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REVIEW

Alleviation of drought and salt stress in vegetables: crop responses and mitigation strategies

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Abstract

In recent decades, the demand for vegetables has increased significantly due to the blooming global population. Climate change has affected vegetable production by increasing the frequencies and severity of abiotic and biotic stresses. Among the abiotic stresses, drought and salinity are the major issues that possess severe threats on vegetable production. Many vegetables (e.g., carrot, tomato, okra, pea, eggplant, lettuce, potato) are usually sensitive to drought and salt stress. The defence mechanisms of plants against salt and drought stress have been extensively studied in model plant species and field crops. Better understanding of the mechanisms of susceptibility of vegetables to drought and salt stresses will help towards the development of more tolerant genotypes as a long-term strategy against these stresses. However, the intensity of the challenges also warrants more immediate approaches to mitigate these stresses and enhance vegetable production in the short term. Therefore, this review enlightens the updated knowledge of responses (physiological and molecular) against drought and salinity in vegetables and potentially effective strategies to enhance production. Moreover, we summarized different technologies such as seed priming, genetic transformation, biostimulants, nanotechnology, and cultural practices adopted to enhance vegetable production under drought and salinity stress. We propose that approaches of conventional breeding, genetic engineering, and crop management should be combined to generate drought and salt resistance cultivars and adopt smart cultivation practices for sustainable vegetable production in a changing climate.

Keywords Climate change · Water scarcity · Salinization · Metabolic responses · Remedies

Introduction

Climate change is increasingly threatening agricultural production via increasing incidents and severity of two types of unfavorable conditions, i.e., biotic (e.g. insects, diseases) and abiotic (e.g. drought, flooding, salinity, heat, frost, nutrients imbalance). Drought and salinity are two major abiotic factors that affect plant growth, development, and ultimately its yield (Niu et al. 2014; Khalid et al. 2019; Zhang et al. 2022a, b). Plants developed several defense mechanisms that cope with the stress to maintain their metabolism and growth (Khalid et al. 2019). Plants such as vegetable crops are capable of surviving under different environmental stresses by natural acclimation and adaptation mechanisms, but these abilities may not be sufficient to cope with the swift climate changes (Dhankher and Foyer 2018). How plants respond to abiotic stresses depend on the species, stress intensity, stress duration, phenological stage of the plant, and the parts of the plant (tissue or organ) involved in the responsive mechanisms. Abiotic stresses cause changes

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in plant physiology and metabolism which can be reversible or irreversible (Seymen 2021). These factors affect the vegetable crops which are usually susceptible to abiotic stresses (Shannon and Grieve 1998; Walter et al. 2013; Devi and Arumugam 2019; Parkash and Singh 2020). To fulfill the future demand for vegetables globally, we urge to develop new cultivation techniques or tolerant genotypes to tackle the pressing drought and salinity issues (Pathak et al. 2018).

Vegetables are a major constituent of the human diet, as they are a rich source of antioxidants, vitamins, minerals, and dietary fibers (Slavin and Lloyd 2012). Vegetables are also consumed for their unique taste, texture, and religious importance. Global vegetable production increased 65% from 446 Mt in 2000 to 1128 Mt in 2019. However, there are still over 770 million undernourished people out of the close to 8 billion global population (FAO 2021). Scientists and growers are investing efforts to increase the production and nutritional value of vegetables under stressful conditions (Gruda et al. 2019). The magnitude of drought and salt stress depends on various environmental factors, such as the occurrence and distribution of solar radiation, evapotranspiration needs, and the ability to retain soil moisture (Khalid et al. 2019). Therefore, sustainable breeding technologies and agricultural management practices should be developed to monitor drought and salt stress in order to minimize their damage to vegetable crops.

Drought and salinity not only affect the production, but also the quality of vegetables. Most vegetables are sensitive to salt with salinity threshold at electrical conductivity (EC) ~ 2.5 dS m^{-1} (Behera et al. 2022) and sensitive to drought at volumetric water content of ~ 20% (Prakash and Singh 2020; Razi and Muneer 2021). Drought- and salinity-induced osmotic, ionic and oxidative stresses lead to the closure of plant stomata in the short-term to result in a decrease in size of plants in the long-term (Safdar et al. 2019) (Fig. 1). Stomatal closure results in reduced CO_2 uptake (Chen et al. 2005; Liu et al. 2014; Cai et al. 2017), limiting carboxylation and lowering internal CO_2 levels, resulting in increased photorespiration (Fig. 1). The production of reactive oxygen species is also enhanced in the plants when exposed to drought and salt stress conditions which lead to oxidative damage to cellular organelles (Fig. 1).

Despite the abundance of research in vegetables in the past few decades, there are still some unfilled knowledge gaps on the responses of vegetables to drought and salinity. This review aims to present the latest knowledge on two major abiotic stresses, drought and salinity in modern agriculture, and the responses of plants to these stresses. We review physiological and molecular responses to drought and salinity in vegetables and potentially effective strategies to enhance production. Moreover, we summarized different technologies such as seed priming, genetic transformation, biostimulants, nanotechnology, and cultural practices adopted to enhance vegetable production under drought and salinity stress For reviews on the mechanisms of drought and salinity tolerance in model plants and crops, the readers are referred to (Cattivelli et al. 2008; Munns et al. 2020; Van et al. 2020).

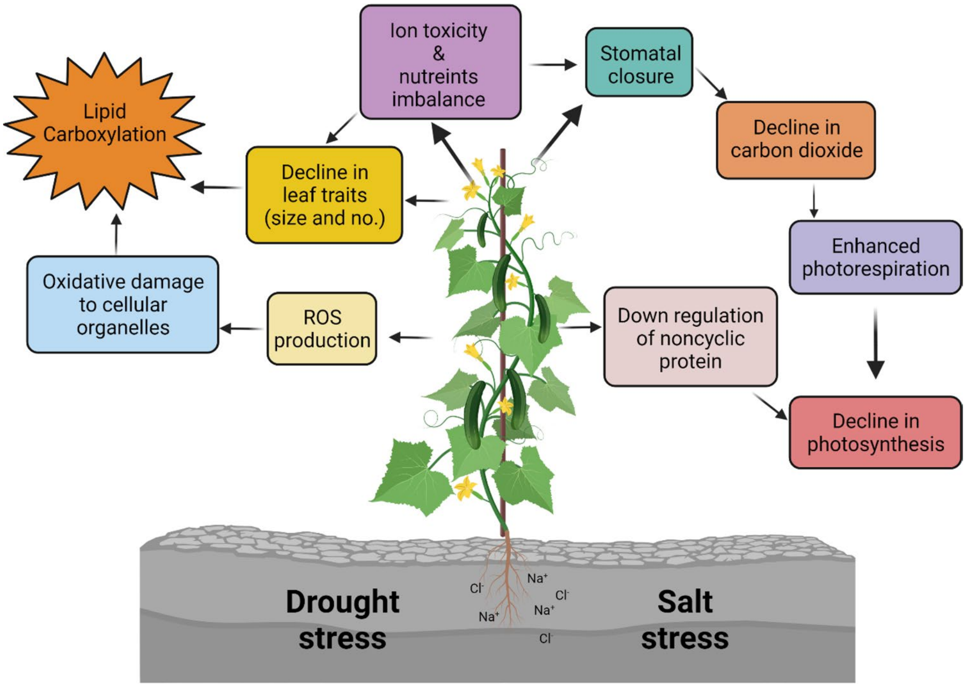

Fig. 1 Effect of drought and salt stress on vegetables and its physiological and molecular response mechanism. The water deficit and accumulation of toxic ions leads to physiological changes in plants, i.e., closure of stomata, decrease in leaf traits, and carbon dioxide, which ultimately enhance the photorespiration and decrease in photosynthesis. At the molecular level, plants responded to drought and salinity with changes in expression of genes, proteins, and metabolites such as the production of ROS, which leads to oxidative damage in the cell and lipid carboxylation

