and PODs further disintegrate the hydrogen peroxide into molecular oxygen and water (Wang et al. 2016). MDAR, GR, and NADH along with APX remove the  $H_2O_2$  via Halliwell- Asada pathway (Uzilday et al. 2012). *Rboh* (Respiratory Burst Oxidase Homolog) genes are code for NADPH oxidases related with plasma membrane have a key role in ROS related signaling transduction (Kwak et al. 2003). SOD act on  $O_2^{\bullet-}$  and convert it into  $H_2O_2$ , further APX, GPX and CAT detoxify the  $H_2O_2$ . Glutathione S-transferase (GST), peroxiredoxin (PRX) and GPX reduce the  $H_2O_2$  into organic hydroperoxidase, via ascorbate independent thiol mediated pathways by using the glutaredoxin (GRX) or thioredoxin (TRX) (Noctor et al. 2014).

Expression of *OsAPX2* reduced MDA and  $H_2O_2$  level and increased the APX activity under drought stress and consequently increased drought tolerance in transgenic plants (Zhang et al. 2013). Moreover overexpressing *OsAPX2* plants were more tolerant to water scarcity than wild plants that significantly increased the fertility during abiotic stresses. In transgenic rice, the overexpression of *OsAPX1*, another gene of APX, increased fertility under cold stress (Sato et al. 2011).

Metallothioneins (MTs) is a group of proteins that have high cysteine (Cys) content, metal binding and low molecular weight. Many Cys residues in MT involved in detoxification of ROS. In transgenic rice, overexpressing *OsMT1a* increased the activity of antioxidant enzymes such as CAT, APX and POD, and increased drought tolerance. *SbMT-2*

gene is also involved to prolong cellular homeostasis by regulation of ROS under drought stress (Chaturvedi et al. 2014).

### Calcium Signaling Induce Drought Tolerance

Calcium ( $\text{Ca}^{2+}$ ) regulates various physiological and cellular processes in plants and a crucial signaling molecule in drought tolerance. It plays an important role in perception and transduction of signals in plants that utilizing calcium-dependent signaling network (Tuteja and Mahajan 2007). Various stresses and phytohormones, like drought and ABA are involved in changing the cytoplasmic  $\text{Ca}^{2+}$  concentration (Li et al. 2015). Plant cellular  $\text{Ca}^{2+}$  signaling are detected and transfer by three classes of calcium sensor molecules; CDPK (calcium-dependent protein kinase), CBLs (calciurein B-like protein) and CaM (calmodulin) (Ullah et al. 2018a). Li et al. (2015) found 41 CDPKs genes from the genome of *Gossypium raimondii*. Their work showed that *GhCDPK2*, *GhCDK3*, *GhCDPK11*, *GhCDPK14*, *GhCDPK16*, *GhCDPK28*, and *GhCDPK35*, genes are involved in drought stress. CBLs interact with CBL interacting protein kinase (CIPKs) to transmit  $\text{Ca}^{2+}$  signaling. The CBL-CIPK complex is associated with tonoplast or plasma membrane (Tang et al. 2015). *GhCIPK6* gene was induced by drought stress and ABA treatment, overexpression of *GhCIPK6* in *Arabidopsis* significantly increased drought tolerance (He et al. 2013). CaM are calcium binding proteins and contain four EF hand motifs. The  $\text{Ca}^{2+}$  attach to EF motifs, conformational transformation undergoes in CaM that increase their catalytic activity, or interaction with downstream target protein. Calreticulin (CRT) and Calnexin (CNX) are important calcium binding protectors of Endoplasmic Reticulum which are responsible to correct the folding of newly synthesized proteins (Sarwat et al. 2013). These studies showed that changes in  $\text{Ca}^{2+}$  ions concentration, transduced  $\text{Ca}^{2+}$  signals via CDPKs, CBLs and CaMs, which phosphorylated the downstream target and then respond to drought stress.

### Scientific Strategies to Improve Drought Tolerance

Scientifically, there are various strategies to further improve drought tolerance in plants for example, exogenous application of substances, plant microbe interactions, plant breeding and transgenic approaches (Fig. 2).

