Agricultural & Forestry Economics and Management (2026) DOI: 10.23977/agrfem.2026.090103
Clausius Scientific Press, Canada ISSN 2616-2202 Vol. 9 Num. 1

Research Progress on Exogenous Spermidine in Plant Responses to Saline-Alkali Stress

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Keywords: Exogenous Spermidine; Salt-Alkali Stress; Plant Growth; Research Progress

Abstract: Global warming exacerbates soil salinization-alkalization, severely limiting plant growth, yield, and agricultural sustainability. Spermidine (Spd), a highly bioactive plant polyamine, effectively alleviates abiotic stress. This review elaborates salt-alkali stress harms: osmotic deficit, ionic toxicity (Na^+/OH^- accumulation), and ROS-induced oxidative burst with membrane lipid peroxidation. It summarizes exogenous Spd's tolerance-enhancing pathways: protecting PSI/PSII and chlorophyll to improve photosynthesis; boosting antioxidant systems (SOD, POD, CAT activity, GSH accumulation); maintaining high K^+/Na^+ ratio via ion transporters; promoting osmolytes (e.g., proline) for osmotic balance; and regulating stress gene transcription to activate defenses. Current limitations are highlighted: unclear Spd-phytohormone crosstalk (e.g., ABA, cytokinins), insufficient spatiotemporal gene regulatory network exploration, and unoptimized field application parameters (dosage, timing, delivery). Finally, it prospects agricultural application via multidisciplinary integration, providing a theoretical basis for improving plant salt-alkali tolerance and efficient saline-alkali soil utilization.

1. Introduction

Global warming intensifies plant environmental stress via precipitation shifts and extreme weather. Saline-alkali stress, a major abiotic stress from surface salt accumulation, affects ~3% of global agricultural land and 20% of irrigated land[1]. China has over 9.0×10^7 hectares of such land, severely restricting plant growth and agricultural sustainability[2].

Spermidine (Spd), a bioactive polyamine (formula: $H_2N(CH_2)_3NH(CH_2)_4NH_2$) in the PAs family (with Put, Spm), enhances abiotic stress tolerance via ROS scavenging, osmotic regulation and ion homeostasis[10]. It alleviates salt-alkali stress in crops by boosting antioxidant enzymes, suppressing Na^+/K^+ ratio and mediating hormone regulation[3].

Salt-alkali stress causes osmotic deficit, ionic toxicity and ROS-induced oxidative damage. Spd mitigates this by protecting photosystems, enhancing antioxidants, maintaining ion balance[13], promoting osmolytes and regulating stress genes. Unclear Spd-hormone crosstalk, inadequate gene network research and unoptimized field parameters limit its use; multidisciplinary integration is prospected for agricultural application[36].

2. The Detrimental Effects of Salt-Alkali Stress on Plant Growth

Under saline-alkali stress, a large amount of Na^+ accumulates in plants, thereby disrupting water and ion balance and causing severe damage to plant growth[4]. This further leads to a decline in plant growth rate, metabolic damage, and a reduction in photosynthetic rate[35]. The adverse effects of Na^+ on plants are the combined result of multiple factors, including osmotic stress, ionic stress, and oxidative stress[14].

2.1. Osmotic Stress

As the dominant factor in the early stage of saline-alkali stress, osmotic stress arises from elevated soil soluble salt concentration, lowering substrate osmotic potential and significantly inhibiting plant root water absorption[5]. Severe cases induce intracellular content leakage, reduced cell water potential, physiological drought, and even plant death[6]. This stress directly suppresses aboveground growth, characterized by decreased biomass accumulation, restricted leaf expansion, and fewer new leaves and lateral branches[9].

Studies have shown osmotic stress reduces relative water content and inhibits growth in wheat seedlings[7]. Marigold research confirms saline-alkali stress impairs biological membrane integrity, increases Electrolyte Leakage Rate (ELR), and induces excessive Reactive Oxygen Species (ROS) accumulation This accelerates membrane lipid peroxidation, raises Malondialdehyde (MDA) content, destroys membrane stability, hinders cell metabolism, and ultimately causes leaf damage[12].

