Review

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# Salinity Stress in Strawberry: Biological Intervention Strategies and Breeding Approaches for Salt-Tolerant Cultivars

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*Review*

# Salinity Stress in Strawberry: Biological Intervention Strategies and Breeding Approaches for Salt-Tolerant Cultivars

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## Abstract

Soil salinity is a major constraint to strawberry (*Fragaria* × *ananassa*) cultivation, adversely affecting plant growth, yield, and fruit quality. Salinity stress triggers complex physiological and biochemical responses, including osmotic adjustment, antioxidant defense, ion homeostasis, and shifts in metabolite accumulation. Genotype-specific variability in tolerance highlights the potential for breeding salt-resilient cultivars. This review summarizes current knowledge on strawberry responses to salinity, emphasizing on the impacts on growth, photosynthesis, water relations, and fruit quality, as well as the underlying mechanisms of tolerance. In addition, it reviews biologically based approaches, including biostimulants, small signaling molecules, and plant–microbe interactions, that help alleviate salinity stress and strengthen plant resilience. By integrating these physiological insights with advances in biological and breeding-based approaches, the review provides a comprehensive framework for improving strawberry performance under saline conditions and guiding future cultivation and genetic improvement strategies.

**Keywords:** strawberry; soil salinity; breeding; tolerance; Fragaria; biostimulants

## 1. Introduction

Agriculture, as the backbone of global food production, faces numerous challenges that threaten its sustainability and capacity to meet the nutritional demands of a growing population. Among these challenges, soil salinity has emerged as one of the most pressing abiotic stresses that hinder crop productivity worldwide. Soil salinization, the process by which soluble salts accumulate in the soil profile, stands as a major form of land degradation that has profound consequences for agriculture, specifically plant growth, yield, soil health, and long-term sustainability [1,2]. Climate change, intensive irrigation practices, and the overexploitation of natural resources contribute to the acceleration of salt accumulation in agricultural [3,4].

### *1.1. Soil Salinity and Its Impact in Agriculture*

Soil salinity is a multifaceted phenomenon encompassing saline, sodic, and alkaline soil types, each defined by distinct types and concentrations of soluble salts and exchangeable cations. Saline soils contain high levels of soluble salts, resulting to reduction of the osmotic potential of the soil solution, thereby impairing plant water uptake, while sodic soils are dominated by sodium ions ($Na^+$), which degrade soil structure, decrease aeration, and restrict water infiltration and movement [1]. Moreover, alkaline soils, often associated with carbonate ion accumulation, exhibit high pH values that further limit nutrient availability and root development [5]. In all cases, the presence of excessive salts in the rhizosphere alters plant–soil–water relationships, ultimately reducing crop yield and quality.

Globally, the magnitude of the problem is striking. According to recent estimates by the Food and Agriculture Organization [4], approximately 424 million hectares of surface soils and 833 million hectares of subsoils are affected by salinity worldwide. Within Europe, salinity affects nearly 15 million hectares of cultivated land, with saline, sodic, and saline-sodic soils coexisting in varying proportions. Salinity is mainly affecting riparian, semi-arid and arid areas [6,7]. According to Shokat et al., 2019 [8], the implementation of sustainable cultivation practices and the cultivation of salinity-resistant genotypes has contributed to the restoration and productive use of problematic soils in developed countries. In contrast, in developing regions, short-term management strategies have failed to yield effective or lasting solutions, thereby exacerbating food insecurity. Mediterranean countries, such as Greece, are particularly vulnerable to salinity due to their semi-arid climate, dependence on irrigation, and overexploitation of groundwater resources [9,10]. In coastal areas, seawater intrusion into aquifers has further aggravated salinity problems, compromising both water quality and agricultural productivity. Climatic projections for the region indicate rising temperatures, reduced precipitation, and increased evapotranspiration, mainly driven by climate change. These developments are expected to accelerate salt accumulation in irrigated soils, ultimately destabilizing yields and compromising crop quality [3,11,12].

The impact of salinity stress or injury to plants (salt injury) depends on the plant species and variety, growth stage, environmental conditions and salt composition [13]. A comprehensive understanding of the physiological, biochemical, and molecular mechanisms that govern plant responses to stress is essential for developing effective mitigation strategies and guiding breeding programs. Such knowledge forms the foundation of sustainable agriculture, which depends on integrating improved management practices with the cultivation of stress-resilient crop varieties [14,15].

### *1.2. Natural and Human-Induced Causes of Soil Salinity*

The development of soil salinity results from both natural and anthropogenic factors operating across varying temporal and spatial scales. Naturally occurring salts derive from the geochemical weathering of parent rock material, which releases ions such as sodium ($Na^+$), calcium ($Ca^{2+}$), magnesium ($Mg^{2+}$), and chloride ($Cl^-$) into the soil solution [16]. In coastal environments and river deltas, seawater intrusion constitutes an additional pathway for salt enrichment. Excessive pumping of groundwater resources intensifies this process, as the decline in freshwater levels allows seawater to encroach into aquifers, leading to salinization of irrigation water and, subsequently, agricultural soils [17].

The use of low-quality water for irrigation threatens long-term agricultural sustainability by promoting salt accumulation in the root zone and soil degradation [18]. This process, commonly referred to as secondary salinization, is closely linked to irrigation and land management practices, as inadequate drainage fosters salt buildup, thereby reducing soil fertility and crop productivity. In arid and semi-arid regions, inappropriate irrigation scheduling and insufficient drainage exacerbate this process [19]. Additionally, groundwater interactions, such as seawater intrusion and water–rock reactions in coastal zones, further intensify salinity risks [20,21]. This salt accumulation also induces osmotic stress by reducing the plant's ability to take up water due to lowered soil water potential, thereby further exacerbating the negative impacts of salinity on plant growth [22].

Human activities exacerbate these natural processes, as inefficient irrigation practices, particularly the use of brackish water combined with inadequate drainage systems, accelerate salt accumulation in the root zone [16]. Over-irrigation promotes waterlogging and reduces leaching efficiency, causing salt to rise into the root zone through capillary action. Once established, excessive salinity is difficult to remediate, as soil restoration is both costly and resource-intensive [23] (Figure 1).