Vegetable production and drought stress

Physiological response

Water is the main constituent of plants as it is required by many vital functions. However, due to climate change, water scarcity is a critical global challenge nowadays especially to agriculture (Khalid et al. 2019). When plants are exposed to drought stress, stomatal closure was induced to retain water in the plant by decreasing leaf transpiration. However, stomatal closure also results in declined photosynthesis and gas exchange. Water use efficiency can be derived by comparing biomass accumulation to transpiration because they are tightly coupled. Genetic analyses showed that a large part of the variation in water use efficiency is controlled by genes in several species, but with low heritability (Chen et al. 2011). Indeed, water use efficiency varies with evaporative demand, time of day, seasons, soil types and crop species. Therefore, breeding plants for high water use efficiency has most often resulted in slow-growing plants that are uninteresting from an agronomical perspective (Blum 2009). For instance, it was shown that increase water use efficiency lead to a 15% yield increase under water deficit condition, but this yield increase was declined with precipitation and nullified with rainfall of 400 mm (Condon et al. 2004).

Protective cell responses to ABA-mediated hydraulic and non-hydraulic signals support a fundamental role of ABA in plant drought signaling (Chen et al. 2017; Xue et al. 2017; Munns et al. 2020). Under drought stress, the photosynthetic rate is slowed down because the captured light cannot be completely converted into chemical binding energy. Meanwhile, the excess energy leads to photoinhibition, that is, a decrease in the maximum quantum yield (Fv/Fm) of the PSII reaction center. Several mechanisms mitigate the negative effects of photoinhibition, such as non-photochemical quenching, photorespiration via Mehler reactions, non-radiative energy dissipation, and chlorophyll content regulation. Fv/Fm values can be used not only as an indicator of water deficit stress conditions but also to distinguish tolerant and sensitive genotypes to drought stress. For example, when drought tolerant genotypes of tomato were subjected to water deficit stress, the PSII activity was not decreased and thus had higher photosynthetic activity compared to sensitive genotypes (Chatterjee and Solankey 2015).

The production of reactive oxygen species (ROS) leads to oxidative damage to the chloroplast, thereby reducing carboxylation. Reducing leaf size also limits carboxylation. Low control of acyclic electron transport inhibits ATP synthesis. These events together lead to a significant reduction in plant photosynthesis. When the plant is exposed to water deficit conditions, the ability to tolerate water deficit stress and maintain water potential is also reduced. Vegetables usually contain more than 90% of water because of their succulent nature. Many physiological and biochemical processes that are involved in plant growth and development are affected by drought stress conditions (Bahadur et al. 2011). Water deficiency during critical growth stages (e.g. flowering, and fruit set stages) of vegetables can severely affects the yield and quality of vegetables. Examples of vegetable affected by water deficiency at some critical growth stages are shown in Fig. 2.

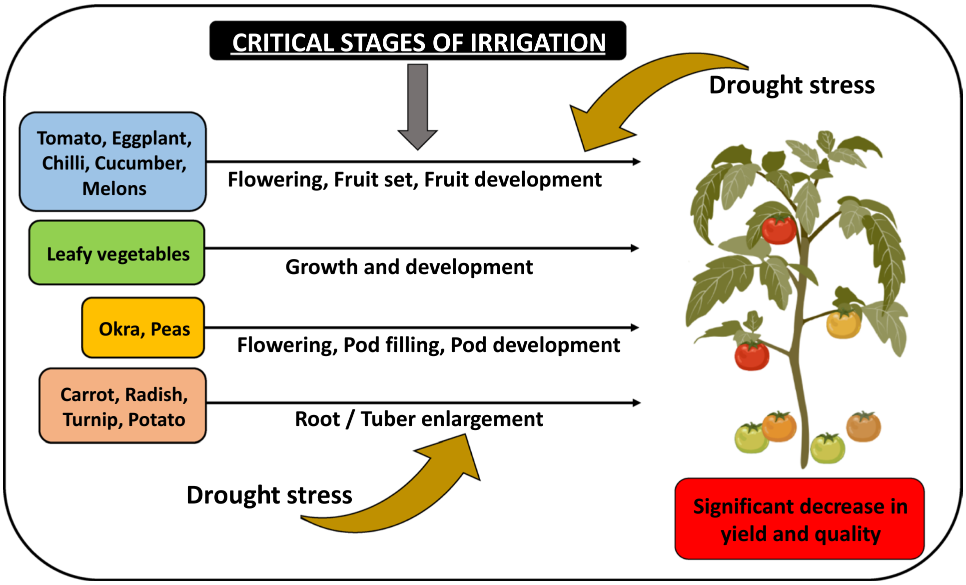

Fig. 2 Critical stages of irrigation that affect the yield and quality of vegetables

Molecular response

Water scarcity forces the plants to close their stomata which increases the production of ROS, i.e., singlet oxygen ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), hydroxyl radical ($OH^{\bullet}$), superoxide radical ($^1O_2$) in cellular organelles. The increase in ROS production will cause oxidative stress which ultimately affects plant growth and production. Subcellular compartments, such as the chloroplast, mitochondria, and peroxisomes, are sites of major metabolic activities and ROS generation (Mittler 2002). The Mehler reaction in chloroplasts, electron transfer in mitochondria, and photorespiration in peroxisomes are the main metabolic activities, leading to cellular ROS accumulation. The balance between production and elimination of intracellular ROS must be tightly regulated and/or metabolized efficiently. This balance is necessary to minimize potential damage to cellular components by ROS, as well as to maintain growth, metabolism, development, and overall plant productivity (Moller and sweetlove 2010). To cope with the destructive consequences of ROS in cellular organelles, plants produce different antioxidative enzymes including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and osmolytes (proline, glycine betaine, etc.) (Mittler 2002; Khalid et al. 2021). SODs are the frontline fighters against the ROS, responsible for the conversion of $^1O_2$ into H_2O_2. CATs play a critical role to convert H_2O_2 into H_2O. APXs help in the conversion of H_2O_2 into H_2O using ascorbate as a specific electron donor (Razi and Muneer 2021) (Fig. 3). Vegetables enhance the production of antioxidant enzymes and osmolytes when they are exposed to drought stress conditions. The tolerant genotypes tend to have higher levels of SOD, POD, CAT, APx, GR, proline, and glycine betaine as compared to the sensitive genotypes. However, this trend may vary among different vegetables. This may underlie the observation of higher levels of H_2O_2 accumulation and lipid peroxidation in drought-sensitive vegetables. In tomato plants, antioxidant activity has been reported to increase when plants are exposed to drought conditions (Zhou et al. 2019). To mitigate the drought stress and enhance the activity of different antioxidative enzymes, researchers have introduced nano-organic fertilizers (Ahanger et al. 2021), foliar application of minerals (Farzane et al. 2021), and grafting techniques (Sanzhez-Rodriguez et al. 2012). Drought-tolerant eggplant and sweet pepper genotypes with strong antioxidant activities were found to tolerate drought stress efficiently at the seedling stage (Maham and Muhammad 2019; Abdelaal et al. 2020a; Kopta et al. 2020; Alabdullah et al. 2021; Mahmood et al. 2021; Semida et al. 2021). Cucumber seedlings also

