

REVIEW ARTICLE

Understanding Abiotic Stress in Lentils: Impacts and Mitigation Approaches

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ABSTRACT

Lentil (*Lens culinaris*) is a vital cool-season legume crop, widely cultivated for its nutritional and economic importance. However, its productivity is severely challenged by various abiotic stresses including heat, drought, cold, and salinity. These stresses disrupt physiological, biochemical, and morphological processes, leading to reduced germination, impaired growth, compromised reproductive development, and significant yield losses. Heat stress accelerates reproductive failure and diminishes seed quality, while drought stress affects water relations, photosynthesis, and nutrient uptake, causing stunted growth and lower biomass. Cold stress, particularly during reproductive stages, hampers flowering and pod formation, resulting in decreased yield and quality. Salinity induces osmotic and ionic imbalances, adversely affecting germination, photosynthesis, and nutrient content. Effective management strategies, such as breeding for stress-tolerant cultivars, improved agronomic practices, and biotechnological interventions, are essential to mitigate these impacts and sustain lentil productivity under changing climatic conditions. This review not only discusses the diverse effects of these abiotic stresses on lentil but also explores current management strategies including breeding for stress-resistant genotypes, agronomic practices, and biotechnological tools aimed at enhancing lentil tolerance. Integrating these approaches is critical for improving lentil resilience under adverse environmental conditions, contributing to sustainable production and food security in the face of climate change.

KEYWORDS

- Lentil • Abiotic stress management • Food security • Heat • Drought • Cold
- Salinity

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INTRODUCTION

Legumes are highly vulnerable to fluctuations brought about by climate change, and the resulting abiotic stresses pose significant challenges to global crop productivity.^{16,80} These stresses include, but are not limited to, high temperatures, drought, soil salinity, and heavy metal toxicity. Collectively, abiotic stressors are the primary cause of crop losses worldwide, often reducing yields by more than 50% in many plant species.¹⁰⁷ These stress factors can act independently or in combination, triggering a cascade of physiological, morphological, biochemical, and molecular responses that negatively impact plant development, growth, and final yield.¹⁸ Key physiological functions affected include photosynthesis, respiration, reproductive development, nitrogen fixation, and oxidative metabolism.⁹¹ Among all environmental stressors, temperature extremes have the most significant and widespread impact on both agricultural and horticultural crops, greatly diminishing their yield potential.^{18,68}

Lentil (*Lens culinaris* Medik.) is one of the earliest crops domesticated by humans, dating back approximately 8,000 to 12,000 years.⁹⁸ It is a cool-season legume primarily cultivated in rain-fed, semi-arid regions of South Asia, North America, Australia, and Africa.^{48,103} This self-pollinating, diploid annual plant has a genome size of 4 Gbp and is particularly vulnerable to high temperatures.^{59,66} Known by various names such as *adas* in Arabic, *mercimek* in Turkish, *messer* in Ethiopian, *masser* in Indian languages, and *Heramame* in Japanese lentils are commonly grown in low-fertility soils. The plant typically has a bushy appearance with soft-haired stems that can be either erect or semi-erect, branching out and reaching heights between 15 and 75 cm.^{28,43} Lentils are nutritionally rich, containing essential vitamins and minerals like potassium, phosphorus, iron, and zinc, as well as proteins and amino acids such as arginine, leucine, lysine, and sulfur.^{43,98} Their ability to fix atmospheric nitrogen and sequester carbon contributes to improved soil health and promotes sustainable agricultural practices.⁸⁶

The *Lens* genus consists of four species: three wild (*Lens ervoides*, *Lens lamottei*, and *Lens nigricans*) and one (*Lens culinaris*) that includes both cultivated and wild subspecies. The wild form is *L. culinaris* subsp. *orientalis*, and the

cultivated form is *L. culinaris* subsp. *culinaris*, commonly known as lentil.¹⁰³ Lentil cultivation faces several abiotic stress challenges, such as drought, cold, salinity, heat, and nutrient imbalances. Of these, heat and drought are the most critical stressors globally.⁶⁶