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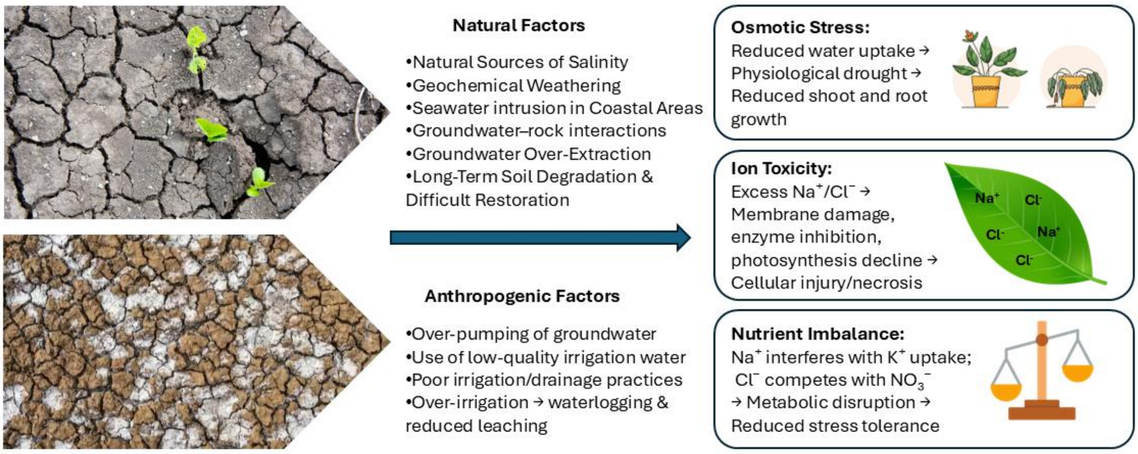

**Figure 1.** Overview of the major physiological and biochemical stress pathways triggered by soil salinity in plants from both natural and anthropogenic factors.

## 2. Salinity Stress and Strawberry Cultivation

### *2.1. Strawberry Cultivation and Salinity Stress*

Strawberry (*Fragaria* × *ananassa* Duch.) represents a particularly important case study for salinity tolerance, due to its high economic value, widespread cultivation, and pronounced sensitivity to soil and water salinity [24,25].

Belonging to the Rosaceae family, strawberries are prized for their unique flavor, nutritional value, and bioactive compounds, including anthocyanins, polyphenols, vitamins, and minerals, which contribute to their recognized health-promoting properties [26,27].

Global demand for strawberries has increased steadily over the past decades, driven by changing consumer preferences and the expanding role of strawberries in functional foods and nutraceuticals. In response to strong market demand, global production has expanded over the past decade, extending into arid and saline regions where irrigation water quality is often poor [28]. However, strawberry plants as glycophytes, are highly sensitive to abiotic stresses, particularly salinity, and exhibit a low threshold of tolerance, with yield reductions observed at soil electrical conductivity (ECe) values as low as 1.0 dS $m^{-1}$ [25]. For each additional unit increase in ECe, yield declines by approximately 33%, making salinity one of the most severe constraints on strawberry cultivation in irrigated regions [16]. Beyond reducing fruit yield, salinity compromises key quality traits such as sugar content, acidity, firmness, and shelf life, attributes that directly influence marketability and consumer acceptance [25,29].

Strawberries are among the irrigated crops increasingly exposed to salt stress because of secondary salinization, whose prevalence has risen with the intensification of agriculture in semi-arid and arid regions. For strawberries, a shallow-rooted crop, the consequences of secondary salinization are especially severe, leading to physiological stress [17,30]. Exposure to elevated salt levels disrupts strawberry growth and metabolism by reducing water uptake due to osmotic effects, while sodium and chloride ions accumulate in tissues, competing with essential nutrients such as potassium and calcium [31]. This ionic imbalance weakens physiological functions such as photosynthesis, stomatal regulation, and enzyme activity. The oxidative stress induced by excess salts promotes the overproduction of reactive oxygen species, which damage cellular membranes and proteins.

Although strawberries possess antioxidant defence mechanisms, their protective capacity is often insufficient under sustained salinity stress, resulting in leaf chlorosis, growth retardation, and overall yield decline. Moreover, the agronomic impacts of salinity in strawberry cultivation extend beyond yield losses, as previously discussed. Secondary salinization alters strawberry fruit quality by modifying sugar and acid balance, as well as affecting secondary metabolites, which are crucial for flavour and nutritional properties. These changes reduce market value and consumer acceptability [32]. An overview of how salt stress influences the growth, development, and productivity of strawberry plants is provided in Figure 2.

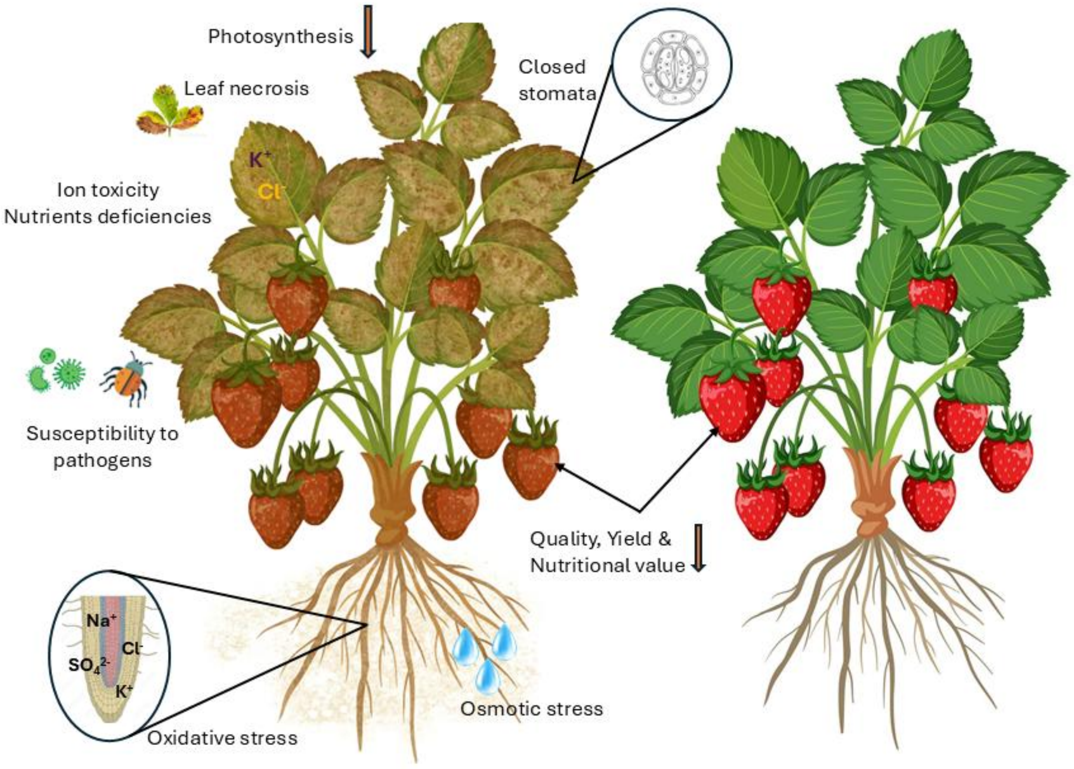

**Figure 2.** Secondary salinization effects on strawberry plants.

The severity of yield and quality losses can escalate when salinity is combined with shallow groundwater tables and waterlogging, which together intensify stress conditions and limit root aeration [19,33]. For strawberry cultivation, strategies such as soil flushing, adoption of salt-tolerant cultivars, and precision irrigation techniques can help mitigate stress and sustain production.

