Review *Plant Protection Science, 61, 2025 (2): 110–151*

https://doi.org/10.17221/83/2024-PPS

Sustainable medicinal plant production – responses of Lamiaceae plants to organic acid elicitors spraying during environmental stress: A review

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Citation: Shahhat I.M.A., Guetat A., Elsheikh Salma Y.S., Abdelwahab A.T., Abdelfattah M.A. (2025): Sustainable medicinal plant production – responses of Lamiaceae plants to organic acid elicitors spraying during environmental stress: A review. Plant Protect. Sci., 61: 110–151.

Abstract: This article provides a review of recent studies on the extent to which the use of organic acid elicitors such as salicylic, jasmonic, humic and ascorbic acids has been successful in alleviating the exposure of *Lamiaceae* plants to unfavourable environmental conditions such as drought and salinity. Overall, the results concluded all organic acid elicitors enhanced the morphological and physiological characteristics of biochemical and secondary metabolite contents. These improvements have enabled plants of the *Lamiaceae* family to adapt to environmental stress conditions to some extent and survive, thus achieving sustainability in the production of plants of this family. It can be recommended to use salicylic acid in concentrations 0.5–2.5 mM, and it should not exceed it so as not to cause poisoning and disruption of the vital and physiological processes within the plant. In contrast, these plants have limited studies on the relationship between jasmonic acid/ascorbic acid and ascorbic acid. Since vitamins such as ascorbic acid are essential for plant metabolism and growth regulation, their effect on these plants remains unstudied at concentrations 2–10 mM under different abiotic stresses. Further research is needed to understand the impact of Nano-SA, JA, HA, ASA, and citric acid on *Lamiaceae* plants under various environmental stress conditions. Limited studies exist on the relationship between jasmonate/humic acid and *Lamiaceae* plants under abiotic stress. The *Lamiaceae* family needs more studies on adaptation to various environmental conditions and the toxicity of stimulants used to confront these conditions. This research contributes to improving agricultural practices in challenging environmental regions.

Keywords: mint family; plant hormones; foliar application; secondary metabolites; stressors

Throughout history, human societies have relied on nature for food and medicine, utilizing medicinal plants as a common resource. Today, ensuring the safety and efficacy of herbal drugs is increasingly important through standardization and evaluation, with collaboration being crucial for preserving traditional knowledge (Jamshidi-Kia et al. 2017). Phytochemicals in plants are bioactive compounds

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Supported by the Deanship of Scientific Research at Northern Border University, Arar, KSA, for funding this research work through the project number "NBU-FFR-2025-860-01".

with significant pharmacological effects, including antioxidant, antibacterial, anti-inflammatory, and antiviral activities (Kaur et al. 2024). They include polyphenols, flavonoids, terpenoids, and alkaloids, which modulate immune responses and provide hepatoprotective benefits (Gupta 2023). They are considered natural and safe alternatives to antibiotics and immunoprophylactics due to their affordability and minimal side effects, providing benefits such as enhanced immunity and antibacterial protection (Van Hai 2015).

Lamiaceae, a large family of aromatic plants, is characterized by external glandular structures that produce essential oils utilized in cosmetics and medicine (García-Caparrós et al. 2019). Environmental stresses, whether abiotic or biotic, negatively affect the growth and yield of plants. Abiotic stressors, such as heavy metal contamination, salinity, soil pH, and drought, lead to issues including generating reactive oxygen species, membrane damage, and reduced photosynthesis. These factors impact crop growth through biochemical, physiological, and molecular processes, resulting in a productivity loss of over 50% (Rajput et al. 2021; Salam et al. 2023).

Plants develop various tolerance mechanisms, including membrane adjustments, maintenance of cell wall structure, and the production of secondary metabolites, antioxidants, and osmolytes. Secondary metabolites are crucial in helping plants cope with stress and function as a defence system. Climate changes can affect the concentration and transport of primary metabolites, precursors for secondary metabolites. Stressful conditions enhance the expression of genes involved in the biosynthesis of natural products. Secondary metabolites contribute to plant survival and defend against biotic stresses (Mahajan et al. 2020). Stressed plants produce diverse protective secondary metabolites, such as morphine and camptothecin, which exhibit anti-inflammatory and antioxidative properties. Terpenoids, alkaloids, and phenolic compounds represent the primary groups of secondary metabolites synthesized in response to abiotic stress, highlighting their potential for drug discovery (Yeshi et al. 2022). With the continuous growth of the global population and the escalating effects of climate change, there is an increasing need to develop and implement sustainable methods for biomass production to support a thriving and sustainable bioeconomy (Antar et al. 2021). Conservation strategies such as *in situ* and *ex situ* methods and effective resource management practices should be prioritized to ensure the sustainable use of medicinal plant resources. Biotechnological methods can enhance plant productivity, including tissue culture and molecular markers (Chen et al. 2016). Accurate nutrient control for horticultural crops presents a significant global challenge, as it primarily relies on chemical fertilizers. Conventional fertilizers can be costly for farmers and harm human health and the ecosystem. This has led to a growing demand for eco-friendly fertilizers, particularly those that demonstrate high efficiency in nutrient utilization.

Phytohormones, also known as plant development regulators, play a crucial role in sensing and signalling environmental conditions such as drought, osmotic stress, chilling injury, and heavy metal toxicity (Lymperopoulos et al. 2018). There are nine major classes of naturally occurring phytohormones, each eliciting distinct responses: auxins, gibberellins, cytokinins, abscisic acid, ethylene, brassinosteroids, jasmonic acid, salicylic acid, and strigolactones (Ali & Baek 2020). This review aims to highlight advancements in the role of foliar organic acids in supporting the production of Lamiaceae, an important family of medicinal plants, under environmental stressors 2015–2024.

METHODOLOGY

To achieve the objectives of this review, relevant keywords such as salicylic acid, citric acid, jasmonic acid and its derivatives, humic acid, ascorbic acid, folic acid, nicotinic acid, secondary metabolites, abiotic stress, and organic elicitors were employed in pertinent research articles. This review examines peer-reviewed papers published 2015–2024. Reputable databases, including Web of Science, Scopus, ScienceDirect, PubMed, and Google Scholar, were utilized to gather articles published during this period. Three interrelated keywords were entered into the databases, focusing on environmental abiotic stressors associated with the Lamiaceae family treated with organic acids. Each research paper was meticulously examined to ensure it included results regarding the impact of one of the aforementioned organic acids on the physiological, biochemical, and secondary metabolites in plants from the Lamiaceae family, particularly under various stress factors such as low salinity, drought, extreme temperatures, and others. Research papers that did not meet these criteria were excluded from the study. The results of each study were summarized and organized into tables, and they were also discussed in various sections of this review article.

Lamiaceae. The Lamiaceae family (Figure 1) is distinguished by several unique characteristics contributing to its taxonomic complexity and economic significance. This family is notable for its diverse morphological, anatomical, and chemical traits, which have implications for taxonomy, medicine, and ecology. It includes approximately 236 different genera and 6 900–7 200 species. *Salvia* is one of the most abundant genera, with around 900 species, followed by *Scutellaria* with 360 species, *Stachys* with 300 species, *Plectranthus* with 300 species, *Hyptis* with 280 species, *Teucrium* with 250 species, *Vitex* with 250 species, *Thymus* with 220 species, and *Nepeta* with 200 species (Ebadollahi et al. 2020; Karpiński 2020). The Lamiaceae family exhibits a variety of inflorescence types, including heteroblastic inflorescences, which host both cleistogamous (closed) and chasmogamous (open) flowers. This phenoplasticity is significant for adaptation and survival in diverse environments. Different flower morphs within a species can lead to variations in pollen fertility, nutlet productivity, and seed viability, which are crucial for understanding reproductive strategies (Amer et al. 2023). Lamiaceae species typically have leaves arranged in a verticillate (whorled) pattern. The leaves are often aromatic due to essential oils (Çatak & Atalay 2022). The stems are frequently quadrangular, a distinctive feature of this family. Additionally, the presence of glandular and non-glandular trichomes is notable. Glandular trichomes are involved in the secretion of essential oils, while non-glandular trichomes vary in form, including unicellular, multicellular, and stellate types (Shukla et al. 2024).

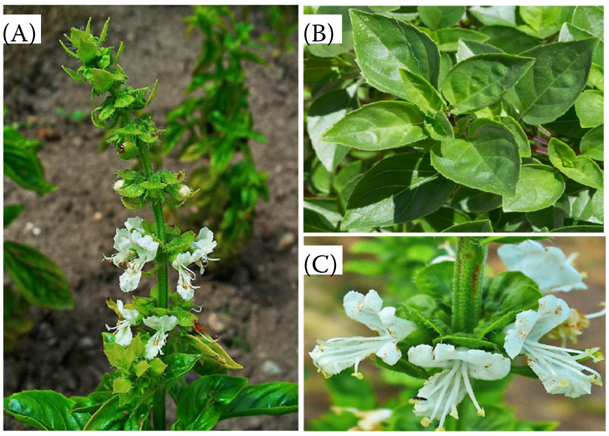

Figure 1. *Ocimum basilicum* as an example of *Lamiaceae* family

A – plant stem; B – leaves; C – flowers

Source: https://es.m.wikipedia.org/wiki/Archivo

Essential oils from the Lamiaceae family are primarily composed of monoterpenes (e.g., limonene, menthol) and sesquiterpenes (e.g., caryophyllene, germacrene) (Isnaini et al. 2024). Studies have identified a wide range of chemical constituents in Lamiaceae essential oils, with significant variations in composition across different species (Sun et al. 2022). Due to their bioactive compounds, species within the Lamiaceae family are utilized in traditional medicine for treating cardiovascular diseases and other health conditions (Patrignani et al. 2021). Lamiaceae plants, rich in non-volatile compounds like iridoids and phenylethanoid glycosides, have medicinal properties (Gamoun & Louhaichi 2024) and have been linked to anti-cancer activities, particularly in modulating apoptosis in human leukaemia cells, indicating potential in chemoprevention and adjuvant cancer therapy. The presence of polyphenolic compounds like rosmarinic acid and caffeic acid further enhances the therapeutic potential of these plants, offering benefits such as enhanced pro-apoptotic effects in cancer cells (Berdowska et al. 2022). While the Lamiaceae family is celebrated for its unique characteristics, polyploidy is a significant factor in the genetic diversity of plants, particularly in the Lamiaceae family. It introduces new genetic material through whole-genome duplication, leading to novel traits and increased variation within species (Wakachaure & Ganguly 2016; D'Agostino & Fasano 2024). Like Ocimum species, polyploid plants have different chromosome numbers and pairing patterns, contributing to intraspecific and interspecific variation (Idowu & Oziegbe 2017). Polyploid plants also create reproductive barriers, promoting the emergence of new species (Scarpino et al. 2014; Mayrose et al. 2010). They also exhibit enhanced adaptability to environmental stresses due to multiple alleles at a locus, leading to unique gene regulations and increased tolerance to abiotic and biotic stresses (Van Hieu 2019). In Lamiaceae, polyploidy can lead to changes in morphology and physiology, such as increased organ size and altered metabolic products, which can enhance the plant's ability to thrive in diverse habitats (Kazi et al. 2015). This genetic plasticity enables rapid adaptation to changing environments, contributing to the ecological success of polyploid species such as Lamiaceae (Yang et al. 2011; Ortiz Ríos 2015).

ABIOTIC ENVIRONMENTAL STRESSES

Drought, salinity, extreme temperatures, heavy metals, chemical pollutants, nutritional deficiencies, and oxidative stress are significant environmental constraints that adversely affect plant development and growth. These factors disrupt various plant processes, jeopardizing crop production. Specifically, they negatively influence developmental, morphological, physiological, biochemical, and molecular processes (Zhang et al. 2022a). Abiotic stresses, such as salinity, drought, cold, and heat, threaten staple food crops, reducing survival rates, biomass production, and overall yield. The Food and Agriculture Organization (FAO) estimates that over 6% of land worldwide is affected by salinity, a major constraint on crop productivity (Parihar et al. 2015). Salinity poses a significant challenge to crop productivity, as elevated salt levels in the soil adversely affect most plants. This situation leads to substantial yield losses as more land becomes affected. Drought and salinity are critical factors restricting crop yields to only 20–50% of their potential. These challenges are anticipated to intensify due to climate change (Shrivastava & Kumar 2015).

The impact of salinity on plant growth and land use is significant, particularly as the population increases and agricultural land diminishes. Utilizing salt-affected land is essential for food production; however, excessive salt can impede plant growth and productivity, affecting critical physiological processes (Safdar et al. 2019). Assessing seedling survival or shoot Na^+ levels in isolation may not yield a comprehensive understanding of salinity tolerance unless overall growth parameters are considered (Negrão et al. 2017).

THE IMPACT OF ABIOTIC ENVIRONMENTAL STRESSES ON PLANTS

When plants are exposed to abiotic stress, they experience negative physiological effects. These negative impacts are summarized in Figure 2 (redrawn with some modifications based on El-Saadony et al. 2022). Plants face various abiotic stresses that lead to evolutionary changes in their defence mechanisms and metabolic functions. These challenges impede agricultural advancement and productivity. To adapt to environmental stresses, plants trigger physiological, metabolic, and molecular responses, reduce water loss through stomata, and produce osmolytes and antioxidants to survive conditions, such as oxidative damage by reactive oxygen species (ROS) (Arbona et al. 2017).

To endure harsh conditions, plants respond to various environmental stressors by altering gene expression, physiology, structure, and metabolism. These responses are complex and influenced by multiple stress factors, including duration, intensity, genotype, combinations of stressors, tissue types, and developmental stages (Mareri et al. 2022). Salinity presents a significant challenge to agricultural systems, as it disrupts water uptake, cellular ion equilibrium, and osmotic balance, leading to ion toxicity and the accumulation of reactive oxygen species (ROS) (Ahmed et al. 2021). Drought negatively impacts the growth of medicinal plants and their production of secondary metabolites, which are rich in phytochemical compounds. Reduced water availability results in smaller plants with altered structures and chemical compositions. Under stress, plants produce higher alkaloids, tannins, and terpenoids, while phenols, flavonoids, and saponins decrease. Moderate drought conditions can enhance the synthesis of secondary metabolites (Shil & Dewanjee 2022). The production of these secondary metabolites is considered a plant's adaptive response to significant stressors (Kulak 2020).

