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Understanding the adverse effects of salinity

on lentil growth: Mechanisms and responses

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Salinity is a major abiotic stress that significantly impairs lentil (Lens culinaris Medik.) *growth, development, and productivity, especially in arid and semi-arid regions. This chapter provides a comprehensive overview of the physiological, biochemical, molecular, and agronomic responses of lentil to salinity stress. Salinity disrupts lentil growth at all stages- germination, vegetative, and reproductive- through osmotic stress, ion toxicity, and nutrient imbalances. Plants respond by accumulating osmoprotectants like proline and glycine betaine, activating antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), and modifying photosynthetic and ionic regulation mechanisms. Advanced understanding of salt tolerance is facilitated by transcriptomics, proteomics, metabolomics, and ionomics, identifying stress-responsive genes, proteins, and metabolites. Breeding efforts involving wild relatives, marker-assisted selection (MAS), and genome-wide association studies (GWAS) are underway, complemented by transgenic and genome editing tools. Integration of high-throughput phenotyping and agronomic practices, such as seed priming and soil amendments, holds promise for developing salt-tolerant lentil varieties. The article underscores a multidisciplinary approach to enhance lentil resilience under salinity for sustainable pulse production.*

Keywords: Antioxidant enzymes, Ion toxicity, Lentil, Osmotic stress

LENTIL (*Lens culinaris* Medik.) is a self-pollinated diploid legume (2n = 2x = 14) that plays a significant role in sustainable agriculture due to its ability to fix atmospheric nitrogen. As a rich source of protein (20–30%), minerals, and dietary fiber, lentil is crucial in the diet of millions, especially in South Asia and the Mediterranean region. However, salinity is a major abiotic stress limiting lentil productivity in arid and semi-arid regions, where soil and water salinization are becoming widespread due to climate change, poor irrigation practices, and high evapotranspiration rates. Salinity affects more than 20% of irrigated agricultural land worldwide, posing a serious challenge to global food security. Lentil, being moderately salt-sensitive, exhibits considerable variation in its tolerance across genotypes. Understanding the physiological, biochemical, and molecular responses of lentil to salt stress is essential for identifying resilient cultivars. In addition, the integration of conventional breeding with modern biotechnological tools offers promising strategies for improving lentil's salinity tolerance. A comprehensive evaluation of lentil performance under salt stress is crucial for designing effective breeding programmes aimed at sustaining yield in salt-affected areas.

Impact of salinity on lentil growth and development

Salinity stress is one of the most detrimental abiotic factors affecting lentil productivity, especially in arid and semi-arid regions where soil salinization is exacerbated by poor irrigation management and climate change. Salt stress disrupts physiological and metabolic functions in lentil at all developmental stages from germination to seed filling, ultimately leading to reduced plant vigour and significant yield losses. Salt stress adversely affects lentil growth at all stages, from germination to pod formation and seed filling. The primary mechanisms include osmotic stress, ion toxicity (mainly Na^+ and Cl^-), and nutritional imbalance, leading to poor germination, stunted growth, reduced nodulation, chlorosis, and ultimately lower yields. High salt concentrations reduce water uptake, disturb hormonal balances, and impair photosynthesis due to stomatal closure and chlorophyll degradation.

Germination under saline conditions is particularly sensitive. Seedlings exposed to electrical conductivity (EC) levels above 6 dS/m show drastic reductions in root and shoot length, fresh and dry weight, and vigour index.

Germination and early seedling growth: The germination stage is highly vulnerable to salinity. Saline soils lead to increased osmotic potential of the soil solution, making it difficult for seeds to absorb water, thereby delaying or inhibiting germination. Furthermore, ion toxicity, particularly from Na^+ and Cl^-, damages embryonic tissues and inhibits enzymatic activities essential for seed metabolism studies have shown that electrical conductivity (EC) levels exceeding 6 dS/m significantly impair germination parameters in lentil. Seedlings subjected to high salinity demonstrate:

- Decreased germination percentage
- Reduced root and shoot lengths
- Lower fresh and dry biomass
- Declined vigour index