Research on strawberry salinity tolerance has expanded considerably in recent years, addressing genotypic differences as well as the morphological, physiological, biochemical, and molecular responses underlying stress adaptation [34–40]. Salinity stress is known to induce pronounced changes in plant morphology, leaf gas exchange, antioxidant activity, and ion homeostasis, reflecting the complexity of the strawberry stress-response network. Advances in molecular biology and genomics have further identified key genes and regulatory pathways associated with salinity tolerance, providing promising targets for breeding efforts and biotechnological applications [41–43]. Research has also focused on the effects of salinity on fruit quality and yield, highlighting significant physiological and metabolic adjustments that influence consumer-relevant traits [25,29,44].

Complementing genetic and molecular approaches, a wide range of agronomic strategies have been evaluated to mitigate the negative effects of salinity on strawberry growth and fruit quality. These strategies include the application of biostimulants [45], plant hormones and growth regulators [46,47], arbuscular mycorrhizal fungi [48], nanoparticles [49] organic fertilizers [50], and plant growth–promoting rhizobacteria [51,52]. Furthermore, the use of complementary light spectra and controlled-environment cultivation has been shown to enhance both stress tolerance and fruit quality [53]. Collectively, these multidimensional strategies reinforce the importance of integrating physiological, genetic, and agronomic methodologies.

Given the high economic and nutritional value of strawberries and their well-documented sensitivity to salinity, there is an urgent need to develop cultivars with enhanced tolerance while promoting sustainable agricultural practices that preserve soil and water resources. By deepening our understanding of strawberry responses to salinity and implementing interdisciplinary approaches, it becomes possible to support resilient and sustainable production systems under increasingly challenging environmental conditions.

### *2.2. Variation in Salinity Responses Across Different Strawberry Species and Cultivars*

Strawberry species and their wild ancestors exhibit distinct responses to salinity stress, largely due to differences in genetic background and genome complexity. The genus *Fragaria* comprises 16 priority crop wild relatives (CWRs) that can be exploited in plant breeding to enhance cultivated strawberries, offering opportunities to improve fruit quality, tolerance to abiotic stresses, and resistance to pests and diseases [54]. Comparative analyses of salinity tolerance mechanisms across *Fragaria* species are therefore essential for identifying key regulatory nodes and molecular pathways underpinning adaptive responses to salinity stress.

Among these CWRs, the Chilean strawberry (*Fragaria chiloensis*), an octoploid wild ancestor of the cultivated strawberry (*F.* × *ananassa*), comprises four subspecies: *F. chiloensis* subsp. *chiloensis*, *F. chiloensis* subsp. *lucida*, *F. chiloensis* subsp. *pacifica*, and *F. chiloensis* subsp. *sandwicensis*. This species is widely regarded as tolerant of abiotic stresses, particularly salinity and drought, and represents a valuable genetic resource for strawberry breeding [55–57].

Consistent with the diversity of stress responses observed among *Fragaria* CWRs, Nikoloudi [58], demonstrated that *F. virginiana* and *F. chiloensis* differ markedly in their responses to salinity stress. Although both species are wild ancestors of the cultivated strawberry, *F. chiloensis* exhibited a substantially greater capacity to withstand saline conditions, highlighting functional divergence within the genus and its relevance for breeding programs.

Subsequent comparative studies involving cultivated varieties and CWRs further substantiated these findings. Garriga et al. in 2015 [59], evaluated salinity effects on growth performance, physiological responses, productivity, and fruit quality in three strawberry genotypes: the commercial cultivar ‘Camarosa’, the cultivated Chilean strawberry Bau (*F. chiloensis* subsp. *chiloensis* f. *chiloensis*), and the wild Chilean strawberry Cucao (*F. chiloensis* subsp. *chiloensis* f. *patagonica*). Notably, *F. chiloensis* f. *patagonica* was largely unaffected by salt stress, indicating superior salinity tolerance among the genotypes examined.

Plant responses to salinity also vary substantially among cultivars within the same species. Because tolerance alone is insufficient for commercial production, breeding efforts increasingly aim to identify cultivars that combine stress resistance with high yield, superior fruit quality, and early production [25,60]. Controlled-environment studies consistently reveal pronounced cultivar-dependent variation in salinity responses. Denaxa et al. [34] reported that ‘Camarosa’ and ‘Rociera’ exhibit moderate salinity tolerance through distinct physiological and biochemical mechanisms, while Demiral et al. [61] identified significant cultivar × salinity interactions in ‘Camarosa’ and ‘Sweet Charlie’, attributable to contrasting $Na^+$ regulation strategies. Specifically, ‘Camarosa’ predominantly restricts $Na^+$ uptake at the root level, whereas ‘Sweet Charlie’ limits $Na^+$ translocation to the shoots.

Morphological traits further contribute to differential tolerance. For example, Elsanta’ exhibits lower stomatal density than ‘Elsinore’ [62], a characteristic associated with improved water-use efficiency under salinity stress [63]. Additional physiological differentiation was documented by Turhan et al. [64], who, building on earlier work [65–67], demonstrated marked differences between ‘Camarosa’ and ‘Chandler’ in stomatal regulation, $LT_{50}$ values, and antioxidant enzyme activity. Similarly, Ghaderi [35] reported greater salinity tolerance in ‘Kurdistan’ compared with ‘Queen Elisa’, associated with enhanced antioxidant capacity and higher relative water content (RWC).

Furthermore, Kortekamp et al. [68] assessed salinity tolerance in an $F_2$ population derived from a cross between the salt-sensitive cultivar ‘Senga Sengana’ and a salt-tolerant *F. chiloensis ssp. lucida* accession. Under greenhouse salt stress, $F_2$ individuals exhibited variable necrotic damage and growth reduction, revealing genetic variation in salt tolerance and identifying genotypes that could serve as a valuable resource for breeding strawberries with enhanced stress resilience.

Beyond whole-plant physiology, cultivars also differ in biochemical, metabolic, and fruit-quality responses to salinity. Alnayef et al. [69] observed increased antioxidant capacity and phenolic accumulation in 'Elsanta' and 'Elsinore' under saline conditions, with mild stress (≤20 mM) even improving fruit quality when combined with appropriate fertilization. At the cellular level, Hussein et al. [37] documented reductions in chlorophyll content, biomass, and growth in 'Fortuna' and 'Festival', accompanied by elevated proline accumulation and antioxidant activity. Similar osmoprotective responses were reported by Pirlak et al. [70], who observed proline accumulation alongside changes in $Na^+$ and $Cl^-$ concentrations in 'Fern' and 'Camarosa'. Under hydroponic conditions, Rahimi et al. in 2011 [71] further demonstrated cultivar-specific ionic imbalances in 'Camarosa', characterized by increased $Na^+$ accumulation, reduced $Ca^{2+}$ and $Mg^{2+}$ uptake, and concomitant growth inhibition.