Plants utilize various mechanisms to sense abiotic stress, including physical sensing, biophysical sensing, metabolic sensing, biochemical sensing, and epigenetic sensing. Physical sensing refers to the mechanical effects of stress on plant or cellular structures, such as the contraction of the plasma membrane during drought conditions. Biophysical sensing involves alterations in protein structure or enzymatic activity, exemplified by inhibiting enzymes during heat stress. Metabolic sensing detects the accumulation of by-products resulting from the uncoupling of electron transfer or enzymatic reactions, such as the accumulation of ROS due to high light intensity. Biochemical sensing encompasses specialized proteins that detect specific

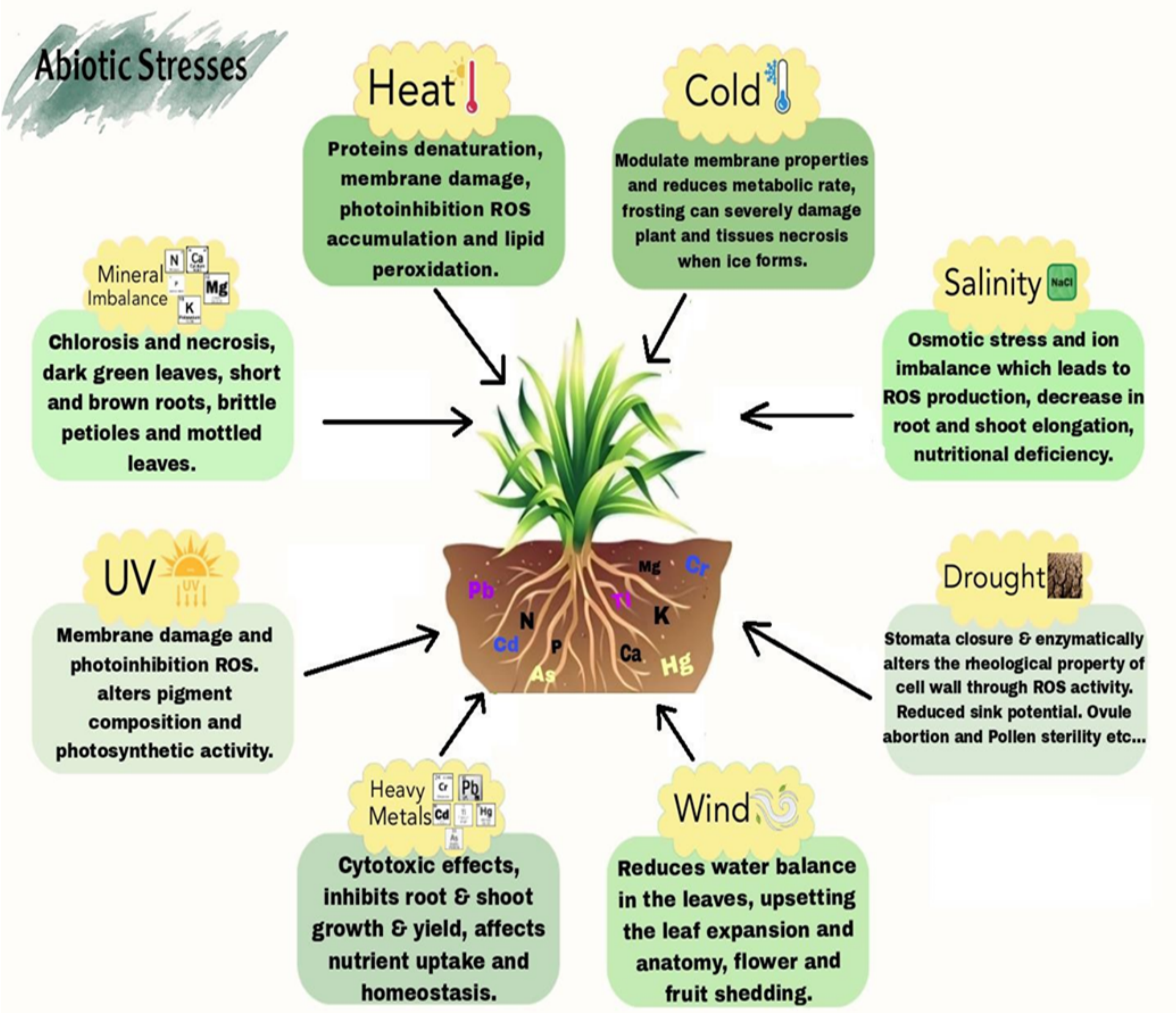

Figure 2. Negative physiological and biochemical effects of various abiotic stresses on plants
Redrawn with some modifications based on El-Saadony et al. (2022)

stresses, such as calcium channels that can disrupt Ca^{2+} homeostasis and respond to temperature changes. In contrast, epigenetic sensing involves modifying DNA or RNA structures without altering the underlying genetic sequences (Hamant & Haswell 2017).

Plants respond to abiotic stressors through signal integration and adaptive responses. Plants perceive stress signals through primary receptors, which may be embedded in their plasma membrane. The broad processes by which plants sense environmental stressors, transduce their signals, and, in a complex and finely coordinated response, combine stress signals, hormone metabolism as ABA (abscisic acid), and adaptive responses that lead to tolerance. Overall, stressors are detected by receptors or membrane-associated proteins, resulting in an ionic imbalance across the membrane and an influx of Ca^{2+} into the cytoplasm. The Sudden rise in Ca^{2+} concentrations in the cytosol initiates a signalling cascade driven by calcium-dependent proteins and kinases, culminating in transcription factor activation, which modifies gene expression associated with plant physiology remodelling (Fu et al. 2020).

EFFECT OF ABIOTIC ENVIRONMENTAL STRESSES ON LAMIACEAE PLANTS

Abiotic stressors, such as drought, salinity, temperature extremes, and heavy metal exposure, significantly impact the growth and development of Lamiaceae plants. These stress factors influence these plants' physiological and biochemical processes, re-

https://doi.org/10.17221/83/2024-PPS

sulting in osmotic stress, ion toxicity, and a reduction in overall growth while concurrently promoting the production of secondary metabolites (Nazari et al. 2023). Notably, drought stress has been shown to increase the percentage of essential oils and stimulate the synthesis of secondary metabolites, including terpenes, which are crucial for plant adaptation and survival in water-limited environments (Sharafzadeh & Zare 2011). For instance, *Salvia* splendens exhibits reversible inactivation of photosystem II under heat stress, accompanied by an increase in antioxidative enzyme activity to mitigate oxidative damage (Liu et al. 2013). In *Origanum* species, temperature variations affect the levels of thymol and carvacrol, with thymol concentrations rising at lower temperatures and carvacrol levels increasing at higher temperatures (Novak et al. 2010). Similarly, *Mentha piperita* demonstrates enhanced accumulation of secondary metabolites, including tannins and terpenoids, when subjected to combined heat and drought stress (Alhaithloul et al. 2019). Under both cold and heat stress conditions, basil has been observed to exhibit increased activity of catalase (CAT), superoxide dismutase (SOD), and peroxidases (POX), which are essential for detoxifying reactive oxygen species (ROS) and maintaining cellular homeostasis (Jakovljević et al. 2021; Mir & Khah 2024). The exposure of Lamiaceae plants to heavy metals can disrupt their normal growth and development by interfering with physiological and biochemical pathways. However, these stressors may also stimulate the production of secondary metabolites, which can provide protective roles against oxidative stress (Mansinhos et al. 2024). For example, *Melissa officinalis* plants subjected to drought stress exhibited a decrease in both root and shoot dry weight (Eshaghi et al. 2022). Drought stress has also been shown to significantly reduce the growth of Satureja hortensis, as evidenced by plant height measurements and fresh shoot weight (Rasouli et al. 2023). *Lavandula latifolia* and *Salvia sclarea* significantly reduce fresh weight and essential oil content under drought conditions (García-Caparrós et al. 2019). Abiotic stress often catalyzes the production of secondary metabolites in Lamiaceae plants. For instance, drought and salinity stress can elevate the concentration of essential oils and phenolic compounds, thereby enhancing their biological activities, such as antioxidant and antibacterial properties (Sharafzadeh & Zare 2011; Mansinhos et al. 2024). Furthermore, abiotic stress increases the production of ROS, leading to oxidative stress, and enhancing the plants' antioxidant defence systems, including enzymes such as catalase and peroxidase, to mitigate damage (Alshammari et al. 2024).

Salinity and heavy metal exposure elicit stress responses that enhance the biosynthesis of secondary metabolites via pathways such as the shikimic acid pathway (Samal et al. 2023). These stressors may result in the accumulation of bioactive compounds, which possess considerable pharmacological and nutraceutical advantages (Toscano et al. 2019). Lamiaceae plants have developed a range of adaptive mechanisms to mitigate abiotic stress, which includes the accumulation of osmolytes, the production of antioxidants, and the enhancement of secondary metabolite synthesis (Nazari et al. 2023).

The role of secondary metabolites in helping medicinal plants cope with abiotic stresses is of considerable importance. Secondary metabolites (SMs) in plants are essential for ecosystem functioning, defence mechanisms, and inter-plant communication, thereby mitigating damage from environmental stressors and addressing various abiotic challenges. Environmental stresses significantly hinder plant growth on a global scale, adversely affecting critical metabolic processes such as water uptake, mineral assimilation, germination, root development, photosynthesis, respiration, and protein synthesis, primarily due to elevated levels of harmful reactive oxygen species (Alnusaire et al. 2022). Secondary metabolites serve multiple functions and roles that enable plants to sustain their vitality. Furthermore, SMs are integral to the plant defence system and facilitate interactions between plants and their surrounding environment (Assaf et al. 2022; Chen et al. 2022). Elicitors play a significant role in regulating biosynthesis through various metabolic pathways, with abiotic and biotic factors influencing the elicitation process and enhancing metabolite production. Abiotic factors, such as temperature and biotic factors, including fungi, are essential for developing improved strategies for producing secondary metabolites (Humbal & Pathak 2023). Notably, moderate salt stress has been shown to increase the levels of secondary metabolites in species belonging to the Lamiaceae family. Furthermore, optimal concentrations of plant growth regulators (PGRs) can significantly enhance the accumulation of metabolites. The combined effects of PGRs have proven effective, although their impact depends on factors such as concentration, application method, and the specific plant species involved. Salicylic acid serves as a pertinent example of a PGR (Assaf et al. 2022).

LAMIACEAE IN RESPONSE TO ORGANIC ACID ELICITORS UNDER ENVIRONMENTAL STRESS CONDITIONS

Elicitors, which are chemical compounds, induce stress responses in plants, leading to increased production of secondary metabolites. Various factors, including the type of elicitor, dosage, and treatment frequency, influence elicitors' effectiveness. The successful accumulation of biomass and metabolites in plants is contingent upon several parameters, such as concentration, cell line, exposure duration, culture age, and nutrient availability (Naik & Al-Khayri 2016). Elicitors represent a category of molecules that enhance multiple defence mechanisms in plants (Jamiołkowska 2020). These stimuli can originate from diverse sources, including living organisms, abiotic components, and environmental factors, all of which can accelerate the production of secondary metabolites in plants (Bharti et al. 2023). In plant physiology, numerous elicitors play a crucial role in stress tolerance mechanisms, generating many secondary metabolites and enhancing resilience to both abiotic and biotic stresses (Rani et al. 2023).

Nutrient sprays have been demonstrated to enhance crop yields and improve resistance to pests, diseases, and drought conditions. This technique is particularly beneficial for cultivating aromatic and medicinal plants within sustainable agriculture and horticulture (Shahrajabian et al. 2022). Furthermore, the excessive use of chemical fertilizers in agricultural practices can result in diminished efficiency and soil-related issues, such as acidification and salinization. Following soil treatment, foliar fertilisers have been shown to increase crop yields and elevate trace element concentrations; however, inorganic fertilizers may impede nutrient absorption (Niu et al. 2021). Foliar treatments allow for the uptake of nutrients through water-based solutions, facilitating the direct transport of these nutrients to various parts of the plant. Additionally, foliar applications can assist in managing adverse environmental conditions, including heat, cold, frost, drought, and salinity, through the utilization of growth regulators, stimulants, or biostimulants (Gao et al. 2018; Godoy et al. 2021).

SALICYLIC ACID

Salicylic acid (SA) is a crucial phytohormone in plants, initially identified in Salix species, and is found in plants either as free phenolic acids or in association with amino compounds. It plays a significant role in plant defence mechanisms, growth regulation, and stress responses. SA is synthesized through two main pathways: the phenylpropanoid pathway and the isochorismate synthase pathway, and it exists in various forms, including free SA and conjugated forms like glycosylated, methylated, and glucose-ester derivatives (Janda et al. 2021; Özden & Kulak 2023). As a natural phenolic signalling molecule, SA modulates the expression of genes and transcription factors involved in stress response pathways, thereby enhancing plant resilience (Devi et al. 2023; Song et al. 2023; Kashif et al. 2024). The salicylic acid signalling pathway (Figure 3) can be elucidated through two scenarios. In the first scenario, under normal cellular conditions (absence of stress), plant cells synthesize low levels of salicylic acid (SA). In this state, NPR1 forms oligomers and remains localized in the cytosol, while NPR3 and NPR4 bind to residual NPR1 in the nucleus, thereby inhibiting the functional activity of NPR1. The complexes containing NPR3 and NPR4 suppress transcription, whereas NPR1 complexes exhibit minimal activity, resulting in an overall low expression of defence-related genes. In the second scenario, SA production increases when plant cells are subjected to stress. This phenomenon results in a biphasic modification of the cellular reduction potential of NPR1, leading to its reduction to a monomeric form (Vidhyasekaran 2015; Mou et al. 2003). Following this process, NPR1 translocates to the nucleus, while the complexes formed by NPR3 and NPR4 are rendered inactive. In this context, SA binds to NPR3 and NPR4, effectively blocking their transcriptional repression activity. Consequently, NPR1 functions as a transcriptional co-activator, whereas NPR3 and NPR4 serve as E3 ligases that facilitate the degradation of NPR1. The inhibition of NPR3 and NPR4 activities by SA promotes the expression of immune regulators (Ali et al. 2018; Ding et al. 2018). Furthermore, NPR1

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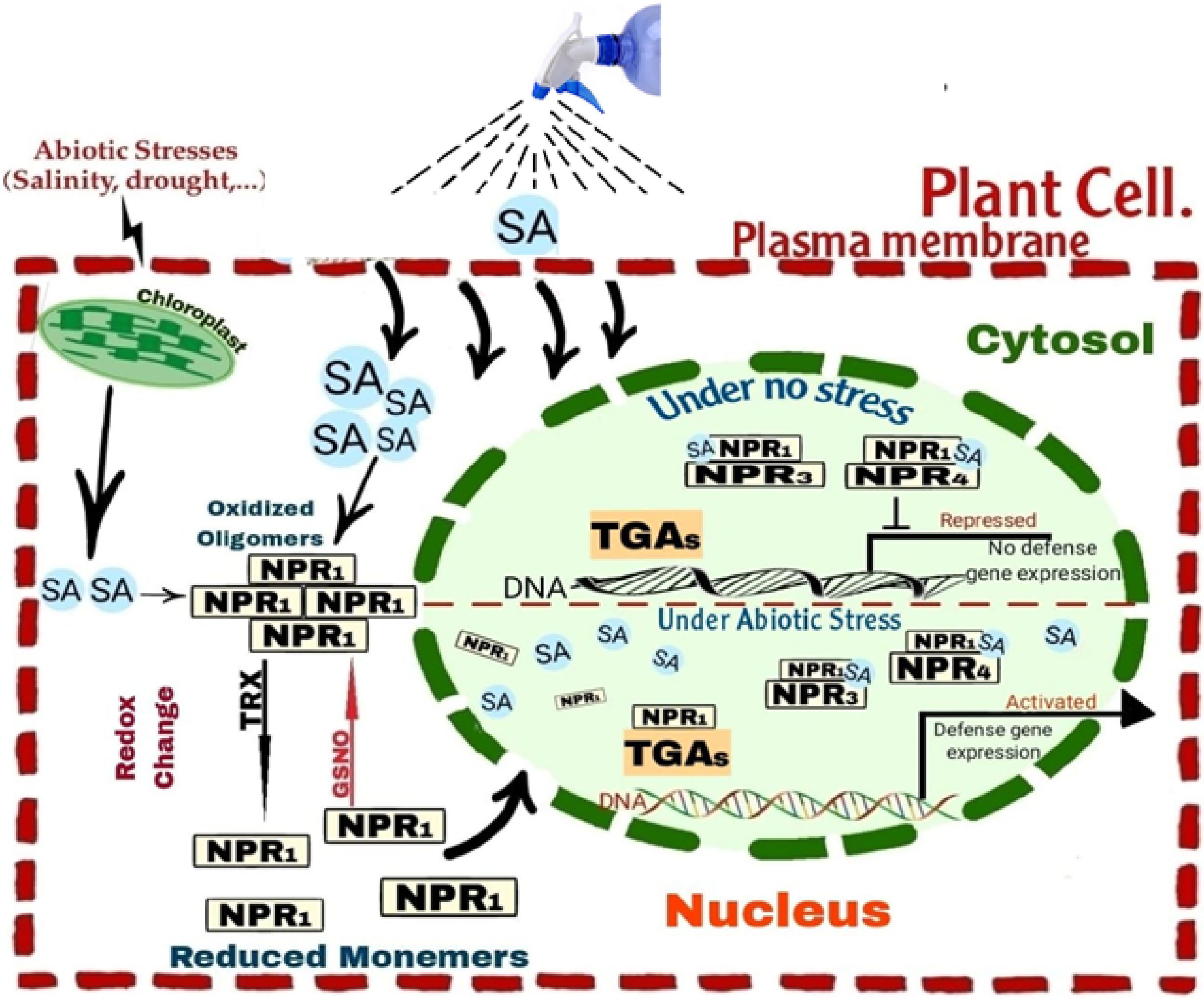

Figure 3. The signaling pathway of exogenous salicylic acid (SA) in response to abiotic stress
NPR1, NPR3, NPR4 – non-expresser of pathogenesis-related genes; TRX – thioredoxin, GSNO – S-nitrosoglutathione; TGAs – TGACG-binding factor, DNA – deoxyribonucleic acid

interacts with TGA proteins at SA-responsive promoters, leading to elevated levels of defence gene expression (Innes 2018; Li et al. 2019).

