

Jasmonic Acid Signaling in Environmental Stress Adaptation of Horticulture Crops

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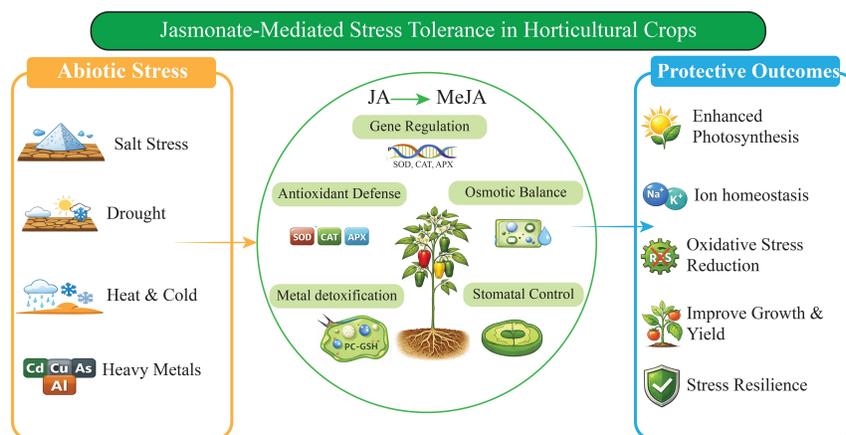
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Highlights

- Jasmonates integrate molecular and physiological defenses to enhance stress tolerance.
- JA and MeJA improve salinity, drought, temperature, and heavy metal tolerance in crops.
- Advanced delivery, breeding, and systems biology are key for JA-based climate-smart horticulture.

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Graphical Abstract



Abstract

Jasmonic acid (JA) and its derivative methyl jasmonate (MeJA) are central lipid-derived signaling molecules that regulate plant growth and stress acclimation. Under abiotic stresses commonly encountered in horticultural production, such as salinity, drought, temperature extremes and heavy metal toxicity. JA accumulation via the octadecanoid pathway and conversion to the bioactive conjugate jasmonoyl-isoleucine (JA-Ile) activate the SCFCOII–JAZ core signaling module. The activation releases transcription factors to coordinate downstream defense and acclimation responses. At the physiological level, exogenous application of JA or MeJA frequently enhances stress tolerance by strengthening antioxidant and glyoxalase systems; promoting osmotic adjustment through the accumulation of proline, soluble sugars and other compatible solutes; maintaining ion homeostasis, modulating stomatal behavior and water-use efficiency, stabilizing cellular membranes and the photosynthetic apparatus; and enhancing detoxification and sequestration processes during metal stress. Moreover, JA extensively interacts with other phytohormones, including abscisic acid (ABA), salicylic acid (SA), ethylene, and brassinosteroids, forming context-dependent hormonal networks that balance growth and defense, ultimately influencing crop yield and quality. In this review, we integrate recent evidence on JA-regulated mechanisms in horticultural crops and propose a conceptual framework that links JA signaling modules to core physiological responses across diverse stress conditions. We also identify key knowledge gaps, including the optimization of dose and timing under field and combined-stress scenarios, cultivar-specific sensitivity to JA, and the need to integrate omics-level markers with agronomic performance. Addressing these challenges will facilitate the rational application of jasmonates to enhance climate resilience in horticultural crops.

Keywords: Climate Change, Abiotic Stresses, Horticultural Crops, Metabolic Functions, Phytohormone

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1. Introduction

Plant hormones play critical roles in regulating growth and quality in horticultural crops and in enabling plants to cope with abiotic stresses such as salinity, drought, temperature extremes, and heavy metals (Rao et al., 2019). These stress responses involve coordinated changes in gene expression, modulation of primary and secondary metabolism, synthesis of stress-responsive proteins, activation of hormonal signal transduction pathways, and enhancement of antioxidant defense systems (Chaudhry and

Sidhu, 2022). At the molecular level, phytohormones are central regulators of gene expression, representing a fundamental mechanism underlying plant physiological processes. This diverse group of naturally occurring compounds includes auxins, gibberellins, cytokinins, abscisic acid, jasmonic acid (JA), salicylic acid (SA), and ethylene, among others (Santner et al., 2009). Although phytohormones have traditionally been recognized for their roles in controlling plant growth and development (Gray, 2004), accumulating evidence highlights their indispensable functions in coordinating complex signal transduction networks during abiotic stress responses, thereby contributing to improved growth, yield, and stress

resilience of horticultural crops (Table 1) (Muhammad et al., 2022).

