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DROUGHT AND SALINITY EFFECTS ON PLANT GROWTH: A COMPREHENSIVE REVIEW

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SUMMARY

Drought and salinity are major environmental constraints that severely affect crop productivity. Plants frequently encounter these abiotic stresses, with salinity-drought combinations posing a significant threat to plant growth. Both stresses induce physiological, biochemical, morphological, and metabolic variations through various mechanisms, ultimately altering plant growth and productivity. Individual stress negatively influences plant growth, photosynthesis, ionic balance, and oxidative status, while integrated salinity-drought stress has a more synergistic effect. The severity caused by each stress varies depending on the plant species and existing environmental conditions. For instance, drought stress may have a more severe effect on photosynthesis compared with salinity, while salinity itself has a more detrimental effect on root biomass. A key difference between the individual and combined stress responses associated with antioxidant production. Plants exposed to individual stress can enhance their antioxidant levels. However, under combined salinity-drought stress, this vital defense mechanism appears compromised, leading to increased oxidative stress. The presented review highlighted the significant negative impact of integrated and individual salinity and drought stresses on plant growth. Understanding the multifaceted plant responses at various levels and the genetic base of plant tolerance to drought and salinity is essential for developing strategies to improve plant resistance to these stressors.

Keywords: Abiotic stress factors, drought, salinity, osmotic and oxidative stress, plant growth, photosynthesis

Key findings: Integrated salinity-drought stress has a more detrimental effect on plants compared with individual stress. The severity of drought and salinity stresses can vary depending on the plant species and environmental conditions. Plants exposed to individual stresses can increase their antioxidant levels, however, comprising this mechanism under combined salinity-drought pressure.

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INTRODUCTION

Drought and salinity cause enormous effects on plant growth and development and eventually productivity (Wu *et al.*, 2023). These abiotic stress factors independently develop physiological, morphological, and metabolic variations within crop plants through diverse mechanisms that ultimately diminish plant growth and yield. Climate change also amplifies the negative effects of drought and salinity stresses and enhanced the intensity of these stresses, particularly in arid and semi-arid environments (Kennish *et al.*, 2023). A considerable portion (40%–50%) of Earth's terrestrial surface comprised arid and semi-arid classifications. These regions mostly experience limitations in crop production due to low precipitation. However, employing irrigation can facilitate agriculture.

A substantial challenge to irrigated agriculture is soil salinization, already indicating its impact to around 20%–50% of irrigated land (Khondoker *et al.*, 2023). Future estimates suggested a further increase in salinized land, reaching 50% of the global arable land by 2050 (Li *et al.*, 2023). Arid and semi-arid regions are particularly vulnerable, as those areas experience low rainfall coupled with high evapotranspiration. The interplay between salinity and drought stresses is especially crucial in coastal and arid/semi-arid regions. Increased soil evaporation boosts the salt concentration within the soil solution, developing a dual stress of drought and salinity for cultivated crops. With the increased prevalence of climate change, future research efforts should prioritize investigating the combined effects of salinity and drought to develop sustainable agricultural practices for these regions (Cao *et al.*, 2023).

High salinity disrupts essential plant cell metabolism through mechanisms, such as Na+ toxicity and ionic imbalance, affecting enzyme activity, protein synthesis, and ribosome function. Moreover, high sodium (Na^+) concentration competitively inhibits the uptake of essential nutrients like potassium (K^+), magnesium (Mg_2^+), ammonium (NH_4^+), nitrates (NO_3^-), and phosphate (PO_4^{3-}) (Shabala and Cuin, 2008). Furthermore, salinity-induced osmotic stress disrupts photosynthetic machinery by reducing stomatal conductance, thereby limiting CO_2 influx and ultimately hindering photosynthesis. The detrimental effects of salinity-induced Na+ toxicity were evident on photosynthetic processes (Safdar *et al.*, 2019); however, the relative severity of salinity and drought stresses on photosynthesis remains unclear. Notably, the combined effects of these two stress factors on photosynthesis cannot be simply predicted based on individual stress responses (Wang *et al.*, 2024).