Metabolic studies further revealed cultivar-dependent sensitivity. Keutgen [32] reported increased malondialdehyde (MDA), amino acids, and proline in 'Korona' and 'Elsanta', with 'Elsanta' exhibiting greater sensitivity and reduced fruit quality. Ondrašek et al. [72] similarly documented declines in fruit yield, number, and size under salinity, along with accelerated leaf senescence and shortened growth duration. Long-term experiments by Keutgen and Pawelzik [31] showed that although salinity reduced yield in both 'Elsanta' and 'Korona', the latter maintained more stable flavor-related traits. Notably, Galli et al. [28] demonstrated that moderate salinity in 'Camarosa' increased sugar content, anthocyanins, phenolics, and abscisic acid (ABA) without reducing yield, suggesting that controlled salinity may enhance nutritional quality.

Taken together, these studies demonstrate substantial genotypic variation in strawberry responses to salinity stress, reflecting complex and genotype-dependent physiological, biochemical, and morphological adaptation strategies. Traits such as efficient ionic regulation, enhanced antioxidant defense, osmotic adjustment, and modified stomatal behavior play key roles in determining tolerance. In particular, the capacity to balance $Na^+$ exclusion with $Cl^-$ compartmentalization, maintain relative water content, and sustain metabolic activity under moderate salinity appears critical for preserving productivity and fruit quality. Collectively, these findings underscore the importance of integrating physiological screening with molecular and agronomic approaches to identify and develop strawberry cultivars capable of thriving under saline conditions,

## 3. Mitigation Mechanisms in Strawberry under Salinity Stress

### *3.1. The Role of Small Signaling Molecules and Biostimulants in Mitigating Salinity Stress in Strawberry*

The external application of small signaling molecules, classified as biostimulants, has been shown to significantly mitigate the adverse effects of various abiotic stresses, including salinity [73]. Among these, 5-Aminolevulinic acid (ALA) serves as the primary precursor for tetrapyrrole compounds, namely chlorophyll, phytochrome and heme [74–76]. Wu et al. (2018) [76] reported that ALA enhance salt stress tolerance by promoting chlorophyll biosynthesis, improving light-harvesting efficiency and photosynthetic performance, and inhibiting thylakoid membrane degradation. Subsequently, they demonstrated that ALA appears to promote root-specific retention of $Na^+$ in strawberry plants, thereby limiting its translocation to the shoots [75,76]. ALA sequentially upregulated the expression of the *NHX1* (Na+/H+ exchanger), *HKT1* (High-affinity K+ uptake), and *SOS1* (Salt overly sensitive 1) genes and increased the hydrogen peroxide ($H_2O_2$) content in the roots, thus enhancing the salt tolerance of *Fragaria x ananassa* cv. 'Benihoppe' strawberry. These findings highlight ALA's potential as an effective agent for improving salt tolerance of strawberry plants under saline conditions.

Melatonin (*N*-acetyl-5-methoxy-tryptamine) is another important small signaling molecule, which plays a vital role as an antioxidant in plant stress responses. During salt stress conditions, melatonin accumulation is commonly observed, functioning as a ROS scavenger and enhancing the cellular antioxidant capacity of plant cells [77–79]. In the study of Zahedi et al. [47], the foliar applications of melatonin have been shown to mitigate the adverse effects of salinity in strawberry leaves, namely increasing the leaf photosynthetic pigments and reducing the changes in macronutrients concentrations induced by salinity. At the same time these melatonin foliar sprays improved fruit yield, size, firmness and fruit chemical parameters. Georgiadou et al. [80], have also demonstrated that preharvest application of melatonin with sodium alginate on strawberry fruit enhanced ellagitannins and ellagic acid derivatives, confirming the beneficial effect of melatonin on the antioxidant mechanism of plants. Continued investigation into the metabolic and regulatory networks of melatonin is essential to optimize its application for enhancing plant resilience to salt stress.

Salicylic acid (SA) is a phenolic compound which is also acknowledged as a signaling molecule that participates in regulating plant responses to various abiotic stress conditions [81]. Karlidag et al. [82], investigated the impact of various SA concentrations on the growth, chlorophyll content, and mineral composition of strawberry plants subjected to salt stress. Regarding growth parameters and nutrient content, SA treatments resulted in higher fresh and dry weight of both shoots and roots along with a general enhancement of nutrient concentrations in both the leaves and roots of strawberry plants exposed to salt stress. Jamali and Eshghi [83], proposed that the time of SA application is a significant parameter to consider, since the pretreatment of strawberry plants with SA before NaCl induced salt stress showed higher levels of root Mg and shoot Ca in comparison to salt-stressed plants treated with the same SA concentration one week after salt exposure. In cv. ‘Gaviota’ strawberries under salt stress, foliar application of 100 µM SA effectively alleviated damage by enhancing PSII efficiency, promoting the accumulation of compatible solutes such as trehalose, and increasing antioxidant enzyme activity and phenolic content [84]. This led to reduced lipid peroxidation and membrane damage, highlighting the role of SA in improving photosynthetic performance and activating defense mechanisms under salinity stress. The results of Roshdy et al. [85], indicate that foliar application of salicylic acid at 90 ppm can mitigate the adverse effects of salinity on the growth of the strawberry cv. ‘Camarosa’. The improvement in key indicators of salinity response, such as Salt Tolerance Index (STI), catalase (CAT), peroxidase (POD) and proline (PRO), following foliar application of SA in strawberries further supports its potential to alleviate the detrimental effects of salinity on the growth of strawberry plants.

Humic acid (HA) has been reported to confer beneficial effects under abiotic stress by improving soil physicochemical properties, such as osmotic and ionic balance, cation exchange capacity, and microbial activity, while also enhancing plant morphological traits, physiological processes (including photosynthesis, chlorophyll concentration, and $CO_2$ assimilation), and overall biochemical responses [22,86,87]. Saidimoradi et al. [50], reported that HA application in two commercial strawberry cultivars under salinity stress stimulated antioxidant enzyme activity and promoted effective osmotic adjustment, thereby enhancing stress tolerance. The addition of humic acid to the nutrient solution significantly reduced $Na^+$ accumulation in both roots and leaves, while simultaneously increasing chlorophyll content in salinity-stressed plants. Moreover, humic acid treatment resulted in increased leaf area and fruit number compared with plants exposed to NaCl alone.

The foliar application of 1mM of acetic acid, one week before the NaCl treatment in strawberry plants enhanced their salinity tolerance [88]. Acetic acid serves as a precursor to acetyl-CoA, a central metabolic intermediate essential for macromolecule biosynthesis and energy production that supports plant cell growth [89]. Treatment with acetic acid under NaCl stress benefited strawberry plants by protecting chlorophyll from degradation, reducing toxic ion accumulation in leaves, and increasing osmoprotectants like soluble carbohydrates and proline, along with non-enzymatic antioxidants such as phenols and ascorbic acid in fruits.

The study of Moradi et al. [41], highlights the promising potential of silicon nanoparticles (SiNPs) and methyl jasmonate (MeJA) in enhancing the physiological responses of strawberry plants

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under salinity stress. While SiNPs were found to significantly improve chlorophyll content and reduce oxidative damage by enhancing antioxidant enzyme activity, the study suggests that the mechanisms by which SiNPs modulate stress-related gene expression, such as for SOS1 and HKT1, still require further exploration. Similarly, MeJA's role in improving plant stress tolerance through upregulation of stress-related genes is well-supported, but optimal concentrations and application methods for maximizing its benefits remain unclear.