#### Exogenous Application of Substances

Exogenous application of substances (Nitric oxide, 24-epibrassinolide, Glycine betaine, Proline) enhances tolerance in plant under different stresses, such as drought (Tanveer

et al. 2018). These exogenous substances promote the accumulation of antioxidant substances to detoxify the ROS and alleviate osmotic adjustment to increase the turgor pressure, thus maintaining composition of membranes structure, macromolecule and enzymes during osmotic stress (Anjum et al. 2011a). For example, exogenous treatment of glycinebetaine and proline has been found fruitful in reducing the harmful effect of osmotic stress on cotton plants (Noreen et al. 2013).

#### Nitric Oxide

Nitric oxide (NO) is gaseous signaling molecule that adapts the plant to stress condition by regulating different physiological processes and increase their survival (Siddiqui et al. 2011). NO is a free radical and form different reactive nitrogen species, like S-nitrosothiols (SNOs), nitrosonium ions ( $\text{NO}^+$ ), peroxyntirite ( $\text{ONOO}^-$ ), nitroxyl anion ( $\text{NO}^-$ ), and nitrogen oxides ( $\text{NO}_x$ ), which are involve in numerous physiological processes (Rio 2015). Various studies showed that NO production increased under drought stress (Cai et al. 2015). Exogenous application of NO enhances drought tolerance and increases the production of ABA. Commonly used exogenous donor of NO in drought stress are S-nitroso-Nacetylpenicillamine (SNAP), Sodium Nitropruside ( $\text{SNP}; \text{Na}_2[\text{Fe}(\text{CN})_5\text{NO}]2\text{H}_2\text{O}$ ), Diethylamine NONOate sodium (DEA-NONOate) and S-nitrosoglutathione (GSNO). These are differ in their bio-physiological response to release NO in various redox form, like GSNO,  $\text{NO}^+$  from SNP and  $\text{NO}^*$  from SNAP (Parankusam et al. 2017). NO increases antioxidant enzyme activity, and cause stomata closure via various steps such as  $\text{Ca}^{2+}$ , cGMP and MAPKs signaling pathways and increase the activities of other protein kinases like osmotic stress activated kinase (Baudouin and Hancock 2014). Exogenous application of NO under drought stress reduced lipid peroxidation and  $\text{H}_2\text{O}_2$  content in maize (Zhang et al. 2012). NO also function as cytoprotectent by interacting lipid peroxidation and induce the expression of antioxidant enzymes besides scavenging of free radicals ( $\text{R}^*$ ) and super oxide ( $\text{O}_2^*$ ). Numerous reports showed that production of NO in guard cell respond to ABA and drought stress (Planchet, et al. 2014). Moreover, stomata conductance is correlated with the increased production of NO under drought stress (Patakas et al. 2010).

#### 24-Epibrassinolide

24-epibrassinolide (EBL) is a byproduct from the brassinolide biosynthesis, has the ability to regulate different metabolic processes like photosynthesis, nucleic acid and protein biosynthesis. EBL protect the plants from adverse effects of abiotic stresses including drought stress (Shahzad et al. 2018). Exogenous application of EBL recovered plant growth and yield during drought stress and thus enhance



crop yield (Anjum et al. 2011b). After exogenous treatment of EBL on maize plant, crop yield was significantly increased under drought stress compared to drought treated plants (Talaat et al. 2015). EBL also increased light harvesting and carbon fixation during drought stress, via improving chlorophyll fluorescence, chlorophyll content and also enhanced the activities of various enzymes which are involved in photosynthesis. It also have important role in the scavenging of ROS and redox regulation under drought stress (Lima and Lobato 2017). Lima and lobato (2017) studied the exogenous application of EBL on Cowpea that increased the scavenging of ROS, by increasing the activities of antioxidant enzymes (CAT, SOD, POD and APX).  $H_2O_2$  production and lipid peroxidation reduced 42% and 31%, respectively, due of EBL application in pigeon pea because EBL increased the production of APX (19%) and SOD (10%) (Shahana et al. 2015). The application of EBL also increase relative water content (RWC) and decrease in transpiration rate in drought stressed plants (Li and Feng 2011; Li et al. 2012).