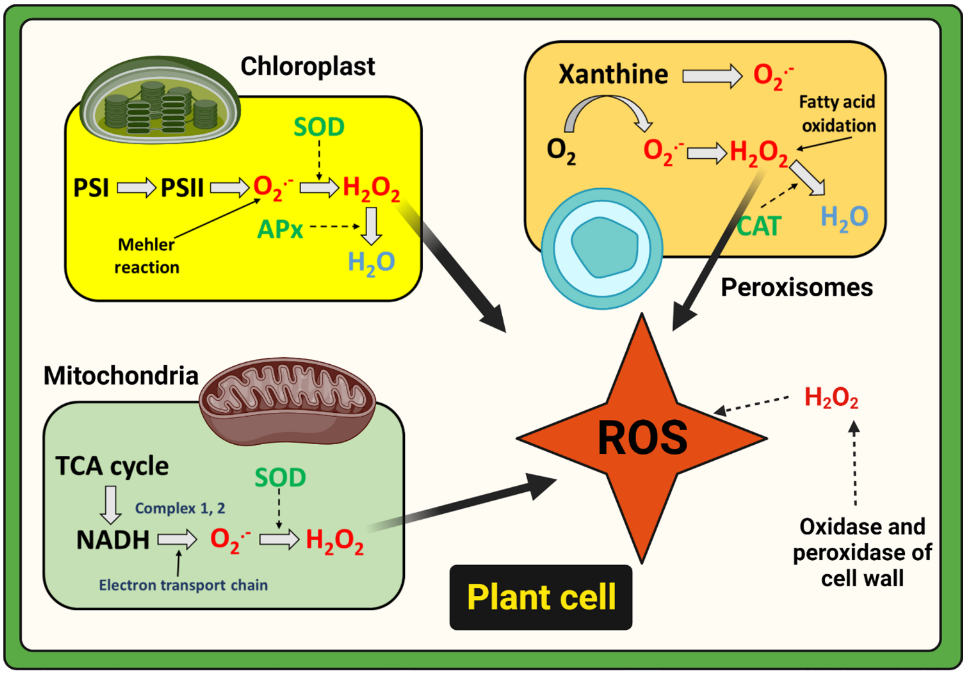

Fig. 3 A model of different cellular organelles (chloroplast, mitochondria, and peroxisomes) where ROS are generated and scavenged by antioxidative enzymes under water deficit conditions. The production of ROS is carried out by electron transport chain via PSI and PSII (Mehler reaction) and conversion of $O_2^{\cdot -}$ into H_2O_2 with the help of SOD in chloroplast. In mitochondria, complex 1 and 2 of electron transport chain are involved in the production of ROS. In peroxisome, xanthine and fatty acids are involved in the production of H_2O_2. $O_2^{\cdot -}$ Superoxide ion, *PSI* II Photosystem I, II, H_2O_2 Hydrogen peroxide, *SOD* Superoxide dismutase, *APX* Ascorbate peroxidase, *CAT* Catalase, *NADH* Nicotinamide adenine dinucleotide, *ROS* Reactive oxygen species

showed a similar result when exposed to drought stress conditions. They increased the production of SOD, POD, CAT, when exposed to water deficit conditions (Jing et al. 2009; Fan et al. 2017).

When plants are exposed to water deficit conditions, roots are the first part that sense the water loss and communicate water deficit as a stress signal to shoot through the xylem. Abscisic acid (ABA) is the main chemical signal that integrates into the roots and moves towards shoots and leaves to regulate stomata under water deficit conditions (Osakabe et al. 2014; Malcheska et al. 2017) or rapidly biosynthesized in leaves in response to stomatal closure (Zhang et al. 2018). ABA helps the regulation of plant growth and development by inducing stomata closure (He et al. 2018) and triggering a complex cascade of signaling pathways and expression of drought responsive genes under the drought stress condition (Chen et al. 2017; Xue et al. 2017).

Under water deficit conditions, plant undergoes different defence strategies and production of cuticular wax is one example. Plant cuticular wax acts as barrier against water deficit conditions (Shepherd and Griffiths 2006; Xue et al. 2017). The cuticle is synthesized by the epidermal cells. As a barrier, it prevents water loss from non-stomatal channels (Xue et al. 2017; Kosma and Jenks 2007) reported that ABA was responsible for the upregulation of 10 cuticle-related genes. The increase in cuticular wax production has been observed in tomatoes (Al-Abdallat et al. 2014) and cucumbers (Wang et al. 2015), contributing to the decrease in non-stomatal transpirations and hence enhanced tolerance against water deficit conditions. By increasing cuticular wax production, *SlSHN1* overexpression reduced tomato cuticular permeability and improved drought tolerance (Al-Abdallat et al. 2014). A major component of cuticular wax in tomatoes is n-alkanes, which are synthesized in both tomato leaves and fruit by *SlCER1s* and *SlCER3s*. Overexpression of *SlCER1–1* resulted in accumulation of n-alkanes in tomato leaves and fruits, which enhance their drought tolerance and postharvest shelf life of fruit (Wu et al. 2022; Liu et al. 2022a, b) found that ectopic expression of orange *CsECR* increases the content of total wax and aliphatic wax fractions in the transgenic tomato plants as well as decreased the cuticle permeability in fruits and leaves.

Aquaporins are critical to the maintenance of hydraulic conductance in roots, maintenance of osmotic homeostasis, the expansion of the tissue structure, the efficiency of water usage, the viability of seeds, the response and recovery after drought stress (Tyerman et al. 2021). A variety of factors play a role in aquaporin regulation and expression, including pH, cations, ROS, stoichiometry, and phytohormones at various stages, including genes, transcripts, and proteins (Patel and Mishra 2021). As a result of drought stress, guard cell-specific aquaporin genes are expressed differently, which alters the stomatal conductance. The overexpression of aquaporin genes *PIP1*, *PIP2*, and *TIP* increase gs, whereas PIP knocked-down mutants have a decrease in gs (Ahmed et al. 2021). For instance, ectopically expressing MdPIP1; 3 increased fruit size and enhanced drought tolerance of tomatoes (Wang et al. 2017).