As a winter crop, lentil thrives in cooler climates and can tolerate cold conditions, but it is highly susceptible to heat stress. Optimal growth temperatures range between 18–30°C, with cooler temperatures being favorable during vegetative growth and warmer temperatures preferred at maturity.^{83,92} Research from various regions confirms that lentils are sensitive to cultivation in hot environments.^{15,83,93} In some parts of the country, especially in central and southern regions, lentils are grown under warmer conditions that frequently exceed optimal temperature ranges, leading to reduced yields.¹⁰³

Furthermore, changing climate patterns have resulted in shorter cool periods and longer hot spells, increasing the risk of heat stress especially during critical reproductive stages of cool-season crops like lentils.^{38,92} Given the ongoing climate changes and evolving cropping systems at both national and global levels, it is essential to assess how different crop species, including lentils, respond to various abiotic stress factors.

IMPACTS OF ABIOTIC STRESSES ON LENTILS

1. Heat stress

Cool-season legumes, such as lentils (*Lens culinaris* Medik.), thrive in temperatures between 10°C and 30°C but begin to suffer heat stress beyond this range.^{88,92} High temperatures, whether short or long-term, can cause morphological, physiological, and biochemical disruptions that adversely affect plant development and yield, depending on species, temperature severity, and exposure duration.³⁸ In lentils, germination drops significantly above 30°C, with 29°C identified as the threshold for 50% germination.⁴⁷ High temperatures (35°C) are useful for screening heat-tolerant genotypes in lentils and chickpeas.^{55,57} Exposure to 30–50°C slows lentil germination and seedling development.²² Heat stress damages lentils before and after harvest, causing symptoms such as leaf scorch, chlorosis, curling, wilting,

and early senescence. It also reduces root and shoot growth, seed set, pod fill, and overall biomass, ultimately leading to yield loss.^{58,92} Reproductive processes are disrupted, with declines in pollen viability, stigma receptivity, and ovule health factors critical for seed formation.^{15,16,92} Pollen performance is optimal at 15°C but declines sharply above 32/20°C (max/min), impacting seed yield and quality.^{25,92} High temperature (33/28°C) has been shown to reduce seed growth rate by up to 44%, shorten seed filling duration, and lower seed yield and weight by 38–58% and 20–39%, respectively.⁹³ Yield reductions of 43–53.5% have been recorded under heat stress in lentil.^{23,27} Additionally, heat stress leads to reduced sucrose levels due to impaired enzyme activity and decreases in minerals, essential amino acids, and storage proteins in seeds.^{15,93,102} Climate change, particularly global warming and rising CO₂ levels, is a major contributor to heat stress. Elevated CO₂ (550 μmol mol⁻¹) was found to enhance lentil yield by 0.5 t/ha, driven by increased biomass, pod number, and harvest index though nitrogen content in grains and plant biomass declined slightly.^{19,20} Hence, heat stress poses a significant threat to lentil production and must be effectively managed to ensure agricultural sustainability and food security (Figure 1).

2. Drought stress

Drought stress is a significant environmental challenge that hampers crop growth, development, and productivity. It occurs when plants face insufficient moisture to support normal physiological functions.⁶¹ A drop in leaf water content below optimal turgor pressure is also indicative of drought.⁷⁷ In lentils, despite their adaptability to dry climates, drought can reduce productivity by up to 54%.^{11,37} Drought stress affects various physiological processes in plants, including cell division, cell expansion, leaf development, stem elongation, root growth, and stomatal function. These disruptions result in reduced water and nutrient absorption, ultimately decreasing water use efficiency.³¹ Early responses include reduced cell swelling and photosynthetic activity, stomatal closure, and metabolic imbalances.^{87,98} These changes result in decreased plant height, branching, leaf number, nodulation, and ultimately lower seed yield. Physiological indicators like foliar relative water content, chlorophyll