### Glycine Betaine

Glycine betaine (BG) is an important component of some foods including mussels, amaranth, calms, wheat, spinach and quinoa (Ross et al. 2014). It protects cellular components from various stresses by maintaining water balance and stabilize the structure of proteins. GB enhances plant growth and prevent from harmful substances produced by drought stress. Exogenous application of GB protect photosynthetic oxygen evolving complex (OEC) and photosystem II (Oukarroum et al. 2012) and regulate the expression of oxidative stress response genes, declining the lipid peroxidation and ROS accumulation (Banu et al. 2010). Due to the application of GB, the wheat leaves raised the accumulation of  $Ca^{+}$  and  $K^{+}$ , it enhanced leaf water potential, and increased the activity of SOD, POD, and CAT (Raza et al. 2014). GB enhance enzymatic activity of plasma membrane for example,  $H^{+}$ ATPase enhance the phosphate uptake and stimulating the phosphate homeostasis (Li et al. 2018a, b).

### Proline

Proline is an amino acid necessary for the primary metabolism. Several studies showed that exogenous application of proline are helpful in plants tolerance exposed to drought and salinity stresses. Proline regulates the genes responsible for stress tolerance and reduces the harmful effects caused by drought stress (Moustakas et al. 2011). It also restores stress injuries through stabilizing of antioxidants system by osmotic adjustment, decrease the effects of ROS, and protect integrity of plasma lemma (Szabados and Savoure 2010). Proline is interconnected with signaling pathways of total

soluble sugars and the quenching of ROS, and thus promotes drought tolerance in *Arabidopsis thaliana*. Proline limits the physiological parameters of plant and improve the quality and yield of seed oil (Ali et al. 2013). Thus, proline reduces stress by working as an important osmolyte and function as ROS scavenging.

### Plant Microbe Interactions

Microorganisms are ubiquitous as their habitat ranges from sub-zero temperature to dessert conditions (Xue et al. 2015; Ullah et al. 2015b). Rhizospheric microbes that live in the vicinity of a plant produce several biocontrol agents and plant growth promoting substances (Ullah et al. 2018a). In addition, they enhance nutrient availability, change soil structure, fertility, pH and oxygen availability (Finkel et al. 2017). Various microbes, such as plant growth promoting bacteria (PGPB) and mycorrhizal fungi assist plant growth and development under biotic and abiotic stresses (Nadeem et al. 2014). The application of these microbes increases drought tolerance capability of plants via numerous process take place in the rhizosphere (Fig. 2).

### Plant Growth Promoting Bacteria (PGPB)

Bacteria are the important microorganisms of rhizosphere that affect plant physiological and biochemical activities. PGPB have important role in plant growth and development, they provide plant growth promoting substances to their host plants and in turn get protection and food in the form mutualistic approach. These bacteria secrete various compounds in the form of osmolytes, antioxidant, phytohormones etc. that enhance the root osmotic potential under drought stress. (Ullah et al. 2017b, 2019a, b). In addition, it also regulate the plant growth under drought stress, either by direct (enhanced production of phytohormones, availability of nutrients) or indirect mechanisms (induce systematic resistance (ISR), suppression of pathogen, synthesizing of lytic enzymes) (Glick 2014; Ullah et al. 2015a, b). For example, *Azospirillum brasilense* increased the ABA level in *Arabidopsis thaliana* under drought stress (Cohen et al. 2015). While, ABA improve drought tolerance via activating transcription of water deficit related genes and the hydraulic conductivity of roots (Jeng et al. 2018). In another study, enhanced auxin synthesis due to the activation of indole-3-pyruvate gene in *Azospirillum* produced morphological changes in xylem coleoptile, and led to increased water conductance and enabled the plant to survive under drought stress (Pereyra et al. 2012). PGPB also influences the expression of genes encoded for ethylene synthesis enzyme, such as *ACC oxidase* and *ACC synthase*. In a case, *Burkholderia phytofirmans* enhanced the expression of *ACO* and *ACS* genes in *Arabidopsis thaliana* (Poupin et al. 2016). A large number