Natural selection has led to plants evolving diverse stress adaptation mechanisms, which include modifying root system architectures to obtain water and nutrients in response to water deficit (Kulkarni et al. 2017). The root system architecture is determined by the angle of root growth, the number and length of primary and lateral roots, and the density and length of root hairs (Gérard et al. 2017; Pagès 2021). Drought stresses significantly alter root system architecture, resulting in the generation of lateral roots and root hairs (Koevoets et al. 2016). It has been shown that phytohormone homeostasis plays a critical role during root initiation and development under normal conditions as well as under abiotic stress conditions (Ranjan et al. 2021). Among the phytohormones that regulate root system architecture under stress, conditions are ABA, auxins, cytokinins, ethylene, and jasmonic acid. A recent report showed that root architecture was significantly enhanced in tomato plants under water deficit conditions when melatonin was applied exogenously (Altaf et al. 2022).

A wide variety of aspects of plant development and stress tolerance are regulated by microribonucleic acids (miRNAs) of 21–24 nucleotides length, which negatively modulate target genes through transcription cleavage and translational inhibition (Deng et al. 2022). It has now been demonstrated that drought stress-induced phytohormone signaling and gene expression have a significant influence on miRNA-mediated root growth and branching regulation, and ultimately determine RSA under stressed conditions (Bakhshi et al. 2016). Transcription factors or genes that are targeted by miRNAs control root growth and patterning. As an example, *miR160* regulates the expression of transcription factors *ARF10* and *ARF16*, which are critical in primary root development (Wang et al. 2005a, b). For instance, in tomato, over-expression of microRNA169 enhanced drought tolerance (Zhang et al. 2011) and miR1916 was reported to be as a negative regulator in drought stress resistance (Chen et al. 2019).

In different species, some novel genes are identified that cause changes in physiological and morphological traits under drought stress. For example, root length and numbers depend on the activity of many genes and the expression of dominant alleles of those genes, while root thickness depends on the expression of recessive alleles (Kumar et al. 2012). Genes involved in solute accumulation (e.g., the *mtlD* gene responsible for mannitol accumulation, or the *P5CS* gene for increased proline accumulation) help to balance the reduction in plant water potential and encode different enzymes required for the synthesis of these molecules (Abebe et al. 2003). In vegetables, overexpression of these genes resulted in specific responses to drought stress: *ABF4* transcription factor genes are not only important in tolerating drought stress in potato but also increase tuber quality and yield (Muñiz García et al. 2018). *SlGRAS4* transcription factor gene is involved in increasing the sensitivity of stomata to ABA (Liu et al. 2021), thereby reducing water loss. *AVP1* gene is involved in root growth (Park et al. 2005). *NADP-Me* gene was involved in the reduction of stomatal conductance and the improvement of water use efficiency (Laporte et al. 2002); *Wilty* gene was involved in the wilting process of tomato leaves under drought stress (Kumar et al. 2012).

Vegetable production and salinity

Physiological response

Soil salinization can be divided into primary salinization and secondary salinization. The saline soil generally contains large amounts of cations such as Na^+, Ca^{2+}, Mg^{2+}, and lower amounts of K^+ and Fe^{2+} while the most common anions are Cl^-, SO_4^{2-}, NO_3^- and HCO_3^-. Most saline soil (primary salinization) is formed through natural processes such as weathering (rock), salt accumulation from rainfall, and deposition of windblown salt. Secondary salinization is the result of human activities, such as the use of poor-quality water and fertilizers, and improper practice of agricultural management, together inducing soil salinization. Currently, 7% of the world's land surface (~ 1 Bha) contains salinized soil (Hopmans et al. 2021; Shahid et al. 2018). This includes approximately ~ 70 Mha of irrigated land which occupies around one-third of the total irrigated land in the Mediterranean Basin. Water quality has become a limiting factor for agriculture due to the overuse of salt water in irrigated land and coastal areas (Petretto et al. 2019; Zhu 2001; Tyerman et al. 2019).

Plant salinity tolerance is a multigenic trait, regulated by multiple genes and associated mechanisms. Bahmani et al. (2015) outlined a myriad of cellular components related to salinity tolerance from very upstream signaling and hormone regulation to cellular protection and ion homeostasis against salinity. These components work interactively to maintain cellular activities under salinity stress via three mechanisms: osmotic modulation, antioxidative regulation, and ion homeostasis. Increasing the level of NaCl in soil solution affects plant water uptake due to osmotic stress (Munns 2002; Munns et al. 2020; Shabala et al. 2020). Ultimately, this osmotic stress has a flow-on effect, resulting in a reduction of the rate of cell expansion in growing tissues and the stomatal opening, as well as a reduction in the amount of nutrient diffusion in the leaves. Also, plants are less likely to be able to fully exploit light absorbed by photosynthetic pigments when stomatal closure is induced by osmosis or when Na^+ is accumulated in the cytosol under saline conditions (Shabala et al. 1998; Tavakkoli et al. 2011).

Salts dissolved in soil solutions are in close contact with roots and affect plant growth because osmosis reduces water uptake by plants, thereby reducing water potential in leaves and tissues (Passioura and Munns 1984). Excessive salt concentrations in plant tissues can affect growth and productivity as they hinder several key processes such as germination, photosynthesis, nutrient balance, and redox balance (Parihar et al. 2015). For example, salinity affects germination because it reduces the osmotic potential of the germination medium for seed adsorption and alters the activities of enzymes involved in nucleic acid and protein metabolism (Parihar et al. 2015). The salinity stress effect on seed germination varies by species, variety, and salinity. In general, there is a negative correlation between salinity and germination rate, such as in carrots (Bolton and Simon 2019), cucumbers (Baghbani et al. 2013), sweet peppers (Chartzoulakis and Klapaki 2000), eggplants (Hannachi and Labake 2018) and tomatoes (Singh et al. 2012). The effect of salinity on plant growth has two consecutive stages (Parihar et al. 2015). In the first stage, saline conditions do not significantly alter plant growth, as Na^+ and Cl^- that enter the xylem are collected in the vacuole, while the meristem continues to grow through the phloem. At this stage, only reduced leaf and root development have been observed (Munns 1993). In the second stage, as the amount of salt accumulated in plant tissues exceeds the storage capacity of the vacuoles, the concentrations in the cytoplasm increase, and the activity of many enzymes is severely inhibited (Munns 2005).

Molecular response

Under salt stress, plants are mainly affected by disturbance of rhizosphere osmotic potential, which is caused by higher salt levels. The accumulation of ions in cellular compartments and organelles can reach toxic levels, hindering many physiological processes, and leading to plant death. Salinity-induced stomatal closure reduces the diffusion of CO_2 into the stomata, reducing the rate of photosynthesis, transpiration, and carbohydrate accumulation (Munns 2002). When plants encounter reduced intercellular carbon dioxide content, this often accelerates ROS accumulation due to photorespiration (Gupta et al. 2016). Although ROS are considered signaling molecules that play an important role in plant defense mechanisms (Mittler 2017), they can also adversely affect cellular metabolism and photosynthesis mechanisms. To protect cellular systems from ROS, plant defense mechanisms produce several oxidative scavenging enzymes (Khalid et al. 2020). When salt accumulates in chloroplasts, it reduces chlorophyll content, affects the photosynthetic transport system, and inhibits the activity of photosystem II. To overcome salinity, plants regulate and sequester toxic ions and produce osmotic substances (e.g. proline, betaine) that help maintain osmotic pressure (Khalid et al. 2020). Under saline conditions, the activity of these antioxidant enzymes, including SOD, CAT, and POD, and the concentrations of inactive compounds, including glutathione and ascorbic acid, are increased. For example, tomato plants showed an increase in antioxidative enzymes when exposed to salt stress conditions, but the tolerant genotype appeared to have more antioxidative enzymes as compared to the sensitive ones (Gharsallah et al. 2016). Similar observations have been also reported for eggplants and sweet peppers, in which salt-tolerant genotypes tend to have more antioxidant enzymes as compared to the sensitive ones (Wu et al. 2012; Fikret et al. 2013; Abdelaal et al. 2020b). Similar findings have been highlighted in salt-tolerant cucumber and potato cultivars that were exposed to salt stress (Zhu et al. 2004; Rahnama and Ebrahimzadeh 2005; Aghaei et al. 2009; Furtana et al. 2010). Increases in enzymatic activity and concentrations of bioactive compounds increase tolerance in plants and can be used to estimate plant salt tolerance.

