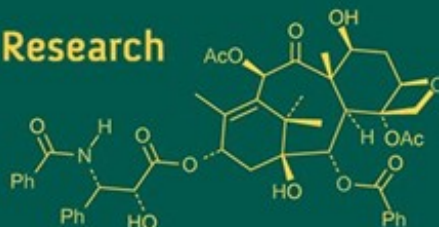


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Salinity tolerance in lentil (*Lens culinaris* Medik.): physiological, biochemical and molecular mechanisms and emerging biotechnological strategies

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ABSTRACT

Soil salinity is a major constraint to global agricultural productivity and is intensifying under climate change, especially in irrigated, arid, and semi-arid regions. Lentil (*Lens culinaris* Medik.), a key grain legume valued for its high protein content, micronutrient density, and biological nitrogen fixation, is moderately sensitive to salinity, particularly during germination, seedling establishment, flowering, and reproductive development. Salinity imposes interconnected osmotic, ionic, nutritional, oxidative, and metabolic stresses that collectively impair plant growth, physiology, and yield.

This review synthesizes current knowledge on lentil salinity tolerance by integrating physiological, biochemical, and molecular mechanisms with recent multi-omics insights. Physiological adaptation involves maintenance of plant water status, photosynthetic efficiency, membrane integrity, and ion homeostasis, whereas biochemical reprogramming encompasses antioxidant defense, osmotic adjustment, redox regulation, and changes in carbon and secondary metabolism. At the molecular level, stress perception and signalling networks including calcium signalling, abscisic acid (ABA) pathways, mitogen-activated protein kinase (MAPK) cascades, and the Salt Overly Sensitive (SOS) pathway interact with transcription factors (DREB, WRKY, NAC, bZIP) and stress-responsive genes to coordinate ion transport, reactive oxygen species (ROS) detoxification, osmolyte accumulation, and cellular protection. Emerging multi-omics approaches (genomics, transcriptomics, proteomics, metabolomics) are beginning to reveal the regulatory architecture and genotype-phenotype relationships underlying salinity adaptation in lentil and related legumes.

Despite major advances, critical gaps remain in linking molecular responses with whole-plant physiology and yield across developmental stages and environments, and in translating candidate genes and markers into robust breeding tools. By integrating mechanistic insights with genomics-assisted breeding, genome editing, nanotechnology, and rhizosphere engineering, this review outlines a framework and research priorities for developing climate-resilient, salinity-tolerant lentil cultivars.

Keywords: Lentil, Salinity stress, Ion homeostasis, Antioxidant defense, Osmotic adjustment, Transcriptomics, Nanotechnology, Climate resilience

Introduction

Soil salinity is considered one of the major environmental constraints to agricultural productivity worldwide, especially in irrigated arid and semi-arid regions. Over the past several decades, the area of salt-affected land has increased dramatically due to inappropriate irrigation, poor drainage, seawater intrusion into the groundwater and climate change. Current estimates indicate that more than 1 billion hectares of land are impacted by salinity and approximately 20–30% of irrigated agricultural land is affected in some way by salt stress (Munns *et al.*, 2008; Van Zelm *et al.*, 2020) [1, 2].

Salinity negatively impacts crop production through a cascade of disturbances in ion homeostasis, oxidative metabolism, nutrient uptake, rhizosphere microbial interactions, and soil physicochemical properties, leading to decreased plant growth and posing a threat to global food security (Munns *et al.*, 2008; Yadav *et al.*, 2026) [1, 3]. It causes osmotic stress, ionic toxicity, imbalance of nutrients and oxidative stress, all of which cause large reductions in plant biomass and yield (Deinlein *et al.*, 2014; Parida *et al.*, 2005) [4, 5]. Recent evidence suggests that salinity should be considered a complex perturbation of the soil-plant system, involving changes in soil structure, microbial communities, nutrient cycling and plant physiology, rather than just osmotic or ionic stress (Yadav *et al.*, 2026) [6].

Lentil (*Lens culinaris* Medik.) is a grain legume of special importance among grain legume crops due to its high protein (22–35%), dietary fibre, essential micronutrients and biological nitrogen-fixing ability (Alexander *et al.*, 2024; Montejano-Ramírez *et al.*, 2024) [7, 8]. Lentil is an essential component of climate-

smart cropping systems as it enhances soil health and sustainability. Lentil is however quite sensitive to salinity especially during germination, seedling establishment, flowering and reproductive development (Singh *et al.*, 2017; Stoddard *et al.*, 2006) [9, 10]. Salinity-induced growth inhibition in lentil is associated with excessive accumulation of ROS, oxidative damage, decreased carbon assimilation and altered metabolism (Panuccio *et al.*, 2022; Muscolo *et al.*, 2014; Pandey *et al.*, 2020) [11, 12, 13].

Salt tolerance in cultivated lentils, wild *Lens* spp. and other legumes has been associated with effective osmotic adjustment, maintenance of cellular ion balance, elevated antioxidant activity and activation of stress responsive regulatory pathways (Dissanayake *et al.*, 2021; Singh *et al.*, 2017) [14, 15]. In recent years, the understanding of complex regulatory networks involved in salinity adaptation in lentil has been greatly enhanced by significant advances in genomics, transcriptomics, proteomics and metabolomics (Singh *et al.*, 2017; Morgil *et al.*, 2019; Singh *et al.*, 2021; Ali *et al.*, 2022) [9, 16, 17, 18]. Studies of the transcriptome, proteome and metabolome show that salinity induces coordinated changes in genes and proteins related to ion transport, stress signalling, antioxidant defence and osmoregulation (Morgil *et al.*, 2019; Dissanayake *et al.*, 2021; Ali *et al.*, 2022) [16, 14, 18].

Given the increasing importance of soil salinization and the growing importance of lentil as an alternative source of protein in sustainable agriculture, a detailed understanding of the mechanisms of salinity tolerance is essential for the successful improvement of crops. Nevertheless, the understanding of the interaction of physiological and molecular mechanisms across developmental stages and environments is still lacking and limits the application of genetic resistance traits in breeding programmes (Singh *et al.*, 2017; Dissanayake *et al.*, 2021) [9, 14]. This review summarises the available information on the physiological, biochemical and molecular mechanisms of salinity tolerance in lentil with a discussion on the recent developments in stress signalling, gene expression, multi-omics technologies and breeding strategies. Critical gaps and future research priorities are highlighted to aid in the development of climate resilient lentil varieties.