Table 1 presents the analyzed and summarized results of various recent studies conducted on species within the Lamiaceae family, specifically focusing on the effects of salicylic acid application on the potential resistance of these plants to abiotic environmental stresses.

Applying salicylic acid (SA) on *Hyssopus officinalis* has significantly enhanced various physiological and biochemical parameters in plants. Specifically, SA treatment has increased dry weights, chlorophyll content, and proline levels, indicating improved stress tolerance and metabolic activity. Furthermore, SA has been linked to a substantial increase in essential oil content and its major constituents. Proline levels increased, enhancing osmotic adjustment and stress tolerance (Fouad et al. 2023). SA improves the uptake of essential nutrients like nitrogen, phosphorus, and potassium, which are crucial for plant growth (Sharma et al. 2023).

Mentha piperita plants respond to all salicylic acid doses without toxicity (Table 1). However, high levels can cause burning and drying at mature leaves' edges due to elevated salicylic acid concentrations. This can increase lipid peroxidation and membrane permeability, causing burn symptoms. Under drought stress, salicylic acid can amplify symptoms by increasing reactive oxygen species production, escalating oxidative damage to plant tissues (Abdi & Karami 2020). Salicylic acid can significantly affect Mentha piperita plant growth and development in saline environments.

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Table 1. Reaction of Lamiaceae to spraying of Salcylic acid (SA) under environmental stresses

Genus	**Species**	**Stress**	**Salcylic acid dose**	**Physiological and biochemical characters**	**Secondary metabolites**	**Effect**	**Reference**
Dracocephalum	*D. moldavic*a	Drought stress (normal irrigation, moderate drought, and severe drought)	1 mM	Chlorophylls and carotenoids, plant biomass relative water content (RWC), Leaf proline content, total soluble sugars, catalase (CAT), peroxidase (POX) and superoxide dismutase (SOD)	Essential oil (EO) %, oil compositions	• SA significantly increased leaf Chl-*a* concentration in all irrigation regimes, with moderate water stress resulting in the highest Chl-*b* concentration (1.17 mg chl-b/g FW). Achieved a 30% higher carotenoid concentration than the water-sprayed control plants. • The leaf TSS content increased by 18% in SA under severe drought. • SA-treated plants under severe drought had higher SOD activities (3.08 Unit mg/g×min), POX activity (2.14 Unit mg/g×min) and CAT activity (2.14 Unit mg/g×min) than control. • Under severe drought, SA increased biomass yield by 18.95 relative to the water-sprayed control plants. • Under moderate drought, SA, increased EO contents by 11.81%, relative to the water-sprayed control plants. • Spraying SA significantly improved chlorophyll, the EO yield by 41.90% and the main essential oil components, including geranial, neral, geranyl acetate and geraniol.	Rezaei-Chiyaneh et al. (2021)
Hyssopus	*H. officinalis*	Drought stress (irrigation at 100 FC, 75–80% FC and at 40-45% FC)	0.0 and 1 mM	Vegetative growth period and the plant height, canopy diameter, number of inflorescences, wet and dry weights and the chlorophyll and proline contents	Essential oil %, oil compositions	• Applying SA enhanced dry weights by 20%. There is a significant increase in chlorophyll *a* and *b* and proline by 31.49, 31.01 and 20.07%, respectively. • Spraying of SA increased essential oil content by about 60.90% and enhanced major constituents like cis- pinocamphene, β-pinene, trans-pinocamphene, *a*-Pinene, and myrtenol by 39.84, 17.39, 14.21, 46.32, 16.11%, respectively.	Danesh-Shahraki et al. (2023)
Mentha	*M. piperit*a	Drought stress [no stress [100% field capacity (FC), 75% FC and 50% FC]	0, 1, 2 and 2.5 mM	Growth (fresh and dry weights of aerial parts and dry leaf weight), membrane permeability, lipid peroxidation, Proline content and ROS scavenger enzymes	Total phenolic content, the flavonoid and essential oil content	• Increasing SA concentration up to 2.5 mM significantly improved plant growth and development without toxic effects. However, the high concentration of SA caused the burning and drying of the edge of some mature leaves in plants. The highest growth values as dry weight of areal parts (increased by 5.79% over control) were treated with only 2 mM of SA. • Plants treated with 2.0 and 2.5 mM of SA showed a significant increase in oil content, reaching 19.06 and 24.43% over No SA, respectively, under moderate water stress (75% FC). While the increased SA under normal conditions (100% FC) reduced oil content. Plants treated with 2.5 mM SA at drought 75% FC showed a reduction in membrane permeability of 37.86%, while those treated with 1.0 mM and drought (50% FC) showed 52.30%. • SA enhanced plant tolerance to water deficiency by decreasing lipid peroxidation and membrane permeability, enhancing antioxidant enzyme activity, and raising essential oil and phenolic content.	Abdi and Karami (2020)

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Table 1. to be continued...

Origanum	*O. vulgare*	Heat (23/12 °C as control and 27/16 °C heat stress in greenhouse)	1 mM	Growth (total fresh and dry weights), photosynthetic pigments (chlorophyll and carotenoids), antioxidant enzymes activities (peroxidase (POD) activity, superoxide dismutase (SOD) activity), oxidative stress indicators (H2O2) levels	Composition of essential oil, total phenol, flavonoids	• Studied traits differed significantly at 27 °C compared to 23 °C in control and stressed plants. • The highest amount of thymol and carvacrol was at 27 °C. Carvacrol levels also increased at 27 °C. • SA treatment at 27 °C increased SOD (11%), total phenol (44%), and H_2O_2 (9%). At 23 °C, this increased peroxidase activity (69%) and carotenoid levels (22%). • SA spraying at 23 °C increased POD (69%) and carotenoid levels (22%). • SA spraying at 23 °C significantly increased thymol methyl ether (93%) and carvacrol methyl ether (7%) and elevated carvacrol levels at 27 °C.	Garoosi et al. (2023)
Origanum	*O. vulgare*	Salinity stress [NaCl (0 and 100 mM)]	1 mM	Growth (total fresh and dry weights), photosynthetic pigments (chlorophyll and carotenoids), antioxidant enzymes activities (peroxidase (POD) activity, superoxide dismutase (SOD) activity), oxidative stress indicators (H_2O_2) levels	Composition of essential oil, total phenol, flavonoids	• SA treatment under salt conditions showed less damage to membrane stability, and H_2O_2 levels increased POD, carotenoids, and flavonoids. • Plants exposed to 100 mM NaCl and treated with SA significantly reduced secondary metabolites, while SA treatment increased flavonoid production. • Spraying of SA to Plants exposed to 100 mM NaCl resulted in increased peroxidase and polyphenol oxidase activities, carotenoids, chlorophyll content, and plant dry weight, but no change in superoxide dismutase activity, carvacrol methyl ether, thymol methyl ether, and total phenol content.	Garoosi et al. (2023)
Ocimum	*O. basilicum*	Drought stress (water deficit)	200 ppm (1.448 mM)	Plant growth (shoot fresh weight, dry weight, and plant height), photosynthetic pigments Chl-*a* and Chl-*b*, and leaf water content (RWC)	Not reported	• SA sprays increased plant weight and height as well as boosted RWC. • SA exhibited higher Mean Productivity index (10.71–13.48) and Harmonic Mean index (9.60–13.23) than non-treated plants. • SA enhanced plant growth parameters, photosynthetic pigments, and RWC under water deficit conditions.	Damalas (2019)
Mentha	*Mentha × piperita*	Salinity stress (0, 50, 100 or 150 mM NaCl)	10^{-6} M	Plant growth (shoot and root length, leaf number, leaf area, shoot and root fresh weight and shoot and root dry weight), photosynthesis, carbonic anhydrase (CA) activity, NPK content, peltate glandular trichome (PGT), increased catalase (CAT), peroxidase (POX) and superoxide dismutase (SOD)and proline content	Essential oil (EO) % and menthol content	• The SA spray significantly improved shoot fresh weight per plant by 46.05%, enhanced CAT activity by 31.46%, increased EO content by 80.00%, EO yield by 154.55%, menthol content by 53.84%, and PGT density by 95.05% compared to the water-sprayed control. NaCl × SA was the best for EO content and PGT density. • At 150 mM NaCl × SA increased CAT, POX, SOD and proline content.	Khanam and Mohammad (2018)

Table 1. to be continued...

Thymus	*Thymbr*a	*Salvia*	*Salvia*
T. vulgaris & T. kotschyanus	*T. spicat*a	*S. officinalis*	*S. ofcinalis*
Drought stress (well-watered and water stress conditions)	Drought stress [80–85 % field capacity (FC) 60–65 % FC and 40-45 % FC]	Salinity stress (NaCl) 150 mM	Zn (40 mM)
0, 100, and 150 ppm (0.0, 0.724, and 1.086 mM)	0.0, 2.5 and 5.0 mM	0.5 and 1 mM	0.0, 0.5 and 1 mM
Plant growth, root and shoot dry weight, chlorophyll, carotenoids, H_2O_2, proline, malondialdehyde (MDA), and total soluble carbohydrate	Not measured	Plant growth (lengths of the aerial and root parts), Na, K, P, Ca contents, total chlorophyll content	Growth (aerial and root length), chlorophyll, Zn, Ca, K and P
Essential oil % & oil composition	Essential oil % & oil components	Essential oil yield, oil compositions	Essential oil content %
• *T. vulgaris* (Urmia and Ghazvin ecotypes) and *T. kotschyanus* (Zanjan) showed significantly higher shoot and root dry weight increases than other ecotypes, with the highest dry weights obtained with 1.086 mM of SA treatment. • SA elevated levels of chlorophyll, leaf carotenoids, proline, and soluble carbohydrates. • SA at 0.724 mM significantly increased essential oils, compositions, and thymol content in *T. kotschyanus* (Zanjan ecotype) by 93.39% under well-watered and water-stress conditions. • Thymol, carvacrol, linalool, *p*-cymene, and γ-terpinene were identified as the main components of essential oils under employed treatments. • The content of cellular damage indicators, including H_2O_2 and MDA was significantly reduced with SA.	• Spraying SA at 2.5 and 5.0 mM significantly increased the essential oil yield by 32% and 48% over control. • Carvacrol, the main component of the essential oil (48.40–79.1%), γ-terpinene (7.27–25.62%), limonene (3.62–10.35%), p-cymene (1.69–6.44%), and β-caryophyllene (1–1.5%) were among the five main chemicals found in the essential oil of *T. spicata* L. • SA at 2.5 mM under drought gave the highest carvacrol content (78%) without affecting other major compounds like γ-terpinene, limonene, p-cymene, and β-caryophyllene.	• Spraying SA at 0.5 mM improved growth, reaching almost 269% for the stem and 88% for the root compared to stressed plants untreated with SA and increased chlorophyll content mainly at 0.5 mM by 79% compared to control. • SA at 0.5 mM significantly increased plant mineral element levels, reaching 64% for Ca, 102% for K, 95% for P in leaves, 143% for Ca, 108% for K, and 81% for P in roots. • SA at 0.5 mM greatly improved essential oils by 112%, SA significantly increased hydrocarbon monoterpenes and oxygenated monoterpenes compared to control plants. At 0.5 mM, major compounds like camphor, α-thujone, thujanone, and 1,8-cineol were increased. At 1 mM, the camphor content increased from 10.00 to 24.62%, α-thujone from 20.20 to 27.58%, and 1,8-cineol from 10.00 to 14.14%. SA at 1 mM significantly increased the camphor content from 10.00 to 24.62%, α-thujone from 20.20 to 27.58%, and 1,8-cineol from 10.00 to 14.14%.	• SA on stressed plants increased aerial and root length at concentrations 1 and 0.5 mM, with 0.5 mM showing the most significant increase, reaching 50% for the aerial part. • SA at 0.5 mM significantly improved chlorophyll synthesis by 501% compared to stressed plants untreated with SA. • SA significantly reduced Zn in roots and its transfer to shoots, especially at 0.5 mM, compared to stressed plants without SA. • SA increased absorption of mineral elements in both leaves and roots, reaching 58% for Ca, 19% for K, 131% for P, 44.54% for Ca, 303% for K, and 59% for P. • Spraying SA on stressed plants increased essential oil yield by 425% at 0.5 mM and 250% at 1 mM compared to stressed plants without SA treatment.
Mohammadi et al. (2019)	Momeni et al. (2020)	Es-Sbihi et al. (2021)	Es-Sbihi et al. (2020)

Table 1. to be continued...

Thymus	*T. vulgaris*	Drought stress: 100%, 75%, 50% and 25% field capacity	0, 1, 2 and 3 mM	Plant growth (height, fresh and dry) weights of plant & antioxidant activity	Total polyphenols content (TPC), total flavonoids content (TFC), essential oil % & oil composition	• SA significantly impacted plant height and weights up to 2 mM, but at 3 mM, it failed to mitigate the negative impact. • With 3mM SA under drought-stressed plants, it gave the highest TPC, reaching 68.5 ± 1.2 mg gallic acid equivalent/gm dry weight compared to 8.5 ± 0.3 mg in control plants. • TFC in drought-stressed plants increased from 6.1 ± 0.3 mg rutin equivalent/gm dry weight in control plants to 32.1 ± 0.1 mg/gm dry weight when sprayed with 3 mM SA. • IC50 decreased by 50.81% in drought-stressed plants (25% FC) sprayed with 3 mM SA. • 2 mM SA in drought-stressed plants (25% FC) gave the highest oil yield (1 ± 0.06 % v/w). • SA at 1 mM under drought stress gave the highest trans-Sabinene hydrate, trans-Geraniol, carvacrol and α-Bisabolene but at 2mM SA the highest were p-Cymene, Camphor, and β-Caryophyllene. • Rosmarinic acid is a major component (25% FC) sprayed with 3mM SA. • Thymol and p-cymene content changes were observed due to drought stress and SA spraying.	Khalil et al. (2018)
Thymus	*T. vulgaris*	Drought stress (well-watered 80% FC and withholding irrigation)	0, 100, 150 and 200 mg/L (0.0, 0.724, 1.086 and 1.448 mM)	Growth (total dry matter)	Total phenols content, essential oil %, oil compounds	• Spraying 1.448 mM SA, the highest dry matter under withholding irrigation. • The highest oil % (2.66%) was achieved with 0.724 mM SA under water stress (withholding irrigation). • SA at 1.448 mM with water stress gave a 58% higher total phenol content (TPC) of 18.431 mg GAE/g DW than control. • The main compounds identified were thymol, carvacrol, p-cymene, linalool, and γ-terpinene. • The highest thymol content was obtained by foliar application of 1.448 mM SA under withholding irrigation. • SA and withholding irrigation decreased the amount of γ-terpinene compound.	Mohammadi et al. (2020)

Under salinity stress, applying salsylic acid (SA) significantly improved growth parameters in *Mentha × piperita*, resulting in a 48.26% increase in shoot dry weight per plant (Table 1). This was due to the hybrid nature of *Mentha aquatica* and *Mentha spicata*, which combines traits from both species (Lin et al. 2022). SA's allelopathic properties can influence other plants' growth, potentially benefiting agricultural systems (Preusche et al. 2022). It also has specific agricultural characteristics, such as high essential oil yield and menthol content, influenced by organic fertilizers (Can & Katar 2021). In *Mentha pulegium*, SA improved its essential oil content and introduced new constituents under salt stress, suggesting that SA modulates the biosynthesis of essential oils in response to environmental stressors (Ghassemi-Golezani & Farhadi 2021).