2.2. Ionic Stress

Ionic stress constitutes a critical component of saline-alkali stress, with excessive Na^+ accumulation being the primary driver of salt toxicity in plants[8]. Excess Na^+, absorbed via roots and translocated into cells, not only disrupts intracellular K^+ homeostasis but also competitively inhibits the uptake of essential mineral elements such as K^+ and Ca^{2+}, triggering ionic imbalance and subsequent ionic toxicity[11]. K^+ deficiency leads to plant wilting and leaf necrosis, while excessive Na^+ further interferes with the distribution of Ca^{2+} within plants[13]. Additionally, surplus Na^+ and Cl^- impair biological membrane structure and enzyme activity, suppress chlorophyll biosynthesis, cause leakage of nutrients and osmotic regulators, compromise cell membrane stability and function, and further induce Reactive Oxygen Species (ROS) accumulation[10]. This damages photosynthetic membranes and proteins, disrupts the operation of the photosynthetic electron transport chain, ultimately reducing photosynthetic efficiency and impairing the synthesis and supply of nutrients[14].

2.3. Oxidative Stress

Reactive Oxygen Species (ROS) are the products of normal metabolism in plant cells, and cells generate energy through the metabolic process of reducing O_2 to H_2O. Under normal growth conditions, ROS maintain a low-level steady state and do not cause obvious harm to the plant[27]. However, under salt-alkali stress, excessive accumulation of ROS can cause oxidative stress in cells, disrupting the dynamic balance between ROS production and scavenging[15]. Excessive ROS can attack enzyme proteins and cause them to become inactive, while also causing oxidative damage to DNA[12], proteins, and lipids, leading to redox imbalance and membrane lipid peroxidation[17]. This severely disrupts the integrity of cell structure and ultimately leads to plant death[6].

3. The Mechanisms by Which Exogenous Spermidine Enhances Plant Saline-Alkali Tolerance

Recent years have seen great progress in studying plant salt-alkali stress response mechanisms and stress resistance regulation(Figure1). Current mitigation strategies include stress-resistant gene mining, soil structure improvement, cultivation optimization, and salt-tolerant germplasm screening, yet these methods are limited by high costs and complex operations[16]. In contrast, exogenous regulators are widely used in agriculture for their low cost, high efficiency, and simplicity[9]. Studies confirm exogenous spermidine (Spd) effectively mitigates salt-alkali stress-inuced growth inhibition, with its regulatory pathways focusing on four aspects[13].