Effect of salinity stress on lentil

Under long-term salinity, the surplus Na^+ gradually builds up in plants, affecting the cell ion homeostasis and competing with K^+ , a key cofactor of many biochemical reactions (Van Zelm *et al.*, 2020; Munns *et al.*, 2008) [2, 1]. The presence of high Na^+ in the soil or irrigation water also influences the uptake of vital nutrients like K^+ , Ca^{2+} , Mg^{2+} and phosphate (PO_4^{3-}) which negatively affects the growth and metabolism (Parida *et al.*, 2005; Hasanuzzaman *et al.*, 2021) [5, 19]. The maintenance of a favourable K^+/Na^+ ratio in cytosol and organelles is dependent on the coordinated regulation of membrane transporters and stress-responsive signalling pathways to maintain ion balance under saline conditions (Tripathi *et al.*, 2025; Singh *et al.*, 2024) [20, 21].

Salinity also disrupts cellular redox homeostasis by inducing overproduction of reactive oxygen species (ROS) and inhibiting antioxidant defences. They generate superoxide radicals, hydrogen peroxide, hydroxyl radicals and singlet oxygen leading to oxidative stress, damage to chloroplasts and mitochondria, lipid peroxidation and disturbance in cellular redox status (Mittler *et al.*, 2004; Yadav *et al.*, 2026) [22, 6]. Salinity at whole plant level inhibits cell division and expansion, root elongation and photosynthetic efficiency, accelerates leaf senescence and ultimately reduces biomass accumulation, reproductive success and grain yield (Muscolo *et al.*, 2014; Pandey *et al.*, 2020) [12, 13].

These processes happening through the course of development lead to lentil yield loss. Salinity reduced generally pods per plant, seed set, 100 seed weight and harvest index with severe yield reduction in sensitive genotypes (Pandey *et al.*, 2020) [13]. Tolerant lentil genotypes

generally accumulate less Na^+ in their tissues, have a greater capacity to exclude and sequester Na^+ and maintain higher K^+/Na^+ ratios which allow metabolic processes to function at moderately high salinity (Panuccio *et al.*, 2022; Singh *et al.*, 2017) [11, 9]. They also generally exhibit higher activities of antioxidant enzymes such as SOD, APX, GPX and CAT leading to lower oxidative damage and enhanced cellular redox homeostasis as compared to sensitive genotypes (Singh *et al.*, 2017; Singh *et al.*, 2019; Singh *et al.*, 2021) [9, 23, 17].

Lentil cultivars and their wild relatives show a wide genetic variation in traits that support growth and reproduction under stress, emphasising the significance of adaptive mechanisms that maintain internal water status, regulate ion homeostasis, support photosynthesis and conserve cellular integrity in saline environments (Singh *et al.*, 2017; Dissanayake *et al.*, 2021) [9, 14].

Physiological adaptations of lentil to salinity stress

The first line of defence for lentil plants to sustain growth, metabolism, and reproduction under saline conditions is physiological adaptation (Gorim *et al.*, 2017; Singh *et al.*, 2017) [24, 9]. An effective adaptation is a coordinated regulation of germination, seedling vigour, water relations, photosynthesis, membrane stability and ion homeostasis to minimise salt-induced damage and maintain productivity (Panuccio *et al.*, 2022) [11].

Root architecture has a major influence in lentil's adaptability to salt. Generally, salt stress decreases root growth and total biomass. However, tolerant genotypes generally produce more extensive and functioning root systems than the sensitive lines, enhancing water uptake, nutrient acquisition and Na^+ exclusion (Foti *et al.*, 2019) [25]. Enhanced root: shoot ratio and deeper rooting can improve access to less saline soil layers and provide greater water-use efficiency (WUE) by optimising carbon fixation against water loss (Foti *et al.*, 2019; Panuccio *et al.*, 2022) [25, 11]. Salinity can be highly detrimental to photosynthesis, with osmotic stress, ion toxicity and oxidative damage together impairing carbon uptake and photochemical efficiency. Restricted stomatal conductance reduces the input of CO_2 and excessive Na^+ and Cl^- can damage the ultrastructure of chloroplasts and photosynthetic machinery (Chaves *et al.*, 2003) [26]. Therefore, salinity generally reduces chlorophyll content, photosynthetic rate and chlorophyll fluorescence indices in lentil, especially F_v/F_m and PSII efficiency (Muscolo *et al.*, 2014; Panuccio *et al.*, 2022) [12, 11]. However, tolerant genotypes generally exhibited higher chlorophyll content, more stable PSII activity and photosynthetic capacity than sensitive genotypes, which allows them to continue biomass accumulation and support reproductive development under saline conditions (Muscolo *et al.*, 2014; Panuccio *et al.*, 2022) [12, 11]. Thus, maintaining photosynthetic efficiency is a crucial predictor of yield stability in saline environments. The physiological adaption also involves the maintenance of membrane integrity and ion balance. Excess Na^+ and Cl^- lead to alterations in membrane permeability, disrupt metabolic processes and interfere with the uptake of critical ions like K^+ and Ca^{2+} (Deinlein *et al.*, 2014) [4]. Salt-sensitive genotypes exhibit increased electrolyte leakage and weaker membrane stability indicators compared to tolerant lines. In contrast, the tolerant lentil genotypes accumulate lower Na^+ and sustain higher K^+ levels leading to a greater K^+/Na^+ ratio in roots and shoots (Singh *et al.*, 2017; Panuccio *et al.*, 2022) [9, 11]. This ionic equilibrium maintains enzyme activity, cellular homeostasis and metabolic function in salinity.

In lentil, the physiological response to salinity is often mediated by the integrated regulation of early seedling growth, root architecture, water relations, photosynthetic performance, membrane stability and ion homeostasis. These features provide a useful basis for screening and breeding salt-tolerant cultivars for physiological traits as outlined Table 1.

Table 1. Core physiological traits used to assess salinity tolerance in lentil (*Lens culinaris* Medik.).