levels, photosynthetic rate, and root and shoot biomass decline under drought. Biochemically, drought induces oxidative stress, marked by increased hydrogen peroxide and lipid peroxidation, damaging membranes and reducing chlorophyll, carotenoids, and photosynthetic efficiency.^{87,97} Although Photosystem II is more drought-tolerant than heat-sensitive, drought still reduces CO₂ uptake and increases photorespiration, further limiting photosynthesis.^{56,77} Lentil seed germination, growth, flowering, and seed set are significantly affected. Reproductive stages are most vulnerable, with drought accelerating flowering and maturity, while decreasing pollen viability, ovary development, and seed quality.⁸⁸ Enzymes involved in starch synthesis are suppressed during flowering, contributing to reduced yield. Drought shortens seed filling duration (from 6.6 to 5.5 days), lowers seed growth rate (by 27.7–34.6%), seed count (15–26.1%), seed weight (15–28%), and individual seed mass (32–43%). Further, drought lowers seed protein and starch content while increasing soluble sugars.⁸⁷ Combined drought and heat stress have more severe impacts than heat alone. Improved tolerance is associated with better water retention and photosynthetic efficiency. As roots play a key role in water uptake, drought significantly reduces root traits like total root length (by 54.6%), projected area (70.1%), and volume (69.85%).⁷⁸ Additionally, drought stress reduces the accumulation of storage proteins, essential minerals (Ca, Fe, P, K, Mg, Zn), and amino acids including arginine, threonine, tryptophan, methionine, and others, ultimately impacting nutritional quality⁸⁷ (Figure 1). Developing lentil varieties with combined tolerance to drought and heat is crucial for sustaining yield and quality under future climate scenarios.

3. Cold stress

Cold stress is a major abiotic factor affecting the growth and yield of many economically important crops, especially those sensitive to temperatures below 10°C.¹⁴ It includes both chilling stress (below 20°C) and freezing stress (below 0°C), and impacts plant development at morphological, physiological, and cellular levels. Low temperatures disrupt cellular homeostasis, alter macromolecules, and impair membrane functions, slowing metabolism and leading to chilling injury.⁸ Cold stress

can reduce germination, cause poor stand establishment, and increase the risk of spring frost damage, ultimately lowering yields.⁸⁵ Morphological symptoms include stunted growth, leaf chlorosis, wilting, necrosis, reduced expansion, anthocyanin accumulation, and impaired reproductive development.^{14,82} Exposure to cold during reproductive stages is particularly damaging, resulting in reduced flowering, poor pod formation, low seed set, and, in severe cases, crop failure.¹⁴ Cool-season legumes such as lentils, chickpeas, peas, and beans are particularly sensitive to stress during the flowering and seed-filling stages.⁶³ Frost during these stages leads to flower abortion, decreased pod set, poor seed filling, and reduced yield quality.⁸ Additionally, cold and wet conditions promote fungal diseases such as *Ascochyta* blight and *Anthraco*se.⁷³ Cold stress also decreases shoot growth and fresh weight in lentils while increasing antioxidant accumulation.⁷¹ The extent of damage varies based on the crop's developmental stage at exposure. Cold acclimation involves metabolic adjustments, including increased levels of soluble sugars, proteins, organic acids, and proline, along with changes in membrane lipid composition.¹³ These adaptations enhance cold tolerance by stabilizing cell structures and maintaining osmotic balance. Lentil seed viability and chlorophyll content are significantly reduced under cold stress.⁵ Notably, soluble sugars, particularly sorbitol, are positively correlated with cold tolerance in legumes, making them key markers in stress response¹ (Figure 1).