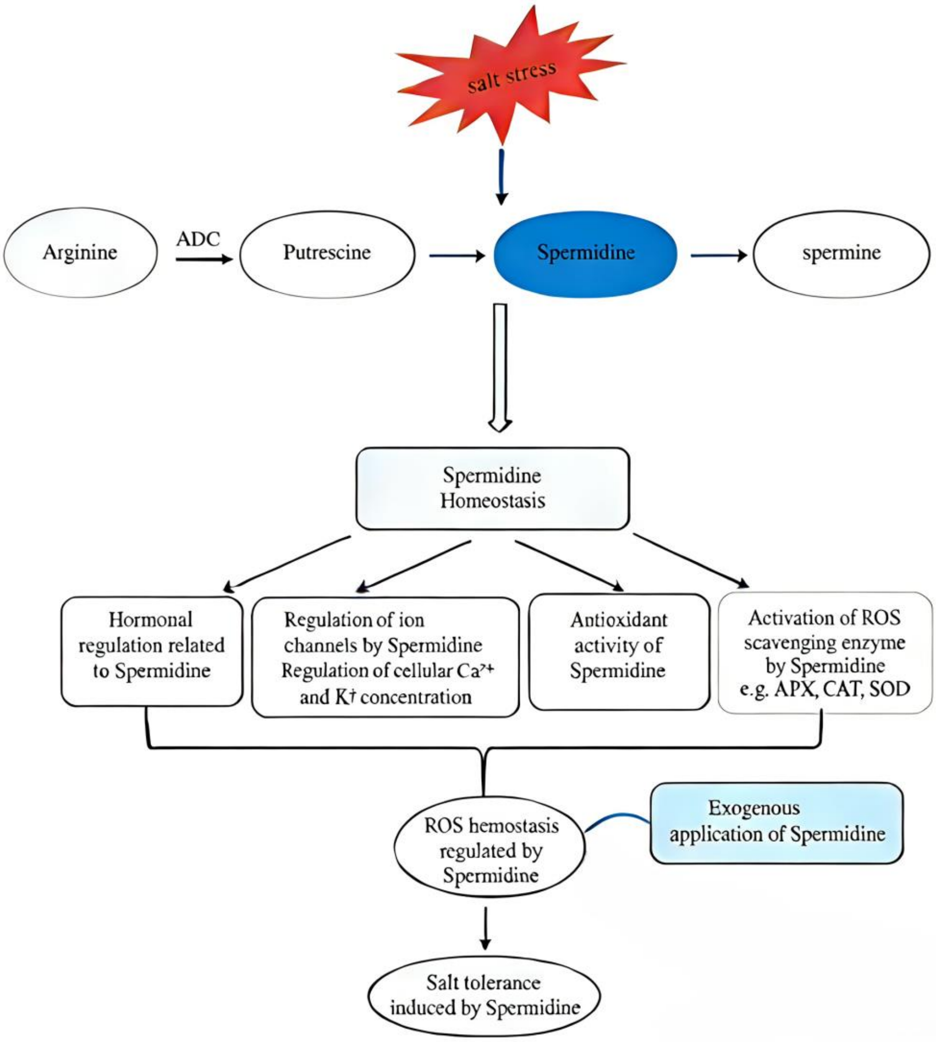

Figure 1: Pathways of Spermidine-Induced Salt Tolerance in Plants

3.1. Oxidative Stress

Exogenous spermidine (Spd) effectively protects plant photosystem structure and function against saline-alkali stress[14]. It enhances growth-related traits (plant height, leaf area, relative leaf water content, fresh biomass) in Sunflower seedlings, and mitigates leaf wilting/yellowing in potato seedlings by increasing chlorophyll content, promoting photosynthesis and dry matter accumulation[34] These results confirm that Spd maintains chlorophyll levels, regulates photosynthetic pigment degradation, protects photosystems and improves plant photosynthetic capacity under saline-alkali stress[19].

3.2. Enhance Plant Antioxidant Capacity

Polyamines perform diverse physiological functions (promoting macromolecule synthesis, stabilizing biomembranes, scavenging ROS, regulating proton gradients, mediating osmotic adjustment) Exogenous polyamines alleviate saline-alkali stress and boost crop productivity[15], with Spd showing superior effects: it scavenges ROS efficiently, upregulates antioxidant enzyme activities (SOD, POD, CAT)[16], and maintains cellular redox homeostasis[17]. Studies on Tomato[25], Cucumber[32], Grape[18] and Rice confirm that Spd interacts with antioxidant systems to inhibit lipid peroxidation, counter oxidative stress[35], repair cell membranes, stabilize intracellular environments and mitigate saline-alkali-induced oxidative damage[20].

3.3. Regulate Intracellular Ion Homeostasis in Plants

A high intracellular K^+/Na^+ ratio is essential for cell membrane integrity/permeability and plant growth. Saline-alkali stress induces Na^+ accumulation, K^+ loss, membrane damage, electrolyte leakage, ion homeostasis disruption, and metabolic impairment[21]. Exogenous Spd alleviates these effects by restoring organ ion balance (marigold)[22], maintaining ion homeostasis (tomato), and downregulating ABA biosynthesis gene transcription[37].Overall, Spd regulates ion homeostasis, preserves membrane integrity, and sustains normal metabolism under saline-alkali stress[23].