Trait group	Key indicators	What they reflect	Use in lentil screening/breeding	References
Germination & establishment	Germination %, seedling vigour index	Ability to overcome osmotic constraints	Fast, low-cost first screen for tolerant accessions	(25,9)
Root system	Primary root length, root biomass, root:shoot	Water/nutrient uptake, Na ⁺ exclusion	Discriminates tolerant genotypes with deeper, denser roots	(25,24)
Water relations	Relative water content (RWC), WUE, stomatal g _s	Hydration status, transpiration control	Identifies lines maintaining turgor and gas exchange	(9,11)
Photosynthesis	Total chlorophyll, A _n (Pn), F _v /F _m	Integrity of photosynthetic apparatus	Non-destructive indicator of sustained carbon assimilation	12,27)
Membrane & ion homeostasis	MSI, EL, leaf/root Na ⁺ , K ⁺ , K ⁺ /Na ⁺ ratio	Membrane stability, ionic balance	Most informative set for physiological salinity tolerance	(9,14)
Productivity	Biomass, pods plant ⁻¹ , 100-seed weight, yield	Integrated whole-season response	Confirms whether physiological tolerance translates to yield	(13)

Abbreviations: A_n, net photosynthetic rate; EL, electrolyte leakage; F_v/F_m, maximum quantum efficiency of PSII; g_s, stomatal conductance; MSI, membrane stability index; RWC, relative water content; WUE, water-use efficiency.

Biochemical reprogramming under salinity stress

Salinity stress induces a broad biochemical reprogramming, which enables lentil plants to maintain cellular homeostasis under osmotic stress, ion toxicity and oxidative imbalance. The biochemical responses represent the metabolic interface between physiological adaptation and molecular regulation and are strongly associated with the genotypic variation in salt tolerance (Muscolo *et al.*, 2014; Singh *et al.*, 2017; Panuccio *et al.*, 2022) [12, 9, 11].

Redox homeostasis and antioxidant defence

Overproduction of ROS such as superoxide (O₂⁻), H₂O₂, hydroxyl radicals (·OH), and singlet oxygen (¹O₂), are among the earliest biochemical responses to salinity, mostly generated in chloroplasts, mitochondria, and peroxisomes because of disturbed electron transport chains (Apel *et al.*, 2004; Mittler *et al.*, 2004) [27, 22]. Moderate levels of ROS are acting as signalling molecules but their uncontrolled accumulation causes oxidative damage to lipids, proteins, nucleic acids and membranes, eventually resulting in impaired growth and productivity. Thus, tolerance to salinity is linked to the maintenance of ROS homeostasis and not to the complete elimination of ROS.

Plants activate an integrated antioxidant defence system with enzymatic and non-enzymatic components to maintain redox balance. The first line of defence is superoxide dismutase (SOD), which catalyses the dismutation of O₂⁻ to H₂O₂, which is then detoxified by catalase (CAT), ascorbate peroxidase (APX) and various peroxidases (POD) (Gill *et al.*, 2010) [28]. Consistent with improved salinity tolerance in lentil and other legumes, increased activities of SOD, CAT and APX are always reported, and the coordinated activation of these enzymes is considered more informative than changes in individual enzymes (Biju *et al.*, 2018; Fardus *et al.*, 2021) [29, 30].

The non-enzymatic antioxidants provide another level of protection. The ascorbate–glutathione (AsA–GSH) cycle is key to redox regulation and carotenoids, tocopherols, phenolic compounds and flavonoids contribute to ROS scavenging, membrane stabilisation and protection of the photosynthetic apparatus (Foyer *et al.*, 2011) [31]. Salt tolerant lentil genotypes generally have a higher antioxidant capacity, more efficient ROS detoxification and less oxidative damage than sensitive genotypes confirming that maintenance of redox homeostasis is a major biochemical determinant of salinity tolerance (Muscolo *et al.*, 2014; Fardus *et al.*, 2021; Panuccio *et al.*, 2022) [12, 30, 11]. The integrated ROS generation, antioxidant defense network, and maintenance of redox homeostasis under salinity stress are summarized in Figure 1.

Salinity-induced osmotic stress and ionic toxicity stimulate ROS production in chloroplasts, mitochondria, and peroxisomes. Balanced ROS signalling regulates stress responses, whereas excessive ROS causes oxidative damage. Enzymatic and non-enzymatic antioxidant systems, together with compatible osmolytes, preserve cellular redox homeostasis and enhance salinity tolerance.

Osmotic adjustment and carbon metabolism

Another important biochemical strategy that allows lentil cells to maintain turgor and hydration under salinity is osmotic adjustment via the accumulation of compatible solutes that do not interfere with normal metabolism (Chen *et al.*, 2002) [32]. Proline is the most studied osmoprotectant in lentil; besides osmotic balance, it stabilises membranes and proteins, scavenges ROS and supports redox homeostasis (Szabados *et al.*, 2010) [33]. Several comparative studies have confirmed the higher accumulation of proline in salt-tolerant than sensitive genotypes of lentil (Muscolo *et al.*, 2014; Panuccio *et al.*, 2022; Yadav *et al.*, 2026) [12, 11, 6]. However, the accumulation of proline is genotype and context-dependent as a direct cause of tolerance or, to a large extent, as a reflection of the intensity of stress.