A study on *Ocimum basilicum* (Table 1) found that drought led to lower shoot fresh weight, dry weight, and plant height in stressed plants compared to non-stressed plants. However, plants treated with 1.448 mM salsylic acid (SA) positively affected these growth parameters. Low concentrations of SA (0.1–0.4 mM) improved vegetative growth and oil yield under water stress, with the highest oil yield observed at moderate stress levels (75% FC) (El-Naggar et al. 2024). SA application with 1.0 mM on *O. basilicum* retained higher chlorophyll content and maintained thylakoid structure under mild drought stress, preserving photosystem II (PSII) efficiency like non-stress conditions. The mechanism involves non-photochemical quenching (NPQ) that reduces singlet oxygen production, thereby protecting PSII functionality (Sperdouli et al. 2021). The relative water content (RWC) value decreased by 29.2% under water deficit, but plants treated with SA significantly increased leaf RWC. Both non-treated and SA-treated plants showed elevated proline content levels under water shortage, possibly due to SA's role as an osmoprotectant, stabilizing proteins and membranes, and scavenging free radicals during stress conditions like drought (Ali et al. 2023; Jahan et al. 2023).

Origanum vulgare is influenced by SA, which is crucial in regulating plant responses to temperature (Table 1). At 27 °C, SA increases the activity of antioxidant enzymes, while at 23 °C, it boosts peroxidase and carotenoid levels, improving stress tolerance and physiological performance. SA application enhances antioxidant enzymes, reducing reactive oxygen species (ROS) levels and enhancing plant resilience (Lee et al. 2022; Kashif et al. 2024). SA increases peroxidase activity at lower temperatures, maintaining cellular integrity and preventing lipid peroxidation. It also enhances carotenoids, contributing to photoprotection and antioxidative defence (Shui DeJu et al. 2013). SA induces the expression of genes coding for proteins involved in stress tolerance, such as antioxidative defence enzymes and heat shock proteins. Low concentrations are generally beneficial, while high concentrations may induce oxidative stress, reducing tolerance. Low SA concentrations are generally beneficial, while high concentrations may induce oxidative stress, reducing tolerance (Miura & Tada 2014).

A salicylic acid (SA) concentration of 0.5 mM effectively alleviates zinc stress in *Salvia officinalis* (Table 1). It enhances aerial chlorophyll synthesis by 501%, reduces zinc accumulation in roots, increases mineral element absorption in leaves and roots, and increases essential oil yield by 425%. When subjected to salinity stress, SA concentration remains optimal, improving plant growth, chlorophyll, mineral element, and oil content by 41.67%. Essential oil production increases by 112% at 0.5 mM, with hydrocarbon and oxygenated monoterpenes enhancements. The concentrations of major compounds increased, including camphor, α-thujone, thujanone, and 1,8-cineol. Salicylic acid (SA) stimulates *Salvia officinalis* at low concentrations. Still, it reduces essential oil content at elevated concentrations due to the disruption of essential nutrients like calcium, potassium, and phosphorus (Yadegari 2018). This affects plant growth and oil production. Lower concentrations of SA enhance nutrient content and oil yield under stress conditions (Es-sbihi et al. 2020). Specifically, 0.5 mM of SA significantly increased essential oil yield and improved the composition by restoring major compounds like α-thujone and camphor levels in copper stress. Low concentrations of SA are economically viable for enhancing plant tolerance to stress, indirectly influencing the composition of essential oils by modifying the plant's metabolic pathways. However, SA may occasionally result in adverse effects, such as growth retardation and decreased yield (Kavulych et al. 2023).

Data from *Thymbra spicata* (Table 1) foliar spraying of SA with 2.5 and 5.0 mM significantly improved essential oil yield 32–48 % compared with control. Compared with control, the carvacrol contents in the essential oil increased in the plants sprayed by SA. The effects of foliar application × soil moisture conditions significantly affected the essential oil; the highest percentage of carvacrol was obtained from SA at 5.0 mM × deficit water stress. Although specific studies on *Thymbra spicata* are limited, similar plants like *Thymus* species have shown improved essential oil yield and composition under stress conditions when treated with foliar applications of growth regulators. The application of SA could potentially enhance the essential oil yield and alter its composition in *T. spicata*, as observed in other thyme species under similar treatments (Alavi-Samani et al. 2015; Momeni et al. 2020).

The data in Table 1 indicate that the *Thymus* genus was examined in two species: *T. vulgaris* and *T. kotschyanus*; these species were subjected to different levels of salicylic acid (SA) solution, namely, 0.724 to 5.0 mM. Both species showed significant positive responses in physiological and biochemical characteristics at different salicylic acid concentrations. The half-maximal inhibitory concentration decreased under drought treatment with 3 mM SA, and the secondary metabolites, total phenolic content and total flavonoid content showed the highest values at 3.000 mM SA under drought. *T. kotschyanus* exhibited superior oil yield to *T. vulgaris*, and both species demonstrated antioxidant properties. Thymol emerged as the predominant component under drought conditions combined with SA treatment, with treatment with 0.724 mM SA significantly increasing thymol content in *T. kotschyanus* by 93.39% under water stress conditions.

The responses of plants to SA vary significantly across species due to genetic makeup, developmental stage, and environmental conditions, impacting growth, stress tolerance, and defence mechanisms through physiological and biochemical responses. It is found that there is a significant variation in salicylic acid response efficiency patterns between the two *Thymus* species (*T. kotschyanus* and *T. vulgaris*) in shoot and root dry weights and essential oil biosynthesis, which may be due to divergent plant adaptation strategies to abiotic stress and the spraying of SA. Different species utilize distinct pathways for SA synthesis, impacting its availability and function (An et al. 2014; Verma & Agrawal 2017). The interaction of SA with other plant hormones varies by species, affecting the overall stress response and defence signalling pathways (Pál et al. 2013). The variation of response in two *Thymus* species may be due to the high genetic diversity in the *Thymus* species, resulting in multiple chemotypes like thymol, carvacrol, linalool, and geraniol, among others, affecting oil yield and quality (György et al. 2020; Dashti et al. 2021). *T. kotschyanus* is more drought-tolerant than *T. vulgaris*, maintaining higher relative water content and stable chlorophyll levels under drought stress. *T. vulgaris* shows increased expression of pyruvate decarboxylase-1 (PDC-1) under severe drought conditions, indicating a different metabolic response to water stress (Ashrafi et al. 2022). On the other hand, climate change and ecological variables also influence essential oil chemistry (Etri & Pluhár 2024). Balsamic time (harvest time) is crucial for maximizing secondary metabolite yield, ensuring essential oils' highest quality and yield during specific growth cycles (Hazrati et al. 2024).

JASMONIC ACID (JA) AND METHYL JASMONATE (MEJA)

Jasmonic acid "3-oxo-2-2'-*cis*-pentenyl-cyclopentane-1-acetic acid, abbreviated as JA and its methyl ester (MeJA) and isoleucine conjugate (JA-Ile) are lipid-derived plant hormones collectively known as Jasmonates. MeJA, initially found in *Jasminum grandiflorum* flowers, is an active jasmonate. JA, originally seen as a stress-related hormone, was isolated from *Lasiodiplodia theobromae* as a plant growth inhibitor. Free acid (–JA) was first identified as a growth inhibitor in *Vicia faba* (Bhatla & Lal 2023). JAs act as signalling molecules, regulating gene expressions in response to abiotic challenges such as salt, drought, heavy metals, micronutrient toxicity, and low temperature, and they promote defensive mechanisms. Plant cells contain JA-Ile, the most bioactive JA, which is low under normal conditions (Fonseca et al. 2009). When stressed, JA undergoes epimerization to form JA-Ile, which accumulates in stressed leaves' cytoplasm. It is transported to the nucleus and adjacent sites for defensive responses (Truman et al. 2007; Li et al. 2017). Both the plasma and nuclear membranes of plant cells contain JAT1, which regulates the dynamics of JA or JA-Ile in the cytoplasm, nucleus, and apoplast during abiotic stress (Wang et al. 2019a).

JA coordinates primary and secondary metabolism, which is crucial for plant growth-defense trade-offs. It promotes the biosynthesis of secondary metabolites, vital for ecological interactions and stress responses. JA-Ile, a derivative of JA, is central to this signalling process. It interacts with other hormones to regulate plant resistance to various stresses. This crosstalk is essential for fine-tuning plant responses to environmental challenges (Zhang et al. 2024).

During normal conditions, the cytoplasm typically maintains a low concentration of JA-Ile, thereby causing JA-associated genes to remain inactive (Wang et al. 2021). Gene promoters exhibit an affinity for various transcription factors (TFs), which are subjected to repression by various transcriptional repressors known as JAZ proteins, thus preventing their activation of jasmonate-responsive gene promoters. JAZ proteins recruit TPL and the adaptor protein NINJA to form an active, closed NINJA-TPL-JAZ complex through the additional recruitment of HDA6 and HDA19. This complex avoids initiating jasmonate-responsive genes (Thireault et al. 2015). During abiotic stresses, the synthesis of JA is elevated, and it is readily converted to JA-Ile within the cellular cytosol. These JA-Ile molecules are then transported across cellular membranes to access the nucleus facilitated by the catalytic activity of jasmonic acid transfer proteins, specifically JAT1. This process marks the initiation of the JA signalling pathway (Wang et al. 2021). Within the cellular nucleus, the SCF complex, composed of kinetochore protein 1 (SKP1), cullin 1 (CUL1), and an F-box protein, acts as an E3 ubiquitin ligase that plays a pivotal role in facilitating JA responses. The initial step involves the translocation of JA-Isoleucine (JA-Ile) into the nucleus, where the protein F-box COI1, an integral component of the SCF complex, recognizes it. The co-receptor complex COI1-JAZ is then activated upon detection of JA-Ile, facilitating the interaction between JAZ (jasmonate ZIM-domain) proteins and COI1. This interaction leads to the degradation of JAZ proteins within the 26S proteasome. Consequently, the depletion of JAZ proteins leads to the transcriptional activation of transcription factors (TFs) and the subsequent expression of genes responsive to JA signalling pathways. Among plant natural products, JAs play a key role in plant defence (Figure 4).

Table 2 contains the summary of studies that explored the effect of Jasmonic acid and its derivatives on Lamiaceae plants regarding physiological and biochemical characteristics and secondary metabolites. The data in this table makes it clear that at *Lavendula officinalis*, JA increases only soluble sugar and proline. Using JA under salinity resulted in a significant reduction of peroxidase and ascorbate peroxidase. This may be due to Jasmonic acid, a plant hormone that significantly af-

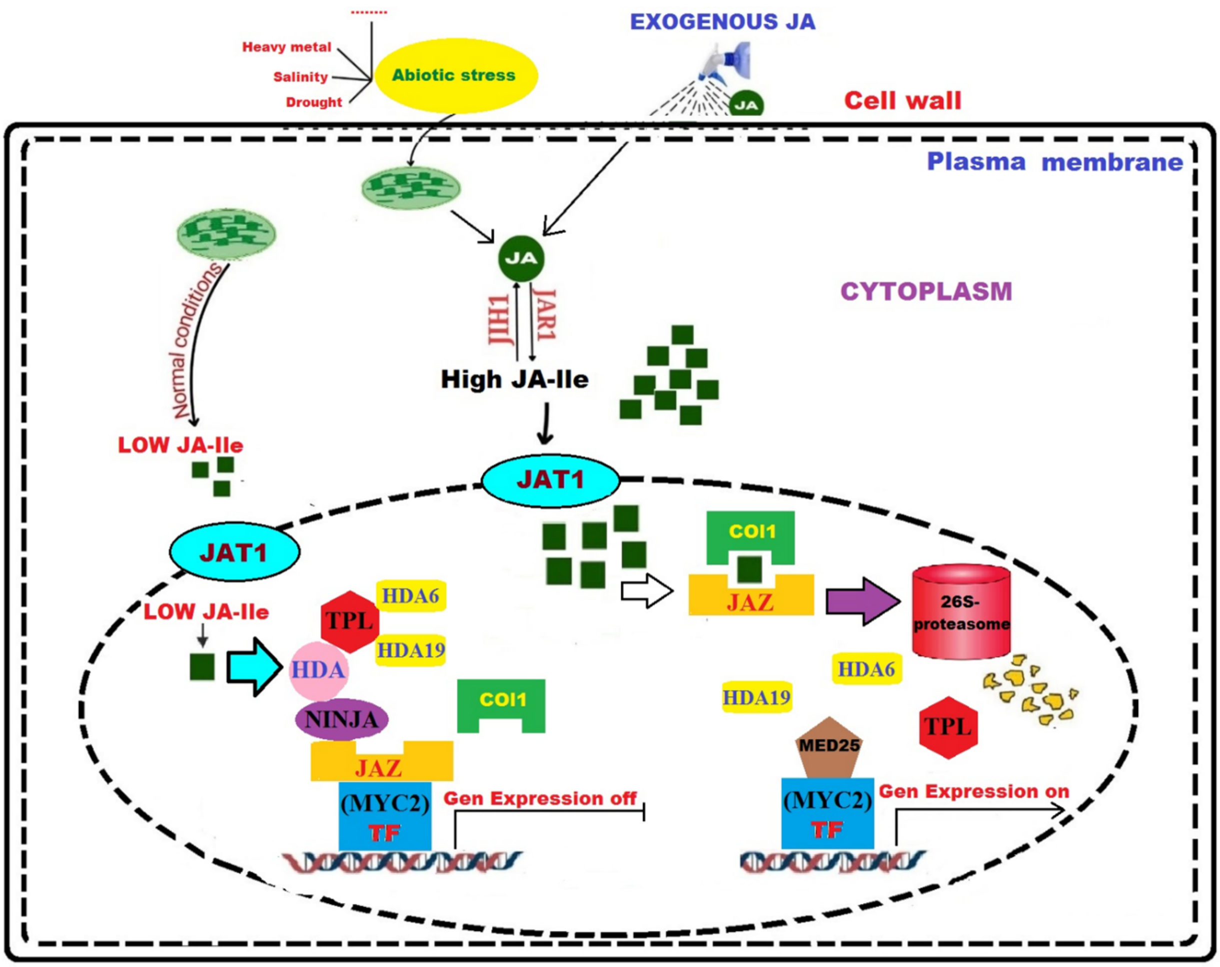

Figure 4. Exogenous jasmonic acid (JA) signalling pathway through the abiotic stress

Modifying and redrawing based on Ali & Baek (2020)

JAT1 – jasmonic acid transfer protein1; TPL – TOPLESS protein; HAD – deacetylases; NINJA – novel interactor of JAZ; JAZ – jasmonate ZIM domain; (MYC2) TF – transcription factor; MED – mediator; 26S protosome – central protease in ubiquitin-mediated protein degradation; HAD – histone deacetylase; COI1 – coronatine Insensitive 1

https://doi.org/10.17221/83/2024-PPS

Table 2. Reaction of Lamiaceae to spraying of jasmonic acid (JA) and methyl jasmonate (MeJA) under environmental stresses

Genus	Species	Stress	Jasmonic acid dose	Physiological and biochemical characters	Secondary metabolites	Effect	Reference
Lavendula	*L. officinalis*	Salinity (0, 25, 50 and 75 mM)	0 and 100 µM	Soluble sugar, proline, activity of antioxidant enzymes (catalase, superoxide dismutase, peroxidase, ascorbate peroxidase and glutathione peroxidase)	Not measured	• However, applied JA under salinity significantly reduced peroxidase and ascorbate peroxidase. • Salinity increases all soluble sugar and proline and increases the activity of antioxidant enzymes. • JA significantly increased only soluble sugar and proline while catalase, superoxide dismutase, peroxidase, ascorbate peroxidase and glutathione peroxidase were significantly decreased under normal conditions. • However, applied JA under salinity significantly reduced peroxidase and ascorbate peroxidase.	Rezaee Nasab et al. (2018)
Melissa	*M. officinalis*	Salinity (0, 25, 50 and 75 mM NaCl).	0 and 100 µM	Chlorophyll *a*, chlorophyll *b*, carotenoids such as carotenes and xanthophylls	Not measured	• Jasmonic acid spraying increased all pigment contents. • 100 µM Jasmonic acids significantly increased. • Chlorophyll *a*, chlorophyll *b*, carotenoids such as carotenes and xanthophylls under salinity stress	Pazoki (2015)
Mentha	*Mentha × piperita*	Drought (FC 100% field capacity, 75 % FCand 50% FC)	50 µM MeJA	Plant growth (leaf and shoot length, fresh and dry weight), proline content, IC_{50}, glucose and other small low-molecular-weight metabolites	Phenolic compounds, flavonoid	• Methyl jasmonate (MeJA) has no significant effect on the growth parameters. • The dry weight (mg/leaf) increased by 5.45% under mild drought (75% FC) with spraying 50 µM MeJA. At moderate drought (50% FC), it increased by 5.37%. • Total phenolic content significantly increased by 72.52% and 16.22% with 50 µM MeJA under mild and moderate drought, respectively. • MeJA significantly increased Flavonoid Content under mild and moderate drought by 70.52% and 37.52%, respectively. • Rosmarinic acid, Hesperidin, and Rutin were the main phenolic components. They increased significantly with MeJA under mild and moderate drought, except Rutin under mild drought. • L-proline increased under moderate drought by 3.25% with MeJA, and soluble carbohydrate such as D-glucose increased by 191.15% and 85.42% with MeJA under mild and moderate drought, respectively. • IC_{50} decreased when using MeJA under mild and moderate drought.	Gholamreza et al. (2019)

https://doi.org/10.17221/83/2024-PPS

Table 2. to be continued...