### *3.2. Microorganisms and Plant-Microbe Interactions under Salinity*

In recent years, increasing attention has been given to the role of beneficial soil microorganisms, particularly arbuscular mycorrhizal fungi (AMF), in enhancing plant tolerance to salinity. These symbiotic fungi form associations with plant roots, facilitating improved water and nutrient acquisition, especially phosphorus and micronutrients, and modulating physiological responses under salt stress [90,91]. Inoculation of strawberry plants with the arbuscular mycorrhizal fungus *Gigaspora margarita* significantly improved salt tolerance by enhancing shoot and root biomass, maintaining chlorophyll content, and reducing leaf browning under 200 mM NaCl stress [48]. Mycorrhizal plants showed lower $Na^+$ accumulation and a reduced $Na^+/K^+$ ratio in both root and shoot tissues compared to non-inoculated controls. SEM-EDX analysis revealed that excess sodium was primarily localized around the vascular bundles, with mycorrhizal plants accumulating less $Na^+$ overall. Additionally, increased cellulose and lignin content in the roots of mycorrhizal plants suggested the formation of a stronger apoplastic barrier, contributing to the suppression of $Na^+$ uptake and improved physiological resilience under salinity stress.

A study by Redondo-Gómez et.al, examined whether Plant Growth Promoting Rhizobacteria (PGPR) isolated from halophytes could improve the growth of eight major crops, including strawberry, commonly cultivated in salinized soils. Using environmental conditions that mimicked future climate scenarios (elevated $CO_2$, higher temperature, and salinity), they indicated that these biofertilizers generally enhanced crop growth and mitigated the negative effects of salt stress. Strawberry and rice demonstrated the strongest positive responses, with notably higher biomass when inoculated with PGPR under saline conditions. Overall, the study demonstrated that halotolerant PGPR can boost crop performance under current and future climate-related stress conditions [92].

In a similar context, a recent study focused on the effects of hydrogen-rich water (HRW) on alleviating salt stress in strawberry 'Benihoppe' seedlings. They presented that HRW improved plant growth, increased root biomass, enhanced antioxidant activity, promoted $K^+$ uptake while it reduced $Na^+$ accumulation, and modulated key metabolites. Transcriptomic and metabolomic analyses revealed that HRW activated genes and pathways related to ion transport, antioxidant defense, and cell wall biosynthesis, with phenylpropanoid biosynthesis and amino/nucleoside sugar metabolism proved particularly important for mitigating salt stress [93].

GABA ($\gamma$-aminobutyric acid) is a non-protein amino acid that acts as a signaling molecule in plants. It helps plants cope with salinity by regulating osmolytes, enhancing antioxidant defenses, reducing oxidative stress, and modulating gene expression related to stress tolerance, photosynthesis, and ion balance. Exploiting that knowledge, recently, Zhang et al. studied the effects of $\gamma$-aminobutyric acid (GABA) on salt tolerance in strawberry seedlings. GABA treatment under salt stress improved osmolyte accumulation, antioxidant capacity, and photosynthesis, while reducing ROS and MDA levels. Transcriptomic analysis demonstrated upregulation of genes related to chlorophyll metabolism and photosynthesis, while 38 transcription factors (WRKY, AP2/ERF, MYB) were identified as potentially contributing to GABA-induced salt tolerance. Overall, GABA enhanced strawberry salt resistance and could be useful in breeding programs by revealing physiological markers and transcriptional targets linked to salt tolerance [42].

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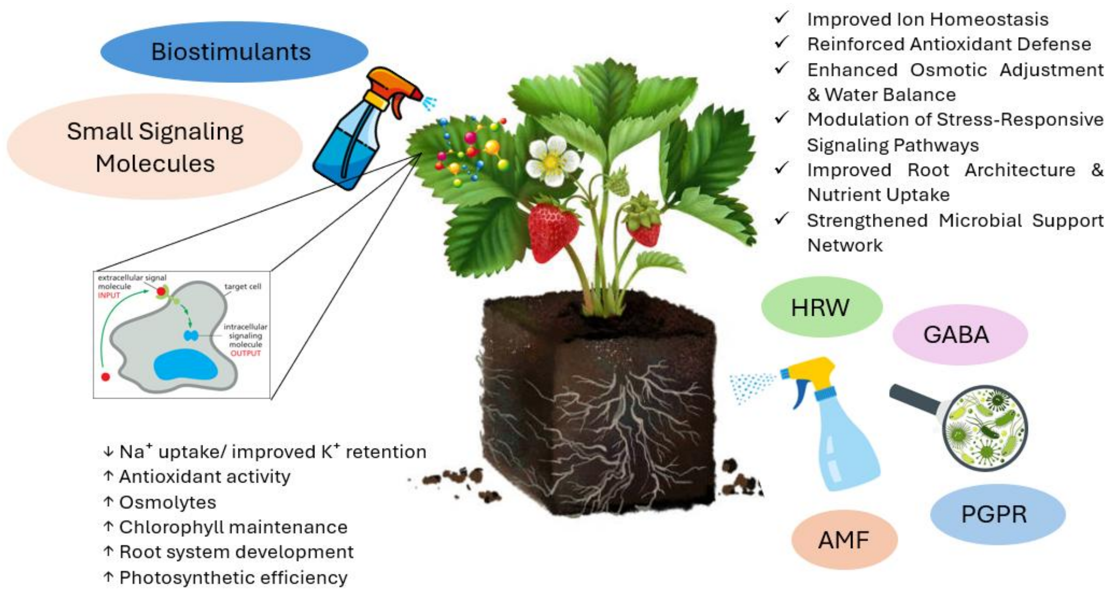

**Figure 3.** Overview of the beneficial effects though the exogenous application of small signaling molecules, biostimulants, and plant–microbe interactions (AMF: Arbuscular Mycorrhizal Fungi; PGPR: Plant Growth Promoting Rhizobacteria; HRW: Hydrogen-rich Water; GABA: $\gamma$-Aminobutyric Acid) enhance salinity tolerance in strawberry.

## 4. Genetic and Molecular Approaches for Improving Salinity Tolerance in Strawberry

### *Gene Identification and Functional Annotation for Breeding Targets*

Recent studies have broadened the genetic understanding of salinity tolerance in strawberry by uncovering novel regulatory genes and elucidating previously unknown stress-response mechanisms [94]. Gene identification and functional annotation provide a critical framework for understanding the molecular mechanisms underlying complex stress-adaptive traits. Such approaches enable the identification of key candidate genes that can be targeted to enhance stress tolerance through breeding [95].