The accumulation of toxic ions in plant cellular organelles leads to the disturbance in ion homeostasis. Transporters regulating Na^+ and Cl^- concentrations in mitochondria and chloroplasts are largely unknown and could be a major source of energy cost (Munns et al. 2020; Chen et al. 2021; Shabala et al. 2020; Jiang et al. 2021). Exclusion of Na^+ from roots, regulation of rhizome transport, cellular compartmentalization of Na^+, and maintenance of cytoplasmic osmotic balance are important mechanisms of salt tolerance (Van Zelm et al. 2020). Plants have evolved ways to eliminate Na^+ ions from the cytoplasm to maintain low levels of ionic Na/H antiporters and transport Na^+ in exchange for H^+ ions. This involves the transfer of Na^+ ions by Na/H ion antiporters to apoplast at the plasma membrane, while Na/H ion antiporter maintains Na^+ ion separation in the vacuole (Fig. 4) (Hussain et al. 2018; Abdelaziz et al. 2019). Similarly, high-affinity potassium transpoter1 (HKT1) type transporters play a vital role in maintaining the Na^+ and K^+ ion homeostasis and decreasing sodium toxicity in plants.

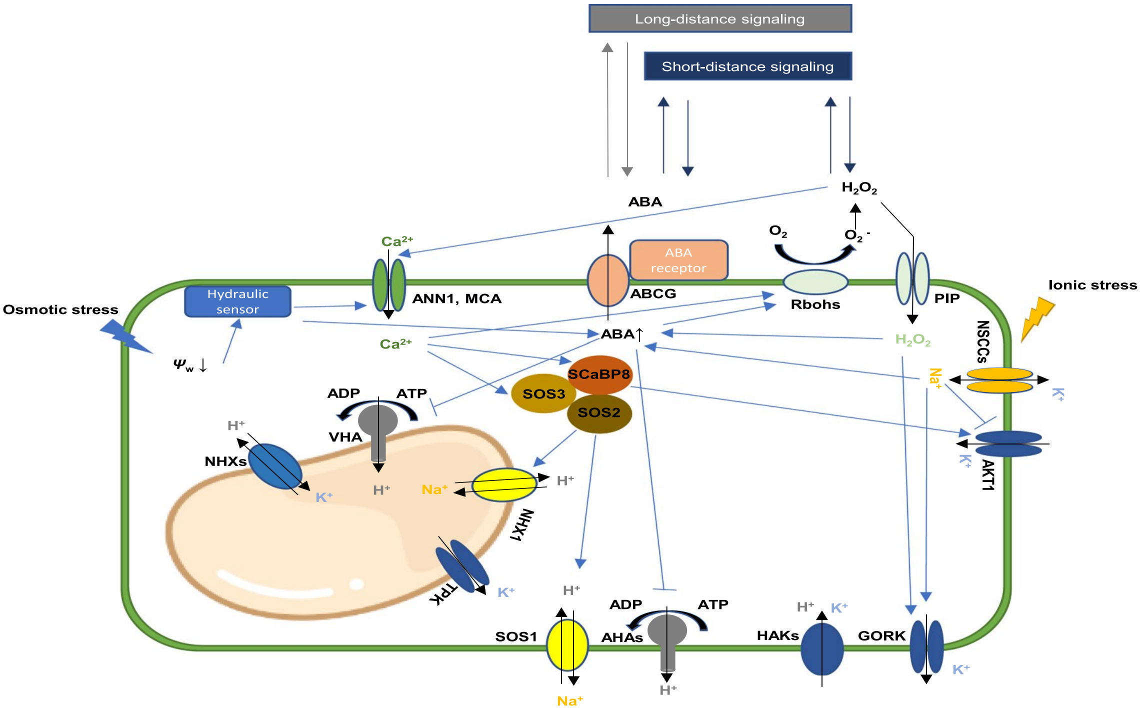

Fig. 4 The diagram illustrates the salinity induced-Ca^{2+} and ROS signaling, and important transporters involved in Na^+/K^+ homeostasis in plant cells. The hydraulic sensor firstly senses turgor pressure via reducing water potential (Ψw). The hydraulic sensor then triggers transient Ca^{2+}, ABA synthesis or both to activate short- and long-distance ROS and ABA signaling. SOS (Salt Overly Sensitive) pathway is a key component that activates Na^+ exclusion and compartmentation from the cytosol through SOS1 (PM Na^+/H^+ antiporter), and NHX1 (tonoplast Na^+/H^+ antiporter). Cytosolic Na^+ content determines ABA and ROS accumulation in cells which inhibits normal cellular functions such as promoting K^+ exclusion via GORK (K^+ outward rectified channel), inhibiting PM and tonoplast-based proton pump- VHA (vacuolar H^+ ATPase), and AHA (PM H^+ ATPase). H^+ ATPase provides a proton source to drive K^+ inward transporters- HAK1 (High-affinity K^+ transporter), NHX2-4 (NHX type2 antiporter), and Na^+ antiporters- NHX1, SOS1 located at PM and tonoplast. ANN (Ca^{2+} permeable channel annexin), MCA (Ca^+ permeable mechanosensitive channels), SCABP8 (SOS3-like Ca^{2+} binding protein 8), RBOH (NADPH/respiratory burst oxidase protein), NSCC (non-selective cation channel)

They exclude the Na^+ ions from the xylem stream and roots to keep the shoots safe from toxic ions (Maser et al. 2002; Horie et al. 2005; Møller et al. 2009). The HKT1 transporters mediate Na^+ ion movement in tomatoes (Almeida et al. 2014; Romero-Aranda et al. 2020) and cucumbers grafted with pumpkin (Sun et al. 2018). In eggplants, the weak induction of HKT1 in roots has demonstrated higher Na^+ ion accumulation in stems and leaves (Assaha et al. 2015).