Thymus	*T. daenensis* & *T. vulgaris*	Drought (irrigation at 100% FC, at 75% FC, and at 50% FC)	0.0, 200, and 400 µL	Growth (plant height, root length, herbage dry weight, number of branches, and LAI (leaf area index), IC_{50} of essential oil	Essential oil % & oil composition	• JA application had no significant effect on both species' measured growth parameters and essential oil yield. • In irrigation (75% FC), the highest increase in herbage dry weight (g/pot) was 29.42% at spraying 400 µL JA in *T. daenensis.* While the spraying of *T. vulgaris* with 200 µL JA under the same irrigation gave the highest reduction percentage (27.78%) of herbage dry weight (g/pot). • At irrigation (50% FC), *T. daenensis* showed the highest reduction in herbage dry weight (g/pot) by 14.92%, while *T. vulgaris* showed an increase of 15.85% with the same JA level. • The highest increase % in essential oil yield of *T. daenensis* was 33.87% at spraying 400 µL JA under 50% FC, while under 75% FC *T. vulgaris* gave the highest increase % in essential oil yield 11.90% at 200 µL. • Thymol is the main component in essential oil, which was the highest value (61.14%) at 200 µL JA under the drought (50% FC) in *T. daenensis.* But in *T. vulgaris,* it was 48.55% at 200 µL JA under the drought (75% FC). • The highest antioxidant activity was obtained from theessential oil of *T. daenensis* under the foliar application of400 µL JA and mild drought stress with IC_{50} = 0.56 mg·m/L.	Alavi-Samani et al. 2015
Satureja	*S. khuzestanica*	salinity (0, 3, 6 and 9 dS/m NaCl)	0, 60 and 120 MeJA (µM)	Plant growth (stem and root lengths, fresh and dry weights), chlorophyll, N, P, K+, K+/Na+, Ca2+, Mg2+, and Na amounts, antioxidant activity, proline, sugar	Total phenol and components	• All concentrations of MeJA significantly affected dry-weight aerial parts (g) under Salinity up to 9 dS/m salt except the treatment 3 dS/m salt × 60 µM MeJA. • The best responses of *Satureja khuzistanica* to MeJA under salinity stress regarding dry-weight aerial parts (g) were increased by 12.27%, 13.27% and 11.08% at 120 µM MeJA × 3 dS/m salt, 120 µM MeJA × 6 dS/m salt and 60 µM MeJA × 9 dS/m salt, respectively. • Chlorophyll, sugar, proline, total phenol and antioxidant activity were significantly affected by MeJA. Under salinity stress, the best chlorophyll was at 60 µM MeJA × 3 dS/m salt, but sugar and proline were obtained at 60 µM MeJA × 9 dS/m salt. Moreover, total phenol and antioxidant activity resulted at 60 µM MeJA × 6 dS/m salt. • MeJA application, especially at 60 µM concentration, decreased Na + and increased all the measured mineral elements such as Ca^{2+}, Mg^{2+}, P, N and K^+ accumulation under salt stress.	Saadatfar and Hossein (2022).

fects stress responses. In *Lavandula officinalis,* JA treatment induces the synthesis of metabolites like rosmarinic acid and caffeic acid, which are associated with increased proline and soluble sugar levels (Nitzsche et al. 2004). The interaction between proline and soluble sugars, possibly mediated by JA signalling, enhances the plant's ability to cope with stress by improving antioxidant defences and maintaining cellular integrity (Moustakas et al. 2011). JA can influence the expression of genes related to antioxidant enzymes. For instance, in Arabidopsis, JA was found to repress the expression of certain antioxidant enzymes like catalase, which could similarly affect peroxidase (POD) and ascorbate peroxidase (APX) under specific conditions (Song et al. 2021). JA treatments improved the transcriptional levels of several antioxidant genes. Still, the overall activity of APX was not significantly increased, suggesting a complex regulatory mechanism where JA might suppress certain pathways to optimize stress responses (Sheteiwy et al. 2021).

Melissa officinalis, applying 100 µM Jasmonic acid foliar significantly increased all evaluated photosynthetically pigments under all salinity stress conditions. This is because JA treatments improved the transcriptional levels of antioxidant genes, which helped maintain higher chlorophyll content under salinity stress (Sheteiwy et al. 2021). However, JA enhances photosynthetic efficiency by improving stomatal conductance, intercellular CO_2 concentration, and maximal photosystem II efficiency. These improvements lead to better utilization of light energy and increased photosynthetic pigment levels (Dhaka et al. 2023).

Mentha × piperita, methyl jasmonate (MeJA) has no significant effect on the growth parameters. This may be because MeJA is primarily recognized for enhancing the production of secondary metabolites rather than promoting growth. Studies have shown that MeJA application increases the content of essential oils and phenolic compounds in *Mentha × piperita*, which are secondary metabolites important for the plant's defence and commercial value (Cappellari et al. 2019; Kandoudi et al. 2023). MeJA is a signalling molecule that triggers stress responses, including activating antioxidant enzymes. This can enhance the plant's ability to cope with environmental stressors but does not necessarily increase growth (Afkar et al. 2013; Afkar & Sharifi 2015). Activating defence mechanisms can reduce growth as the plant reallocates energy and resources to bolster its defence systems rather than expanding biomass (Krzyzanowska et al. 2012). The genetic makeup and developmental stage of *Mentha × piperita* can influence how the plant responds to MeJA. Certain genes involved in growth and secondary metabolism may be differentially expressed in response to MeJA, affecting overall growth (Taheri 2019; Abu El-Leel et al. 2021). MeJA, a signalling molecule, significantly increases plants' total phenolic and flavonoid content under mild and moderate drought conditions. This is due to its role in triggering the expression of genes involved in the biosynthesis of phenolic and flavonoid compounds, including the upregulation of enzymes and transcription factors in the phenylpropanoid pathway (Horbowicz et al. 2011; Zuo et al. 2024). L-proline and soluble carbohydrates also increase, but the IC50 decreases. Soluble carbohydrates are an immediate energy source and contribute to osmoprotection by stabilizing cellular structures and maintaining osmotic balance (Araniti et al. 2024). MeJA treatment upregulates genes involved in the biosynthesis of these metabolites, indicating a genetic basis for observed metabolic changes. MeJA enhances the biosynthesis of secondary metabolites, including proline and carbohydrates, by modulating stress-responsive pathways, leading to improved drought tolerance and increased antioxidant capacity in plants (Qi et al. 2018; Gholamreza et al. 2019; Kandoudi et al. 2023). Drought stress combined with MeJA treatment leads to the accumulation of osmolytes, such as proline and sugars, which help maintain cellular homeostasis and contribute to the plant's stress tolerance (Alhaithloul et al. 2019). Under drought stress, MeJA significantly increases *Mentha*'s flavonoid and total phenolic content, which are crucial for antioxidant activity (Gholamreza et al. 2019).

Satureja khuzestanica, methyl jasmonate (MeJA) significantly affects the physiological and biochemical responses of *Satureja khuzestanica* under salinity stress, enhancing its tolerance to such conditions. It affected dry-weight aerial parts under salinity up to 9 dS/m salt, except for the 3 dS/m salt × 60 µM MeJA treatment. Moreover, chlorophyll, sugar, proline, total phenol and antioxidant activity were significantly affected by MeJA. This, due to MeJA may similarly contribute to maintaining membrane stability, increases proline and sugar levels, aiding in osmotic balance and stress mitigation and ion homeostasis under saline conditions (Mulaudzi et al. 2023; Wang et al. 2023). Optimal responses of *S. khuzistanica* to MeJA, particularly at 60 µM concentration, decreased Na^+ and increased mineral element accumulation (Ca2$^+$, Mg^{2+}, P, N and K^+) under salt stress. This may be attributed to MeJA reduces Na^+ accumulation in plants by increasing the expression of ion transporters, such as OsHKT and OsHAK genes, which regulate Na^+ and K^+ transport. In rice, MeJA increased OsHKT and OsHAK gene expression (Hussain et al. 2022), while in sorghum, it decreased the Na^+/K^+ ratio, indicating effective Na^+ exclusion (Mulaudzi et al. 2023).

Thymus daenensis and *T. vulgaris* showed insignificant responses to jasmonic acid (JA) regarding growth and essential oil. This may be attributed to JA prioritising defence mechanisms over growth by interfering with the gibberellin (GA) signalling pathway, which is crucial for plant growth. This interference can reduce plant growth rates, as seen in other species like Arabidopsis, where JA delays gibberellin-mediated degradation of growth-promoting proteins (Yang et al. 2012). The antagonistic relationship between JA and GA could explain why *thyme* does not exhibit significant growth responses when treated with JA, as the hormone may inhibit growth-promoting pathways (Heinrich et al. 2013). *Thyme*'s physiological responses to JA, including changes in chlorophyll content and antifungal properties, suggest that JA may be more effective in enhancing stress resistance than promoting growth or oil production. This aligns with the general role of JA in mediating plant defence responses, as suggested by Alavi-Samani et al. (2015), and Kamińska (2021). *Thyme* species showed differences in response to JA treatments in growth and volatile compounds of essential oil, with *T. vulgaris* superior and Thymus daenensis superior in antioxidant activity (Azimzadeh et al. 2023). This may be due to the expression of specific genes like γ-terpinene synthase and CYP71D180, which are upregulated differently in these species. The complexity of the JA pathway, regulated by JAZ repressors, suggests genetic differences can lead to varied responses in *thyme* species (Zhang et al. 2022b). JA affects terpenoid metabolism in *thyme*, affecting defence and stress response. Different species' upregulation of genes like γ-terpinene synthase affects response, resulting in essential oil composition and stress tolerance (Kamali et al. 2024).

HUMIC ACID

Humic acids (HA) are chemical priming substances that trigger physiological and molecular responses against plants' abiotic stresses like salinity, drought, and heavy metal toxicity. They also enhance the plant's antioxidant defence mechanisms, crucial for mitigating oxidative stress caused by abiotic factors. It also induces both enzymatic and non-enzymatic antioxidants, which help reduce oxidative damage in plants under stress conditions. HA supports enhanced primary and secondary plant metabolism and improves growth and stress resilience (Abu-Ria et al. 2024; Atero-Calvo et al. 2024). Humic acids contain hydroquinone and naphthoquinone fragments that act as inhibitors of oxidation reactions. These fragments can neutralize radicals, thereby enhancing the antioxidant capacity of humic acids via the transcriptional regulation of EcSOD, EcCAT1, EcAPX1, and EcGR (Yarkova & Gyul'maliev 2021; Volikov et al. 2021). The findings of this study indicate that HA treatment may confer protective effects on finger millet seedlings against salt stress while simultaneously attenuating oxidative stress by promoting the expression of genes involved in the reactive oxygen species scavenging pathway (Figure 5 redrawing based on Rakkammal et al. 2024).

Humic acids (HA) play a crucial role in plant defence mechanisms, enhancing tolerance to both biotic and abiotic stresses. They influence the expression of stress-responsive genes, such as abscisic acid, gibberellic acid, and auxins, which help prepare the plant's defence mechanism before stress onset (Canellas et al. 2020; Souza et al. 2021). Humic acids also induce cytosolic acidification in plant cells, activating stress response pathways. This process

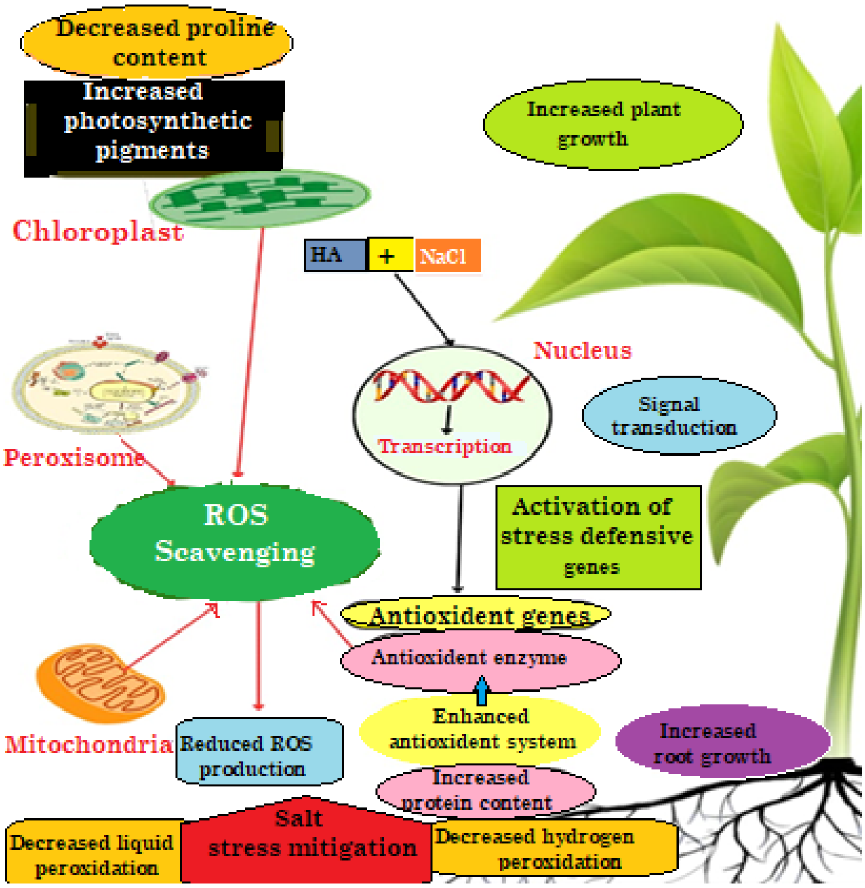

Figure 5. Exogenous humic acid (HA) signaling pathway through the abiotic stress Redrawing based on Rakkammal et al. 2024)

ROS – reactive oxygen species

is linked to the activation of ion transport systems, such as plasma membrane H^+-ATPase and Ca^{2+}-dependent protein kinases (CDPKs) (Baia et al. 2020). Humic acids upregulate genes encoding WRKY transcription factors, which regulate plant responses to biotic and abiotic stresses. These transcription factors integrate multiple signalling pathways, including those mediated by abscisic acid (ABA) and reactive oxygen species (ROS), to upregulate stress-related genes (Cha et al. 2021; Wani et al. 2021; Wang et al. 2024). Humic acids also regulate the expression of the P5CS gene, which is involved in proline biosynthesis, a key osmoprotectant that helps in osmotic adjustment under salt stress. The application of HAs reduces the relative expression of P5CS and its downstream products, indicating a complex regulatory mechanism that balances osmotic stress responses (Meng et al. 2023).

Many studies examined the impact of humic acid on physiological and biochemical parameters and secondary metabolites of various Lamiaceae plants under abiotic environmental stresses, as summarized in Table 3.

Dracocephalum moldavica, humic acid, significantly increases the essential oil content of *Dracocephalum* under stress due to its role as a biostimulant that enhances plant growth and stress tolerance. This effect is primarily attributed to humic acid, which helps mitigate the effects of abiotic stress, such as drought and salinity, by enhancing the plant's physiological and metabolic processes. It stimulates the production of secondary metabolites, including essential oils, often upregulated in response to stress (Amador et al. 2018; El Gohary et al. 2023). Under salt stress, humic acid has been shown to increase the concentration of key essential oil components like geranial and neral, which are part of the plant's adaptive response to stress (Aziz et al. 2013). In *D. moldavica*, humic acid application increases essential oil yield and improves morphological traits under normal and stressful conditions (Samadimatin & Hani 2017). Other studies on related species, such as *Majorana hortensis* and *T. kotschyanus*, have also demonstrated the positive impact of humic acid on essential oil content and plant growth under water stress (Massoud et al. 2010; Saber et al. 2021).