Devinder Sandhu [96], explored the relationship between salinity tolerance and the expression of seven genes associated with Na$^+$ transport (*SOS1, SOS2, SOS3, NHX1, NHX2, AKT1, SAL1*) and four genes involved in Cl$^-$ transport (*CLC_G, CLC_C, SLAH3, ALMT12*). The study assessed biomass production, ion accumulation (particularly Na$^+$ and Cl$^-$), and a range of physiological and genetic parameters across eight genotypes of *F. vesca*. Notably, the upregulation of genes involved in Na$^+$ and Cl$^-$ transport was strongly associated with the plant's ability to sequester or exclude toxic ions, thereby influencing overall performance and survivability under saline conditions. The findings underscore the importance of deciphering the genetic mechanisms that mediate salt tolerance, as such insights may inform the development of commercially viable, salt-tolerant strawberry cultivars.

Several studies have employed similar strategies to explore other stress-related regulatory networks. Li et al. [97], focused on the Growth-Regulating Factor (GRF) gene family in *F. vesca*). Ten *FvGRF* genes were identified and classified into five subfamilies, with several members, specifically *FvGRF3*, *FvGRF6*, and *FvGRF8*, showing significant upregulation in response to salt stress. These GRF proteins, characterized by the conserved Glutamine–Leucine–Glutamine (QLQ) and Tryptophan–Arginine–Cysteine (WRC) DNA-binding domains, are implicated in chromatin remodeling and transcriptional regulation. Their putative involvement in ABA signaling pathways further supports a role in the plant's abiotic stress response network; however, functional validation in transgenic strawberry lines is still required.

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Husaini et al. [98], reported that transgenic strawberry plants expressing the *osmotin* gene showed enhanced tolerance to salinity stress compared with control plants. These plants accumulated higher levels of proline and total soluble proteins, maintained greater chlorophyll content, and performed better under high salinity conditions, tolerating electrical conductivity levels up to 20 dS $m^{-1}$. The improved stress tolerance was associated with elevated osmotin expression, indicating that this gene plays a key role in salinity adaptation and represents a promising target for improving salt tolerance in strawberry.

Through a targeted analysis of *superoxide dismutase (SOD)* genes in octoploid strawberry cv. 'Benihoppe', Zhang et al. [99], identified specific isoforms, such as Manganese Superoxide Dismutase 5 *(*FaMSOD5*)*, with salinity-induced expression patterns, highlighting their potential role in stress mitigation. However, the absence of functional validation limits their immediate use as breeding targets, underscoring the need for further molecular and physiological studies to confirm their contribution to salt tolerance.

Broadening the molecular understanding of salinity responses, Kong et al. [100], explored enzymatic responses associated with salt-induced oxidative stress in woodland strawberry (*F. vesca*). Among 41 identified *Laccase* (*FvLAC*) genes, 20 representative members were analyzed under salt treatment using qRT-PCR. The expression of *FvLAC7*, *FvLAC24*, *FvLAC32*, and *FvLAC51* increased steadily over 12 hours of NaCl exposure. Functional validation in transgenic yeast revealed contrasting roles: *FvLAC51* enhanced salt tolerance, while *FvLAC24* and *FvLAC32* reduced it. These results suggest that members of the laccase family play differential roles in the regulation of redox balance and cell wall remodeling under saline conditions, with *FvLAC51* acting as a potential positive regulator of salt tolerance in strawberries.

Transcription factors (TFs) are gene families which play many roles in plants' biological processes including regulation of salinity stress tolerance [101]. Indicatively, the NAC gene family includes several transcription factors, which are known to regulate various aspects of plant development, tissue differentiation, and responses to abiotic stress [102]. Zhang et al. in 2018 [103], investigated the NAC transcription factor family in woodland strawberry. They identified 37 *FvNAC* genes and systematically analyzed their gene structures, conserved motifs, and expression patterns across different tissues. Expression analyses under abiotic stresses (cold, heat, drought, and salt), biotic stresses (pathogen infection), and exposure to signaling molecules revealed that several *FvNAC* genes responded strongly to stress, particularly under cold and $H_2O_2$ treatments. In addition, some *FvNAC* genes were either upregulated or downregulated during pathogen infection. More specifically, for the fungal *Colletotrichum gloeosporioides*, genes *FvNAC04*, *FvNAC28*, *FvNAC29* found upregulated, while *FvNAC09*, *FvNAC18*, *FvNAC20* presented down regulated. Regarding the *Ralstonia solanacearum* bacteria, significant down regulation was detected for *FvNAC02*, *FvNAC13*, *FvNAC14*, *FvNAC21*, *FvNAC26*, and *FvNAC32* genes. These findings highlight stress-responsive regulation of specific *FvNAC* genes and identify them as potential candidates for improving salinity stress tolerance in woodland strawberry.

More targeted research on the *FvNAC* gene family, identified *FaNAC2*, a transcription factor from the ATAF sub-family in 'Benihoppe' strawberry, as a key regulator in stress responses [104]. *FaNAC2* expression is induced under various abiotic stresses and is predominantly localized in the shoot apical meristem and older leaves. Its overexpression in *Nicotiana benthamiana* enhanced tolerance to salt, cold, and drought stress, likely through upregulation of proline biosynthesis and ABA biosynthesis genes. These results suggest that *FaNAC2* plays a beneficial role in enhancing abiotic stress tolerance and represents a promising target for improving stress tolerance in strawberry.

In a more recent study, Wenhui Li et al. [105], cloned the *FvNAC29* gene from *F. vesca*. The study indicated a potential link between *FvNAC29* expression and the plant's molecular mechanisms for coping with high salinity stress. Transgenic lines exhibited reduced accumulation of reactive oxygen species (ROS) and malondialdehyde (MDA) along with elevated levels of proline and chlorophyll. In addition, there was an up regulation in the activities of key antioxidant enzymes: CAT, SOD, and

POD. These findings suggest that *FvNAC29* may contribute to enhanced salinity tolerance by modulating both oxidative stress responses and osmoprotective pathways.

In a follow-up study, Wenhui Li et al., cloned the *FaTINY2* gene from the octoploid strawberry. *FaTINY2* is a member of the APETALA2/Ethylene Responsive Factor (AP2/ERF) transcription factor family, which is involved in diverse biological functions, including plant morphogenesis, stress signaling pathways, hormone regulation, and secondary metabolite biosynthesis [106]. The expression of *FaTINY2* in transgenic lines was associated with enhanced antioxidant defense, as evidenced by reduced levels of ROS and MDA. In addition, transgenic plants exhibited increased concentrations of proline and chlorophyll, along with elevated enzymatic activities of CAT, SOD, and POD. Collectively, these findings indicate that *FaTINY2* plays an important regulatory role in salinity tolerance by coordinating antioxidant defense mechanisms and osmotic adjustment [107].