of PGP bacterial strains also synthesized Cytokinin (Glick 2012). For examples, *Pseudomonas fluorescens* are capable of cytokinin synthesis, it increased the isopentenyl riboside and zeatin riboside level (Pallai et al. 2012). The *Platyclusus orientalis* plants inoculated with *Bacillus subtilis* produced Cytokinin were reported more tolerant to drought stress than drought treated plants (Liu et al. 2013). PGPB also facilitate the plant under drought stress by enhancing their capability to increase root surface area and number of root tips (Vacheron et al. 2013). PGP rhizobacteria also involve in improving scavenging system of ROS under drought stress. The inoculation of PGPR alleviates the accumulation of antioxidant enzymes, like SOD, APX, POD and CAT to minimize the oxidative injury under drought stress. For example, *Bacillus pumilus* and *B. firmus* increased the levels of APX and CAT under drought stress and reduced oxidative damage (Gururani et al. 2013). Drought tolerant and PGPR enhance water potential, biomass, and decrease the loss of water from plants under drought stress. These inoculants increase the production of amino acids, sugar and proline and also decline the antioxidant activity in plants (Vardharajula et al. 2011). The photosynthetic machinery is affected under drought stress, *Pseudomonas putida* overcome this effect and enhanced the chlorophyll content and shoot length (Kang et al. 2014). Some other examples of bacterial assisted drought tolerance in plants have been listed in Table 2.

## Fungi

Mycorrhizal association of fungi with host plant increase drought tolerance by involving in several, physiological and molecular processes. External hyphae increase their size in soil and build extremely branched mycelia that can connect plants together in a network called mycorrhizal network (Simard et al. 2015). The mycelium can absorbed water from deeper soil, which is then transport to cortical tissues, here it is then join to water transport through apoplastic pathways. Arbuscular mycorrhizal fungi (AMF) are one of the most important soil microbes and function as symbionts with roots of plants (Brundrett and Tedersoo 2018). AMF also enhance the growth of host plant via promoting water uptake and nutrients to control abiotic stresses, like drought stress (Bowles et al. 2018). It also improve the efficiency of photosynthetic product and photosystem II under osmotic stress (Ruiz-Lozano et al. 2016). Moreover, AMF colonization could elevate JA level in plants and consequently improve tolerance capacities (Hause et al. 2007). Vallino et al. (2014) observed that Arbuscular mycorrhizas in rice enhanced root branching via increase in lateral roots by the mechanism of hypothetically involved AMF signaling or by the changing in plant nutrient status. This AMF association and root architecture response may be very beneficial for plant adaptation

to osmotic stress. Inoculation of AMF helps in increasing water use efficiency and maintaining the hydraulic conductivity of roots by the increase of aquaporin expression under water scarcity (Bárcana et al. 2014). Table 1 enlisted fungus enhanced drought tolerance in plants with their beneficial characteristics.

## Transgenic Approach

Transgenic plants are the ones, whose DNA is modified using genetic engineering techniques, which are generally resistant to biotic and abiotic stresses. Plants respond to various stresses by altering their gene expression (Deeba et al. 2012; He et al. 2017a). Regulation of various stress response genes is the important factors that cope the plant with abiotic stresses and increase stress tolerance against these conditions (Hozain et al. 2012; Ullah et al. 2020). A large number of genes in plants have been reported that are involved in drought stress tolerance. For example, *AtNAC2* gene (related with phytohormones signaling like ABA) play crucial role in drought stress. The overexpression of *AtNAC2* enhanced drought tolerance in transgenic plants (Patil et al. 2014). In addition, *AtNHX1* gene induces salinity and drought tolerance in plants, its overexpression in *Arachis hypogaea* (groundnut) improved the drought resistivity than wild type plants (Asif et al. 2011). In another study the transformation of gene, *ScALDH21* from *Syntrichia carlinervis* enhanced drought tolerance in cultivar cotton (Yang et al. 2016). In addition, genome editing technologies like, transcription activator-like effectors nucleases (TALENs), zinc fingers nucleases (ZFNs), homing meganucleases and clustered regularly interspaced short palindromic repeats (CRISPR) have enabled us to produce targeted genetic modification in organisms of choice (Martignago et al. 2019). For example, CRISPR/Cas9 was used to create *slnpr1* mutants, to determine its role in response to drought stress in tomato. The resulted *slnpr1* mutants exhibited reduced drought tolerance with higher electrolytic leakage, increased stomatal number, H<sub>2</sub>O<sub>2</sub> and MDA content. These superior achievements of genetic engineering improved physiological traits related to drought stress for example, higher soluble sugar and proline level, photosynthesis, and lower lipid peroxidation. These finding encouraged the scientists to develop such drought resistance plant by genetic engineering. Different transgenic plants have previously produced through inserting stress related genes. However, engineering several genes in the same variety could be more fruitful because drought tolerance is a horizontal resistance in plants.