Elevated salinity and drought stresses disrupt the plant growth through a multitude of physiological mechanisms. Increased root zone salinity induces a state of physiological drought, leading to varied stomatal functions, reducing photosynthetic activity, and hindering crop plants' growth and development. Rapid increase in soil salinity causes a decline in cell volume and turgor pressure within leaf cells and consequently, reduces leaf production and size (Bhusal *et al.*, 2023). Comparatively, drought stress disrupts nutrient homeostasis and photosynthetic capacity within plants. Water shortage also leads to a loss of turgor pressure in plant cells, consequently limiting growth (Yavas *et al.*, 2024). Thus, it is consistent that combined salinity and drought stresses exert a more pronounced negative impact on physiological and growth processes compared with individual stresses. However, a quantitative assessment of growth reduction with integrated stress conditions remains relatively unexplored. Based on the above discussion, the latest study aimed to investigate the differential effects of individual and combined effects of salinity and drought stresses on plant growth and to quantify the differential responses of crop plants.

Drought effects on plant growth

Drought significantly hinders plant growth in several ways (Figure 1).

Reduced water uptake

Water is the lifeblood of crop plants that plays a primary role in the physiological process,

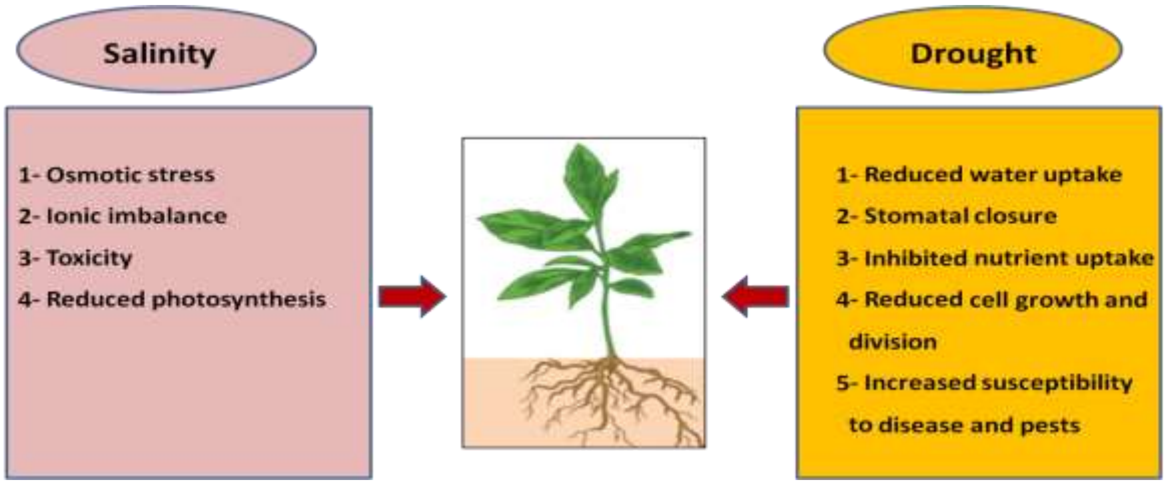

Figure 1. Impacts of drought and salinity on plant growth and development.

from germination to photosynthesis and growth. During droughts, this vital resource becomes scarce, throwing a wrench into the delicate balance within a plant (Gies, 2022). Dry soil has a lower water potential and the plants require more energy to extract moisture from the soil. It also develops a tug-of-war between plant roots and the soil, and plants need more energy to access moisture. Plants also have a defense mechanism via tiny pores on their leaves called stomata. The stomata are essential for gas exchange, however, also responsible for water loss through transpiration. Drought triggers stomatal closure, reducing water loss but also limiting CO_2 uptake for photosynthesis. This develops a difficult trade-off – to conserve water or maintain growth. Beyond the stomata, drought can also affect the root system, and the plant's lifeline for water uptake (Bachofen *et al.*, 2024). As drought develops, the soil dries out, creating air gaps around the roots. Air gaps between the soil particles and roots make it harder for plants to absorb more water. Additionally, under drought stress conditions, plants may even limit root growth, prioritizing water conservation over expanding their reach for water (Vadez *et al.*, 2024).

