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Salt Stress Tolerance in Medicinal and Aromatic Plants: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

ABSTRACT

Soil salinity is a globally pervasive issue, significantly affecting crop productivity and quality. This review provides a comprehensive overview of salt stress tolerance in medicinal and aromatic plants, plants known for their unique metabolic capabilities and resilience to abiotic stress. The

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adverse impact of salt stress on plant development, growth, and chemical composition is examined, emphasizing the specific effects on medicinal and aromatic plants, such as reduced biomass, altered yield, and modification of chemical composition. We delve into the complex responses exhibited by plants under salt stress, including physiological, biochemical, and molecular mechanisms. Physiological responses such as osmotic adjustment and ion homeostasis, biochemical responses including antioxidant production and compatible solute synthesis, and molecular responses like the upregulation of salt stress-responsive genes and hormone modulation, all contribute to salt stress tolerance. Understanding these intricate mechanisms offers valuable insights into the plants' resilience under salt stress. This review also discusses strategies to enhance salt stress tolerance in medicinal and aromatic plants, encompassing breeding and genetic modification, management strategies, and the utilization of beneficial soil microbes. The potential of selective breeding and genetic engineering in developing salt-tolerant plants is explored, along with the implementation of efficient irrigation systems and the use of salt-tolerant rootstocks. Additionally, the potential role of beneficial soil microbes such as mycorrhizal fungi and plant growth-promoting rhizobacteria in alleviating salt stress is highlighted. Lastly, we present potential future directions and applications for this research. The findings and strategies elaborated upon in this review have far-reaching implications, including the improvement of salt stress tolerance in other crops, promoting sustainable agriculture in saline soils, and potential therapeutic implications due to altered biochemical composition under salt stress. The continuation of research in this field is critical to tackling soil salinity challenges and maximizing the medicinal and aromatic plants' potential under salt stress. This review underscores the importance of studying salt stress tolerance mechanisms in medicinal and aromatic plants to contribute to sustainable agricultural practices and the advancement of the pharmaceutical industry.

Keywords: Salt-stress; tolerance; medicinal; aromatic; agriculture.

1. INTRODUCTION

Salt stress, a type of abiotic stress, is defined as the negative physiological effects experienced by plants due to high salt concentration in the soil, typically resulting from irrigation practices or natural processes such as sea water intrusion and mineral weathering [1]. Salt stress encompasses two main components: an immediate osmotic stress that inhibits plant growth and a longer-term ionic stress resulting from the accumulation of toxic ions in the plant tissue, primarily sodium and chloride [2]. Salt stress poses a serious and increasing threat to agriculture worldwide. Approximately 20% of the world's irrigated lands and nearly 50% of all arable lands are affected by salinity [3]. It has been estimated that by 2050, more than 50% of arable land worldwide could be affected by salinity [4]. The impact of salinity stress on crop productivity is substantial, leading to reduced yield, quality, and economic value. For example, wheat yield can decrease by more than 50% under moderate salt stress conditions [5]. Medicinal and aromatic plants play significant roles in various sectors, including healthcare, cosmetics, and food industry, due to their therapeutic properties and flavors [6]. They serve as a rich source of bioactive compounds like essential oils, antioxidants, and other secondary metabolites with antimicrobial, anti-inflammatory, and antitumor activities [7]. Some well-known medicinal and aromatic plants include lavender, rosemary, and thyme, which have been extensively used in traditional medicine for their healing properties. For instance, lavender is known for its calming effect, rosemary for its potential to improve memory, and thyme for its antimicrobial properties [8]. These plants also contribute significantly to the economy, particularly in countries where they are cultivated extensively. Just like other crops, medicinal and aromatic plants are not immune to the detrimental effects of salt stress. High salinity can lead to a reduction in plant growth, biomass, and yield, affecting the overall productivity of these plants [9]. Moreover, salt stress can alter the composition of the bioactive compounds in these plants. For instance, studies have reported changes in essential oil content and composition in rosemary and lavender under salt stress conditions [10]. However, it is noteworthy that some medicinal and aromatic plants exhibit considerable tolerance to salt stress, and understanding these mechanisms could offer ways to improve salt tolerance in other plant species [11]. Given the increasing threat of soil salinization and its impact on plant productivity, understanding the mechanisms behind salt stress tolerance in medicinal and aromatic plants has gained significant importance. This review aims to elucidate these mechanisms and