## Plant Breeding

Development of stress tolerant plants that have stable production under stress condition is a crucial approach to

**Table 2** Microbes assisted drought tolerance in plants

Bacteria	Host plant	Plant part used for isolation	Inoculated plant/s	Beneficial features related to drought tolerance	References
<i>Bacillus subtilis</i>	<i>Cicer arietinum</i> (chickpea)	Leaves	<i>Cicer arietinum</i> (chickpea)	Proline content, lipid per-oxidation, and activities of antioxidant enzymes (CAT, APOX, POD, and SOD) increased in response to drought stress	(Khan et al. 2019)
<i>Pseudomonas fluorescens</i>	<i>Setaria italica</i> L	Roots	<i>Setaria italica</i> L	Efficiently colonized the root adhering soil, increased soil moisture, and enhanced the root adhering soil/root tissue ratio	(Niu et al. 2018)
<i>Bacillus amyloliquefaciens</i>	<i>Grapevine</i>	Roots	<i>Grapevine</i>	Secreted melatonin, reduced MDA, H <sub>2</sub> O <sub>2</sub> and O <sub>2</sub> <sup>-</sup>	(Jiao et al. 2016)
<i>Spingomonas</i>	<i>Tephrosia apollinea</i>	Leaves	Soya bean ( <i>Glycine max</i> )	Enhanced ABA and jasmonic acid content, Increased plant biomass (dry), glutathione, glutamine, photosynthetic pigments, glycine and proline	(Asaf et al. 2017; Khan et al. 2014)
<i>Streptomyces coelicolor</i> , <i>S. olivaceus</i> and <i>S. geysiriensis</i>	Bui ( <i>Aerva tomentosa</i> ), Keeker ( <i>Acacia nilotica</i> ), Kheep ( <i>Leptadenia pyrotechnica</i> ), Phog ( <i>Calligonum polygonoides</i> ) and Bajra ( <i>Pennisetum glaucum</i> )	Roots	Wheat ( <i>Triticum aestivum</i> )	Enhanced auxin and IAA production, higher seedling vigor and yield	(Yandigeri et al. 2012)
<i>Pantoea alhagi</i>	<i>Alhagi sparsifolia</i>	Leaves	Wheat ( <i>Triticum aestivum</i> )	Increased soluble sugars, IAA, EPS, siderophore, ammonia and protease production, decreased proline and MDA accumulation and chlorophyll degradation	(Chen et al. 2017)
<i>Pseudomonas azotoformans</i>	<i>Alyssum serpyllifolium</i>	Leaves	<i>Trifolium avense</i>	Relative water content, chlorophyll content, SOD, POD, CAT, proline and plant biomass increased	(Timmusk et al. 2014)
<i>Burkholderia phytofirmans</i> and <i>Enterobacter</i> sp.	Onion ( <i>Allium cepa</i> )	Roots	Maize ( <i>Zea mays</i> )	Leaf area, shoot and root biomass, photosynthesis, chlorophyll content and photochemical efficiency increased	(Naveed et al. 2014b)

Table 2 (continued)