In contrast to vegetables, tissue compartmentalization and exclusion of toxic ions plays an important role in redistribution of toxic ions in older or mature leaves in grasses (Liphschitz and Waisel 1974) and exclusion is carried out by salt glands or bladders. In many grasses, salt glands and bladders play a vital role in building tolerance of salinity (Ramadan and Flowers 2004; Yong et al. 2022). Salt glands mostly appear in epidermal cells, but they are usually found in mesophyll tissues in C4 grasses (Marcum 2006). The exclusion of salt toxic ions from salt glands in grasses is highly selective (Worku and Chapman 1998). The movement of toxic ions to salt glands is energy-dependent (Naidoo and Naidoo 1999). Other ions are also excreted from salt glands but in small quantities (Marcum and Murdoch 1994). There are many types of salt gland cells and epidermal bladder cells (EBCs) are an example (Shabala et al. 2014). EBCs take part in several roles, including acting as an external water reserve, depository of metabolites, a reservoir for ROS and osmolytes, and restricting sites for excessive toxic ions (Steudle et al. 1975; Agarie et al. 2007; Oh et al. 2015). Therefore, genetic engineering of salt glands in existing salt-sensitive vegetables and selection of new vegetable crops with salt glands will be among the promising molecular strategies for improving the salinity tolerance of vegetables.

Accumulation of toxic ions induces imbalances in other ions, i.e., K^+ and Ca^{2+} (Munns and Tester 2008). Calcium ions play a vital role in transmitting external stimulus signals. These Ca^{2+} signals are communicated downstream by Ca^{2+}-binding proteins (Hashimoto and Kudla 2011), ultimately transferring information to the systems that regulate the physiological and biochemical processes or gene expression (Kurusu et al. 2015). TPC_1 cation channel is involved in the production of salinity stress-triggered systemic Ca^{2+} signal in roots and may contribute to whole-plant resistance to salinity stress (Choi et al. 2014; Gilroy et al. 2014). The development of high-resolution calcium biosensors and the identification of the downstream CBL-CIPK pathway have helped the establishment of Ca^{2+} waves as early signals of the sodium response and led to the identification of a novel cation sensing mechanism (Van Zelm et al. 2020). Tolerant plants seem to have certain genes that are not in sensitive plants. According to the literature, the genes involved in salt tolerance can be categorized into three groups: (i) genes that regulate salt absorption and distribution; (ii) genes involved in osmotic control; (iii) genes associated with plant growth. Analysis of sensitive Arabidopsis mutations in high external Na^+ concentrations enabled the identification of three *SOS* genes involved in salt tolerance (i): *SOS1* encapsulates the Na^+/H^+ code of the plasma transporter membrane involved in the exclusion of Na^+ to the apoplast; *SOS2* incorporates protein kinase, which activates *SOS1*; *SOS3* incorporates calcium-binding protein and activates *SOS2*. In addition, the fourth gene (*SOS4*), appears to regulate *SOS1*, as it binds the cofactor, pyridoxal-5-phosphate, which binds *SOS1*. In addition to activating *SOS2*, there is also the protein *SCaBP8* regulated by *SOS2* (Parihar et al. 2015). In Arabidopsis plants where excessive exposure to *SOS* genes has been observed, salt tolerance and low Na^+ concentration, and high K^+ concentration have been reported (Yang et al. 2009). The relationship between genetic interactions *SOS1*, *SOS2*, and *SOS3*genes, salt stress tolerance, and high Na^+/K^+ levels have also been demonstrated in brassica (Kumar et al. 2009) and potato (Jaarsma and de Boer 2018) other genes include osmolytes or osmoprotectants or related solutes. These osmolytes are divided into four classes: N-containing solutes, such as proline and glycine betaine; sugars such as sucrose and raffinose; straight-chain polyhydric alcohols (polyols), such as mannitol and sorbitol; and cyclic polyhydric alcohols (cyclic polyols). The genes involved in plant growth are associated with signal molecules, hormones, and transcription factors, and are more common in other stress conditions. Depression molecules acting as protective molecules can be metabolites that change their concentrations or proteins that change their structures in response to drought, salt, and cold from roots to shoots to promote salt stress tolerance (Munns 2015).

Strategies to enhance vegetable production

Molecular breeding toward drought and salinity tolerance vegetables

To understand the complex mechanisms of drought and salinity and to augment their production, the focus of research is entering the era of omics. The implementation of multi-omics and improved breeding strategies is a dynamic step towards drought and salt tolerance in vegetables. The identification of drought and salt-responsive genes, proteins, metabolites, and miRNAs has become possible through studies of genomics, transcriptomics, metabolomics, proteomics, micromics, and phenomics. Many omics methods, tools, and resources have been developed for vegetable yield and quality improvement (Chaudhary et al. 2019). However, further investigation on the latest omics technologies will need to explore the myriad of pathways involved in drought and salt tolerance. Additionally, genome-wide association studies (GWAS) and quantitative trait loci (QTL) mapping techniques have made an impressive contribution to improving plant responses to drought and salt stresses. Regarding the drought stress condition, the *SiDHN* gene induced in tomato plants showed drought tolerance by maintaining their photosynthetic machinery and antioxidative defence mechanism (Guo et al. 2019). The overexpression of gene *CsATAF1* enhanced the drought tolerance in cucumber seedlings by regulating ABA-dependent pathways and more efficient coping of ROS load (Wang et al. 2018). The tomato plants produced by crossing homozygous lines have showed upregulation of salt tolerance related genes *LeNHX2* and *SlSOS2* which are involved in improving the plant growth, water uptake, and yield under salt stress conditions as compared to their parental plants (Baghour et al. 2019). Similarly, the *HAL1* gene responsible for salt tolerance in yeast was introduced in tomato plants. The overexpression of *HAL1* significantly increases the crop tolerance under salt stress by improving the K^+/Na^+ ratio which leads to sustainable growth (Gisbert et al. 2000). The Arabidopsis gene *LOS5* increases the salt tolerance in cucumber seedlings by enhancing germination, plant biomass, ABA, sugars, and antioxidative enzymes (Liu et al. 2013).

Priming

Seed priming is a major strategy to sustain or increase vegetable production in the current climate change scenario. Priming not only increases germination, but also helps the plant to tolerate different biotic and abiotic stress factors. It also enhances seedling establishment under harsh environmental conditions (Chen et al. 2012). Abiotic stresses such as drought, extreme temperatures, salinity, and heavy metals are major factors limiting global crop productivity and sustainability. Among them, drought has become a serious environmental constraint for horticultural production, especially in arid and semi-arid regions, and under rapidly changing climate scenarios (Khalid et al. 2019). Seed priming may help cells respond to drought stress through multiple mechanisms, including modulation of antioxidant defense systems, and upregulation of osmoprotectants and phenolic compounds (Savvides et al. 2016). The seed priming technique appears to be very much effective in water deficit conditions. Chakma et al. (2021a) observed that tomato plants primed with silicon showed higher fruit yield and quality as compared to controls under 75% and 100% field capacity. Cucumber plants when primed with ascorbic acid and pyridoxine improved the plant physiological and biochemical attributes under 65 and 80% field capacity. Pea primed with *Bacillus thuringiensis*, silicon, potassium silicate, and carrot extract, and onion primed with polyethylene glycol (PEG) and gibberellic acid showed improved germination, higher biomass, and better biochemical attributes at 50% deficit irrigation conditions (Arafa et al. 2021; Arvin and Kazemi 2003). Arvin and Kazemi (2003) also observed that seed priming of onion with PEG and gibberellic acid increased the tolerance against 85 mM salt stress. Di Stasio et al. (2020) showed that priming the tomato seeds with sea-weed extract enhances tomato production by up to 50% under salt-affected soils (6.3 dS m^{-1}). In terms of priming techniques, osmopriming is regarded as the most efficient for sweet pepper against 60 and 80 mM NaCl (Shumaila and Ullah 2020). Similarly, various studies have been conducted to understand the priming compounds and techniques on vegetable seeds to mitigate the negative effect of drought and salt stress conditions (Table 1).