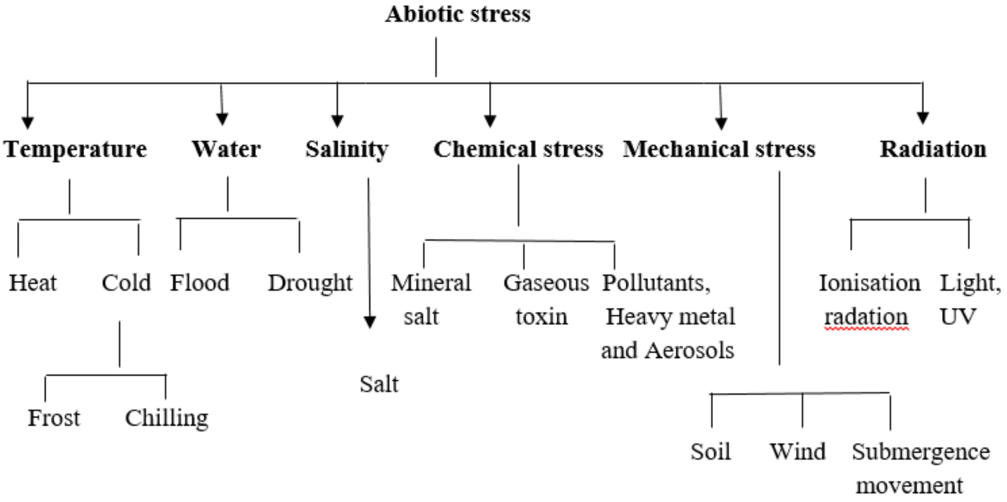

Fig. 1. Several abiotic stress signalling affect plants [12]

provide a comprehensive understanding of how these plants cope with salt stress. Furthermore, the review intends to highlight potential strategies for enhancing salt stress tolerance in these economically and therapeutically important plants. By doing so, this review hopes to contribute to sustainable agricultural practices and the continued cultivation of medicinal and aromatic plants in saline soils.

2. THE EFFECT OF SALT STRESS ON PLANTS

One of the earliest responses to salinity is osmotic stress, which is caused by the high concentration of salt in the soil solution [13]. This high salt concentration reduces the soil water potential, making it more difficult for plants to extract water. This results in an immediate inhibition of root and shoot growth [14]. The osmotic stress caused by high soil salinity can induce a series of metabolic and physiological changes in plants, such as reducing photosynthesis and transpiration rates [15]. Ionic toxicity is a subsequent effect of salinity that occurs when the plant absorbs excessive sodium and chloride ions. These ions accumulate over time and can reach toxic levels, causing cellular damage [16]. Sodium ions, in particular, are known to interfere with potassium uptake and disrupt essential metabolic processes, leading to cellular dysfunction [17]. Chloride ions, while less toxic than sodium ions, can also cause toxicity symptoms at high concentrations [18]. Salinity stress often leads to nutrient imbalance in plants. High concentrations of sodium in the soil solution can interfere with the absorption of other essential cations such as potassium, calcium, and magnesium, which can cause nutrient deficiencies and impair plant metabolic process [19]. For example, potassium, which plays a crucial role in maintaining cell turgor, enzyme activation, and stomatal opening, can be severely affected by high sodium concentrations [20].

3. SALT STRESS ON THE GROWTH OF MEDICINAL AND AROMATIC PLANTS

One of the significant effects of salt stress in medicinal and aromatic plants is a reduction in plant biomass. High salt levels can lead to a decrease in both root and shoot growth, resulting in smaller plant size [21] For instance, a study on the effects of salinity stress on rosemary (Rosmarinus officinalis) demonstrated that increased salinity led to a significant decrease in the plant's total biomass [22]. Similarly, salt stress reduced the total dry weight of lavender plants (Lavandula angustifolia) in a dose-dependent manner [23]. In addition to biomass reduction, salinity stress can lead to decreased yield in medicinal and aromatic plants. The reduced plant growth due to osmotic stress, ionic toxicity, and nutrient imbalance ultimately results in lower flower and leaf yield, the parts of the plant most commonly used for their medicinal properties and aromatic oils [24]. For instance, high salt levels significantly reduced the flower yield of chamomile (*Matricaria chamomilla*), a popular medicinal and aromatic plant [25]. Apart from growth and yield, salt stress can significantly alter the chemical composition of medicinal and aromatic plants. Changes in the concentration of bioactive compounds, including essential oils and antioxidants, have been observed under high salinity conditions [26]. For instance, rosemary plants grown under saline conditions demonstrated changes in their essential oil composition, with an increase in certain compounds and a decrease in others [27]. Similarly, in lavender plants, salt stress caused a significant alteration in the essential oil profile, affecting its quality [28].