Stomatal closure

Drought-induced stomatal closure is a crucial adaptation that helps plants to survive under dry conditions. However, it comes at a cost, potentially reducing plant growth and productivity. During drought stress, plants rely on abscisic acid (ABA) signaling to regulate the water balance. Roots perceive drying soil conditions and trigger ABA production. Then, the ABA signal proceeds translocation to the shoots, where it mediates various physiological responses, including stomatal closure to conserve water loss. The surge in ABA acts like a molecular switch, triggering a series of events that lead to stomatal closure (Tiwari *et al.*, 2023). The ABA alters the movement of ions within the guard cells that control the stomatal opening. The ionic shuffle disrupts the turgor pressure inside the guard cells. As the turgor pressure decreases, the guard cells lose their plumpness and become limp, causing the stomata to close. An effective reduction of water loss through transpiration can occur by closing the stomata and conserving the precious water during drought. However, stomata are also vital in the carbon dioxide uptake required for photosynthesis process. Therefore, stomatal closure restricts CO_2 uptake and potentially hindering plant growth and food production. The degree of stomatal closure also varies depending on plant species and drought severity.

Nutrients uptake inhibition

Drought not only starves plants of water, but also hinders their ability to access the essential nutrients from the soil (Imtiaz *et al.*, 2023). Nutrient deficiencies can lead to several visual symptoms in crop plants, including stunted growth, chlorosis (yellowing of leaves), and decreased crop yield. This creates adverse effects and reduces water movement in the soil, which eventually hinders plant growth and development. Furthermore, drought makes it difficult for dissolving nutrients to move freely through the soil profile. Imagine nutrients stuck in molasses — becoming less accessible to plant roots. Drought also directly affects root systems, and the roots may struggle to reach new areas containing moisture and nutrients. Additionally, some plants may even limit root growth under drought stress, prioritizing water conservation over expanding their reach for nutrients (Vadez *et al.*, 2024). Plants require energy for transport mechanisms to move nutrients from the soil into their roots. Under water deficit conditions, plants need to use more energy to extract water from the soil. This energy shortage limits the resources available for nutrient uptake, creating a bottleneck in the system.

Reduced cell growth and division

Drought disrupts the foundation of plant growth: cell division and expansion. Under water scarcity conditions, plants experience adverse effects in these vital processes. Plant tissues rely on turgor pressure, the pressure exerted by water against the cell wall, to maintain their shape and facilitate expansion. During drought, water falls out of plant cells, leading to a significant decrease in turgor pressure. This lack of turgor pressure makes it difficult for cells to expand, hindering growth (Al-Yasi *et al.*, 2020). Cell division and growth are resource-intensive processes, requiring a steady supply of building blocks like proteins and nucleic acids. Water-deficit conditions hamper the movement of these essential building blocks, limiting the materials available for cell construction. Drought also brings variations in plant hormone levels. The ABA is crucial in stomatal closure. However, it also has an inhibitory effect on cell division. The surge in ABA during drought slows down the cell cycle through reduced cell division and overall growth. Drought disrupts the delicate balance of metabolic processes within the plant cell (Brookbank *et al.*, 2021). Water is a vital component of various enzymatic reactions, and less water availability develops hindrances in these reactions. This can accumulate harmful byproducts and a decline in overall metabolic efficiency, plant growth and development.

Increased susceptibility to diseases and pests

Drought weakens plants' defense systems, making them more vulnerable to disease and pests (Candeias, 2021). Drought disrupts the plant's internal processes; reduced water uptake weakens cell walls, hindering their ability to act as a barrier against pathogens. Additionally, essential nutrients crucial for defense mechanisms become less available under drought stress conditions. Plants even produce various compounds to fight off diseases and pests. However, drought stress diverts resources away by producing those chemicals, leaving plants with a weak immune system. Drought reduces available water, and the pathogens on the plant surface can become more concentrated, with an increasing chance of infection. Moreover, specific fungi and bacteria flourish well in dry conditions. Drought can favor these pathogens, allowing them to compete with beneficial microbes and overwhelm the weakened plant's defense system (Cao *et al.*, 2024).