Agronomic practices

The abiotic stresses cannot be addressed without management practices in the field. For instance, many agronomic practices have been developed by the Asian vegetable research and development center (AVRDC) now known as the World vegetable center to enhance vegetable yield under stress. To overcome water scarcity, the method of irrigation plays a pivotal role. It was reported by AVRDC (2005) that the use of drip irrigation enhances water use efficiency of capsicum by approximately 50–80% and the production was also increased as compared to furrow or flooding. Fewer chances of disease (fusarium wilt) were also reported in watermelon. The use of mulching is also very much important to maintain soil moisture and enhance nutrient conservation. Crop rotation, intercropping, crop diversification, use of organic mulches are important agronomic traits to conquer the stresses (Naik et al. 2017). These practices enhance the soil organic matter and nutrients in the soil which help the vegetables to tolerate abiotic stress conditions. The efficient use of fertilizers also helps the vegetables to tolerate abiotic stresses. The use of nutrients can also help under salt stress conditions. For example, potassium has been reported to increase tuber yield (Elkhatib et al. 2004). Phosphorous can promote radish plant health (De Oliveira et al. 2010). Sulphur seems to activate defense mechanisms in brassica and legumes (Rausch and Wachter 2005), and zinc application can reduce the uptake of sodium in pepper plants (Aktas et al. 2006).

Grafting

To counter the negative effects caused by climate change and to increase production, grafting is an environmentally friendly technique. Similar to perennial fruit crops, the rootstock and scion compatibility and their tolerance support each other. Tomato drought-tolerant rootstocks (cv. Fraidah, Zarina, Beaufort) grafted on drought-sensitive scions (cv. Unifort, Josefina, M28) has demonstrated maintenance of efficient growth, proper nutrients uptake, enhanced osmotic adjustment and improved fruit yield and quality (Ibrahim

Table 1 The effect of seed priming on tolerance against drought and salinity in vegetables

Stress	Crop	Priming compound	Stress level	Changes	References
Drought	Tomato	Silicon	50, 75, and 100% field capacity	Priming increases the yield and fruit quality at 75 and 100% FC.	Chakma et al. (2021a, 2021b)
	Cucumber	Water, Ascorbic acid, and Pyridoxine	65%, 85% and 100% field capacity	Pyridoxine and ascorbic acid increase plant photosynthesis and antioxidant defense enzymes.	Mombeini et al. (2021)
	Pea	*Bacillus thuringiensis*, Silicon, Potassium silicate, Carrot extract	50% deficit irrigation	*Bacillus thuringiensis* and carrot extract priming showed the maximum tolerance against drought stress by physiological, growth, and biochemical attributes.	Arafa et al. (2021)
	Onion	Polyethylene glycol 6000, Gibberellic acid	50% deficit irrigation	Increase germination and biomass attributes.	Arvin and Kazemi (2003)
	Cabbage	Water, Potassium nitrate, Urea	0, − 1.0, − 2.0, − 3.0, − 4.0 and −5.0 MPa osmotic potential	Priming increased the germination, antioxidative enzymes and accumulation of osmolytes.	Yan (2015)
Salinity	Sweet pepper	Osmopriming, hydropriming, and thermopriming	60 and 80 mM NaCl	Osmopriming induced more tolerance by maintaining photosynthetic pigments, accumulation of osmolytes and antioxidative enzymes.	Shumaila and Ullah (2020)
	Cucumber	Triacontanol	50 mM NaCl	Increased germination, photosynthesis, biomass, chlorophyll, and enhance osmolytes accumulation.	Sarwar et al. (2017)
	Cabbage	Hydropriming	0, 50, 100, 150, 200 and 250 mM NaCl	Increased germination, seedling vigor, chlorophyll, and antioxidant enzymes and osmolytes.	Yan (2016)
	Tomato	Seed-weed extract	6.3 dS m^{-1} NaCl	Increased in yield to 50% in control, increased biomass and nutrients balance.	Di Stasio et al. (2020)
	Melon	Sodium chloride	4.5, 9.0, 13.5 and 18.0 dS m^{-1} NaCl	Increased potassium, calcium, and osmolyte accumulation.	Sivritepe et al. (2003)
	Onion	Polyethylene glycol 6000, Gibberellic acid	85 mM NaCl	Increase germination and biomass attributes.	Arvin and Kazemi (2003)

et al. 2014; Sanchez-Rodrigues et al. 2014; Altunlu and Gul 2012). Pepper cv. Verset used as rootstock and grafted with sensitive scion cv. Atlante showed better osmotic adjustment and strong photosynthetic machinery under water deficit conditions (Penella et al. 2014). Similarly, salt-tolerant *Cucurbita* hybrids rootstock cv. P360, PS1313 grafted with salt-sensitive cucumber scion cv. Akito and melon cv. Cyrano showed great tolerance against salt stress conditions by less decline in photosynthetic attributes and strong defence mechanisms (Rouphael et al. 2012; Colla et al. 2012).

Plant growth-promoting rhizobacteria

Salt and drought stresses are serious environmental challenges that greatly reduce the yield of vegetables. The application of plant growth-promoting microorganisms in vegetable crop production has yet to attract research attention. Enhanced use of plant growth-promoting rhizobacteria (PGPR) is a new option to address agricultural challenges posed by soil environmental stress. The few reports published underline that PGPR can enhance plant productivity by counteracting the negative effects of salt and water deficit stresses on plant growth, even in stressful environments. PGPR promotes plant growth through a variety of mechanisms, such as triggering osmotic responses, providing growth hormones and nutrients, acting as a biological control agent, and modifying plant root shoot signaling. The development of salt-tolerant crops is still being planned. Thus, the only viable alternative is the use of PGPR to increase vegetable yields in stressful environments. Under abiotic stress conditions, the complex and dynamic interactions between microorganisms and plant roots influence not only the plants themselves, but also the physical, chemical, and structural properties of soils. Selecting microorganisms from stressed ecosystems and their applications under stress conditions to alleviate the effects of abiotic stress on soils may increase the yield of soil vegetables under drought and salt stress conditions (Table 2). Similarly, Arbuscular mycorrhizal fungi (AMF) are also involved to mitigate the negative effects of drought and salinity on vegetable production (He and Huang 2013). Mycorrhizae have been reported to increase the absorptive surface area of plants. In salt-stressed and water-deficient soils, nutrients absorbed by hyphae of mycorrhizae can promote plant growth and reproduction and reduce abiotic environmental stress (Baum et al. 2015). The tolerance of salt stress in tomatoes was increased by using arbuscular mycorrhizal fungi (Latef and Chaoxing 2011), grafting (He et al. 2009), and application of phytohormones (Szepesi 2008). Salinity imposes negative effect on AMF but, still some studies showed that AMF could help the plant to tolerate more stress by enhancing host-plant nutrition, maintaining K^+/Na^+ ratio and better osmotic adjustment with improved photosynthesis, which together increase the plant tolerance against salinity (Baum et al. 2015). The inoculation of AMF in tomato (He and Huang 2013), pepper (Beltrano et al. 2013), and lettuce (Aroca et al. 2013) showed higher tolerance against salinity stress. Regarding the water deficit condition, the vegetables inoculated with AMF showed better tolerance by altering their physiology