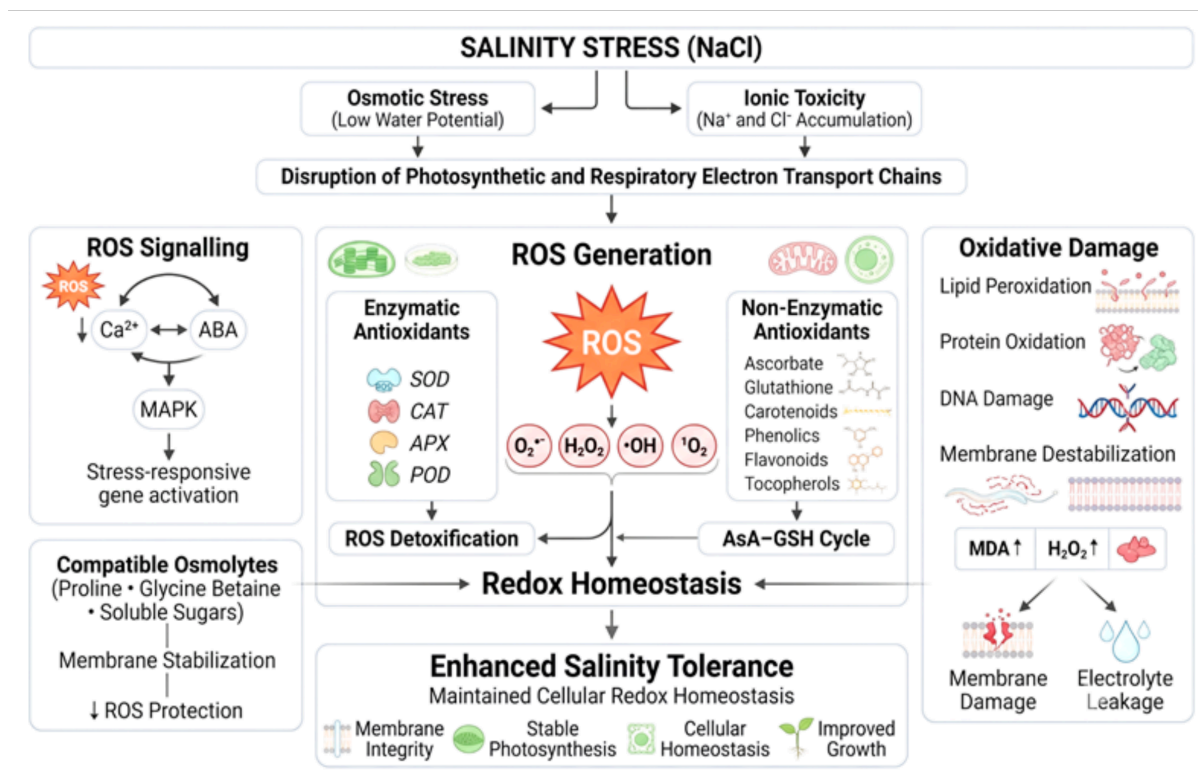


Figure 1. Reactive oxygen species (ROS) generation, antioxidant defence, and maintenance of cellular redox homeostasis during salinity stress in lentil

Other compatible osmolytes such as glycine betaine and soluble sugars (sucrose, glucose, fructose and raffinose-family oligosaccharides) also help for osmotic adjustment, membrane stabilisation and protection of cellular frameworks under salinity (Couée *et al.*, 2006; Singh *et al.*, 2017; Singh *et al.*, 2021) [34, 15, 17]. Salt stress is often accompanied by changes in carbohydrate metabolism, including decreased starch synthesis and changes in sugar partitioning, leading to the accumulation of soluble sugars, which function as osmoprotectants and signalling molecules. Thus, the ability to efficiently partition carbon between growth, energy supply, and osmoprotective compounds is an important biochemical determinant of salinity tolerance in lentil, although the interactions between carbohydrate metabolism and stress signalling remain poorly characterised (Couée *et al.*, 2006; Panuccio *et al.*, 2022) [34, 11].

Secondary metabolism and biochemical markers

The biochemical defence system induced by salinity stress presents a significant non enzymatic component constituted by secondary metabolites, mainly phenolic compounds and flavonoids. Under salinity, the phenylpropanoid pathway is activated, leading to the accumulation of phenolics and flavonoids that scavenge ROS, stabilize membranes and are involved in stress signalling, with higher levels typically found in salt tolerant genotypes (Yasir *et al.*, 2021; Goncharuk *et al.*, 2023) [35, 36].

MDA and H₂O₂ are commonly used biochemical markers to assess oxidative damage under salinity. High MDA levels indicates significant lipid peroxidation and membrane damage, while high H₂O₂ indicates redox homeostasis disruption and insufficient detoxification (Muscolo *et al.*, 2014) [12]. Salt tolerant genotypes have been observed to accumulate lower amounts of MDA and H₂O₂ than salt sensitive genotypes under identical saline circumstances in studies on lentil demonstrating their stronger antioxidant defence and redox regulation (Fardus *et al.*, 2021; Panuccio *et al.*, 2022) [30, 11]. Therefore,

MDA, H₂O₂, total antioxidant capacity and correlated features are valuable biochemical indicators for screening of salinity tolerance in lentil breeding and physiological research. To summarise, biochemical adaptations to salt in lentil are associated with a co-ordinated regulation of antioxidant systems, suitable solutes, carbohydrate metabolism and secondary metabolites, which together sustain cellular frameworks, minimise oxidative damage and facilitate development under saline circumstances. Table 2 thoroughly shows these responses and offers realistic biochemical markers for evaluating genotypic differences in salt tolerance.

Molecular networks governing salinity tolerance

Salinity tolerance in lentil is regulated via interconnecting molecular networks comprising stress detection, signal transduction, transcriptional regulation, ion transport and downstream cellular protection (Singh *et al.*, 2021; Morgil *et al.*, 2019; Dissanayake *et al.*, 2021) [17, 16, 14]. Physiological qualities may be evaluated directly, whereas salinity tolerance is a more complex feature determined mostly by network-level integration. Molecular adaptation entails dynamic interactions among signalling pathways and regulatory modules. The major signaling pathways and regulatory networks governing salinity tolerance in lentil are illustrated in Figure 2.

Stress perception, signal transduction and ion homeostasis

Salinity stress is initially seen as changes in the osmotic potential of the cell and ion concentration that activate membrane-associated receptors, ion channels and receptor-like kinases that activate downstream signalling cascades (Van Zelm *et al.*, 2020; Zhu, 2016) [2, 37]. Rapid early reactions include depolarisation of plasma membrane potential, brief elevations in cytosolic Ca²⁺, bursts of ROS and changed phytohormone levels, which together activate several signal-transduction pathways (Dodd *et al.*, 2010; Batistič *et al.*, 2012) [38, 39].

Table 2. Key biochemical markers associated with salinity tolerance in lentil (*Lens culinaris* Medik.).

Component group	Key markers (examples)	Role under salinity	Interpretation in tolerant genotypes	References
Enzymatic antioxidants	SOD, CAT, APX, POD	Stepwise detoxification of ROS	Higher, well-coordinated activities; lower ROS load	(29,30)
Non-enzymatic antioxidants	Ascorbate, GSH, carotenoids, flavonoids	Redox buffering, ROS scavenging, membrane protection	Larger pools; stronger total antioxidant capacity	(32,36)
Compatible osmolytes	Proline, glycine betaine	Osmotic adjustment; protein and membrane protection	Higher accumulation without growth penalty	(12,11)
Soluble carbohydrates	Sucrose, glucose, fructose, RFOs	Osmoprotection and signalling; carbon storage	Better maintenance/redistribution under stress	(35,9)
Secondary metabolites	Total phenolics, flavonoids	Additional ROS scavenging, signalling	Elevated levels linked with reduced oxidative injury	(36,37)
Oxidative damage markers	H ₂ O ₂ , MDA, protein carbonyls	Reflect ROS accumulation and cellular damage	Lower values indicate effective protection	(12,31)