3.4. Maintain Plant Osmotic Homeostasis

Saline-alkali stress elevates soil salinity, hindering plant water uptake, inducing solute leakage and osmotic stress. Plants resist via accumulating osmotic regulators (free proline, soluble proteins/sugars)[24]. Exogenous foliar Spd boosts these substances in Mulberry seedlings[25], regulating osmotic potential and preserving enzyme/membrane integrity—an effect verified in Oats [26]and Sugar beets[27]. Overall, Spd enhances osmolyte accumulation, maintains homeostasis and alleviates saline-alkali-induced growth inhibition[28].

4. Mechanisms Underlying Spermidine-Mediated Regulation of Plant Responses to Saline-Alkali Stress

Plant science evidence confirms that spermidine (Spd), a bioactive polyamine, regulates plant responses to abiotic stresses[29].Exogenous Spd improves plant growth, antioxidant capacity, enzyme activity, osmolyte accumulation and ion homeostasis[38]; studies on Rice, Cucumber, Tomato and Marigold show it alleviates saline-alkali stress by enhancing antioxidants/osmolytes, reducing membrane permeability, MDA, O_2^- and H_2O_2 levels, and rebalancing ion homeostasis (e.g., K^+ retention, Na^+ reduction)[30].

Under NaCl/saline-alkali stress, 0.25 $mmol \cdot L^{-1}$ foliar Spd promotes Rapeseed seedling growth, increases chlorophyll, salicylic acid contents and SOD/POD activities; 0.9 $mmol \cdot L^{-1}$ Spd enhances Potato root vitality, chlorophyll content, antioxidant capacity and osmolyte accumulation to mitigate growth inhibition[31].

At the molecular level, Spd has little effect on polyamine synthase gene expression under non-stress conditions but upregulates it significantly under saline-alkali stress[32]. In Tea plants, 0.5 $mmol \cdot L^{-1}$ Spd upregulates CsRbcL to improve photosynthetic efficiency; in Cucumbers, it alleviates downregulation of carbon assimilation genes, promotes light energy utilization and upregulates chlorophyll biosynthesis genes (CsHEMA1, CsCHLH, CsPOR, CsCAO), thus enhancing stress tolerance[33].

5. Conclusions and Future Perspectives

Soil salinization severely limits global agricultural productivity. Saline-alkali stress disrupts plant physiology (cellular water deficit, ion imbalance, metabolic perturbation), inhibiting growth, reducing yields, or causing mortality—threatening agricultural sustainability and economic stability. In recent decades, using exogenous substances to enhance plant salt-alkali tolerance has become a focus in plant stress physiology.

Mounting evidence shows spermidine (Spd), a key polyamine, stabilizes plasma membrane integrity, regulates plant growth/senescence, and mediates abiotic stress responses. Exogenous Spd improves salt-alkali tolerance in crops (tomato, rice, cucumber) by enhancing photosynthetic efficiency, antioxidant capacity, ion homeostasis, and osmotic balance—alleviating core damages from osmotic, oxidative, and ion stresses.

However, critical gaps remain:

1) Cross-talk between exogenous Spd and plant hormones: Synergistic/antagonistic interactions between Spd and phytohormones (e.g., melatonin, salicylic acid) under stress, and whether combined application outperforms single agents, are largely uncharacterized.

2) Molecular mechanisms of Spd-mediated stress regulation: While phenotypic/physiological studies outline Spd's effects, underlying signaling networks (key transduction molecules/pathways) are nascent. Integrative multi-omics analyses are urgently needed to decode Spd-responsive gene/metabolite regulatory patterns.

3) Field-scale application feasibility: Though Spd boosts tolerance in labs, critical agronomic parameters (optimal dosage, timing, delivery) and field efficacy in real saline-alkali soils remain unclear. Future research must prioritize translational studies combining lab insights with field validation to develop Spd-based biostimulants or seed priming technologies.

In summary, exogenous Spd is a cost-effective, eco-friendly approach to mitigate salt-alkali stress. Future interdisciplinary research should clarify its mechanisms and accelerate translation to practice, supporting improved crop resilience and yield stability in salinized agroecosystems.

Acknowledgments

Fund Project: School Enterprise Cooperation Project (Project Number: 2024390)

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