Humic acid significantly improved growth characteristics in *Melissa officinalis* under drought stress, leading to a 41.33% increase in plant dry weight. This is due to its ability to improve the bioavailability and absorption of essential nutrients, which are crucial under drought conditions. Humic acid also exhibits hormone-like activity, influencing the phytohormone profile of plants, which helps maintain growth and development processes even under stress conditions. It enhances primary and secondary metabolism, vital for sustaining plant growth and increasing biomass (Hayati et al. 2022; Atero-Calvo et al. 2024). A concentration of 400 mg/L of humic acid significantly increased essential oil content by 75.68% at 50% field capacity (Saber et al. 2021; Hayati et al. 2022). Humic acids enhance the availability and uptake of nutrients, which are crucial for maintaining plant metabolic activities under stress conditions. This improved nutrient uptake can lead to increased synthesis of secondary metabolites, including essential oils (Goel & Dhingra 2021). However, humic acid did not significantly affect essential oil in *Melissa officinalis* under high drought stress. The plant's physiological state under extreme drought may not allow humic acid's full benefits to manifest, suggesting that specific pathways influenced by humic acid may not directly enhance essential oil biosynthesis under such stress (Saber et al. 2021).

The study compared the height of *Ocimum basilicum* var. basilicum and *O. basilicum* var. Genovese, revealing significant differences in plant height and essential oil content. While no significant difference was observed in height, treating humic acid significantly enhanced plant height, with more pronounced increases for var. basilicum. The highest value of linalool (72.23%) was observed in var. basilicum, followed by eucalyptol, while estragole disappeared. In contrast, var. Genovese showed the highest value of eucalyptol (19.37%), increasing by 24.57%. These differences can be attributed to genetic variation, differential stress tolerance, and the specific effects of humic acid on plant physiology (Ciriello et al. 2023). The response to humic acid varies between basil varieties due to their inherent genetic makeup and physiological traits. Humic acid also increased proline content, a marker of stress tolerance, and improved photosynthetic efficiency, contributing to better growth under stress conditions (Lasheen et al. 2024).

Satureja khuzistanica is highly responsive to humic acid under salinity stress, improving photosynthesis, respiration, and stomatal conductance. It increases substomatal CO_2 and proline content,

https://doi.org/10.17221/83/2024-PPS

Table 3. Reaction of *Lamiaceae* to spraying of humic acid (HA) under environmental stresses

Genus	**Species**	**Stress**	**Humic acid dose**	**Physiological and biochemical parameters**	**Secondary metabolites**	**Effect**	**Reference**
Dracocephalum	*D. moldavica*	salinity stress s (0, 50, 100 and 150 mM)	0, 100 and 200 mg /L	Not measured	Essential oil % & oil composition	• Humic acid significantly increased the essential oil content at 100 and 200 mg/L under high salinity with 100 and 150 mM. Spraying by 200 mg/L of humic acid increased essential oil % by 51.61%. • Geranial, neral, geraniol, and geranyl acetate were identified as the main components with 100 mg/L of humic acid treatment under 50 mM salt.	Narimani et al. (2020).
Melissa	*M. officinalis*	Drought (100 field capacity, 75% FC and 50% FC)	0.0, 200 and 400 mg/L	Plant growth (plant height, fresh and dry weight, number of lateral branches, stem diameter and root dry weight),	Essential oil %	Humic acid significantly improved all growth characteristics under drought stress, which increased the plant's dry weight by 41.33%. • All humic acid doses up to 400 mg/L significantly gradually affect essential oil content (%) at high drought stress (irrigation of 50% FC). So, 400 mg/L of humic acid under drought stress (irrigation of 50% FC) increased oil content by 75.68%, while there was no significant effect of all humic acid doses under drought stress (75% FC).	Gorgini et al. (2017)
Ocimum	*O. basilicum* var. basilicum and *O. basilicum* var. Genovese	Salinity (salty soil conditions)	1.5 %	Growth (number of branches, fresh weight, dry weight, plant height), proline content	Essential oil % & oil composition	• Both *Ocimum basilicum* var basilicum and Genovese gave significant results in growth characters in terms of plant height and number of branches. • Spraying HA with 1.5% significantly increased dry weight (g/plant) growth by 29.64% in *O. basilicum* var. basilicum but insignificantly increased by 7.93% in var. Genovese. • *Ocimum* showed a significant response to humic acid treatment in both varieties in the case of proline % and essential oil content in var. basilicum where the increases were 100% and 61.54% for proline and essential oil content, respectively. While var. Genovese showed a significant increase of 60% for proline only, and the essential oil content was unaffected. • The major compounds in *ocimum* were linalool, estragole, and eucalyptol. There were significant differences between the two varieties in the content of the major compounds in var. basilicum, the humic acid treatment showed the highest value of linalool (72.23%) with increasing by 4.29% and enhanced eucalyptol, increasing by 51% compared to control, while estragole disappeared. On the other hand in *O. basilicum* var. Genovese showed the highest value of eucalyptol (19.37%), increasing by 24.57%. • In var. *basilicum* oxygenated monoterpenes (90.81%) were reduced with applied humic acid by 5.52%, while monoterpene hydrocarbons, Sesquiterpene hydrocarbons and oxygenated sesquiterpenes were increased with humic acid application by 300, 64.29 and 200.72% compared to control, respectively. • This trend was also in var. Genovese oxygenated monoterpenes reduced with applied humic acid by 6.71%, while monoterpene hydrocarbons, Sesquiterpene hydrocarbons and oxygenated sesquiterpenes were increased with humic acid application by 42.95, 31.78 and 51.80% compared to control, respectively.	El Gohary et al. (2023)

Table 3. to be continued...

Thymus	*Thymus vulgaris*	drought stress (irrigation of 100% FC and 50% FC)	2 g/L	Plant growth (plant height, branches, and dry weight), chlorophyll, nutrient uptake (N, P, and K), relative water content (RWC), antioxidant enzymes activities (catalase (CAT) activity, ascorbate peroxidase (APX), superoxide dismutase (SOD) activity), enzymes and antioxidant activity.	Essential oil % & oil composition, phenol content, and flavonoid	• Humic acid significantly enhanced plant growth parameters, where the total dry weight (g/plot) increased by about 57.59% under drought stress. • The RWC, chlorophyll *a* and chlorophyll *b* significantly increased with humic acid, where RWC increased by 42.02% under drought compared to no humic applied. • Total phenols, flavonoids and total soluble sugar were significantly enhanced by 51.05%, 60.38%, 66.98%, respectively, using Humic acid compared to no humic applied. On the other hand, proline content was significantly reduced by 42.11% with the application of humic acid under drought stress. • Humic acid increased N by 29.10%, P by 39.13%, and K by 13.25% compared to without applied humic acid. • CAT, SOD, and APX were increased by 65.5%, 46.16%, and 39.10% µmol/g when humic acid was applied under drought stress. • The essential oil content was significantly enhanced by 55.56% when treated with humic acid under drought.	Rahimi et al. (2022).
Satureja	*S. khuzistanica*	Salinity stress (0, 25, 50, 75 and 100 mM of NaCl)	0, 10, 20, 30 and 40 mg/kg of soil	Plant growth (length of stem and root, leaf area), photosynthesis and transpiration, stomatal conductance and substomatal cavity CO_2 concentration, organic matter percentage, ash percentage, relative water content (RWC) of leaf, proline and soluble sugar.	Not measured	• Higher humic acid (40 mg/kg of soil) under all salinity stress boosted growth parameters. The highest values of stem length, root length, leaf length, leaf width and leaf area were 27.7 cm, 17.8 cm, 3.86 cm, 385 mm and 80.5 mm^2, respectively, were obtained at 40 mg/kg of soil under 25 mM of NaCl compared to no humic applied. Humic acid enhanced photosynthesis, respiration and stomatal conductance under salinity, where the best values were at 40 mg/kg of soil under 25 mM of NaCl. Humic acid increased substomatal CO^2 under salinity stress, where the highest value was shown at 40 mg/kg of soil under 100 mM of NaCl. • Proline content rose with salinity but dropped with increased humic acid. The highest value of proline content is observed at 10 mg/kg of soil under 100 mM of NaCl. • Both salinity doses up to 100 mM NaCl and humic acid at 10 mg/kg of soil-raised soluble sugar content. • Relative water content fell with salinity, unaffected by humic acid.	Zaremanesh et al. (2019).

with the highest proline content found at 10 mg/kg of soil under 100 mM NaCl. Both salinity doses and humic acid at 10 mg/kg of soil raise soluble sugar content, but relative water content falls with salinity. Humic acid treatments improve photosynthetic rate by enhancing chlorophyll content and reducing oxidative damage through the activation of ascorbate peroxidase, catalase, and superoxide dismutase enzymes (Ennab et al. 2023; Meng et al. 2023). HA also enhances the tricarboxylic acid cycle and glycolysis, which is critical for respiration and supports energy production and metabolic processes (Bera et al. 2024). HA application increases stomatal conductance, facilitating better gas exchange and water use efficiency, especially under salinity stress. It ensures a higher concentration of CO_2 in the substomatal cavity, which is essential for maintaining photosynthetic efficiency and carbon fixation (Meng et al. 2023; Lasheen et al. 2024).

Under drought stress, humic acid significantly improved plant growth parameters in *Thymus vulgaris*, increasing total dry weight by 57.59%. This was due to stimulating plant growth hormones such as auxins, which promote root and shoot growth, increase biomass production and improve plant vigour (Qin & Leskovar 2020). Humic acid also increases the production of secondary metabolites, such as phenolic compounds and antioxidants, which affect stress tolerance. These compounds contribute to *T. vulgaris*' ability to withstand drought stress. The interaction between humic acid and drought stress also increased proline and soluble sugar content, important osmoprotectants that help maintain cellular integrity and function under stress. In contrast, proline content in *T. vulgaris* was reduced by 42.11% when treated with humic acid under drought. This may be because humic acid may alter this balance by reducing the perceived stress level, thus decreasing the need for proline accumulation as an osmoprotectant (Sorkhi 2020). The application of humic acid has been shown to increase both the fresh and dry biomass of *T. vulgaris*, as well as the yield and composition of essential oils. This is attributed to humic acid's improved nutrient uptake and stress mitigation effects (Juárez-Rosete et al. 2012). Humic acid can enhance the antioxidant capacity of plants, potentially reducing oxidative stress and the need for proline as a protective agent. The interaction between humic acid and drought stress can lead to changes in other osmolytes and stress markers, potentially compensating for reduced proline levels (Farag et al. 2019; Sorkhi 2020).

ASCORBIC ACID

Plants produce ROS under abiotic stress, including hydrogen peroxide (H_2O_2), hypochlorous acid (HClO), ozone (O_3), singlet oxygen ($1O_2$), superoxide anion radicals (O_2–), hydroxyl radicals (OH–), perhydroxyl radicals (HO2•), organic alkoxy (RO•), and organic peroxyl radicals (ROO•). Which damages cell composition and disrupts growth and development (You & Chan 2015; Choudhury et al. 2017; Nadarajah 2020). Ascorbic acid (ASA) is a non-enzymatic compound essential for plant development, cell division, osmotic adjustment, hormone biosynthesis, and as an enzymatic cofactor. The concentration of ASA varies between organs and plant species, and in most plant species, it may not be sufficient to combat abiotic stress effectively. So, the Exogenous application of ASA can enhance endogenous levels and boost antioxidant capacity in plants, particularly under abiotic stress conditions (Celi et al. 2023) as well as the physiologically active form of ASA is ascorbate, which is effective in scavenging ROS (Pu 2022). ASA's major roles include antioxidant to scavenge accumulated ROS, cofactor involved in plant metabolism where protection of lipids and proteins, regulation of the photosynthetic rate, transpiration, photosynthetic pigments, increase in proline content, a decrease in lipid peroxidation and regulator to coordinate the actions of various signal pathways under abiotic stress (Wang et al. 2019b; Elkelish et al. 2020; Farooq et al. 2020; Xiao et al. 2021, Celi et al. 2023). ASA can scavenge both radical and non-radical ROS through direct and indirect pathways. In chloroplasts, ASA efficiently scavenges both types of ROS, assisting plants in maintaining photosynthesis-related ROS (Foyer 2018; Khorobrykh et al. 2020; Xiao et al. 2021). Superoxide dismutase reduces the ROS O_2– radical to H_2O_2, which ASA peroxidases (APXs) can be eliminated using ASA as an electron donor (Maruta & Ishikawa 2018; Pu 2022). ASA can directly scavenge non-radical ROS $1O_2$ and reduce carotenoids and tocopherols oxidized by $1O_2$. As an enzyme cofactor, ASA is essential for abiotic stress responses by altering plant cell composition, coordinating phytohormone production, controlling gene expression, and indirectly removing reactive oxygen species (Xiao et al. 2021).

ASA can act as a violaxanthin de-epoxidase (VDE) cofactor to eliminate ROS indirectly. VDE uses ASC as a substrate to reduce the xanthophyll pigment violaxanthin to zeaxanthin, which can dissipate excess excitation energy in the photosystem II light-harvesting complex and protect the photosynthesis system from photooxidative stress (Yang et al. 2017). In addition to being a reducing substrate, ASC is also a cofactor involved in several oxidase enzymatic reactions; among these, 2-ODDs play a role in a number of metabolic functions, including the synthesis and metabolism of phytohormones and protein hydroxylation. These metabolic activities significantly impact plants' growth and development and their responses to abiotic stress (Alegre et al. 2020; Broad et al. 2020; Foyer et al. 2020).

Ascorbic acid significantly influences multiple signalling pathways (Figures 6 and 7 modified and redrawing according to Xiao et al. 2021), including ROS and phytohormone, integrating their actions and coordinating plant abiotic stress responses by regulating cell redox states (Bellini & De Tullio 2019; Bilska et al. 2019; Yu et al. 2019). ROS causes oxidative damage and functions as signalling molecules that activate plants' responses to abiotic stresses (Choudhury et al. 2017). Con-

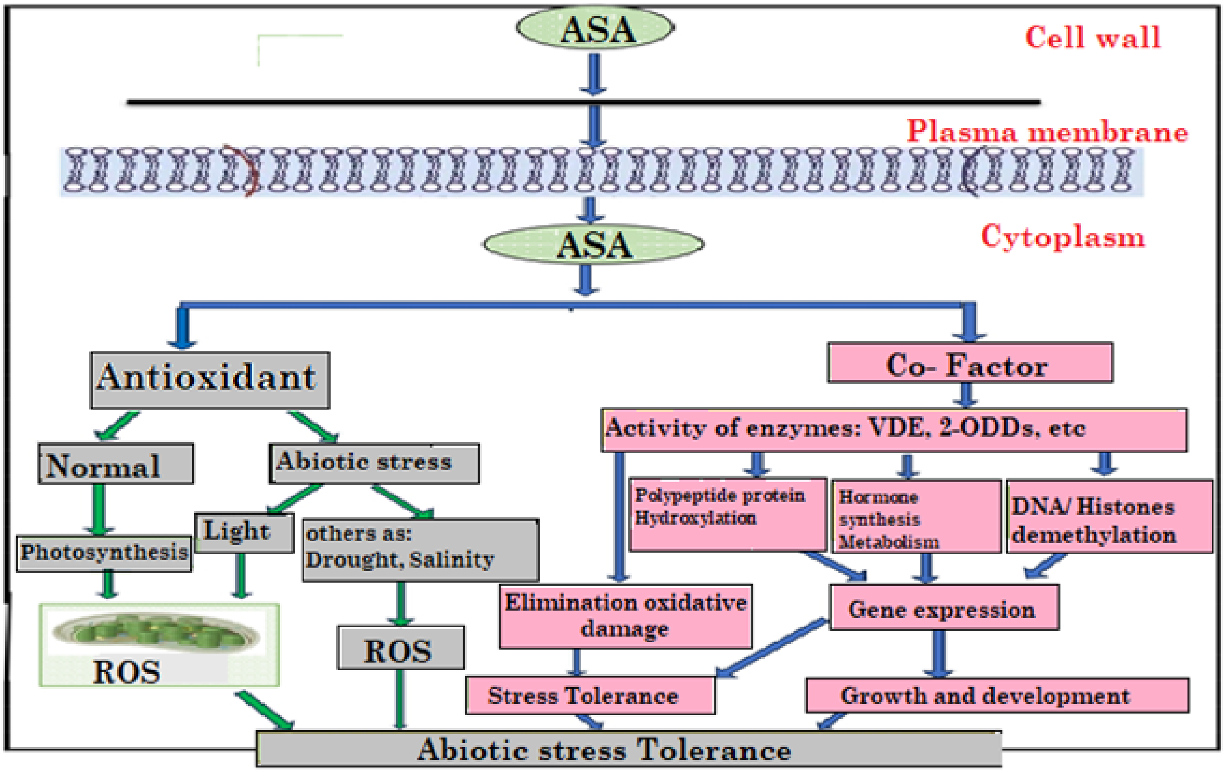

Figure 6. Exogenous ascorbic acid (ASA) as co-factor and antioxident pathway through normal and abiotic stress conditions