Building on the understanding of transcriptional and metabolic responses to salinity, Li et al. [108], analyzed two contrasting strawberry cultivars, the salt-tolerant 'Sweet Charlie' and the salt-sensitive 'Benihoppe' using integrated transcriptomic and metabolomic profiling. The tolerant cultivar showed a more robust response to salt stress, with a higher number of differentially expressed genes and metabolites compared to the sensitive one. Notably, genes associated with cell wall restructuring and ion regulation were more frequently upregulated in 'Sweet Charlie', suggesting these pathways play a central role in its adaptive capacity. A distinct pattern was also observed for genes encoding ATP-binding cassette (ABC) transporters, which were linked to coordinated changes in metabolite accumulation, particularly in pathways involving secondary metabolism. These differences indicate that enhanced activation of transport systems and reinforcement of cell wall architecture may underpin varietal differences in salt stress tolerance, providing potential targets for breeding programs focused on stress resilience in cultivated strawberry.

The MYB transcription factor family represents a promising target associated with salt stress tolerance in strawberry [109]. A novel MYB transcription factor gene *FvMYB82*, isolated from *F. vesca*, has been characterized by Wenhui Li et al. [110], characterized. Functional analyses in transgenic lines revealed elevated proline and chlorophyll levels, together with enhanced activities of key antioxidant enzymes, including SOD, POD, and CAT. These results suggest that *FvMYB82* plays a central regulatory role in the strawberry salt stress response by integrating osmotic adjustment and antioxidant defense pathways.

In a complementary study on the MYB transcription factor family, Wang et al. in 2021 [109], characterized *FvMYB24*, an R2R3-MYB transcription factor from *F. vesca* and demonstrated its functional role in salinity tolerance using transgenic *Arabidopsis thaliana* lines. Plants overexpressing *FvMYB24* exhibited improved performance under salt stress, including increased germination rates, root elongation, fresh biomass, and chlorophyll content. Physiological assays revealed elevated proline levels and antioxidant enzyme activities (SOD, POD, CAT), alongside reduced malondialdehyde (MDA) content, indicating enhanced cellular redox regulation and oxidative stress mitigation. Gene expression analysis showed that key salt-responsive genes, including *AtSOS1*, *AtNHX1*, *AtLEA3*, were upregulated in the transgenic lines. Importantly, *FvMYB24* was shown to bind the SOS1 promoter, acting as a positive regulator of SOS1-mediated $Na^+$ transport.

Kula et al. [111], compared the responses of two strawberry cultivars, 'Petaluma' and 'Cabrillo', to 0, 150, and 300 mM NaCl for ten days, combining physiological assays with gene expression analysis (qRT-PCR) to associate transcription factor activity with stress tolerance. Their findings revealed that 'Petaluma' displayed superior tolerance, maintaining growth parameters more effectively, experiencing lower oxidative damage, and significantly increasing anthocyanin accumulation compared with 'Cabrillo'. At the molecular level, Petaluma showed strong upregulation of the MYB5 transcription factor, which correlated almost perfectly with anthocyanin accumulation, and early induction of *ATF*1-2, a stress-responsive regulator. These coordinated physiological and molecular adjustments underpin Petaluma's enhanced ability to withstand high salinity, highlighting the importance of transcription factor regulation in strawberry salt tolerance.

In addition to gene expression and protein regulation, salt stress influences epigenetic mechanisms that control gene activity in strawberry. In this context, López et al. [112], found that epigenetic modifications, particularly DNA methylation, mediate stress responses in *F. vesca*. More specifically, salt stress triggered widespread hypomethylation, particularly in the CHG and CHH sequence contexts, with differentially methylated regions (DMRs) primarily located in promoter and intergenic regions. RNA-seq analysis revealed over 5,000 salt-responsive genes, enriched in functions related to transport, homeostasis, hydrolase and motor activity, as well as pyrophosphatase activity. Notably, MYB transcription factors represented the most enriched regulatory group among these DEGs. A subset of these salt-responsive genes showed concurrent methylation and expression changes, suggesting that DNA methylation acts as a context-specific modulator of gene activity. These findings indicate that epigenetic remodeling under salt stress may influence the expression of genes involved in key physiological processes, contributing to adaptive responses in *F. vesca*.

Chu et al. [113], isolated and characterized *FaTEDT1L*, a transcription factor from octoploid cultivated strawberry, which shares high homology with *AtEDT1/HDG11* of Arabidopsis. Functional validation in transgenic Arabidopsis demonstrated enhanced tolerance to both drought and salt stress, with transgenic lines showing increased root growth, decreased water loss, and upregulated expression of SOS pathway genes (SOS1, SOS2, and SOS3). These findings suggest that *FaTEDT1L* may act as a master regulator of osmotic stress response and could be a strong candidate for engineering salinity-tolerant strawberry cultivars.

A genome-wide association study (GWAS) is a genomic approach that scans genetic variation across an organism's entire genome to identify associations between specific genetic variants and phenotypic traits. Unlike studies limited to a few candidate genes, GWAS surveys the whole genome to find variants correlated with trait variation, providing researchers with a deeper understanding of the species under study [114].

Lei et al. [115], performed GWAS of the glucose-6-phosphate dehydrogenase (*G6PDH*) gene family in strawberry, identifying 19 members involved in redox regulation via the pentose phosphate pathway. Several *G6PDH* genes responded to salt stress, indicating their role in protecting cells from oxidative damage through NADPH production. *G6PDH* genes contribute to cellular detoxification and redox homeostasis under salinity conditions [116]. The integration of transcriptional and metabolic strategies appears critical for engineering effective salinity tolerance in strawberry.

Crizel et al. [117], conducted genome-wide identification and characterization of the calcium-dependent protein kinase (CDPK) gene family in *Fragaria × ananassa* cv. Camarosa, identifying 35 *FaCDPK* genes with diverse structural domains and expression patterns. Under salt stress, several members, particularly *FaCDPK11*, *FaCDPK15*, and *FaCDPK27*, showed pronounced upregulation, indicating their active involvement in salinity tolerance. These findings highlight the pivotal role of CDPK-mediated calcium signaling in the salt stress response, wherein $Ca^{2+}$-dependent phosphorylation pathways activate specific downstream genes and physiological processes that collectively enhance the plant's ability to maintain ion homeostasis and mitigate cellular damage under saline conditions.

Recent studies have provided additional insights into the molecular mechanisms underlying salinity tolerance. Li et al. [118], examined another important gene family involved in stress regulation. They conducted a comprehensive GWAS of the C2H2-Zing Finger Proteins (C2H2-ZFPs) C1-2i subclass in 'Benihoppe' cultivar. C2H2-ZFPs are crucial regulators of plant responses to diverse environmental stresses. Under salt stress, the expression levels of nineteen variants of *FaZAT8, FaZAT10*, *FaZAT11* and *FaZAT12* were elevated in roots relative to untreated control. Transcriptome data highlighted *FaZAT10* as exhibiting the highest expression in roots under these conditions, indicating that it may serve as a key regulator in stress signal transduction.