Vegetative growth: During the vegetative phase, salinity causes stunted plant growth due to inhibited cell expansion and division. Ion toxicity results in chlorosis (yellowing of leaves) and necrosis due to oxidative stress and nutrient imbalances. Salt stress often induces a deficiency of essential nutrients such as K^+, Ca^{2+}, and Mg^{2+} by competitive inhibition with Na^+ and Cl^-. This imbalance interferes with metabolic activities and reduces photosynthetic capacity. Key effects observed include:

- Shortened internodes and plant height
- Reduced number of leaves and leaf area
- Disturbed water relations and turgor maintenance
- Impaired nodulation and nitrogen fixation, affecting overall plant nutrition

Reproductive development: Salt stress adversely affects flowering, pod formation, and seed filling, which are critical for yield determination. The hormonal imbalance under stress, particularly altered levels of auxins, cytokinins, and abscisic acid (ABA), leads to flower and pod abortion, reduced pollen viability, and poor fertilization. Salinity-induced stress during reproductive stages results in:

- Delayed flowering and maturity
- Reduced number of pods per plant
- Lower seed set and smaller seeds
- Poor seed quality (protein and micronutrient content)

Physiological and biochemical disruptions: High salt concentrations affect key physiological processes:

- Photosynthesis inhibition due to chlorophyll degradation and stomatal closure
- Decreased relative water content (RWC) and water use efficiency (WUE)
- Altered enzyme activities and energy metabolism
- Oxidative stress from reactive oxygen species (ROS), leading to membrane damage

These combined effects significantly compromise lentil productivity under saline conditions.

Physiological and biochemical responses

Salt stress profoundly affects the physiological and biochemical processes of lentil, disrupting normal metabolic functions and leading to growth retardation and yield loss. Plants under saline conditions experience both osmotic stress and ionic stress, which collectively impair essential physiological activities. Under salt stress, lentil plants accumulate osmolytes such as proline, glycine betaine, and soluble sugars to maintain osmotic balance. Increased antioxidant enzyme activity, including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), helps mitigate oxidative stress induced by reactive oxygen species (ROS). Photosynthetic efficiency decreases significantly under salinity, with reduced chlorophyll content, disturbed gas exchange parameters (e.g. net photosynthetic rate, stomatal conductance), and altered chlorophyll fluorescence (Fv/Fm), indicating stress-induced damage to the photosystem II (PSII).

Osmolyte accumulation: One of the primary adaptive responses of lentil to salinity is the accumulation of osmoprotectants or compatible solutes, such as proline, glycine betaine, and soluble sugars. These low molecular weight compounds contribute to maintaining cellular osmotic balance, protecting macromolecules and membranes, and stabilizing proteins and enzymes under stress conditions. Among these, proline plays a particularly crucial role in osmotic adjustment, ROS scavenging, membrane stabilization, and signaling for stress responses. Glycine betaine helps protect the photosynthetic apparatus and maintain chloroplast integrity, while soluble sugars serve as both osmolytes and signaling molecules influencing stress gene expression.

Antioxidant defense mechanism: Salt stress triggers the overproduction of reactive oxygen species (ROS) such as superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^-), which cause oxidative damage to cellular structures. To mitigate this oxidative damage, lentil plants activate an enzymatic antioxidant defense system comprising:

- **Superoxide dismutase (SOD):** Catalyzes the dismutation of superoxide radicals into hydrogen peroxide and oxygen.
- **Catalase (CAT):** Decomposes hydrogen peroxide into water and oxygen, thus preventing H_2O_2 accumulation.
- **Peroxidases (POD):** Help detoxify peroxides using various electron donors.

This enhanced antioxidant activity is vital for maintaining cellular redox homeostasis and protecting the integrity of cellular components under salinity stress.

Photosynthetic impairment: Salinity also negatively impacts photosynthesis, which is a central physiological process directly linked to plant productivity. Key photosynthetic responses under salt stress include:

- **Reduced chlorophyll content:** Due to degradation of chlorophyll pigments or inhibited chlorophyll biosynthesis, resulting in chlorosis and reduced light-harvesting capacity.