4. MECHANISMS OF SALT STRESS TOLERANCE IN PLANTS

Plants, being sessile organisms, have developed a variety of mechanisms to deal with environmental stressors such as high salinity [29]. These mechanisms range from physiological and biochemical responses to changes at the molecular level. They are often interconnected, and collectively contribute to a plant's ability to tolerate and adapt to salt stress. One of the primary physiological responses to salt stress is osmotic adjustment. This involves the accumulation of organic and inorganic solutes in the plant cells to maintain cell turgor and water uptake under high external salt concentrations [30]. This allows the plant to continue growing even under osmotic stress. For example, proline, a common osmolyte, has been found to accumulate in various medicinal and aromatic plants under salt stress, aiding in osmotic adjustment [31]. Maintaining ion homeostasis is another important physiological response to salt stress. High concentrations of sodium ions can disrupt cellular ion balance, affecting metabolic processes and leading to toxicity [32]. To counter this, plants have developed mechanisms to exclude sodium from uptake, sequester excess sodium into the vacuole, or excrete it through salt glands or bladders [33]. These mechanisms help to maintain the cytosolic sodium concentration at non-toxic levels and ensure the optimal functioning of cellular processes.

5. BIOCHEMICAL RESPONSES TO SALT STRESS

Salt stress leads to the production of reactive oxygen species (ROS), which can cause oxidative damage to proteins, lipids, and DNA [34]. To combat this, plants have a sophisticated antioxidant defense system, including enzymes like superoxide dismutase, catalase, and peroxidase, and non-enzymatic antioxidants like ascorbate and glutathione. These antioxidants scavenge ROS, thereby preventing cellular damage [35]. Compatible solutes, also known as osmolytes, are small organic compounds that can accumulate in high concentrations without disrupting cellular functions [36]. These include amino acids like proline, quaternary ammonium compounds like glycine betaine, and sugars like trehalose. Compatible solutes play a key role in osmotic adjustment and also protect cellular structures from damage caused by high salt concentrations [37].

6. MOLECULAR RESPONSES TO SALT STRESS

At the molecular level, numerous genes are activated or repressed in response to salt stress. These salt stress-responsive genes encode proteins involved in a variety of functions, including ion transport, osmotic adjustment, antioxidant production, and signal transduction [38]. For instance, several genes involved in the synthesis of compatible solutes, such as P5CS (proline) synthesis) and TPS (trehalose synthesis), have been identified to be upregulated under salt stress [39]. Plant hormones play a crucial role in the regulation of plant responses to salt stress. Abscisic acid (ABA) is one of the primary hormones involved in this process. ABA levels rise in response to salt stress, triggering stomatal closure to reduce water loss and activating stress-responsive genes [40]. Other hormones, such as ethylene, gibberellins, and jasmonates, also participate in the complex network of salt stress responses [41].

7. SALT STRESS TOLERANCE IN MEDICINAL AND AROMATIC PLANTS

Numerous strategies have been proposed and implemented to enhance salt stress tolerance in medicinal and aromatic plants, ranging from traditional breeding techniques to modern genetic engineering approaches, from agronomic management to leveraging beneficial soil microbes. These strategies aim at preserving and improving the productivity of these plants in saline conditions. Selective breeding or traditional breeding is a time-tested strategy for enhancing salt tolerance in plants [42]. By selecting parent plants with desirable traits, such as salt tolerance, and cross-breeding them, the resulting offspring may exhibit enhanced salt tolerance. This strategy has been utilized in several crops, including rice and wheat, with successful results [43]. However, the application of this strategy to medicinal and aromatic plants is still in its early stages and demands further

Table 1. Role of PGPR on medicinal plants in amelioration of salt stress. PGPR refers to plant growth-promoting rhizobacteria

PGPR	Medicinal Plants	Effect	References
Bacillus megaterium	*Catharanthus roseus*	Plant growth, enhanced secondary metabolites content	[54]
Pseudomonas extremorientalis	*Silybum marianum*	Increased biomass	[55]
Azotobacter chrooccocum	*Catharanthus roseus*	Increased biomass	[54]
Pseudomonas putida	*Ocimum basilicum*	Increased biomass and secondary metabolites content	[56]
Bacillus lentus	*Ocimum basilicum*	Increased biomass	[56]
Exiguobacterium oxidotolerans	*Bacopa monnieri*	Increased herb yield and bacoside-A content	[57]
Bacillus pumilus	*Bacopa monnieri*	Plant weight, bacoside-A content	[57]
Bacillus coagulans	*Glycyrrhiza glabra*	Increased biomass and secondary metabolites content	[58]
Azospirillum brasilense and Pseudomonas fluorescens	*Catharanthus roseus*	Increased biomass and ajmalicine content	[54]
Halomonas desiderata	*Mentha arvensis*	Increased herb yield	[59]
Exiguobacterium oxidotolerans	*Mentha arvensis*	Increased herb yield	[59]