Salinity effects on plant growth

Osmotic stress

Plants’ root hairs facilitate the water uptake through osmosis. Osmosis is the passive movement of water molecules across a semi-permeable membrane from a region of lower solute concentration (hypotonic solution) to a region of higher solute concentration (hypertonic solution). In normal conditions, the cytoplasm inside the plant cell acts as the hypotonic solution compared with the soil solution (more concentrated). This allows for water to flow into the plant cell (Zheng *et al.*, 2024). With high soil salinity levels, the soil solution becomes hypertonic relative to the plant cells. It also disrupts the natural water balance of plants, making it difficult for them to absorb water from the soil. As a result, the plant may experience water stress even if the soil is moist. This water stress can lead to stunted growth, wilting, and even death of crop plants (Bhattacharya, 2021).

Ionic imbalance

High salinity develops more concentration of ions outside cells, which creates an osmotic pressure, drawing out water from cells to equalize the concentration on both sides of the cell membrane. This dehydration can disrupt cellular functions. Cells rely on specific processes to move the ions in and out. With high salinity, specific abundant ions, such as sodium (Na^+), can overwhelm these processes. It further disrupts the uptake of essential ions, i.e., potassium (K^+), which are crucial for maintaining plants' electrical signals and other cellular processes. In soil, higher salinity can slow down plant growth, and eventually, wilting occurs with reduced crop yields. Plants have different mechanisms to adapt to salinity; however, its exceeding ratio can cause ionic imbalances (Majeed and Siyyar, 2020).

Toxicity

Specific ions, particularly sodium (Na^+) with higher concentrations, can be directly toxic to plant cells. Excessive sodium uptake by plants can disrupt enzyme activities and damage cellular structures. It can lead to issues like leaf scorch, where leaf tips and margins turn brown, then die. Similarly, other ions, such as chloride (Cl^-), can also be toxic to plants at higher concentrations. This can also damage plant cells and tissues, leading to leaf scorch, reduced growth, and even death (Balasubramaniam *et al.*, 2023).

Reduced photosynthesis

High salinity in the soil can impair photosynthesis by damaging chloroplasts and reducing chlorophyll content. This reduction likely occurs due to increased production of reactive oxygen species (ROS) under salinity stress conditions, which oxidize and degrade chlorophyll. The severity of chlorophyll loss often interlinks with salinity levels (Taïbi *et al.*, 2016). Plant response to salinity varies depending on the species, salt concentration, and their interaction with existing environmental conditions. Higher salinity can cause osmotic stress and ionic toxicity in crop plants. Furthermore, short-term exposure to salinity disrupts the internal structure of chloroplasts and photosynthesis sites in plants. This abiotic stress conditions cause swelling of the thylakoids, the membranes within chloroplasts capturing the light energy, and accumulation of starch. Salt stress reduces photosynthetic rates and severely damages chloroplast structures and the photosynthetic apparatus at moderate to higher concentrations in rice, eggplant, purslane, and physic nut (Hussein *et al.*, 2023).

Drought and salinity combined effects

The combined effects of drought and salinity significantly reduce crop yields by disrupting physiological and morphological processes. These combined stresses disrupt the nutrient and ionic balance within the plants and hinder physiological and biochemical pathways crucial for growth and development. Numerous studies have explored the individual and combined effects of these stresses on various crops (Hameed *et al.*, 2021). Research on crops like cotton, barley, wheat, and maize consistently showed combined effects of drought and salinity stresses have a more detrimental impact on plant growth compared with either single stress. Drought and salinity negatively affect plant growth, reducing their overall biomass production. Interestingly, limited water availability per se seems to have minimal influence on shoot size, and shoot and root dry weights. Under drought stress, plants tend to grow longer roots to access water and nutrients from deeper soil layers, which explains the less effect on root dry weight by drought alone compared with combined stresses (Kim *et al.*, 2020). Combined drought and salinity pressures have a more notable impact on plant height and growth rate than the individual stress. The combined stress conditions disrupt key physiological and biochemical processes, hindering plant growth and development (Zhang *et al.*, 2012).

Response mechanisms to drought and salinity

Plants employ complex signaling networks to detect and respond to drought and salinity stresses, triggering stress-responsive defense mechanisms. The Figure 2 illustrates the morphological, physiological, biochemical, and metabolic responses.