Methyl jasmonate (MeJA) and JA, collectively referred to as jasmonates (JAs), have attracted considerable attention due to their multifaceted roles in horticultural crop management (Fig. 1). Exogenous application of JAs has been shown to regulate key developmental and physiological processes, including tuber formation, pigment metabolism, and stress adaptation. For example, foliar application of JA enhances sugar beet productivity and improves tolerance to various abiotic stresses (Koda, 1992). Exogenously applied JAs can also modulate endogenous phytohormone levels, triggering a signaling cascade that amplifies plant defense and stress-responsive mechanisms. Moreover, MeJA treatment has been reported to enhance oxidative defense by upregulating antioxidant metabolites, thereby improving drought tolerance in cauliflower (Meyer et al., 1984). Collectively, these findings indicate that JA-based foliar applications can effectively enhance yield and stress resilience in fruit and vegetable crops across diverse horticultural production systems.

In horticultural crops, jasmonates function as critical defensive signaling molecules against a broad spectrum of environmental challenges. These compounds provide particular protection to crops grown under extreme drought and salinity conditions, making them valuable tools for managing climate-related risks in horticultural production systems (Raza et al., 2021). Accumulating evidence suggests that JA-mediated defense mechanisms have evolved as adaptive responses to diverse environmental stresses, including waterlogging stress in pepper plants (Yun-xia et al., 2010). In the context of the increasing frequency and intensity of climate extremes, JAs exhibit substantial potential as protective agents for enhancing the resilience and sustainability of horticultural crops (Ruan et al., 2019). The involvement of both endogenous and exogenously applied JA and its derivatives in plant defense mechanisms under abiotic stress conditions has been extensively investigated (Xing et al., 2020). Plant cells maintain dynamic concentrations of multiple phytohormones, and fluctuations in these levels are closely associated with differential expression of genes involved in hormone biosynthesis and the downstream regulatory pathways they control under both stress and non-stress conditions. Numerous studies have demonstrated that JA plays a central role in mediating plant responses to environmental challenges, including salinity, heavy metal toxicity, and water deficit (Cohen et al., 1993). Foliar application of JA under saline conditions significantly enhances crop salt tolerance and reduces salt accumulation in both roots and leaves. These effects are attributed to increased tonoplast H⁺-ATPase activity and alterations in root system architecture, which together contribute to improved ion compartmentalization and maintenance of cellular redox homeostasis (Munné-Bosch et al., 2007). Furthermore, a strong correlation between endogenous JA levels and abiotic stress tolerance has been well documented across plant species (Fig. 2) (Riemann et al., 2015).

To ensure sustainable crop productivity under increasingly harsh environmental conditions, plant scientists emphasize the development of integrated management strategies that incorporate stress-mitigation technologies. Among the available approaches, the exogenous application of phytohormones has emerged as a promising strategy for alleviating the adverse effects of abiotic stresses on vegetable production systems. Phytohormones have received considerable research attention due to their multifunctional roles in mediating plant responses to diverse environmental stresses and their demonstrated effectiveness in enhancing yield and resilience of horticultural crops under stress conditions. In this review, we critically examine the application and underlying mechanisms of phytohormones, with particular emphasis on jasmonates, in horticultural crops exposed to multiple environmental stresses. We further provide comprehensive insights into the physiological, biochemical, and molecular reprogramming processes that enable plants to withstand climate-related extremes.

2. Impact of Environmental Stresses on Horticultural Crops

Jasmonates, comprising JA and MeJA, are multifunctional signaling

compounds that regulate both plant developmental processes and stress responses. Beyond their well-established roles in growth regulation, JAs orchestrate a wide range of physiological processes, including photosynthesis, root elongation, stomatal development, leaf senescence, chlorophyll metabolism, and nutrient homeostasis (Fig. 2) (Peña-Cortés et al., 2004). The pivotal role of JA in mediating stress tolerance and plant adaptability has been extensively documented across diverse plant species, with substantial evidence demonstrating that JA application enhances resistance to multiple environmental stressors.