Focusing on a different aspect of salt stress response, Jiang et al. [119], performed GWAS of the U-box E3 ubiquitin ligase gene family. Among the 155 identified FaU-box genes, several exhibited marked transcriptional responses to salt stress. qRT-PCR analysis revealed that *FaU-box9*, *FaU-box18*, *FaU-box52*, and *FaU-box65* were rapidly induced within three hours of NaCl treatment, whereas *FaU-*

*box3*, *FaU-box83*, and *FaU-box142* showed gradual upregulation, peaking at 12 hours before slightly declining. The authors suggested that U-box E3 ubiquitin ligases may regulate salinity tolerance through targeted ubiquitination of specific signaling proteins, influencing their stability and degradation to adjust cellular responses under stress.

**Table 1.** Key genes and proteins involved in strawberry salinity tolerance related to ion homeostasis, osmotic adjustment, and stress signaling pathways.

| Gene / Protein | Function / Role In SalinityTolerance | Mechanism / Pathway | Reference |
|---|---|---|---|
| SOS1 | Plasma membrane $Na^+/H^+$ antiporter; removes $Na^+$ from cytoplasm | $Na^+$ transport / ionhomeostasis | [96,120] |
| SOS2 | Part of SOS pathway; regulates $Na^+$ homeostasis | $Na^+$ transport / signaltransduction | [96] |
| SOS3 | Part of SOS pathway; regulates $Na^+$ homeostasis | $Na^+$ transport / signaltransduction | [96] |
| NHX1 | Vacuolar $Na^+/H^+$ antiporter; sequesters $Na^+$ into vacuoles | $Na^+$ compartmentalization / ion homeostasis | [96,120] |
| NHX2 | Vacuolar $Na^+/H^+$ antiporter; ion compartmentalization | $Na^+$ compartmentalization / ion homeostasis | [96] |
| HKT1 | $Na^+$ transporter; regulates $Na^+$ uptake and distribution | $Na^+$ transport / ionhomeostasis | [96,120] |
| AVP1 | Vacuolar $H^+$-PPase; generates proton gradient for ion sequestration | Proton gradient / ioncompartmentalization | [120] |
| Osmotin | Enhances proline, total soluble protein, chlorophyllcontent; improves salinitytolerance | Osmotic adjustment / stress-responsive protein | [98,121] |
| FvGRF3 | Growth-Regulating Factor; involved in chromatin remodeling and ABA-mediated stress response | Transcriptional regulation / ABA signaling | [97] |
| FvGRF6 | Growth-Regulating Factor; involved in chromatin remodeling and ABA-mediated stress response | Transcriptional regulation / ABA signaling | [97] |
| FvGRF8 | Growth-Regulating Factor; involved in chromatin remodeling and ABA-mediated stress response | Transcriptional regulation / ABA signaling | [97] |
| FvMYB82 | MYB transcription factor; increases proline, chlorophyll, and antioxidant enzyme activity | Transcriptional regulation / antioxidant defense | [110] |
| FaNAC2 | NAC transcription factor; regulates proline and ABA biosynthesis under stress | Transcriptional regulation / osmotic adjustment | [104] |
| FvNAC29 | NAC transcription factor; reduces ROS and MDA, enhances antioxidant enzymes and osmotic adjustment | Transcriptional regulation / oxidative stress & osmoprotection | [105] |
| FaTINY2 | AP2/ERF transcription factor; coordinates osmotic adjustment and antioxidant defense | Transcriptional regulation / stress signaling | [107] |
| FaTEDT1L | HDG11-like transcriptionfactor; enhances root growth, reduces waterloss, upregulates SOS genes | Transcriptional regulation / osmotic stress response | [113] |
| G6PDH gene family | Redox regulation via pentosephosphate pathway; protects cells from oxidative | Redox homeostasis / ROS detoxification | [115] |

| | | | |
|---|---|---|---|
| | stress and contributes to NADPH production under salinity | | |
| AKT1 | $K^+$ channel; maintains ionbalance under salinity stress | $K^+$ transport / ionhomeostasis | [96] |
| SAL1 | Phosphatase involved in stress signaling and ionhomeostasis | Signal transduction / stress signaling | [96] |
| CLC_G | Chloride channel; regulates $Cl^-$ transport and homeostasis | $Cl^-$ transport / ionhomeostasis | [96] |
| CLC_C | Chloride channel; regulates $Cl^-$ transport and homeostasis | $Cl^-$ transport / ionhomeostasis | [96] |
| SLAH3 | Anion channel; contributesto $Cl^-$ homeostasis under salt stress | $Cl^-$ transport / ionhomeostasis | [96] |
| ALMT12 | Malate transporter; contributes to ion balance and stress response | Organic acid transport / ion balance | [96] |

## 5. Future Prospects

Future research on strawberry salinity tolerance will benefit from integrating multilevel approaches that span genetics, physiology, molecular biology, and agronomy. The rapid identification of key regulatory genes, such as members of transcription factors (NACs, AP2/ERFs, MYBs), ion-transport regulators and redox-related genes, provides promising targets for breeding programs aimed at improving salt tolerance while preserving fruit quality. These findings highlight the need for functional validation, gene pyramiding, and the translation of candidate genes into marker-assisted selection, genomic selection, and CRISPR/Cas-based engineering to accelerate the development of elite cultivars. The genetic diversity of wild relatives, particularly *F. chiloensis*, offers additional reservoirs of tolerance traits that can be introgressed into commercial cultivars.

At the same time, advances in biostimulants and small signaling molecules (e.g., ALA, melatonin, salicylic acid, silicon nanoparticles, acetic acid) show strong potential for mitigating salinity effects by enhancing antioxidant capacity, osmotic adjustment, ion homeostasis, and stress-responsive gene expression. Future studies should establish standardized application protocols and test these compounds under field conditions. Similarly, plant–microbe interactions, including arbuscular mycorrhizal fungi and plant growth–promoting rhizobacteria, represent eco-friendly tools that can complement genetic improvement by enhancing nutrient uptake, reducing $Na^+$ toxicity, and reinforcing root structural barriers. Integrating these biological approaches with precision irrigation, soil salinity monitoring, controlled-environment horticulture, and sustainable water management will allow growers to maintain salinity within manageable thresholds—especially given evidence that mild salinity can enhance fruit nutritional quality in certain cultivars.

Collectively, future progress will depend on bridging molecular insights with practical cultivation strategies, combining advanced genomic resources with optimized agronomic and microbial interventions. Such a holistic perspective will be essential for developing resilient strawberry production systems capable of sustaining yield and fruit quality under increasingly saline and resource-constrained environments.

## 6. Conclusions

Soil salinity is a major abiotic constraint that severely limits both the productivity and nutritional quality of strawberry crops. This review synthesizes current knowledge of strawberry responses to salinity stress, with emphasis on the underlying physiological, biochemical, and molecular mechanisms. Salinity impairs plant growth, photosynthetic performance, water relations, and fruit quality, while inducing osmotic adjustment, activation of antioxidant defenses, and shifts in primary and secondary metabolite profiles. Significant genotypic variation shapes the degree of tolerance, underscoring the need for identifying and developing salt-tolerant cultivars. By integrating evidence from diverse studies, this review provides a framework for breeding strategies aimed at enhancing strawberry resilience to saline environments and offers practical insights to support growers managing production in salt-affected regions.

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