Morphological responses

Drought stress interrupts various physiological processes, hindering plant growth. Reduced water leads to stunted growth and decreased yield in crops like barley, wheat, and maize (Kamara *et al.*, 2024). This may occur due to several factors, including lower water content within the plants, increased sunlight intensity, and higher temperatures (Tamrazov, 2022; Demichev *et al.*, 2024). Drought can also disrupt respiration, photosynthesis, and enzyme activities. In the early stages of drought stress, plants may prioritize root growth over shoot growth to maintain water uptake (Bardhan *et al.*, 2022). Under moderate drought, plants may exhibit minimal variations in growth patterns and only a slight increase in root mass (RMF). This indicates a prioritization of resource allocation toward aboveground biomass maintenance, potentially to prolong competitive interactions for light and space. However, under severe drought conditions, plants significantly increase their RMF, primarily due to decreased stem growth (Weigelt *et al.*, 2021).

Drought also restricts nutrient availability and their uptake in crop plants. Water facilitates nutrient transport to roots. During drought, reduced water flow limits nutrient diffusion and mass flow of soluble nutrients. The soil with higher salinity can impede seed germination, hinder plant growth and development, and ultimately cause significant reductions in crop yield. Salinity stress disrupts seed germination by altering the ABA levels through variations in the expression of a gene called nine-cis-epoxycarotenoid dioxygenase (*NCED*).

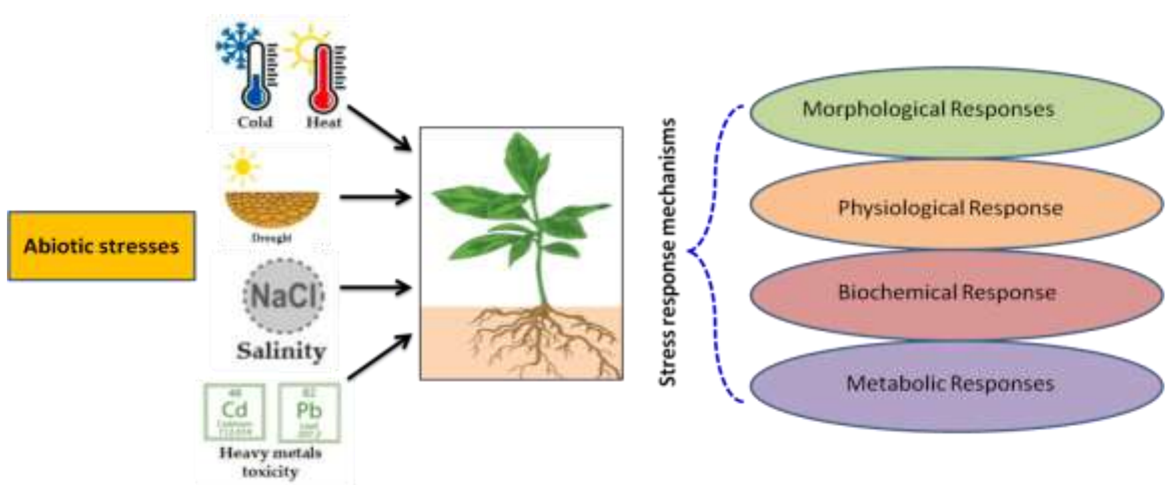

Figure 2. Plant responses to different abiotic stresses.

Additionally, salinity upsets the enzymes responsible for ethylene biosynthesis in plants. Ethylene usually promotes seed germination in various plant species by counteracting ABA's effects, and can even contribute to salinity tolerance in seeds. Therefore, a delicate balance between ethylene and ABA is essential for regulating seed germination under salinity stress conditions (Liu *et al.*, 2022).