4. Salinity stress

Soil salinity is the accumulation of salts like sodium chloride, calcium and magnesium sulfates, and bicarbonates in the soil or irrigation water.⁴² It poses a significant challenge, particularly in arid and semi-arid regions, which make up approximately 40% of the Earth's land area. Pulses, particularly lentils, are more sensitive to salt stress than cereals and many other crops, making salinity a significant barrier to lentil cultivation in saline-prone areas.⁷⁶ Salinity imposes stress in two primary ways: **osmotic stress**, which limits water uptake, and **ionic stress**, caused by toxic ion accumulation.⁹⁵ It disrupts key physiological processes such as photosynthesis, respiration, nitrogen fixation, and carbohydrate metabolism,⁵¹ and negatively

affects seed germination and early seedling growth.^{32,72} Seedlings are more vulnerable to salinity as salt tends to accumulate in the upper soil layers where seeds germinate.⁴ Salinity reduces relative water content, membrane stability, chlorophyll levels, and key nutrient balances (Na^+ , K^+), while also limiting plant height, leaf area, and yield.⁷⁴ Excess Na^+ and Cl^- ions lower water potential, causing water uptake issues and toxicity.⁵²

Salt stress initially damages older leaves before spreading to younger ones.⁵⁸ It impairs growth by reducing leaf area and dry matter through inhibited cell expansion.¹² Chlorophyll levels decline due to impaired synthesis or increased degradation.² Reduced photosynthesis is also linked to stomatal closure, decreased transpiration, and elevated leaf temperature.¹⁰ Salt stress hindered the growth of lentil seedlings and led to a decline in photosynthetic pigments (chlorophylls and carotenoids), water content, and overall survival. It also triggered oxidative damage, evident from elevated levels of hydrogen peroxide, malondialdehyde (MDA), and increased electrolyte leakage. This damage was associated with a disrupted antioxidant defense system and excessive accumulation of toxic Na^+ ions.²⁹ Salt stress causes both **primary effects** (osmotic and ionic stress) and **secondary effects**, such as reactive oxygen species (ROS) production, K^+ inhibition, and membrane dysfunction.²⁹ Severe yield losses have been reported up to 100% at 3.1 dS/m salinity in lentil cv. 6796.⁷ High salinity also reduces flowering, pod formation, carbon fixation, and overall productivity²⁹ (Figure 1). Furthermore, salt stress reduces nitrogen and micronutrient uptake (Fe, Cu, Mn), adversely affecting lentil seed quality and yield.⁶⁹ Overall, salinity remains a critical constraint to lentil cultivation, especially in regions with poor water quality and saline soils.

MANAGEMENT OF ABIOTIC STRESSES IN LENTILS

1. High Temperature Stress

The two main management strategies to prevent excessive temperatures during later growth phases are timing of planting and choosing an appropriate planting/sowing time.⁷⁹ Heat stress causes significant water

loss and is therefore frequently linked to water scarcity. Consequently, it may be assumed that timely irrigation and using the proper irrigation techniques to apply water is a beneficial practice.³⁹ For high yields, appropriate nutrition availability is crucial. Applying micronutrients is another effective way to reduce plant stress. Boron, iron, and zinc (B+Fe+Zn) applied as a foliar fertiliser at a rate of 0.5% to lentils resulted in the highest plant height, nodule number, flower count, and yield, and is therefore effective in reducing heat stress.⁶⁰ Foliar applications of boron and iron may be beneficial for subtropical regions' sustainable lentil production by reducing heat stress and soil moisture.¹⁰² Another micronutrient, selenium, may help to reduce heat stress by boosting antioxidant activity.⁴⁹ Zinc (Zn) is a crucial element that shields plants from the damaging effects of heat stress by preserving membrane integrity and ensuring enough Zn supply.⁷⁵ All of these justifications imply that sufficient mineral nutrition is necessary to maintain plant function under stress in order to ensure good production. Proline and other osmolytes hold promise as signalling molecules to combat heat stress in plants. One method to create heat-resistant plants is to engineer the plants with proline generating genes or exogenously apply proline.⁵⁰ Salicylic acid was observed to be the most effective in study on the effectiveness of salicylic acid, abscisic acid, or CaCl₂ in correcting oxidative damage brought on by heat stress in lentil.²² By pre-treating plants with these compounds, it may be possible to increase their capacity for growth at higher temperatures. An effective and affordable strategy being utilised worldwide to boost agricultural establishment is seed priming (SP).³¹ Seed priming enhances the production of several metabolites, including proline and glycine betaine, which keep the heat shock proteins (HSPs) stabilised and maintain relative water content and osmotic adjustment to safeguard the photosynthetic system. Seed priming also encourages the biosynthesis of phenolics, which can function as hydrogen donors by detoxifying ROS in the stability of membranes.⁶² Heat priming is the preparation of plants for upcoming high-temperature occurrences by treating them at a moderate temperature.⁶⁴ It has been reported that the non-protein amino acid δ aminobutyric acid (GABA) functions as a signalling molecule

