

# Understanding the mechanistic basis of plant adaptation to salinity and drought

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## ABSTRACT

Plant growth and development is adversely affected by environmental constraints, particularly salinity and drought. Climate change has escalated the effect of salinity and drought on crops in varying ways, affecting agriculture and most importantly crop productivity. These stressors influence plants across a wide range of levels, including their morphology and physiological, biochemical, and molecular processes. Plant responses to salinity and drought stress have been the subject of intense research being explored globally. Considering the importance of the impact that these stresses can have on agriculture in the short term, novel strategies are being sought and adopted in breeding programs. Better understanding of the molecular, biochemical, and physiological responses of agriculturally important plants will ultimately help promote global food security. Moreover, considering the present challenges for agriculture, it is critical to consider how we can effectively transfer the knowledge generated with these approaches in the laboratory to the field, so as to mitigate these adversities. The present collection discusses how drought and salinity exert effects on plants.

**Keywords:** antioxidants, drought, mechanism, oxidative stress, photosynthesis, ROS, salinity, tolerance.

## Introduction

The abiotic stresses of foremost importance, such as salinity and drought, threaten crop cultivation and agricultural production (Huang *et al.* 2012). In the current scenario of climatic changes, salinity and drought stresses are gradually becoming more severe, particularly in arid and semi-arid regions (Kumar *et al.* 2019). When the threshold of salinity and drought stress is exceeded, the plant becomes stressed, followed by activation of a complex signalling pathway, resulting in variable alterations of molecular, biochemical, and physiological mechanisms (dos Santos *et al.* 2022; Zhang *et al.* 2022) in various plant species to acclimatise to individual or combined stresses (Saharan *et al.* 2022). Drought and salinity are major environmental stresses resulting in secondary stresses such as osmotic and oxidative stress. Osmotic stress is induced by drought, and salinity affects the plant by hindering development, growth, seed germination, flowering and fruiting (Kumar *et al.* 2021). To survive osmotic stress, plants have adapted a range of integrated mechanisms including morphological changes (in leaf thickness, rolling, wax or cutin deposition, and alteration in root system architecture), biochemical adjustments (accumulation of osmolytes such as sugars and phenols, antioxidant enzymes for reactive oxygen species [ROS]), molecular responses (expression of stress-induced genes), and physiological adaptations (stomatal aperture) (Cao *et al.* 2023; Hasanuzzaman *et al.* 2023). However, understanding the underlying mechanisms for improving crops' tolerance to salinity and drought stress is challenging (Waseem *et al.* 2023). Therefore, it is pivotal to develop new strategies, tools, methods, and equipment to predict the changes that could be caused by salinity and drought stresses at the current time. This will make it possible to reduce production losses and increase crop tolerance.

## New insights into salinity and drought adaptation in plants

The members of the Solanaceae family include important plant food species such as *Solanum tuberosum*, *S. lycopersicum*, *S. melongena*, and *Capsicum annuum* (Samuels 2015). Salinity is one of the devastating environmental stresses and affects approximately 20% of agricultural land, and significantly reducing crop yields (Negrão et al. 2017). In the current scenario of global warming, the magnitude and frequency of salinity have amplified, impacting the productivity of solanaceous crops. Altaf et al. (2022) discuss the impact of salinity on various traits of solanaceous crop plants including relative growth rate, transpiration, water relations, water use efficiency, senescence, ion homeostasis, hormonal balance, rate of photosynthesis, yield and yield-related components. They summarise key mechanisms, including (1) water relations, photosynthesis, source–sink relationships, and nutrient uptakes; (2) antioxidant enzymes of ROS, osmolytes accumulation and osmo-protectant; (3) alterations in hormonal balance; (4) protein functions, and gene expression. We hope that this review will provide pertinent information to researchers for performing proficient assays and interpreting results from salinity tolerance experiments.

In recent years melatonin has gained much attention as a multifunctional bioactive and powerful antioxidant compound associated with plant growth and regulation (Ahmad et al. 2023). Melatonin regulates plant responses either directly, by preventing accumulation of reactive oxygen species (ROS) and reactive nitrogen species (RNS), or indirectly by affecting stress-responsive pathways (Zeng et al. 2022).

Drought has a strong impact on the agro-economics of the Mediterranean region due to persistent rain deficiency (Toreti et al. 2022). *Capsicum annuum* is an important crop in the Mediterranean region that is impacted by drought, which hinders root nutrient absorption, particularly nitrogen at the root–soil interface (Wang et al. 2019). Kaya and Shabala (2023) demonstrated melatonin-mediated drought tolerance in *C. annuum*. The exogenous application of melatonin minimises the impact of oxidative stress by modulating the activities of enzymes related to nitrogen metabolism, including nitrite reductase, nitrate reductase, glutamate synthetase, glutamine synthetase, and glutamine dehydrogenase. Leafy vegetables belonging to Compositae family, including lettuce (*Lactuca sativa* L.), are rich in antioxidants, minerals, vitamin, and fibre, (Camejo et al. 2020). However, environmental perturbations, including salinity, significantly reduce growth and yield of lettuce (Al-Maskri et al. 2010). Ascorbic acid, a water-soluble vitamin with antioxidant properties, is effective under salt stress (Foyer and Noctor 2011). Foliar application of ascorbic acid is one of the effective strategies to mitigate stress effects (Billah et al. 2017). Similarly, Naz et al. (2022) demonstrated that foliar application of ascorbic acid encourages the accumulation of superoxide dismutase, peroxidase, catalase,

and phenolic content in lettuce. These studies suggest that exogenous application of melatonin and ascorbic acid has the potential to mitigate the adverse effects of salinity and drought and could serve as a cost-effective and sustainable solution for crop productivity.