research. Genetic engineering is a powerful tool that can directly introduce genes conferring salt tolerance into plants. For instance, overexpression of the gene SOS1, a sodium ion transporter, has been shown to enhance salt tolerance in transgenic Arabidopsis plants [44]. Similarly, transgenic approaches have been used to overexpress genes involved in the synthesis of compatible solutes, such as proline and trehalose, resulting in improved salt tolerance [45]. However, the use of genetic engineering in medicinal and aromatic plants must be cautiously approached due to potential impacts on the production of secondary metabolites. Efficient irrigation management is a practical approach to mitigate salt stress. For instance, the use of fresh water for leaching can help to reduce salt accumulation in the root zone [46]. However, the availability of fresh water is often a limiting factor, especially in arid and semi-arid regions. Alternative strategies, such as the use of treated wastewater or partial root-zone irrigation, can also be employed to manage salt stress [47]. The use of salt-tolerant rootstocks can confer salt tolerance to the grafted scion, as demonstrated in citrus and grapevines [48]. Similarly, the concept of companion planting, where salt-tolerant plant species are grown alongside salt-sensitive medicinal and aromatic plants, can also help to alleviate salt stress. The salt-tolerant plants can absorb excess salts, reducing the overall salinity of the soil and creating a more favorable environment for the growth of medicinal and aromatic plants [49]. Mycorrhizal fungi form symbiotic relationships with plant roots and can enhance plant tolerance to salt stress. They improve nutrient uptake, water absorption, and also secrete compounds that mitigate salt stress [50]. Studies have shown that mycorrhizal inoculation can enhance the growth and productivity of various medicinal and aromatic plants under salt stress [51].

Certain soil bacteria, known as PGPR, can promote plant growth and enhance salt tolerance. These bacteria can produce plant growth-promoting substances, induce systemic resistance, and facilitate nutrient uptake [52]. Recent studies have highlighted the potential of PGPR in enhancing salt tolerance in medicinal and aromatic plants [53].

8. FUTURE DIRECTIONS AND POTENTIAL APPLICATIONS

The research on salt stress tolerance in medicinal and aromatic plants holds promising prospects for other crops, sustainable agriculture, and potential therapeutic applications. Below, we will delve deeper into these topics and elaborate on the future directions this research may take. The elucidation of salt stress tolerance mechanisms in medicinal and aromatic plants has implications beyond these specific plant groups. By understanding how these plants deal with salt stress, we can transfer this knowledge to improve salt stress tolerance in other crop plants [60]. For example, the genes identified in these plants responsible for osmotic adjustment, ion homeostasis, antioxidant production, and synthesis of compatible solutes could be potential targets for genetic engineering in other crops [61]. Similarly, the beneficial association between mycorrhizal fungi and plant growth-promoting rhizobacteria can be explored in other plant species [62]. The strategies identified to enhance salt stress tolerance in medicinal and aromatic plants hold significant potential for sustainable agriculture in saline soils. Given that soil salinity is a growing problem worldwide, these strategies could help increase crop productivity in affected areas [63]. For example, through selective breeding and genetic engineering, we could develop salt-tolerant plant varieties. These could be cultivated in saline soils, reducing the need for freshwater irrigation and mitigating the adverse environmental impact of conventional agriculture [64]. Moreover, the use of beneficial soil microbes could promote a more sustainable agriculture system by reducing the dependence on chemical fertilizers and pesticides [65]. Salt stress can induce changes in the biochemical composition of medicinal and aromatic plants, which can affect their therapeutic properties [66]. For instance, some studies have reported increased concentrations of essential oils and phenolic compounds – key contributors to the medicinal properties of these plants – under salt stress [67]. Understanding the influence of salt stress on the biosynthesis of these metabolites could enable us to manipulate growing conditions to maximize the production of desirable compounds. This offers exciting potential for the pharmaceutical industry, particularly in the production of natural health products [68].

9. CONCLUSION

The review provides comprehensive insights into salt stress tolerance in medicinal and aromatic plants. It covers the detrimental effects of salt stress, physiological, biochemical, and molecular responses to salt stress, and strategies for enhancing salt tolerance. The implications of this research extend beyond these plants, offering prospects for other crops, sustainable agriculture, and potential therapeutic applications. The possibility of using the knowledge in breeding salt-tolerant crops, adopting sustainable agricultural practices in saline soils, and leveraging changes in biochemical composition for therapeutic benefits are promising future directions. Continued exploration in this field is crucial for addressing soil salinity challenges and optimizing the benefits of medicinal and aromatic plants under such conditions.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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