- **Disturbed gas exchange:** Decline in net photosynthetic rate (Pn), stomatal conductance (gs), and transpiration rate, primarily due to stomatal closure aimed at conserving water under osmotic stress.
- **Altered chlorophyll fluorescence parameters (Fv/Fm):** Indicating photo inhibition and damage to Photosystem II (PSII), a critical site for light energy conversion in the thylakoid membrane.

These impairments collectively lead to reduced carbon assimilation, growth, and eventually lower biomass and yield.

Ion homeostasis and membrane stability: Under salinity stress, lentil plants experience ion toxicity, primarily due to the accumulation of Na^+ and Cl^- ions in tissues, which disrupt the K^+/Na^+ balance and enzyme function. Salt-tolerant genotypes exhibit better ability to exclude Na^+, maintain higher K^+ levels, and restrict ion transport to shoots. Additionally, these genotypes demonstrate enhanced membrane stability, often assessed by parameters such as electrolyte leakage and lipid peroxidation, with lower levels indicating stronger cell membrane integrity under stress.

Molecular and genetic mechanisms: Salinity tolerance in lentil is a quantitative trait governed by multiple genes, including those involved in ion transport, osmotic regulation, and transcriptional regulation. Genes such as NHX1 (Na^+/H^+ antiporter), SOS1, HKT1, and P5CS (Δ1-pyrroline-5-carboxylate synthetase) have been studied for their roles in ion compartmentalization and proline biosynthesis under salt stress.

Transcriptome studies under salt stress have identified differentially expressed genes associated with stress signaling pathways, hormone metabolism, and transcription factors such as MYB, bZIP, NAC, and WRKY. These gene families modulate various downstream responses for cellular protection and adaptation.

Screening and breeding for salt tolerance

Conventional screening methods in lentil involve evaluating germplasm in hydroponics, sand culture, and saline field conditions for traits like germination rate, seedling vigour, Na^+/K^+ ratio, biomass, and yield components. Several landraces and wild relatives (e.g. *Lens orientalis, Lens ervoides*) have shown promise for salt tolerance and can be used in pre-breeding programmes. These wild species often possess adaptive traits such as efficient ion homeostasis, deeper root architecture, and higher antioxidant enzyme activities. To ensure reliable phenotyping, multi-environment trials and standardized protocols are crucial for identifying stable, high-performing genotypes. Controlled screening under simulated salt conditions allows for early-stage selection, reducing field-level variability. Integration of high-throughput phenotyping tools, such as imaging and chlorophyll fluorescence sensors, is enhancing the precision of salt tolerance screening.

Molecular markers (e.g. SSRs, SNPs) linked to salt-tolerance QTLs have been identified, though, limited compared to major crops. Genomic-assisted breeding using marker-assisted selection (MAS) and genome-wide association studies (GWAS) is still emerging for lentil.

Biotechnological and omics approaches

Biotechnological interventions offer promising tools for dissecting and enhancing salt tolerance. Genetic transformation studies introducing AtNHX1, BADH, or P5CS genes in lentil have improved salt tolerance, though stable transformation remains challenging due to genotype dependency and low transformation efficiency.'Omics' approaches, such as transcriptomics, proteomics, metabolomics, and ionomics, provide system-level insights into stress responses. Integration of multi-omics datasets is facilitating the identification of candidate genes and molecular pathways involved in salinity tolerance in lentil. Salinity stress exerts a significant negative impact on lentil productivity by disrupting physiological, biochemical, and molecular processes such as osmotic balance, nutrient uptake, photosynthesis, and antioxidant defense. Conventional breeding for salt tolerance has been limited by complex inheritance patterns, polygenic control, and genotype-environment interactions. In this context, biotechnological and 'omics'-based tools provide novel avenues for understanding and enhancing salt tolerance in lentils.