Bacteria	Host plant	Plant part used for isolation	Inoculated plant/s	Beneficial features related to drought tolerance	References
<i>Burkholderia phytofirmans</i>	Onion ( <i>Allium cepa</i> )	Roots	Wheat ( <i>Triticum aestivum</i> )	Photosynthetic rate, water use efficiency, chlorophyll content, grain yield, ionic balance and antioxidant level improved	(Naveed et al. 2014a)
<i>Glucoacetobacter diazotrophicus</i>	Sugarcane ( <i>Saccharum officinarum</i> )	Roots and shoots	Sugarcane ( <i>Saccharum officinarum</i> )	Activation of drought stress responsive genes, ABA and ethylene signaling pathways	(Vargas et al. 2014)
Fungi					
<i>Rhizophagus irregularis</i>	<i>Zea Mays</i> (Maiz)	Roots	<i>Zea Mays</i> (Maiz)	Higher root biomass, enhanced stomata conductance, reduced oxidative damage and enhanced hydraulic conductivity	(Quiroga et al. 2017)
<i>Glomus</i> spp.	<i>Chlorophytum borivilianum</i> (Musli)	Roots	<i>Chlorophytum borivilianum</i>	Enhanced antioxidant enzyme activities, alleviated oxidative damage of biomolecules	(Dave and Taraftar 2012)
<i>Rhizophagus irregularis</i>	<i>Cicer arietinum</i> (Check pea)	Roots	<i>Cicer arietinum</i> (Check pea)	Improved shoot and root length, number of primary branches and root density	(Hashem et al. 2018)
<i>Funneliformis mosseae</i>	<i>Poncirus trifoliata</i> (Orange)	Roots	<i>Poncirus trifoliata</i>	Increased root and root hairs density, length and diameter, IAA level	(Liu et al. 2018)
<i>Flammulina velutipes</i>	<i>Solanum lycopersicum</i> (Tomato)	Leaves	<i>Solanum lycopersicum</i>	Formation of a waxy layer reduced transpiration from surface of plants, provided an effective waterproof barrier resulting in improved protection from drought	(Kamthan et al. 2012)
<i>Rhizophagus irregularis</i>	<i>Zea mays</i> (Maize)	Roots	<i>Zea mays</i>	Efficiency of photosystem II, membrane stability, accumulation of soluble sugars and plant biomass increased	(Quiroga et al. 2017)
<i>Rhizophagus</i> spp.	<i>Cupressus atlantica</i>	Roots	<i>Cupressus atlantica</i>	Higher relative water content and water potential, promoted growth	(Zarik et al. 2016)
<i>Glomus intraradices</i>	<i>Foeniculum vulgare</i>	Root	<i>Foeniculum vulgare</i>	Leaf nutrient content and osmotic adjustment parameters was higher	(Zardak et al. 2018)

**Table 2** (continued)

Bacteria	Host plant	Plant part used for isolation	Inoculated plant/s	Beneficial features related to drought tolerance	References
<i>Glomus intraradices</i>	<i>Cicer arietinum</i>	Root	<i>Cicer arietinum</i>	Enhanced the growth and yield under drought stress condition through enhancing nutrient and water uptake	(Weisany et al. 2018)

protect future food security (Godfray et al. 2010). In past, most of the breeders aimed to develop high yielding crops, as a result very few of the modern varieties are tolerant to stresses (Gilliam et al. 2017). Modern plant breeding strategies aims to increase stress tolerance by going back to conventional landraces (Dwivedi et al. 2016) or/and wild relatives of the important crops for beneficial stress tolerance alleles (Li et al. 2018a, b). Wild crop relatives may provide a solid platform to promote new gene discoveries and mechanisms of physiological adaptations (Isayenkov 2019). During domestication of different plant species, close traits were selected to determinate larger seed size and decrease seed shattering (Meyer and Purugganan 2013). Orthologous genes to be involved in domestication of various plant species, usually for the species which are phylogenetically closed (Lenser and Theißen 2013). For example, loss of orthologous gene function in *Arabidopsis* terminal flower 1 (*TFL1*) determinate the growth in *Fabaceae* and *Solanaceae* (Lenser and Theißen 2013), which is a desire character for the mechanized harvesting of some crops. He et al. (2017b) reported that drought resistant Soybean consistently have smaller leaf area and have lower stomata conductance under drought stress, which is significant contribution to yield during water stress. The hybrids which have the largest dry root weight in all layers of soil during the entire growing season, consequently this type of hybrids can take out large amount of water from soil to sustain development and shoot growth under water scarcity condition. However, this trait may be restricted by consistent and regular drought stress in arid and semi-arid environment (He et al. 2017b). Root crown is important determinate for capturing of soil resources; hybrids which have reduce root crown number have deeper root system and enhanced water accession capability from dry soil (Gao and Lynch 2016). Seminal root system is also particularly responsible for the water uptake from deeper soil profile (Singh et al. 2010). Therefore, drought resistant hybrid has the best capability to uptake water from deep soil.