Table 2 Plant growth-promoting rhizobacteria mitigate drought and salt stress in different vegetables

Stress	Crop	PGPR	Stress level	References
Drought	Cucumber	*Burkholderia cepacia* *Promicromonospora* sp.	15% Polyethylene glycol for 10 days withholding	Sang-Mo et al. (2014)
	Tomato	*Citrobacter freundii*	45% and 35% field capacity	Ullah et al. (2016)
	Pepper	*Bacillus liheniformis*	Withholding water 15 days	Lim and Kim (2013)
	Tomato	*Bacillus subtilis*	30% Field capacity	Arkhipova et al. (2007)
	Cabbage	*Bacillus megaterium* *Peanibacillus polymyxa*	75%, 50% and 25% evaporated water	Samancioglu et al. (2016)
Salinity	Lettuce	*Pseudomonas mendocina*	2 and 4 g NaCl/Kg soil	Kohler et al. (2009)
	Eggplant	*Pseudomonas sp.*	0.57, 1, 2, and 3 g NaCl/Kg soil	Fu et al. (2010)
	Cucumber	*Pseudomonas putida* *Gigaspora rosea*	50, 100 or 200 mM	Gamalero et al. (2010)
	Pepper	*Brevibacterium iodinum* *Bacillus licheniformis* *Zhihengliuela alba*	100, 150 and 200 mM	Siddikee et al. (2011)
	Tomato	*Streptomyces sp.*	180 mM	Palaniyandi et al. (2014)
	Cucumber	*Burkholderia cepacia* *Promicromonospora sp.*	120 mM	Sang-Mo et al. (2014)
	Okra	*Enterobacter sp.*	25, 50, 75, and 100 mM	Habib et al. (2016)

and gene expressions (Baum et al. 2015). Lettuce plants with AMF exposed to drought stress condition showed tolerance by increasing abscisic acid concentration which helps maintain balance in water movement through roots to leaf transpiration (Aroca et al. 2008). AMF also enhance the tolerance of pepper plants (Davies et al. 1992) by maintaining turgor pressure, leaf water potential and water content in leaves.

Plant growth regulators

Plant growth regulators (PGRs) are used in vegetables to improve plant health and yield in stress conditions. It was reported by Grand View Research that by 2025 the PGR market is expected to grow about 4.14 billion USD (GVR 2018). They can enhance plant growth and productivity, interact with several plant processes in response to stress, and increase the accumulation of antioxidant compounds that reduce plant susceptibility to stress. The application of gibberellic acid increases the relative water content and antioxidant defence mechanism of basil plants to tolerate drought stress conditions (Kiapour et al. 2015). Synthetic PGRs, i.e., melatonin (Ibrahim et al. 2020), salicylic acid (Chakma et al. 2021b) and strignolactones (Visentin et al. 2016) also showed improved tolerance in tomato plants and enhanced the fruit quality under water deficit condition. Similarly, strignolactones in tomato (Liu et al. 2022a, b), lettuce (Aroca et al. 2013), cucumber (Zhang et al. 2022a, b) and melatonin in cucumber (Zhang et al. 2020) and eggplant (Sofy et al. 2021) induced tolerance against salt stress environments. Natural or plant based PGRs also play vital role in tolerance mechanisms of vegetables against abiotic stresses. Foliar application of moringa leaf extract on pumpkin showed sustainable growth, maintained photosynthetic pigment, increase in proline and sugar content under water deficit conditions (Abd El-Mageed et al. 2017). Similarly, application of liquorice root extract increases the nutrient uptakes, vegetative growth, biochemical attributes, and yield in peppers (Desoky et al. 2019) and beans (Rady et al. 2019).

Nanoparticles

Nanotechnology is now widely used in many fields, such as pharmaceutical, engineering, agriculture, etc. It has an enormous potential in the agriculture sector and provides a green and important alternative for crop management. Many studies showed that the use of nanoparticles as foliar, soil, and priming enhances the crop performance in biotic and abiotic stress conditions (Aqeel et al. 2021; Alabdallah and Alzahrani 2020) observed that foliar application of zinc oxide nanoparticles enhanced crop growth and production of okra seedlings under saline conditions. Similarly, zinc, boron, silicon, and zeolite nanoparticles enhanced potato plant growth in salt-affected soils (Mahmoud et al. 2019). Cucumbers also showed resistance in a saline environment by inducing early stimulation of defence responses (antioxidative enzymes) when treated with cerium oxide nanoparticles (Chen et al. 2022) and manganese oxide nanoparticles (Lu et al. 2020). Nanoparticles also mitigate the drought stress in different vegetables. The cucumber (Ghani et al. 2022), tomato (El-Zohri et al. 2021) and eggplant (Semida et al. 2021) plants showed tolerance against drought stress when treated with zin oxide nanoparticles by enhancing their antioxidative enzymes and osmolytes accumulation. Alabdallah et al. (2021) also reported that silver nanoparticles enhanced the proline accumulation and upregulated the antioxidant enzymes in eggplant under water deficit conditions.

Conclusion and future perspectives

Climate change causes different biotic and abiotic stress factors which affect crop production. Among various abiotic factors, drought and salinity are the major factors that hinder vegetable production around the world. Droughts and salinity stresses affect the vegetable plant health which ultimately leads to the reduced yield. When vegetables are exposed to drought and salt stress conditions, they respond by activating specific genes and particular mechanisms (e.g. antioxidant defence mechanism) which enable tolerance against these stresses. To enhance their tolerance, different strategies can be adopted, including proper cultural practices, priming, grafting, and the use of PGPR, nanotechnology, and omics. Omics alone or together with other cutting-edge biotechnological technologies have revolutionized vegetable breeding by accelerating the identification of candidate genes, and non-coding RNAs, such as lncRNAs, miRNAs, and circRNAs for high yield, quality and stress response. However, limited research work has been conducted on key genes and some non-coding RNAs in regulating to drought and salt stress tolerance in vegetables. More research on key genes and some non-coding RNAs action under drought and salt stress in vegetables can therefore provide additional resources and tools for developing drought- and salt-tolerant vegetables. Genetic transformation has successfully improved vegetable varieties; however, public approval of GMOs using recombinant DNA hamper the genetically engineered vegetable crops in many countries. This issue may be solved in the near future with the development and application of CRISPR/Cas systems in vegetable breeding programs. To date there are very few drought and salt tolerance vegetable cultivars. The expansion of such cultivars should not focus on only yield attributes of vegetables but also those attributes which are directly affected by drought and salt stresses during plant growth and development. To manage the salt and drought stress is a complex matter that involves approaches of breeding, genetic engineering of salt and drought resistance cultivars, smart cultural practices and the use of mitigators for sustainable agriculture.

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