Recent studies highlight the broad-spectrum protective effects of JA across various stress conditions and horticultural crops. Under cold stress, exogenous MeJA application enhances cold tolerance in peach by maintaining reactive oxygen species (ROS) homeostasis and upregulating antioxidant defense systems (Meyer et al., 1984). Similarly, JA treatment strengthens antioxidant defense mechanisms in grape seedlings exposed to high-temperature stress. In sugar beet, JA supplementation significantly improves productivity by enhancing antioxidant enzyme activity and increasing tolerance to water stress. MeJA treatment in pomegranate markedly elevates secondary metabolite accumulation and antioxidant enzyme activity while alleviating chilling injury symptoms (Ghasemi Pirbalouti et al., 2014). Likewise, MeJA application to loquat fruit under cold stress effectively reduces chilling injury and enhances antioxidant enzyme activity (Fan et al., 1997). Under saline conditions, JA application improves growth traits, proline accumulation, and metabolite content while reducing oxidative damage in bitter melon (Fan et al., 1997). Furthermore, low-dose MeJA treatment significantly reduces lipid peroxidation, as indicated by decreased malondialdehyde (MDA) levels, while promoting root development, enhancing antioxidant enzyme activity, and maintaining chlorophyll content in chili plants exposed to cadmium stress (Noor et al., 2015; Awang et al., 2013). In addition, MeJA pretreatment induces substantial increases in antioxidant capacity in strawberry seedlings subjected to salt stress.

Comprehensive studies across a wide range of horticultural species have demonstrated the multifaceted roles of JA in mitigating the adverse effects of abiotic stresses through diverse physiological mechanisms. These include promotion of vegetative growth in eggplant, enhancement of seed germination in okra, stimulation of pigment biosynthesis in strawberry, optimization of stomatal conductance and leaf gas exchange in cauliflower, increased accumulation of osmolytes in tomato, suppression of ROS production in *Malus crabapple*, and reduction of heavy metal uptake and translocation in several horticultural crops. Among the jasmonates, JA is the most extensively studied, best characterized, and most abundant naturally occurring form. It plays a central regulatory role in activating defense mechanisms in horticultural crops exposed to a broad spectrum of abiotic stresses, including drought, salinity, temperature extremes (both heat and cold), alkalinity, and heavy metal toxicity (Zhu et al., 2014).

Previous research has further revealed that under abiotic stress conditions, JA regulates multiple physiological and biochemical processes, such as growth enhancement in eggplant, improved seed germination in okra, increased pigment accumulation in strawberry, improved leaf gas exchange and antioxidant defense capacity in cauliflower, elevated osmolyte content in tomato, reduced ROS generation in *Malus crabapple*, and decreased heavy metal accumulation in numerous horticultural crops (Raza et al., 2021). In citrus fruits, MeJA treatment modulates phenolic metabolism and upregulates antioxidant enzyme activity, collectively leading to a reduction in chilling injury severity. Similarly, JA application significantly enhances proline biosynthesis and antioxidant enzyme activity while alleviating ROS-induced oxidative damage under stress conditions (Du et al., 2021).

3. Crosstalk between jasmonic acid and environmental stresses

Decades of research on phytohormonal dynamics under abiotic stress have revealed highly complex and often context-dependent responses. A single phytohormone may enhance stress adaptation under certain conditions while impairing stress tolerance under others, depending on factors such as

stress intensity and duration, plant developmental stage, and interactions with other signaling pathways (Table 2). These findings suggest that phytohormones primarily function as integrators of multiple upstream signals rather than acting as primary stress sensors (Amiard et al., 2007).

Accordingly, a comprehensive understanding of upstream signaling networks is critical for elucidating JA-mediated stress responses and their physiological outcomes in horticultural crops (Table 3).