Modified and redrawing according to Xiao et al. (2021)

ROS – reactive oxygen species

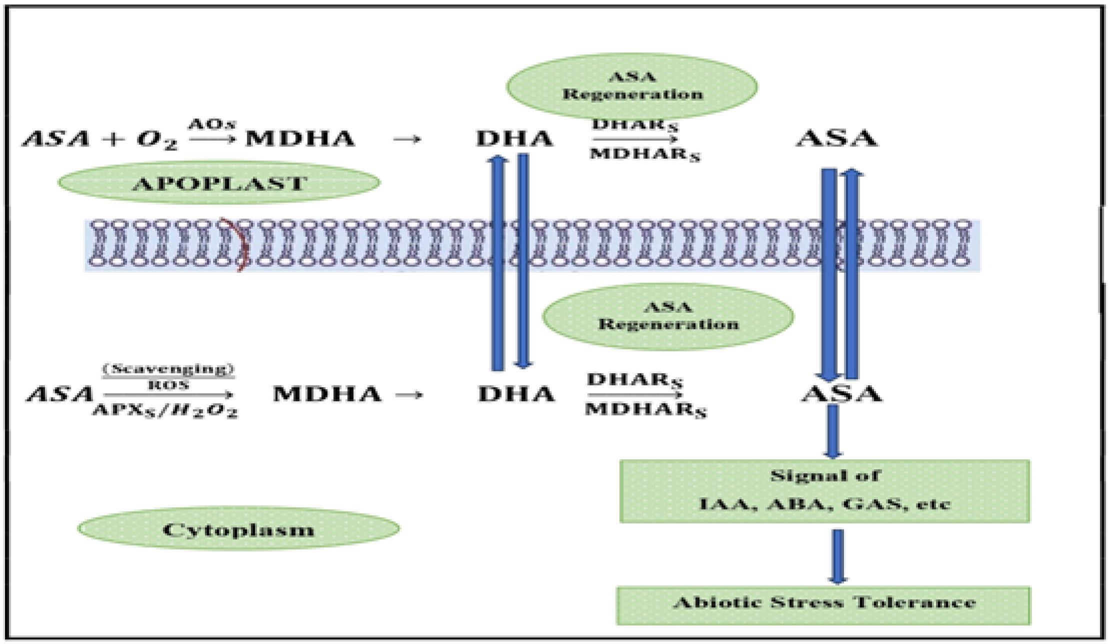

Figure 7. Exogenous ascorbic acid (ASA) signalling pathway through the abiotic stress

Modified and redrawing according to Xiao et al. (2021)

MDHA – monodehydroascorbate; AOs – ascorbate oxidases; DHA – dehydroascorbate; DHARs – DHA reductases; MDHARs – MDHA reductases; APXs – peroxidases sequently, controlling ROS homeostasis is essential for plants to adapt to abiotic stresses (Nadarajah 2020). Ascorbic acid can control ROS signal transduction by regulating ROS homeostasis (Cobley et al. 2015; Bellini & De Tullio 2019; Foyer et al. 2020). The enzymes that perform ASC metabolism and regeneration are also critical in regulating cell redox signals (Bellini & De Tullio 2019). ASC peroxidases (APXs), distributed in the cytoplasm, play an important role in ROS scavenging and the activity of various cell signalling pathways. APXs oxidize ASC to monodehydroascorbate (MDHA); MDHA can then be disproportionate to dehydroascorbate (DHA), ASC can be regenerated from MDHA and DHA by MDHA reductases (MDHARs) and DHA reductases (DHARs), respectively.

The AsA/DHA (dehydroascorbate) redox pair involves redox state-based signalling mechanisms, influencing gene expression and protein levels to enhance stress tolerance (Miret & Müller 2017). Therefore, ASC regeneration can provide more ASC for ROS scavenging and thus helps to maintain cell redox homeostasis and decrease oxidative damage under abiotic stress (Broad et al. 2020; Xiang et al. 2020). On the other hand, the Ascorbate oxidases (AOs), located in the cell wall, oxidize apoplastic ASC to monodehydroascorbate (MDHA) by using O_2 are involved in cell signal transduction (Li et al. 2017; Bellini & De Tullio 2019; Pan et al. 2019). In the apoplast, MDHA formed as a result of ASC oxidation by AOs can be converted to DHA and rapidly transported into the cytoplasm, where it can then be recycled into ASC by DHARs. In contrast, the reduced ASC in the cytoplasm can be transferred to the apoplast, resulting in ASC exchange between the apoplast and cytoplasm. This DHA-ASC exchange is critical for maintaining redox homeostasis in the apoplast and cytoplasm (Pan et al. 2019; Foyer et al. 2020). Under abiotic stress, the DHA flux from the apoplastic oxidization of ASC increases rapidly and disrupts the balance of the redox state in the apoplast and cytoplasm; this acts as a signal to initiate a response to adverse environmental conditions (Xiao et al. 2021).

This review analyzed studies 2015–2024 on Lamiaceae plants (Table 4), including *Dracocephalum moldavica* under drought stress. Results from this plant showed that ascorbic acid (ASA) increased biomass yield by 8.39% and 12.72% under moderate and severe water stress, increased leaf chlorophyll-*a* and chlorophyll-*b* concentrations, and increased leaf TSS and RWC content. ASA-treated plants also showed enhanced proline and oxidase enzyme activity, with catalase, superoxide dismutase, and peroxidase increasing significantly under severe water stress. Severe water stress significantly impacted essential oil content, with the most identified compounds obtained through ASA treatment. This may be due to the role of ascorbic acid in boosting the activity of antioxidant enzymes such as catalase, superoxide dismutase, and peroxidase, which are crucial for scavenging reactive oxygen species (ROS) generated under stress conditions (Halimeh et al. 2013; Rezaei-Chiyaneh et al. 2021). This enhancement in enzymatic activity helps maintain cellular redox homeostasis, thereby protecting plant cells from oxidative damage. ASA preserves chlorophyll-*a* and chlorophyll-*b* concentrations, which are essential for light absorption and energy conversion in photosynthesis (Xu & Huang 2017; Ali et al. 2019); this preservation delays leaf senescence and maintains photosynthetic efficiency, contributing to higher biomass yield (Veljović-Jovanović et al. 2017). ASA also increases proline accumulation, which acts as an osmoprotectant, helping the plant to maintain cell turgor and water balance under drought conditions (Halimeh et al. 2013), as well as increases the total soluble sugars (TSS) and relative water content (RWC) further supports osmotic adjustment, contributing to improved drought tolerance (Rezaei-Chiyaneh et al. 2021). The increased production of essential oils under stress conditions may be linked to the plant's adaptive response to enhance its defence mechanisms (Halimeh et al. 2013).

Also*, D. moldavica,* under salinity stress**,** the essential oil content decreases. However, ascorbic acid can improve its essential oil profile by enhancing specific components like alpha-pinene, beta-pinene, camphene, camphor, alpha-thujone, nerol, and thymol. This improvement is particularly noticeable when applied at 100 mg/L and 200 mg/L concentrations under varying salinity conditions. Salinity stress negatively impacts the biosynthesis and metabolism of essential oils, with components like geranial and neral increasing with salinity while others like geranyl acetate decrease with stress, indicating a shift in the plant's metabolic pathways under stress (Aziz et al. 2013). Ascorbic acid, an antioxidant, stabilizes essential oil production by mitigating oxidative stress from high

Table 4. Reaction of *Lamiaceae* to spraying of ascorbic acid under environmental stresses

Genera **Species**	**Stress**	**ASA dose**	**Physiological parameters**	**Secondary metabolites**	**Effects**	**Reference**
Dracocephalum *D. moldavica*	Drought stress (normal irrigation, moderate water stress, and severe water stress)	10 mM	Chlorophylls and carotenoids, plant biomass Relative water content (RWC), Leaf proline content, Total soluble sugars, catalase (CAT), peroxidase (POX) and superoxide dismutase (SOD).	Essential oil (EO) %, oil compositions	• Under severe drought, ASA increased biomass yield by 8.39% and 12.72% under moderate and severe water stress, respectively. • The application of ASA treatment markedly enhanced the concentration of leaf chlorophyll-*a* across all irrigation regimes, exhibiting an increase of 9.9% to 52.8%. Similarly, the concentration of chlorophyll-*b* was enhanced by 62% and 76% under moderate and severe drought conditions, respectively. Water-stressed plants had higher carotenoid concentrations than those under normal irrigation, which increased with foliar application of ASA. • ASA significantly increased the leaf TSS content by 29% and 21.2% under moderate and severe water stress, respectively. • ASA application enhanced RWC across all irrigation regimes, especially under moderate and severe water stress, with 18.11% and 22.44%, respectively. • Foliar ASA, applications increased leaf proline contents. • ASA-treated plants showed enhancement of oxidase enzyme across all irrigation regimes, where catalase, superoxide dismutase and peroxidase increased by (17.22–27.78%), (12.38–70.51%) and (8.76–13.11%), respectively. The highest values of oxidase enzymes were recorded under severe water stress. • ASA treatment increased EO contents by 7.3% and 12.57% under moderate and severe water stress, respectively; additionally, The most identified compounds were obtained in the AA treatment (99.86%) under severe water stress.	Rezaei-Chiyaneh et al. (2021)
Dracocephalum *D. moldavica*	salinity stress (0, 50, 100 and 150 mM)	0, 100 and 200 mg/L (0.57 and 0.85 mM)	Not measured	Essential oil (EO) %, oil compositions	• The concentration of essential oils exhibited a notable decline in response to escalating salinity stress, whereas incorporating salt stress mitigators such as ascorbic acid significantly ameliorated this characteristic. Under varying salinity stress levels combined with 100 and 200 mg/L, ascorbic acid enhanced alpha-pinene, beta-pinene, camphene, camphor, alpha-thujone, nerol, and thymol.	Narimani et al. (2020)
Mentha *M. piperita*	Drought (irrigation at 4, 8 and 12 days)	0, 100, 150, 200, 250 mg/L (0, 0.57, 0.85, 1.14 and 1.42 mM)	Plant growth (plant height, number of leaves and yield fresh weights)	Essential oil % & oil composition	• ASA (100–200 ppm) caused significant increases in vegetative growth characteristics, essential oil percentage and yield. Increasing ASA led to increasing growth in terms of fresh weight essential oil percentage and oil yield up to 200 mg/L when over that fresh weight decreased. The major components in plants were menthol, menthone, 1,8-cineole, limonene, and menthyl acetate, with varying percentages based on stress level and ASA concentration. The highest menthol percentage was achieved under severe stress at 200 mg/L for 12 days, followed by moderate stress at 8 days with the same concentration. It is worth mentioning that the menthol percentage in the 2nd cut is higher than that of the 1st and 3rd cut. Under moderate stress, the interaction with 200 mg/L ASA in the 1st and 3rd cut produced 34.32 and 34.86%, respectively, while under severe stress, the interaction with 200 mg/L AsA produced 34.57 and 32.83%. When 150 mg/L ASA was applied for drought (irrigation after 8 days), it produced 7.58 and 5.95% in the first and 3rd cuts and 3.86% in the second. Under severe stress (12 days), 200 mg/L ASA produced higher percentages.	El-Naggar et al. (2022)

Table 4. to be continued...

Ocimum *O. basilicum*	Salinity stress (200, 400 and 600 ppm NaCl)	300 ppm (1.7 mM)	Plant growth (height, primary branches, leaves, and total leaf area, fresh herb yield), chlorophylls, carotenoids, free proline levels, and basil leaf anatomy	Essential oil % & oil composition	• Spraying ascorbic acid at 300 ppm under all salinity stress levels significantly improved growth in fresh herb yield, where it was increased by 19.33%, 28.83%, and 63.77% under salinity 200 ppm, 300 ppm, and 600 ppm, respectively. • Photosynthetic pigments (Chl-*a*, Chl-*b* and carotenoids) also significantly increased compared to unsprayed stressed plants. In contrast, proline content gradually and significantly decreased when sprayed with 300 ppm ASA under all salinity levels. • Spraying basil plants with 300 ppm ascorbic acid in the presence of 6 000 ppm salinity stress enhanced volatile oil (%) and yield, where they increased by 18.75 and 94.48%, respectively. • Salinity stress at 600 ppm NaCl + spraying with 300 ppm ASA increased linalool by 18.32% and decreased neural and phenol (Iso-eugenol) by 8.13 and 15.80%, respectively, but there is no effect on geranial in volatile oil components compared to unsprayed stressed plants.	Nassar et al. (2019)
Ocimum *O. basilicum*	Drought (Optimal irrigation Medium tension and sever tension)	2 mM	plant height, number of leaves per plant, relative leaf water content, ion leakage. stomatal function, proline content, auxin and biological yield	Leaf essential oil %	• Drought significantly decreased biological yield by (36.38% under moderate water stress), plant height by (13.4%), number of leaves per plant (66.39%), relative leaf water content (61.67%), stomatal Function by (34.73) and auxin by (45.49%) under severe water stress. While it increased ion leakage by (31.19%), leaf essential oil by (67.63%) and proline contents by (169.26%) under severe water stress. • Foliar application of ASA at 2mM enhanced biological yield across all drought levels, with the highest effect (41.83%) recorded under moderate drought. • Plant height and number of leaves per plant improved by ASA treatment across all irrigation regimes with ratios ranging between (7.50–11.39%) and (4.96–11.11%), respectively. Where the highest effect recorded under moderate water stress. • ASA significantly increased the leaf water content by 14.94% and 5.01% under moderate and severe water stress, respectively. • Plants treated with ASA decreased ion leakage across all irrigation regimes with a ratio ranging between (4.05–5.02%). • Foliar application of ASA enhanced auxins concentration across all irrigation regimes, with the highest effect (15.49%) under moderate water stress. • Stomatal function and leaf essential oil improved by ASA application by a ratio ranging between (7.71–9.22%) and (10.2–13.49%) respectively with the highest effect under severe water stress. • Foliar ASA, applications decreased leaf proline contents across all irrigation regimes with a ratio ranging between 12.93–19.59%.	Hamidi et al. (2022)

https://doi.org/10.17221/83/2024-PPS

Table 4. to be continued...