Abbreviations: APX, ascorbate peroxidase; CAT, catalase; GSH, glutathione; MDA, malondialdehyde; POD, peroxidase; RFOs, raffinose-family oligosaccharides; ROS, reactive oxygen species; SOD, superoxide dismutase

Cytosolic Ca^{2+} is an important second messenger, which is decoded by Ca^{2+} binding proteins such as calmodulin (CaM), calcium dependent protein kinases (CDPKs) and calcineurin B like (CBL) proteins (Batistič *et al.*, 2012) [39]. These sensors interact with CBL–CIPK modules that control ion channels and transporters under salt stress. Ca^{2+} dependent signalling is tightly linked to abscisic acid (ABA) pathways; ABA perceives osmotic stress via PYR/PYL receptors and relays signals through PP2C–SnRK2 modules to control stomatal conductance, osmotic adjustment, antioxidant metabolism and stress-responsive gene expression (Cutler *et al.*, 2010; Yadav *et al.*, 2026) [40, 6]. These pathways are also further regulated by ROS and phytohormones resulting in a big interaction between Ca^{2+} , ABA and redox signalling.

Mitogen-activated protein kinase (MAPK) cascades are responsible for amplifying and integrating Ca^{2+} , ABA and ROS signals and transducing extracellular inputs into transcriptional and metabolic responses (Zhu, 2016) [37].

For plants to survive in saline environments, these signalling networks must maintain intracellular ion homeostasis; failure to control Na^+ accumulation leads to enzyme inhibition, membrane dysfunction and impaired nutrient uptake (Munns *et al.*, 2008) [1].

The Salt Overly Sensitive (SOS) pathway is a central regulator of Na^+ homeostasis. Increased cytosolic Na^+ under salinity induces a Ca^{2+} signal that activates SOS3 (CBL4), which forms a complex with the kinase SOS2 (CIPK24) to phosphorylate and activate SOS1, a plasma-membrane Na^+/H^+ antiporter (Shi *et al.*, 2000; Halfter *et al.*, 2000; Guo *et al.*, 2001) [41, 42, 43]. Activated SOS1 mediates Na^+ efflux from the cytosol, while vacuolar NHX antiporters sequester Na^+ into vacuoles and HKT transporters regulate Na^+ loading and retrieval in the xylem, collectively maintaining cytosolic K^+/Na^+ balance (Munns *et al.*, 2008; Yadav *et al.*, 2026) [1, 3]. Expression of SOS pathway components has been detected in salt-stressed lentil, suggesting a conserved role for this pathway in ion homeostasis across species (Singh *et al.*, 2021) [17]. However, functional validation of many candidate ion transporters in lentil remains limited, with most mechanistic evidence inferred from model plants.

Beyond classical Na^+ transporters, genome-wide analyses in lentil have identified additional transporter families, including MATE, ALMT and ABC transporters, which contribute to ion detoxification, organic acid transport and broad membrane transport processes during salinity adaptation (Tripathi *et al.*, 2025; Singh *et al.*, 2024) [20, 21].

Salinity-induced osmotic stress, ionic toxicity, and oxidative stress activate calcium signaling, ABA-dependent pathways, MAPK cascades, and ROS signaling. These pathways regulate major transcription factors including DREB, WRKY, NAC, and bZIP, which coordinate the expression of stress-responsive genes involved in ion homeostasis (SOS1, SOS2, SOS3, NHX1, HKT1), antioxidant defense (CuZnSOD, MnSOD, CAT, APX, POD), osmotic adjustment (LEA, HSP70, ASR), and carbon metabolism (SPS and F-box proteins). Coordinated molecular regulation results in physiological and biochemical adaptation, improved ion balance, reduced oxidative damage, and enhanced salinity tolerance. Integration of multi-omics approaches facilitates identification of candidate genes for crop improvement

Transcriptional regulation and stress-responsive genes

Transcriptome sequencing has become a key tool for elucidating salinity tolerance mechanisms in lentil by identifying differentially expressed genes involved in ion transport, hormone signalling, an-

tioxidant defence, osmotic adjustment, secondary metabolism and stress-responsive transcriptional control (Morgil *et al.*, 2019; Singh *et al.*, 2021; Singh *et al.*, 2022) [16, 17, 44]. Stress signals converge on transcription factors (TFs) that regulate large networks of downstream genes.

The DREB (AP2/ERF), WRKY, NAC and bZIP TF families are particularly important in plant salinity tolerance. DREB proteins activate genes associated with osmotic adjustment, antioxidant defence and dehydration tolerance, while WRKY TFs regulate ROS metabolism, defence signalling and hormone-responsive pathways (Agarwal *et al.*, 2006; Rushton *et al.*, 2010) [45, 46]. NAC proteins integrate developmental and stress-response pathways and contribute to osmotic and oxidative stress tolerance (Puranik *et al.*, 2012) [47]. bZIP TFs participate in ABA-dependent signalling and control genes related to osmoprotection and cellular protection (Jakoby *et al.*, 2002) [48]. Although many of these TF families are conserved across higher plants, relatively few members have been functionally characterized in lentil, highlighting a gap between transcriptomic discovery and gene-function validation (Singh *et al.*, 2021; Dissanayake *et al.*, 2021) [17, 14].

Genome-wide expression studies in lentil have also identified ABA-responsive genes, including *NCED* (involved in ABA biosynthesis), dehydrins, late embryogenesis abundant (LEA) proteins and ABA-responsive transcription factors, as major regulators that coordinate physiological and molecular adaptation under abiotic stress (Singh *et al.*, 2022) [49]. Numerous antioxidant-related genes (e.g. *CuZnSOD*, *MnSOD*, *CAT*, *APX*, *POD*) are strongly induced by salinity and are thought to contribute to redox homeostasis and cellular protection (Morgil *et al.*, 2019; Ali *et al.*, 2022) [16, 18]. There is increasing evidence of crosstalk among DREB, WRKY, NAC and bZIP TF networks, with these regulators jointly modulating genes controlling ion transport, ROS detoxification, osmolyte biosynthesis and secondary metabolism.

Despite this progress, functional validation of candidate TFs and stress-responsive genes through reverse genetics, transgenics or genome editing remains limited in lentil, and represents a major bottleneck in translating molecular insights into breeding applications (Singh *et al.*, 2021; Dissanayake *et al.*, 2021) [17, 14].