Biotechnological interventions: Genetic engineering has enabled the functional characterization and transfer of stress-responsive genes from model systems into lentils and other legumes. Some key transgenic strategies employed include:

- Overexpression of AtNHX1 (Arabidopsis Na^+/H^+ antiporter) gene, which mediates vacuolar sequestration of excess Na^+ ions, thereby improving cellular ion homeostasis under salinity stress.
- BADH (betaine aldehyde dehydrogenase), which catalyzes the synthesis of glycine betaine, an osmoprotectant, has been introduced into lentil and chickpea to improve osmotic adjustment under saline conditions.
- P5CS (Δ^1-pyrroline-5-carboxylate synthetase), involved in proline biosynthesis, enhances osmotic tolerance and antioxidant defense when overexpressed in legumes.

Although such transgenic approaches show promising physiological improvements (e.g. better chlorophyll retention, higher K^+/Na^+ ratio, and increased yield under salt stress), stable transformation of lentil remains a major bottleneck, owing to genotype dependency, low regeneration frequency, and poor transformation efficiency. Hence, there is a need to optimize tissue culture protocols and explore genome editing tools such as CRISPR/Cas9 for more targeted and efficient genetic manipulation.

Omics approaches: The rapid development of high-throughput omics technologies has revolutionized plant stress biology by enabling a system-level understanding of complex traits like salinity tolerance. In lentil, multiple omics approaches are being integrated to identify stress-responsive genes, proteins, metabolites, and ionomic signatures:

- **Transcriptomics:** RNA-seq studies have revealed differentially expressed genes (DEGs) related to ion transporters (NHX, SOS1), transcription factors (DREB, WRKY, NAC), and antioxidant enzymes under salinity stress in salt-tolerant vs. sensitive lentil genotypes. These data form the basis for marker development and candidate gene selection.
- **Proteomics:** Protein profiling under salt stress has identified upregulated proteins related to ROS detoxification (e.g. superoxide dismutase, peroxidase), photosynthesis, and chaperones (e.g. HSPs), supporting enhanced cellular protection mechanisms.
- **Metabolomics:** Metabolite profiling has detected higher accumulation of compatible solutes like proline, sugars, and polyols in tolerant genotypes. These metabolites help in osmotic adjustment, ROS scavenging, and maintaining membrane integrity under saline conditions.
- **Ionomics:** Ionomic analyses reveal the ability of tolerant genotypes to exclude Na^+, maintain high K^+/Na^+ ratios, and accumulate beneficial ions like Ca^{2+} and Mg^{2+}, indicating efficient ion homeostasis and signalling.

Multi-omics integration

Recent advances now allow integration of transcriptomic, proteomic, metabolomic, and ionomic datasets, enabling the construction of gene regulatory networks and the identification of hub genes or master regulators. Such integrative omics approaches are essential for the discovery of novel molecular markers, QTLs, and biotechnological targets for lentil improvement under salinity.

Tools like WGCNA (Weighted Gene Co-expression Network Analysis) and machine learning algorithms are being used to correlate molecular data with physiological traits, making omics-guided breeding more precise and effective.

Management strategies and agronomic practices

Agronomic strategies can complement genetic approaches to mitigate salt stress in lentil. These include:

- ***Soil amendments:*** Gypsum and organic matter to improve soil structure and reduce Na^+ toxicity.
- ***Seed priming:*** Using salt solutions, hormones (GA_3, SA), or osmoprotectants (proline, PEG) improves germination and early growth under salt stress.
- ***Irrigation management:*** Using saline water judiciously with proper leaching and drainage.
- ***Crop rotation:*** Including salt-tolerant crops like barley can reduce salt accumulation.

Integrated management combining tolerant genotypes with improved agronomy holds the key for sustaining lentil production in saline soils.

SUMMARY

Salt stress poses a significant threat to lentil production globally. Advances in genomics, transcriptomics, and high-throughput phenotyping are paving the way for dissecting complex salt-tolerance traits. Developing multi-stress-resilient lentil varieties through integrated breeding and biotechnological tools, along with farmer-friendly agronomic practices, will ensure sustainable lentil production in the face of increasing soil salinization.

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