Physiological responses

Drought and salinity stresses trigger the water shortage in plants, leading to stunted growth, reduced stomatal conductance, and nutrient deficiencies (such as K^+ and Ca^{2+}). However, prolonged exposure of plants to salt adds ionic stress to dehydration. This disrupts photosynthesis by causing leaf senescence and hindering pigment synthesis. Under salinity conditions, chloride may accumulate in thicker roots. Additionally, excessive sodium ions can damage photosynthetic components, reducing enzyme activity, and pigment production. Reduced CO_2 assimilation due to limited utilization of absorbed light can trigger ROS production, leading to cellular oxidative stress. However, in contrast, plants with long-term drought stress prioritize root elongation, possibly to reach deeper water sources (Shoaib *et al.*, 2022). Particular plant species have mechanisms to exclude salt from their cells or minimize its concentration within the cytoplasm. These strategies involve compartmentalizing salt in the vacuoles. It also helps mitigate the negative impact on photosynthesis and other vital processes.

Biochemical responses

Drought and salinity stresses can also boost the production of harmful ROS within plant cells. A higher ROS accumulation also damages cell membranes, proteins, and DNA (Hasanuzzaman *et al.*, 2021). However, plants also have defense mechanisms to combat the higher ROS level. These mechanisms involve two main components, i.e., non-enzymatic antioxidants (glutathione, flavonoids, ascorbates, phenolics, and tocopherols**),** and enzymatic antioxidants (peroxidase, ascorbate catalase, and superoxide dismutase).

Drought and salinity tolerant cultivars of crops, such as maize, tomato, and marigold, exhibited increased production of antioxidants (Mir *et al.*, 2022). This highlights the potential of antioxidants in mitigating the oxidative stress caused by drought and salinity stress conditions. Plants with high levels of antioxidant activity have better means to face these stresses and minimize the damage. The ability of these enzymes to scavenge ROS and lessen their harmful effects interconnects with genotypes tolerance to drought and salinity stresses. These stresses can negatively impact various parts of a plant cell (vacuole, cytoplasm, and nucleus), and even damage the entire organs and plant health (Hameed *et al.*, 2021).

Metabolic responses

Stressful conditions significantly manipulate the plant metabolism, leading to major variations in how to produce, transport, and store metabolites. A rapid metabolic response in a stress event allows plants to recover functions more quickly, essential for survival. Metabolomics studies can be a powerful tool for identifying key stress metabolites. These metabolites can serve as indicators of a plant's ability to adapt with drought and salinity stress conditions. Additionally, they reveal how groups of compounds adjust to mediate stress tolerance and how a species can modify its primary metabolic pathways to tolerate with different stresses (Jorge and António, 2018). Metabolic variations in stress conditions involve adjustments in both primary and secondary metabolites. Primary metabolites, indispensable for plant growth, development, and reproduction, exhibit greater abundance consistency within a species. Conversely, the secondary metabolites, although not strictly vital for survival, contribute significantly to a plant's ecological interactions. As a result, the secondary metabolites tend to vary more across different species (Jorge and António, 2018).

Genes and transcription factors involved in drought and salinity tolerance

Plants have developed a complex genetic system to survive under unfavorable environments like drought and salinity. The management of is type of tolerance has multiple genes working together rather than a single magic bullet. For instance, transcription factors (TFs) act as master switches, turning on and off the expression of other genes in response to different stresses. Important gene families involved in drought and salinity tolerance include bZIP, NAC, AP2/ERF, and MYB (Gahlaut *et al.*, 2016). They become an on and off switch by a process called reversible phosphorylation, where the adding or removal of a phosphate group occurs from the protein. This modification allows them to control the expression of other genes involved in drought tolerance. Salinity tolerance requires plants to regulate the uptake and efflux of ions like sodium (Na^+) and chloride (Cl^-). Genes encoding ion transporters and channels are crucial for this process. For instance, some plants overexpress the genes for vacuolar Na^+/H^+ antiporters to pump excess sodium out of the cell (Sun *et al.*, 2024). In the same context, LEA (late embryogenesis abundant) genes encode proteins that protect cells during dehydration by stabilizing membranes and proteins.

CONCLUSIONS

Combined drought and salinity stresses inflict greater harms significantly on crop plants compared with the individual stress. Understanding plant responses across various levels is crucial for developing stress-tolerant genotypes in different crops. This review emphasizes the importance of investigating combined stress responses to refine breeding strategies for improved crop resilience. Unraveling the complex genetic mechanisms of drought tolerance holds the key to engineering crops that can thrive under challenging environmental conditions.

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