Crop breeding strategies for achieving salt tolerance

Breeding for salinity tolerance in lentil is challenging because tolerance is a complex, quantitative trait influenced by multiple loci, strong genotype $\times$ environment interactions, and developmental-stage specificity (Kumar *et al.*, 2016; Ismail *et al.*, 2017) [50, 51].

However, substantial progress has been achieved by combining conventional breeding, introgression from wild *Lens* species and contemporary genomics-assisted techniques. Natural variation in salinity tolerance has been exploited by using conventional breeding approaches such as hybridisation, selection, introgression from wild relatives specifically for traits such as seedling vigour, root architecture, K^+/Na^+ homeostasis and yield stability under saline conditions (Afzal *et al.*, 2016; Singh *et al.*, 2017; Dissanayake *et al.*, 2021) [52, 9, 14]. However, these approaches are hindered by the low genetic variation of cultivated gene pools, linkage drag from wild donors, reproductive obstacles, and the labour expensive nature of phenotypic selection under changeable field circumstances (Kumar *et al.*, 2016; Esmaili *et al.*, 2022) [50, 53].

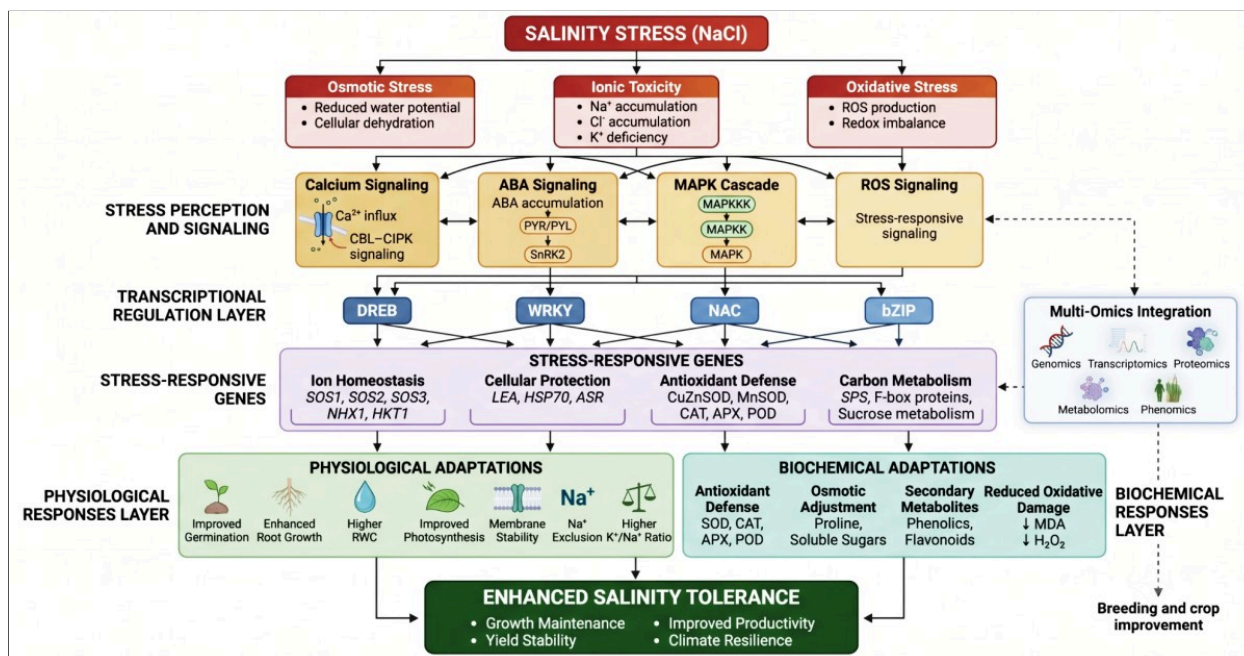


Figure 2. Integrated molecular signaling network regulating salinity tolerance in lentil

Mutational breeding, twofold haploid production and marker assisted selection (MAS) provide complementary options for accelerated genetic gain. Mutagenesis has been effectively exploited to produce novel alleles that improve ionic control and tissue tolerance in the presence of salt in grains and legumes (Yousefirdad *et al.*, 2018) [54]. MAS allows selection for tolerance associated loci using DNA markers associated with QTLs for ion homeostasis, antioxidant capacity or yield under stress which lessens the need for expensive multi environment phenotyping (Ismail *et al.*, 2017; Geetha *et al.*, 2017) [51, 55]. For confident identification of genotypes with consistent salinity resistance across habitats, these methods would have to be combined with strong physiological and biochemical screening in lentil.

Utilization of QTL knowledge on salt tolerance

Quantitative trait loci (QTLs) and marker-assisted selection offer substantial benefits over direct phenotypic screening for complicated traits such as salinity tolerance. Salinity tolerance is often controlled by many quantitative trait loci (QTLs) with additive and dominant impact each explaining a small percentage of phenotypic variance (Ismail *et al.*, 2017; Turki *et al.*, 2023) [51, 56].

For rice and other crops, multiple important QTLs for salinity tolerance have been found, including the famous “Saltol” locus linked with high K^+/Na^+ ratios and low Na^+ uptake at the seedling stage (58,59). QTL mapping and association studies in *Brassica* and other legumes have also identified loci associated with ion homeostasis, membrane stability and yield under salinity and candidate genes such as Bra003640 associated with salt tolerance (Lang *et al.*, 2017) [57].

Compared to major cereals, QTL studies in lentil are still relatively few. Emerging studies have started to identify genomic regions associated with salt-responsive traits such as germination, early vigour, root traits, K^+/Na^+ ratio and yield components under saline conditions (Singh *et al.*, 2021; Dissanayake *et al.*, 2021) [17, 14]. Such QTLs, when verified across several environments, are useful candidates for MAS and genomic selection. With the introduction of high throughput genotyping and development of dense genetic linkage maps, finer mapping and identification of candidate genes is now possible, which ultimately can allow for more precise pyramiding of favourable alleles for salinity tolerance in lentil (Ismail *et al.*, 2017; Pramanik *et al.*, 2021) [51, 58].

Genetic engineering and genome editing of salt tolerance

Recombinant DNA technologies, functional genomics and genome editing have significantly increased the tools for engineering salinity tolerance in crops by targeting specific genes and regulatory ele-

ments. Genes involved in ion transport, osmoprotectant production, ROS detoxification and transcriptional control have been altered in various species to improve tolerance under saline circumstances (Gupta *et al.*, 2014; Wani *et al.*, 2020) [59, 60].