Wheat is the second essential staple cereal crop after rice among those cultivated worldwide. Wheat production is significantly affected by climate factors, mainly drought and heat stress (Waseem et al. 2023). Al-Quraan et al. (2022) explored the Jordan's durum wheat (*Triticum durum* L.) germplasm by evaluating agronomic adaptations for drought tolerance. A panel of four durum wheat cultivars, including Umqais, Hurani75, Sham1, and Acsad65, were selected to assess the functional role of genes involved in the gamma-aminobutyric acid (GABA) shunt pathway, dehydrin gene expression (*dhn*; *Dehydrins* and *wcor*; wheat cold regulated (*cor*)), and ROS accumulation. Gaining insight into the genetic mechanisms underlying drought tolerance in cultivated and advanced wheat lines helps us to understand the phenomic variation in modern wheat cultivars. The application of high-throughput approaches for functional genes elevation is a prerequisite for a modern molecular breeding program (Waseem et al. 2022). A panel of 40 wheat genotypes were selected from Pakistan's wheat germplasm by Rubab et al. (2023) using Kompetitive allele specific polymerase chain reaction (KASP) assays integrated with agronomic traits. The authors selected eight functional KASP markers and nine morphological traits to demonstrate that Aas, China 2, Chakwal42, Bhakar Star, and Markaz performed better under drought stress. The data collected by Al-Quraan et al. (2022) and Rubab et al. (2023) can be used for breeding programs to enhance climate resilience in wheat for sustainable food production and global food security.

Soybean is one of the important oil crops with desirable traits and is regarded as low-cost meat alternative (Abbasi 2020). Soybean is highly susceptible to drought stress (Ayman et al. 2016) and intensive research efforts have been to develop drought-tolerant cultivars (Suhartina et al. 2022). Similar efforts have been made by Castro-Valdecantos et al. (2023) by investigating a panel of drought-sensitive (*Williams 82* and *Union*) and drought-tolerant (*Jindou 21*, *Long Huang 1*, and *Long Huang 2*) genotypes of soybean subjected to varying soil moisture levels, to understand the role of endogenous ABA (abscisic acid) concentrations and leaf water relations in regulating stomatal behaviour. Although ABA is a prime mediator of drought stress tolerance, this tolerance can also be brought about in an ABA-independent manner. Waseem et al. (2023) found that leaf water potential relations play a dominant role in regulating stomatal closure across soybean cultivars.

Ben Hamed et al. (2023) reported a comparative analysis of the effect of water stress for 23 days followed by rewatering for 7 days on *Pistacia vera* and *P. atlantica*, considering various factors such as leaf gas exchange, chlorophyll content, and mineral nutrition, particularly Zinc (Zn) and Iron (Fe).

This study showed that *P. atlantica* exhibited enhanced water relations, leaf chlorophyll content, gas exchange, and Zn/Fe content relative to *P. vera*.

Abbasi *et al.* (2023) explores the impact of silicon supplementation (50 mg L<sup>-1</sup>) on enhancing salt tolerance in sugarcane (CPF-246). The research reveals improvements in chlorophyll content and photosynthesis, attributing these effects to silicon's regulation of ion concentrations. The element limits the uptake of sodium by roots while promoting essential elements in both roots and shoots. Positive outcomes were observed not only in CPF-246 but also in other genotypes (HSF-240, CPF-250). The findings suggest that silicon supplementation could serve as a viable strategy for enhancing crop growth in saline soil. The study recommends further investigation into silicon-mediated gene expression in sugarcane protoplasts for broader applications in cultivating crops in saline areas.

Ahmed *et al.* (2023) focused on examining the impact of salinity and alkalinity stress on root system traits and ion content in 21 accessions of *Avena* species. Various treatments were applied, revealing significant variations in root traits and ion levels among genotypes. Principal component analysis identified key traits contributing to stress tolerance, and biplot analysis highlighted significant correlations. Specific oat genotypes, such as IG-20-1183, IG-20-894, and IG-20-425, exhibited tolerance to particular stress conditions. The study conducted multi-trait stability index analysis, identifying three stable genotypes (IG-20-714, IG-20-894, IG-20-425) suitable for cultivation in salinity–alkalinity affected areas.

## Concluding remarks and future outlooks

Collectively, recent research on salinity and drought stress has significantly advanced our knowledge, providing insights into the response, signalling, and the adaptive mechanisms operating in plants. This compilation offers invaluable cues for the better understanding of salinity and drought stress. We anticipate that the accumulated knowledge will not only assist but also pave the path for new studies and breeding programs aimed at developing crops with enhanced salinity and drought tolerance. To comprehend salinity and drought tolerance in plants more comprehensively, a combination of integrated variety improvement, theoretical research, and field management is essential. We sincerely appreciate the efforts and significant contributions of the authors, editors, and peer reviewers who made this research topic possible. We hope that our readers can identify valuable information from this topic of research and find appropriate collaborators to promote their great success.

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