in plants and affects the pathways, activities, and defense mechanisms. Heat priming of hydrated lentil seeds with GABA significantly improved the tolerance of lentil plants to heat stress by reducing leaf damage, boosting antioxidant enzyme activity and osmolyte accumulation, enhancing photosynthetic efficiency, and ultimately leading to improved yield.¹⁶ Heat tolerance can also be achieved by applying growth-regulating hormones such as salicylic acid, NO, and polyamines.⁹⁰ NO has been shown to shield plants from a variety of stresses. Also in lentil, foliar application of NO has been shown to increase water status, lower oxidative stress, increase chlorophyll concentration, fix carbon, have better absorption abilities, and increase reproductive and yield functions under high temperature circumstances⁹⁴ (Figure 1). These methods can be effectively employed to mitigate heat stress in lentil, thereby improving crop resilience, yield stability, and overall productivity under rising temperature conditions.

2. Drought Stress

Plant productivity is severely hampered by water shortages. Various strategies have been proposed to mitigate the impact of drought stress, including mass screening and breeding for tolerant varieties, marker-assisted selection, application of exogenous hormones and osmoprotectants to seeds or plants, and genetic engineering for enhanced drought resistance.³¹ Supplementary irrigation is the most common method used to avoid drought. When supplementary irrigation was applied to lentil plants, Hosseini *et al.*⁴⁶ reported a maximum 60% increase in yield compared to the treatment without irrigation. Therefore, supplemental irrigation is essential for growing lentils, especially in dry areas.^{11,101} By making more water available and burning soil organic carbon at extremely high temperatures with little oxygen, biochar can help plants withstand drought stress and reduce ionic and osmotic toxicity.¹⁰⁰ By promoting growth and drought resistance, biochar improves water use efficiency (WUE), water bioavailability, and crop nutrient uptake.⁹ Rhizobacteria promote growth and increase plant resistance to drought in semi-arid and arid regions. Inoculating lentil with the cytokinin-producing bacteria *Methylobacteriumoryzae* improved seed germination, transpiration, water use

effectiveness, photosynthetic activity, and yield.⁵⁴ Additionally, cytokinins enhance drought resistance by improving transpiration efficiency, photosynthesis, and delaying senescence. Arbuscular mycorrhizal fungi improve soil structure and water retention by stabilising and forming soil aggregates. This facilitates plant development during times of drought.⁹⁶ A variety of crop species have used seed priming to combat the effects of drought stress because it is one of the most effective short-term solutions. By partially hydrating seeds, a technique known as “seed priming” can be used to start germination-related metabolic processes but prevent radicle emergence. Primed seeds exhibited a higher germination rate, improved uniformity, and an increased germination percentage compared to non-primed seeds.³¹ Ghassemi-Golezani *et al.*³⁴ evaluated the impact of different seed priming methods hydro priming, halo priming (using 1.5% KNO₃ and NaCl at 15 mS/cm), and osmo priming (with polyethylene glycol 6000 at -0.8 MPa) on the vigour of lentil seedlings. They found that hydro priming had more favourable effects and it was therefore the best treatment for enhancing seedling vigour during drought. Hydro priming led to improved imbibition rate, germination rate, shoot, root growth, seedling dry weights, and seed vigour index. Hydro priming enhanced several seedling traits, including faster imbibition and germination rates, improved shoot and root development, greater seedling dry weight, and a higher seed vigor index.