Transgenic approaches overexpressing vacuolar Na^+/H^+ antiporters (NHXs), plasma-membrane Na^+/H^+ antiporters (SOS1), high-affinity K^+ transporters (HKTs), and vacuolar H^+ -pyrophosphatases (AVP1) have conferred greater Na^+ sequestration, improved K^+ retention and enhanced growth under salinity in several crops (Apse *et al.*, 1999; Gaxiola *et al.*, 2001; Pehlivan *et al.*, 2016) [61, 62, 63]. Co-overexpression of complementary genes, such as AVP1 with SOS1, NHX1 or other regulatory proteins, has further increased tolerance by simultaneously improving ion sequestration, Na^+ exclusion and vacuolar energization (Pehlivan *et al.*, 2016; Balasubramaniam *et al.*, 2022) [63, 64]. While most of these studies have been conducted in *Arabidopsis*, rice, cotton and other model or major crops, they provide a conceptual framework for similar strategies in lentil once efficient transformation and regeneration systems are in place (Esmaeili *et al.*, 2019; Esmaeili *et al.*, 2021) [65, 66].

Genome editing technologies, particularly CRISPR/Cas systems, now allow precise modification of structural genes, regulatory genes and cis-elements associated with salt-stress pathways (Pramanik *et al.*, 2021; Shelake *et al.*, 2022) [58, 67]. For example, translational enhancer elements have been included in SOS1 targeted editing in rice to promote greater salt tolerance (Lu *et al.*, 2020) [68]. Editing of vacuolar H^+ pyrophosphatase genes (HVP10) in barley has uncovered their pivotal function in Na^+ sequestration and growth under salt stress (Fu *et al.*, 2022) [69]. Genome editing in lentil is still in its infancy due to technical constraints. However, similar targets such as ion transporters (SOS1, NHX1, HKT1), key transcription factors (DREB, WRKY, NAC, bZIP) and protective proteins (LEA, ASR, HSPs) are logical candidates for future manipulation (Singh *et al.*, 2021; Esmaeili *et al.*, 2022) [17, 53].

Small RNA mediated regulation (miRNAs and siRNAs) and RNA interference (RNAi) give additional levels of control over stress response genes. Stress induced miRNAs can fine tune expression of critical transcription factors, ion transporters and hormone signalling components and so altering salinity responses (Kumar *et al.*, 2018; Abdellatef *et al.*, 2021) [70, 71]. For example, overexpression of miR172a in soybean improved systemic signalling under stress and boosted salt tolerance (Pan *et al.*, 2016) [72]. Identification and functional characterisation of salinity-responsive miRNAs and their targets in lentil and its allied legumes may open new avenues for engineering tolerance (Kumar *et al.*, 2018; Wani *et al.*, 2020) [70, 60].

Overall, although transgenic and genome-editing approaches for salinity tolerance in lentil are still at an initial stage, lessons from other crops clearly demonstrate the potential of precise manipulation of ion transporters, transcriptional regulators and protective proteins to generate a stronger and more durable tolerance. Such solutions will need to be functionally validated and rigorously tested in the field before widespread implementation in lentil improvement projects.

Emerging management and biotechnological strategies

The restricted number of lentil cultivars available with high salinity tolerance necessitates complementing management and biotechnology options to boost performance in salty environments and to enable genetic enhancement. Plant growth promoting microbes, nano enabled interventions and rhizosphere engineering have been highlighted as potential strategies to improve ion homeostasis, antioxidant defence, nutrient uptake and photosynthetic efficiency under salinity in recent studies (Nadeem *et al.*, 2014; Yadav *et al.*, 2026; Kumari *et al.*, 2025) [73, 3, 74].

Plant growth promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungus (AMF) and symbiotic rhizobia can enhance nutrient uptake, regulate phytohormones levels, improve antioxidant systems and improve ion balance to promote growth and nodulation in salty soils (Nadeem *et al.*, 2014) [73]. Salt resistant rhizobial isolates have been found to enhance lentil growth, nodulation, and physiological performance under high salt, suggesting the potential of microbiome assisted selection and development of inoculants (Kumari *et al.*, 2025) [74]. The nano enabled rhizosphere engineering further endeavours to improve beneficial microbial colonisation, nutrient cycling and root-microbe interactions by means of functionalised materials to control soil chemistry and microbial habitats (Yadav *et al.*, 2026) [3].

Nanotechnology offers additional methods for the management of saline stress. Biogenic and green synthesised nanoparticles can provide nutrients, change cellular redox state, activate stress responsive pathways and alleviate salt-induced damage (Sharma *et al.*, 2025; Yadav *et al.*, 2026) [75, 3]. Engineered nanobiochar combines the sorptive and structural features of biochar with the reactivity of nanoparticles, providing enhanced ion buffering, nutrient retention, microbial stabilisation and reduction of oxidative stress (Yadav *et al.*, 2026) [3]. In particular, TiO₂ nanoparticles synthesised by green methods have been found to stabilise photosystems, improve carbon assimilation, and enhance antioxidant activity to relieve photoinhibition under saline conditions (Yadav *et al.*, 2026) [3].

Despite these promising results, the efficacy of nanoparticles is significantly dependent on particle size, concentration, application method and environmental context, and there are real concerns regarding their long term biosafety and ecological consequences (Sharma *et al.*, 2025; Yadav *et al.*, 2026) [75, 3]. Therefore, careful risk evaluation, dose optimisation and regulatory structures will be necessary before wide scale adoption in lentil production systems.

Knowledge gaps and future perspectives

Although much progress has been made, some gaps remain important in translating salinity tolerance research to lentil improvement effectively. Most studies have concentrated on germination and early seedling stages, although reproductive development (flowering, pod set, seed filling and maturation) is both extremely salinity-sensitive and relatively understudied. Future work should be focused more on reproductive stage physiology and yield stability in field-relevant salinity regimes as final yield is mainly defined at these phases. Current understanding is primarily acquired from distinct physiological, biochemical and molecular research performed in diverse genotypes and situations, with few studies combining these levels of organization into the same genetic background. Mechanistic linkages between gene regulation, metabolic adjustment, physiological features and yield consequences are still poorly understood. Integrated multi omics studies combining genomics, transcriptomics, proteomics,

metabolomics and high throughput phenotyping in well characterised mapping populations and breeding lines are required for a systems level understanding of salinity tolerance and for the identification of robust biomarkers for selection (Morgil *et al.*, 2019; Singh *et al.*, 2021; Ali *et al.*, 2022) [16, 17, 18].