Ocimum *O. sanctum*	Salinity stress (100mM NaCl)	Ascorbate acid (ASA) (0.1, 0.5 and 1.0 mM)	Peroxidase (POX) catalase (CAT), and superoxide dismutase (SOD), antioxidant activity and antimicrobial activity	Phenolic and flavonoids content	• ASA treatment (0.5 mM) enhanced CAT activity to alleviate the effect of salt stress by about 2.25 folds compared to control. • ASA treatment improved SOD activity across all concentrations, with the highest value of 66.1 units/mL recorded with 0.5mM ASA compared to salinity-stressed plants at 40.7 units/mL. • The plants treated with 0.1 mM, 0.5 mM, and 1mM ASA along with 100 mM NaCl gave a significant increase in the value of POD activity as 4.7, 5.8, and 4.8mg/g, respectively, compared to salinity-stressed plants 3.6 mg/g. • Flavonoid and phenolic contents improved by ASA application by a ratio ranging between (13.40–22.42%) and (2–25.3%) respectively, with the highest effect with 0.5 mM ASA compared to salinity-stressed plants. • Plants treated with 0.1 mM, 0.5 mM, and 1 mM ASA along with 100 mM NaCl showed a significant increase in the value of antioxidant activity as 51.67, 52.96, and 50.63%, respectively, compared to 40.03% recorded by salinity-stressed plants. • Antimicrobial activity of the plant extracts obtained from the plants were treated with 0.1 mM, 0.5 mM, and 1 mM ASA significantly increased the zone of inhibition by 1.15 cm, 2.12 cm, and 1.6 cm compared to the control (0.6); in contrast, it decreased by application of ASA along with 100 mM NaCl compared to salinity stressed plants (2.1 cm), except against *Staphylococcus aureus* (2.12 cm) observed in plants treated with 0.5 mM ASA.	Munir et al. (2021)
Satureja *S. hortensis*	Salinity stress (0, 25, 50, and 75 mM)	Ascorbate (0 and 4 mM)	Proline, protein, soluble and non-soluble carbohydrates	Not measured	• Ascorbate enhanced soluble carbohydrates, non-soluble carbohydrates, proline and protein for shoot and root under all salinity level up to 75 mM • The highest values of soluble carbohydrates were increased by 13.12% at 4 mM ascorbate × 25 mM salt and 64.78% at 4 mM ascorbate × 50 mM salt for shoot and root, respectively. While non-soluble carbohydrates were 59.27% at 4 mM ascorbate × 50 mM salt and 56.21% at 4 mM ascorbate × 75 mM salt for shoot and root, respectively. • The highest values of proline were increased by 27.32% at 4 mM ascorbate × 50 mM salt and 21.89% at 4 mM ascorbate × 75 mM salt for shoot and root, respectively. • The highest values of protein were increased by 121.19% and 92.23% both at 4 mM ascorbate × 75 mM salt for shoot and root, respectively.	Pazoki and Niki Esfahlan (2016)

salinity levels. It enhances the concentration of essential oil components like alpha-pinene and beta-pinene, which are crucial for plant aromatic and therapeutic properties (Golestani 2022). Plants adapt to salt stress through ion homeostasis, osmotic adjustment, and stress-responsive gene activation, enhancing plant resilience and essential oil quality under saline conditions (Kumari et al. 2019; Zhou et al. 2024).

Ascorbic acid (ASA) significantly increased vegetative growth, essential oil percentage, and oil yield in *Mentha piperita* under salinity stress. ASA, which contains menthol, menthone, 1,8-cineole, limonene, and menthyl acetate, was the most effective in reducing oxidative damage and protecting cellular components from oxidative damage. The menthol percentage varied depending on the stress level and ASA concentration applied to the plants. The highest menthol percentage was observed under severe drought stress with 200 mg/L ASA, possibly due to maturation processes and genetic factors affecting terpene biosynthesis. The study also found that the concentration of menthol in the second cut exceeded that in both the first and third cuts, possibly due to maturation processes or genetic determinants preventing the biosynthetic pathway. ASA also influenced the activity of enzymes involved in essential oil biosynthesis, leading to increased production of menthol and other components (Tausif 2015). Under severe stress, 200 mg/L ASA produced higher percentages due to its role in scavenging reactive oxygen species (ROS) and influencing enzymes involved in essential oil biosynthesis (Emami Bistgani et al. 2023). Ascorbic acid supports better water and nutrient uptake, improving vegetative growth (Lamsaadi et al. 2024). The highest menthol percentage was observed under severe drought stress with 200 mg/L ASA, possibly due to maturation processes and genetic factors affecting terpene biosynthesis (Silva et al. 2019). The mitogen-activated protein kinase pathway regulates essential oil metabolism under salinity stress (Li et al. 2016).

In *O. basilicum* plants, the application of ascorbic acid (ASA) at 2 mM significantly improved biological yield, plant height, leaf number, water content, ion leakage, auxins concentration, stomata function, and leaf essential oil under moderate and severe drought stress. However, leaf proline contents decreased due to increased auxin concentration, which supports cell elongation and division and reduces ion leakage by stabilizing cell membranes. It also increases the production of leaf essential oils, which play a role in stress adaptation (Mohammadi & Moradi 2013). ASA also helps regulate stomatal function, maintaining gas exchange and transpiration rates under stress (Eltayeb et al. 2006). Additionally, SA influences proline metabolism by modulating gene expression in proline biosynthesis and degradation. It enhances the expression of proline biosynthesis genes while downregulating ProDH, leading to increased proline accumulation under drought stress (La et al. 2019).

In *O. basilicum*, ascorbic acid spraying at 300 ppm under salinity stress improved growth and yield with increased photosynthetic pigments and proline content. Basil plants also showed increased volatile oil percentage and yield under 6 000 ppm salinity stress. Linalool increased by 18.32% under 600 ppm NaCl spraying with 300 ppm ASA. These results can be discussed as ASA application under salinity stress improves plant growth by enhancing antioxidant activity, which mitigates oxidative damage caused by stress (Munir et al. 2021). Proline is a compatible solute that accumulates in plant cells under osmotic stress, such as salinity and drought, helping to balance the osmotic potential between the cytoplasm and vacuole (Escalante-Magaña et al. 2024). AsA is a powerful antioxidant, protecting plant cells from reactive oxygen species (ROS) generated during photosynthesis under stress conditions. This protection helps maintain cellular redox homeostasis, crucial for sustaining photosynthetic efficiency (Mishra et al. 2024). The increase in linalool content suggests that ASA influences specific pathways involved in volatile oil biosynthesis. The decrease in neral and phenol content indicates a shift in the metabolic pathways, possibly due to ASA's role in modulating stress responses. The unchanged geranial content suggests that ASA's effect is selective, possibly due to the specific regulatory mechanisms involved in its biosynthesis (Alves et al. 2015).

O. sanctum, the exogenous application of ASA, significantly enhances the antioxidant potential of *O. sanctum* under salt-stress conditions. ASA application increases enzymatic antioxidant activities, including catalase, peroxidase and superoxide dismutase, crucial for scavenging ROS generated under salt stress. The highest catalase activities, peroxidase and superoxide dismutase are recorded with 0.5 mM ASA and 100 mM NaCl, indicating a robust antioxidant response (Munir et al. 2021). Additionally, it promotes the accumulation of beneficial compounds, including flavonoids (13.40–22.42%) and phenolics (6.67–25.3%). The antimicrobial activity of plants treated with ASA increased the zone of inhibition but decreased with ASA application along with 100 mM NaCl.

O. sanctum, ASA application significantly enhances the antioxidant potential under salt stress conditions. ASA increases enzymatic antioxidant activities, such as catalase, peroxidase, and superoxide dismutase, which are crucial for scavenging ROS generated under salt stress. The highest catalase, peroxidase, and superoxide dismutase activities are recorded with 0.5 mM ASA and 100 mM NaCl, indicating a robust antioxidant response. ASA also promotes the accumulation of beneficial compounds, including flavonoids and phenolics (Munir et al. 2021) ASA application has been shown to increase the activities of SOD and CAT, which are essential for the detoxification of superoxide radicals and hydrogen peroxide, respectively. This enhancement helps reduce oxidative damage in plants under stress conditions such as salt stress in peanut plants (Alves et al. 2022). Salt stress causes membrane depolarization, activat-

https://doi.org/10.17221/83/2024-PPS

ing ion channels and increasing electrolyte leakage. This can disrupt cellular homeostasis, leading to metabolic changes and cell death (Hryvusevich et al. 2022). Proline and glycine betaine are key osmoprotectants that accumulate in response to salt stress, stabilizing proteins and membranes, protecting cellular structures, and maintaining osmotic balance (Umar et al. 2018; Reddikavitha & Sathiavelu 2024). ASA can modulate these pathways, enhancing plants' ability to cope with salt-induced oxidative stress by scavenging reactive oxygen species and maintaining ion homeostasis. ASA also enhances antioxidant capacity, reducing oxidative stress and stabilizing cell membranes. The effectiveness of ASA in mitigating salt stress varies with its concentration, with optimal concentrations enhancing stress tolerance, while suboptimal levels may not provide significant benefits (Arif et al. 2020).

Ascorbate is a key antioxidant in *Satureja hortensis*, enhancing the accumulation of soluble carbohydrates, non-soluble carbohydrates, proline, and protein in plant shoots and roots under salinity stress up to 75 mM. It reduces oxidative stress by scavenging ROS, allowing for better maintenance of cellular functions and growth (Ali et al. 2014; Hamed & AbdElgawad 2018). Ascorbate also enhances the activity of antioxidase enzymes, protecting plant cells from oxidative damage (Al Othaimen 2015). Soluble carbohydrates, such as sucrose and glucose, are essential for osmotic adjustment and cellular structure protection (Gil Ortiz et al. 2011; Gil et al. 2013). Increasing soluble and non-soluble carbohydrates at 4 mM ascorbate × 50 mM salt is linked to enhanced carbohydrate metabolism and transport (Curtis et al. 1988; Ebrahim 2005; El-Sayed & El-Sayed 2013). Proline, an osmolyte, accumulates in plants under stress, providing osmotic balance and protecting cellular proteins and membranes (Sarkar & Roy 2021). Ascorbic acid can enhance proline synthesis or reduce degradation, improving stress tolerance (Ebrahim 2005; El-Sayed & El-Sayed 2013). Proteins, crucial in stress response, play a role in protein synthesis and degradation. The significant increase in protein content at 4mM ascorbate × 75 mM salt suggests that ascorbic acid may enhance protein synthesis or reduce degradation, supporting growth under adverse conditions (Ebrahim 2005; Abdel Fatah & Sadek 2020; Sarkar & Roy 2021).

CONCLUSION AND FUTURE ASPECTS

Conclusion. Abiotic stress, such as drought, salinity, extreme temperatures, heavy metals, chemical pollutants, and oxidative stress, produce excessive ROS, including hydroxyl radicals, superoxide radicals, hydrogen peroxide, and singlet oxygen. These ROS interact with cellular biomolecules like lipids, proteins, carbohydrates, and nucleic acids, causing structural and functional modifications. Abiotic stressors cause osmotic stress, ion toxicity, membrane disruption, loss of enzyme activity, and mutations ultimately affecting their physiological and biochemical processes that affect plant growth and development and significantly impact the growth and development of Lamiaceae plants. This review investigated the peer-reviewed papers using organic elicitors, such as organic acids, to improve plant resilience to abiotic stress published between 2015 and 2024. It discusses Lamiaceae plants' adaptive and signaling mechanisms and antioxidant defence systems, providing an understanding of how they cope with oxidative stress induced by abiotic factors. Lamiaceae plants have developed adaptive mechanisms to mitigate abiotic stress, including accumulating osmolytes, producing antioxidants, and enhancing secondary metabolite synthesis.

The signalling pathway of exogenous salicylic acid in response to abiotic stress was summarized in this review as a text and Figure 3. Salicylic acid that was sprayed on different stressed plants of Lamiaceae showed an enhancement in the plant growth parameters, total phenolic and flavonoid contents, total soluble sugars, proline, anti-oxidant enzymes, essential oil content, and essential oil compositions (Table 1). While the papers do not specify a toxic threshold for salicylic acid in Lamiaceae plants, the absence of reported toxicity at a range between 0.5 mM and 2.5 mM concentration suggests this level is safe. These concentrations enhanced the Lamiaceae plants regarding physiological, biochemical, and secondary metabolites, leading to acclimated plants with abiotic stress that exposed them. In contrast, *Mentha x piperita* was sprayed with minor SA concentration (10^{-3} mM) under salinity stress and showed a positive response. On the other hand, *Thymbra spicata* sprayed with a major concentration of SA (5 mM) under drought stress gave good results regarding essential oil content and its compositions. While salicylic acid is beneficial for enhancing certain plant properties, its application must be carefully managed to avoid potential toxicity. The concentration of SA that leads to toxicity can vary depending on the plant species and environmental conditions.

Jasmonic acid and its derivatives act as signalling molecules, regulating gene expressions in response to abiotic challenges such as salinity, drought, heavy metals, micronutrient toxicity, and low temperature, and they promote defensive mechanisms. The signalling pathway of Jas was explained in this review (Figure 4). Data in Table 2 indicated that two forms of Jasmonate (JA and MeJA) were used to explore the effect of these elicitors on tolerating Lamiaceae plants to drought and salinity stresses. The Lamiaceae family plants showed varying responses to MeJA, with *Mentha* × *piperita* showing no growth effect under drought stress and *Satureja khuzestanica* showing a good growth response under salinity stress. This may be attributed to the difference in plant species, stress, or low MeJA concentration used with the *Mentha* × *piperita*. Jasmonate derivatives enhanced the ability of plants to cop the abiotic stresses by increased photosynthetic pigments, antioxidant activity, soluble carbohydrate, decreased Na^+ and increased all the measured mineral elements such as Ca^{2+}, Mg^{2+}, P, N and K^+ accumulation, proline and some secondary metabolites as thymol. The limited studies on the relationship between jasmonate and Lamiaceae plants under environmental stress conditions hinder the accurate determination of the appropriate concentration of jasmonate.

Humic acid (HA) is a biostimulant that effectively mitigates various types of stress in plants, enhancing growth and physiological functions. It is particularly effective in abiotic stresses like salinity, drought, and heavy metal contamination, improving plant resilience and promoting better growth and yield under stress conditions. Exogenous humic acid signalling pathway through the abiotic stress was summarized and shown in Figure 5. Humic acid increased the growth of different plants belonging to Lamiaceae (Table 4). Total phenols, flavonoids and total soluble sugar, NPK, antioxidant enzyme activities, and secondary metabolites were significantly enhanced when using HA. The concentration and method of humic acid application play a crucial role in determining its effects. Higher concentrations or inappropriate application methods may lead to adverse effects, while optimal concentrations can enhance plant resilience to stress. The potential negative impacts of humic acid on plants under stress are not extensively documented.

ASA, commonly known for its antioxidant properties, is often used to mitigate plant stress. However, its application can sometimes have negative effects, particularly under certain stress conditions. ASA generally enhances plant tolerance to various abiotic stresses by modulating antioxidant systems and improving physiological functions. Figures 6 and 7 showed exogenous ascorbic as a co-factor and antioxident pathway through normal and abiotic stress conditions and exogenous ascorbic acid signalling pathway through the abiotic stress, respectively. Table 4 contains the summary of result papers from 2015 to 2024. It was noticed that different levels of ascorbic acid were used from 0.5 to 2.0 in most Lamiaceae plants except *Dracocephalum moldavica* it was 10 mM; all these ASA concentrations increased the morphological, physiological, biochemical, and secondary metabolites (Table 4). These effects may be due to the antioxidant properties of ASA, which helps detoxify ROS, thereby protecting plant cells and maintaining cellular homeostasis. The application of exogenous ASA has been shown to bolster the antioxidant system, improve photosynthesis, and enhance overall plant resilience under stress conditions.

Further research is needed to understand the impact of Nano-SA, JA, HA ASA, and citric acid on Lamiaceae plants under various environmental stress conditions. There are limited studies on the relationship between jasmonate/humic acid and Lamiaceae plants under environmental stress conditions. Since vitamins such as ascorbic acid are essential for plant metabolism and growth regulation, their effect on these plants remains unstudied at concentrations between 2 mM and 10 mM under different abiotic stresses. The Lamiaceae family needs more studies on the possibility of its adaptation to difficult environmental conditions by treating it with natural products and conducting research that includes two or more types of natural stimulants. This family, Lamiaceae, also needs further studies on the toxicity resulting from the use of stimulants to confront difficult environmental conditions. By exploring the effects of abiotic stress and potential mitigation strategies, the paper contributes to improving agricultural practices, particularly in regions where Lamiaceae plants are cultivated under challenging environmental conditions. Nanotechnology can enhance agricultural productivity by improving nutrient uptake, stress tolerance, and photosynthesis efficiency, but it can also cause toxicity, affecting plant health and the environment. Therefore, there is an urgent need to conduct studies on the toxicity of using nanotechnology in plant nutrition.

Acknowledgement:

Supported by the Deanship of Scientific Research at Northern Border University, Arar, KSA, for funding this research work through the project number "NBU-FFR-2025-860-01".

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Received: May 24, 2024
Accepted: February 3, 2025