On the other hand, osmo priming (1% CaCl₂) was found by Farooq *et al.*³⁰ to be superior to hydro priming in terms of enhancing lentil growth, biomass production, calcium accumulation, and sugar metabolism in both well-watered and water-deficient conditions. The crucial element of silicon (Si) is crucial for plants’ ability to withstand environmental stresses. Under PEG-induced drought, Si influenced lentil genotypes’ seed germination and seedling vigour in a positive way. Additionally, it was discovered that selenium (Se) can increase drought tolerance by modifying antioxidant defence responses and nitro-oxidative homeostasis.¹⁷ Application of selenite increased the lentil grain yield and also increased the antioxidant activity.²⁶ It was determined that Se fertilisation helps

to increase lentil yield. Using poly ethylene glycol (PEG) at 0, -0.4, -0.6, -0.9, and -1.1Mpa levels, Hojjat⁴⁴ reported a positive effect of silver nanoparticles (0, 10, 20, 30 and 40 g ml⁻¹) on lentil seed germination under drought stress. Compared to controls, silver nanoparticles significantly increased the percentage of seeds that germinated. Similarly, researchers investigated the impact of zeolites on the productivity, efficiency of protein and biomass in lentil under drought stress conditions.³ A significant impact on biomass, protein yield, and protein harvest index was seen when two levels of irrigation [irrigation at field capacity (FC) and 50% FC] and four levels of zeolites (0, 10, 20, and 30 tons/ha) were used. It was determined that zeolite can counteract the negative effects of water stress and its application can lengthen irrigation intervals.³ Plant growth regulators, both natural and synthetic, can be applied topically to plants to promote growth and reduce a range of abiotic stresses. By enhancing the seedlings’ water status and partially sustaining protein synthesis, gibberellin can counteract the effects of drought stress on hypocotyl length and fresh weight. Exogenous administration of 1-aminocyclopropane-1 carboxylic acid, along with other hormones, increases drought tolerance by postponing senescence.¹⁰⁶ The negative impact of drought stress on lentil can be mitigated by applying melatonin. Foliar application of melatonin has been found to promote plant growth and biomass accumulation, enhance photosynthetic pigment levels and gas exchange efficiency, and increase the activity of both enzymatic and non-enzymatic antioxidant defense systems.

Additionally, it increases proline accumulation, thereby reducing oxidative damage under drought conditions.¹⁰⁵ When a drought-stressed lentil was treated with the exogenous antioxidant α -tocopherol, it protected the membranes by preventing lipid peroxidation, boosting the activity of anti-oxidative enzymes (APX, CAT, POD, and SOD), and accumulating osmolytes like glycine betaine, proline, and sugar⁸⁹ (Figure 1). These approaches can be effectively utilized to mitigate drought stress in lentil, enhancing plant performance, physiological stability, and yield under water-limited conditions.

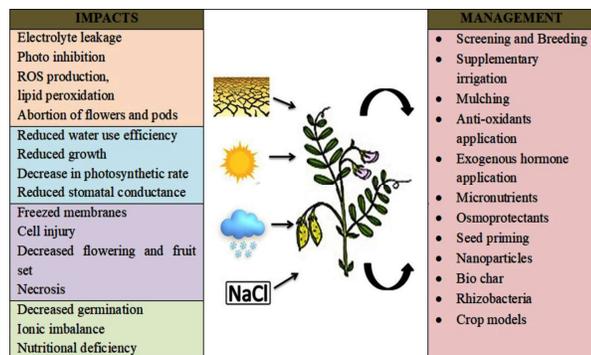


Figure 1: Effects of different abiotic stresses on lentil and their management to provide abiotic stress tolerance