### Quantitative Trait Loci (QTLs)

QTL is a chromosomal region which is responsible for a part of phenotypic variation. Various number of QTLs related to leaf and root morphology traits are identified. Obara et al. (2010) identified a QTL for root length in water scarcity condition and found that QTL *qRL6.1* facilitated the root length under different concentration of  $\text{NH}_4^+$ , which increase rice production in molecular breeding program. A QTL, *Dro1* is responsible for the deep rooting and Uga et al. (2011) identified that *Dro1* gene is involved in increasing the ratio of deep rooting system which is important approach to drought tolerance in rice. The role polygene has been evaluated via traditional methods, but QTL mapping and DNA markers made it convenient and possible to analyze the complex



traits (Ashraf 2010). QTLs for the leaf morphology are distributed throughout the genome of plants which is related to leaf shape and size. The most notably chromosome are c1 and c9 containing two QTLs, c6 containing three, c15 containing six QTLs, and c17 containing four QTLs, whereas c2, c3, c4, c5 c10, c12, c18, c22 and c25 having one QTLs of each (Said et al. 2013). A study conducted from 2 years under well water and drought condition, 11 morphological and physiological characters were recorded. As a result of the QTL mapping, 67 QTLs were identified under drought stress and 35 QTLs were identified under well water condition. Most important chromosome are c2 containing 7, c9 containing 12 and c16 containing 13 QTLs, respectively (Zheng et al. 2016).

## Conclusions and Future Recommendations

Even though, the green revolution increased plant production enormously; however, ever increasing world population and global warming (which are causing drought stress) once again challenging our capability to feed the world. So, there is an international interest in increasing yield and plant drought tolerance due to the severe lost in crop production in last few decades by drought stress. The aim of the current study was to aggregate various drought tolerance mechanisms and to further improve these processes. Plants generally respond to drought stress in the form of morphological, physiological, biochemical and molecular processes. The morph-physiological processes include changes in leaf structure, root development and stomata regulation. The biochemical processes are changes in phytohormonal level such as ABA, JA, Auxins, Ethylene, Gibberellins, Cytokinin and Brassinosteroids. The phytohormone level of plants generally increase upon drought stimulus and lead to the activation of morph-physiological and other biochemical pathways. These pathways may include MAPK signaling pathway, calcium signaling pathway, regulation of transcription factors and increased level of antioxidant enzymes and other substances to mitigate the effect of drought stress on plant. On the other hand, scientists are also trying to further improve these mechanisms via exogenous application of substances (Nitric oxide, 24-epibrassinolide, Proline, Glycine betaine), plant breeding, and transgenic approach. In addition, microorganisms such as bacteria and fungi are also consider very important in increasing plant growth, yield and drought tolerance of plants. In order to be prepared for the upcoming food and shelter crisis, high yielding drought tolerant crops should be developed via integrating these approaches. In this regard, various technologies are still using to determine the high yielding drought tolerant mechanisms and subsequently improve these processes. New technologies containing gene selection (GS), microarrays,

transcriptomics, next generation sequencing, RT-PCR, immunofluorescence, Western blotting, ELISA, AFLP, TALEN, CRISPR, will enable the scientists to understand and improve drought tolerance in major crops.

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## Compliance with ethical standards

**Conflict of interest** There is no conflict of interest between the authors.

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