Many potential genes associated with ion transport, ROS detoxification, osmotic adjustment and stress signalling have been discovered, however functional confirmation in lentil is currently restricted. Priority targets include SOS pathway components, DREB and WRKY transcription factors, LEA and ASR proteins, and key antioxidant enzymes that are validated using reverse genetics, transgenics, and CRISPR-based genome editing to determine their causal regulation on salinity tolerance rather than just stress-inducible markers (Pramanik *et al.*, 2021; Esmaeili *et al.*, 2022) [58, 53]. Functional investigations require the development of effective transformation and regeneration methods for lentil.

A key restriction is the prevalence of trials in controlled environments like hydroponic, greenhouse or growth chamber settings, generally under single stress condition. In natural production systems, salinity is often combined with drought, heat and nutrient constraints. Field trials over multiple years and locations on naturally saline soils, together with factorial experiments with salinity and other abiotic stresses, are crucial to understand stress crosstalk, to refine selection criteria and to identify genotypes with wide adaptation (Ismail *et al.*, 2017; Yadav *et al.*, 2026) [51, 76].

In future, lentil salinity management will depend on integration of conventional and genomics assisted breeding with nanotechnology, microbiome engineering, multi omics, artificial intelligence and precision agriculture. Predictive breeding frameworks combining genomic selection, machine learning and high throughput phenotyping with systems biology insights can speed up the identification of superior alleles and production of climate resilient crops (Pramanik *et al.*, 2021; Yadav *et al.*, 2026) [58, 76]. A comprehensive framework integrating physiological screening, molecular regulation, multi-omics technologies, functional genomics, genome editing, and AI-assisted breeding for developing salinity-resilient lentil cultivars is presented in Figure 3.

Salinity stress initiates osmotic, ionic, nutritional, and oxidative stress, which activate signaling pathways involving calcium, ROS, ABA, MAPK cascades, and the SOS pathway. These signaling networks regulate stress-responsive transcription factors and downstream genes controlling ion homeostasis, antioxidant defense, osmotic adjustment, and photosynthetic protection. Integration of physiological responses with genomics, transcriptomics, proteomics, metabolomics, phenomics, and functional genomics provides a systems-level understanding of salinity adaptation. These multi-omics resources support genome-wide association studies (GWAS), marker-assisted breeding, genomic selection, CRISPR/Cas-mediated genome editing, and precision breeding for the development of climate-resilient, high-yielding lentil cultivars.

Conclusion

Soil salinity remains as one of the most major restrictions to the production of lentil worldwide and is likely to increase with continuous climate change and land degradation. Salinity causes coupled osmotic, ionic, nutritional and oxidative stressors which collectively limit growth, impair physiological function and lower yield.

The salinity tolerance in lentil is controlled by the co-ordinated physiological, biochemical and molecular regulatory networks rather than any single adaptive mechanism. Physiological activities including maintenance of plant water status, photosynthetic efficiency, membrane integrity and ion homeostasis interact with biochemical mechanisms like antioxidant defence, osmotic control, carbon metabolism and secondary metabolite production. At molecular level, integrated signalling networks including Ca²⁺ signalling, ABA mediated regulation, MAPK cascades, the SOS pathway and multiple transcription factor families orchestrate gene expression and cellular protection un

der salt stress (Morgil *et al.*, 2019; Singh *et al.*, 2021; Dissanayake *et al.*, 2021) [16, 17, 14].

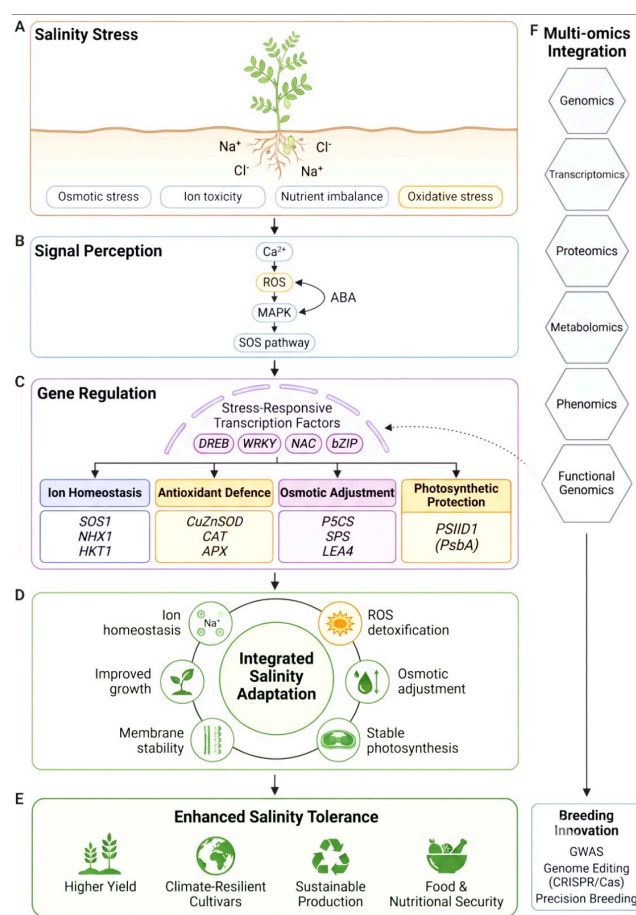


Figure 3. Integrated systems biology framework for developing salinity-tolerant lentil cultivars

Sustainable salinity tolerance in lentil will require integrated strategies combining detailed physiological and biochemical phenotyping with functional genomics, multi omics, genomics assisted breeding, genome editing and complementary agronomic interventions, including beneficial microbes and nanotechnology where appropriate (Esmaeili *et al.*, 2022; Yadav *et al.*, 2026; Kumari *et al.*, 2025) [53, 3, 74]. Multidisciplinary and on-farm verified methodologies linking controlled-environment studies to real-world production systems will be critical to transfer mechanistic findings into resilient cultivars capable of maintaining productivity under saltier and climate-challenged circumstances.

This review, by collating existing knowledge and recognising key research gaps, provides a framework to accelerate the development of salinity resilient lentil cultivars, and highlights the larger role of lentil in contributing to global food and nutritional security in the face of increasing soil salinization.

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