3. Cold Stress

One of the methods to avoid negative effects of cold stress is to grow cold tolerant varieties. Screening for cold/frost/chilling tolerance is the widely used method to identify cold tolerant genotypes.⁹¹ The ideal approach is to breed for cold-tolerant lentils that are very adaptable to autumn cultivation in cold climates. In many high-altitude areas of West Asia and North Africa, lentil is cultivated as a spring crop to avoid harsh winter cold. However, late-fall sowing of winter-hardy lentil varieties offers greater production potential in these regions. Another approach to enhance cold tolerance is cold acclimation, where plants are gradually exposed to low temperatures within the freezing damage range, allowing them to adapt and survive better. According to Ali¹ lentil plants that had not previously been exposed to cold temperatures were unable to withstand subfreezing temperatures. According to Croser *et al.*,²⁴ cold acclimatization results in changes to cellular structures, metabolic processes, levels of sugars, soluble proteins, prolines, organic acids and lipid membrane composition. At reproductive stages, glycine betaine is reported to counter chilling injury by stabilizing enzyme activity, membranes and photosynthetic apparatus.⁷⁰ Furthermore, the exogenously applied glycine betaine during cold stress treatments has been found to improved flower function and yield.⁴⁰ Plants employ various internal mechanisms, including the production of phytohormones such as abscisic acid, cytokinins, jasmonic acid, salicylic acid, gibberellic acid, brassinosteroids, indole-3-acetic acid, and strigolactones, to cope with stressful environments. Under cold stress, these phytohormones play a vital role in regulating processes related to plant growth and development, acting as key endogenous

signaling molecules that coordinate a wide range of physiological, biochemical, and molecular responses through stress-responsive regulatory pathways⁸¹ (Figure 1). Based on research, lentil genotypes MLC409 and MLC70 are recommended for cultivation in cold regions, while MLC33, MLC47, MLC409, and MLC454 are better suited for temperate climates.⁶⁷ These methods offer effective solutions to reduce the impact of cold stress in lentil and enhance crop performance in cooler climates.

4. Salinity Stress

Harb *et al.*³⁶ investigated the impact of a brief pre-exposure to low salt concentration (10 mM) on shoot growth, oxidative stress, and antioxidant enzyme activity in lentil plants subjected to high salt stress (300 mM). They concluded that this short low-salt treatment enhanced the plants' tolerance to subsequent high salinity.

Giannakoula *et al.*³⁵ studied the impact of applying various plant growth regulators gibberellin, indole-3-acetic acid, kinetin, prohexadione-calcium, and furprimidol on lentil growth, proline and carbohydrate levels, lipid peroxidation, and tolerance to salinity stress. They found that treatment with gibberellin or kinetin alongside NaCl improved plant performance and quality indicators under salt stress.

Consequently, by acting as an effective antioxidant mechanism, kinetin and GA₃ protected plants from harm caused by oxidative stress brought on by salinity. Calcium ions (Ca²⁺) mitigate the harmful effects of NaCl on plant growth and photosynthesis by modulating the activities of antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), and catalase.⁹⁹ According to Hossain *et al.*,⁴⁵ Ca₂⁺ plays a protective effect in salt stress by increasing K⁺ ion concentration. Sabaghnia and Janmohammadi⁸⁴ investigated the impact of SiO₂ nanoparticles on 25 lentil genotypes under salt stress and found that genotypes treated with SiO₂ had improved germination, high shoot fresh and dry weight, and seedling early growth. This was consistent with the findings in maize.³³ Osmolytes like proline and salicylic acid were identified as useful in overcoming the negative effects of salt stress. Proline content was shown to increase by 5 folds in shoots and 1.1 folds in roots with a 100 Mm NaCl + 0.5 Mm SA treatment,

demonstrating that shoots always have a higher amount of proline than roots. Proline oxidase activity was suppressed whereas that of the enzymes Pyrroline-5-carboxylate reductase and -glutamyl kinase increased.⁶⁵

Pretreating lentil seedlings with 10 mM L-glutamic acid (L-Glu) helped reduce salt-induced damage by restricting Na⁺ buildup, maintaining ion balance, and enhancing the activities of antioxidant enzymes like catalase and ascorbate peroxidase. Consequently, oxidative stress from salinity was diminished, leading to better seedling growth, higher levels of photosynthetic pigments, and increased survival rates. These findings suggest that L-Glu plays a protective role in supporting lentil seedling development under salt stress conditions.²⁹ In another study the exogenous sodium nitroprusside (SNP) application, especially at 100 µM, effectively mitigated salt stress by modulating plant growth and biochemical responses, making it a promising strategy for enhancing lentil performance in saline conditions.¹⁰⁴ Seed priming with salicylic acid (SA) and silicon (Si) enhanced germination and promoted seedling growth under salinity stress by supporting better shoot development and improving root system architecture. Overall, priming with SA and Si offers a cost-effective and sustainable approach to mitigating salt stress in lentil cultivation.²¹

The effect of chitosan coating (concentrations 0, 1, 3, and 6 g/l) on seed germination and salt tolerance of lentil at five levels of salinity was examined by Al-Tawaha & Al-Ghzawi.⁶ Lentil seeds primed with 3 g/l chitosan showed the highest germination rate, along with the greatest hypocotyl and radical lengths, as well as the highest dry weights for both hypocotyl and radical. It was therefore determined that by priming seeds with chitosan, lentil's salt tolerance may be increased. Islam *et al.*⁵³ assessed the effects of salinity-tolerant rhizobacterial strains on lentil growth under salt stress and observed enhanced growth, nodulation, and yield. Therefore, using these rhizobial strains as bio fertilizers can improve lentil production in saline environments. To predict how climate, soil conditions, and agriculture methods affect crop growth and yield, scientists have devised crop models. SALTMED is an agricultural technique designed to manage soil salinity by regulating water and solute movement, evapotranspiration, and crop water uptake⁴¹ (Figure 1). Researchers assessed the potential

for productivity in lentil cultivation using saline water irrigation systems.⁷ They used the SALTMED model to determine threshold crop yields based on the salinity of irrigation water in equilibrium with the surrounding soil solution. During calibration and validation, the model demonstrated a strong correlation between predicted grain yields and the actual yields observed in the field.

CONCLUSIONS

Abiotic stresses like heat, drought, cold, and salinity present major obstacles to lentil cultivation, impacting all stages of plant growth from germination to seed filling. These stresses interfere with essential physiological and biochemical processes such as photosynthesis, respiration, nutrient absorption, nitrogen fixation, and reproductive development, resulting in significant reductions in both yield and quality. Among these, heat and drought stresses are particularly detrimental during the reproductive stage, causing flower abortion, poor seed set, and reduced grain weight. Salinity impairs seedling growth and mineral balance, while cold stress leads to metabolic disruptions, tissue damage, and increased disease susceptibility. Given the increasing frequency and intensity of these stresses due to climate change, effective management strategies are crucial. These include the development and deployment of stress-tolerant lentil varieties through conventional breeding and modern molecular techniques. Agronomic practices such as optimized irrigation scheduling, use of mulches, soil amendments (e.g., gypsum in saline soils), and timely sowing can mitigate stress impacts. Additionally, the integration of biofertilizers, plant growth-promoting rhizobacteria (PGPR), and exogenous application of osmoprotectants (e.g., proline, glycine betaine) can enhance stress resilience. In conclusion, addressing abiotic stress in lentil requires a multifaceted approach combining genetic improvement, agronomic management, and physiological interventions. Strengthening research on stress tolerance mechanisms and promoting sustainable practices will be essential to ensure stable lentil production under future climatic uncertainties.

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