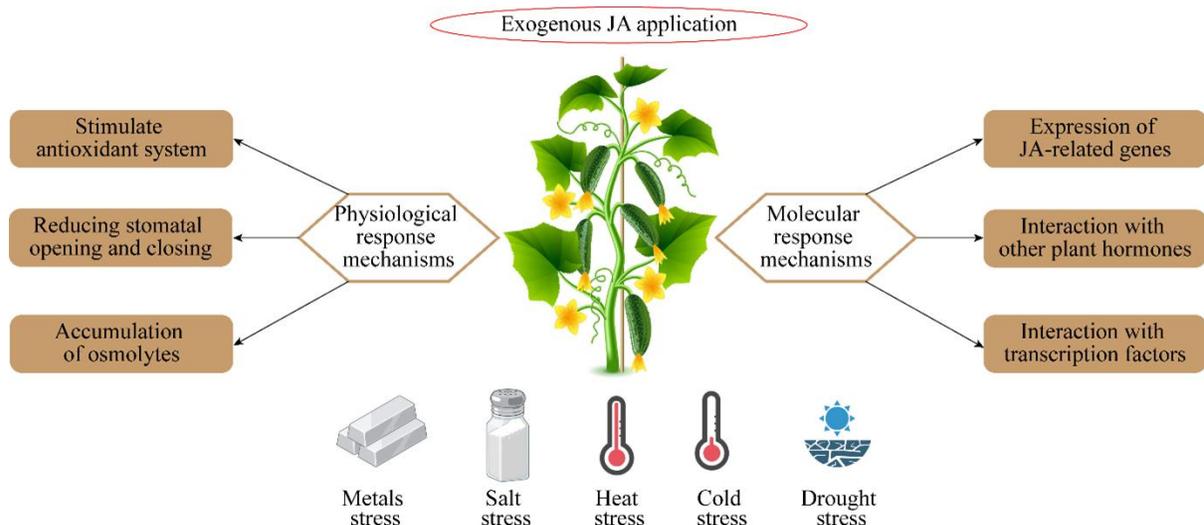


Fig. 1. Exogenous application of jasmonic acid enhanced physiological and molecular mechanisms in plants under abiotic stress conditions.

Table 1. Adverse effects of abiotic stress on sustainable production of horticultural crops.

Stress types	Horticultural crops	Key impacts	References
Heat	Strawberry (<i>Fragaria × ananassa</i>)	The physiological, biochemical, and molecular basis were disturbed due to abiotic stressors	(Gulen & Eris, 2004)
Drought and cold	Apple rootstocks (<i>Malus domestica</i>)	The Myb4 transcription factor was expressed ectopically, which altered metabolite accumulation and improved physiological and biochemical response to cold and drought stress. Based on these findings, it may be worthwhile to use Osmyb4 as a strategy to increase woody perennial productivity under stressful environmental circumstances.	Pasquali et al., (2008)
Salinity	Cucumber (<i>Cucumis sativus</i>)	The use of 50 mM NaCl, which may be controlled by spraying various phytohormones on vegetable crops, had a negative effect.	Duan et al., (2008)
Cold	Pear (<i>Pyrus communis</i>)	A thorough examination of the Chinese white pear revealed the bHLH genes for the first time and showed that PbrbHLH195 is involved in the formation of ROS in response to cold stress, indicating that members of the PbrbHLH family are crucial to the pear's ability to withstand stress.	Dong et al., (2021)
Salinity	Lettuce (<i>Lactuca sativa</i>)	Because salinity inhibited plant productivity, lettuce performance suffered from adversities occurring abiotic stresses.	Babaousmail, M., et al., (2022)
Cd toxicity	Tomato (<i>Solanum lycopersicum</i>)	The relative leaf water capacity of vegetables may be decreased by the overexpression of several genes, including StJAZ1.	Jing et al., (2022)
Heat	Peppers (<i>Capsicum annum</i>)	Extreme temperature is a crucial factor in the denaturation of proteins, which affects optimal production and development. Adoptive mechanisms are required for the alleviation of problems brought on by heat stress in plants.	Gisbert-Mullor et al., (2021)
Drought	Cucumber (<i>Cucumis sativus</i>)	Drought triggers osmotic and oxidative stress, leading to reduced growth and yield and altered defense-related activities in cucumber.	Liu et al., (2016)
Chilling	Mango (<i>Mangifera indica</i>)	There was a suggestion that the effect of oxalic acid or SA on mango CI ⁻ was likely due to ascorbate and glutathione having a higher reducing status, which led to less O ₂ buildup and more H ₂ O ₂ accumulation.	Ding et al., (2007)
Drought	Potato (<i>Solanum tuberosum</i>)	Electrolyte leakage, lipid peroxidation, and MDA were increased. Phytohormones can effectively lower lipid peroxidation and MDA generation.	Abou El-Yazied et al., (2022)
Heat	Date palm (<i>Phoenix dactylifera</i> L.)	Date palm seedlings experience stress in the hot summer months, increase ROS in the atmosphere	Du et al., (2019)

3.1. Jasmonic Acid and Salinity

Endogenous phytohormones function as pivotal signaling mediators that orchestrate plant stress responses, extending well beyond their classical

roles in growth regulation. These low-molecular-weight signaling molecules influence nearly all aspects of plant growth, development, and stress adaptation through distinct yet highly interconnected signaling pathways (Tavallali and Karimi, 2019). Phytohormonal regulatory networks are characterized by extensive crosstalk, whereby individual hormones modulate

multiple physiological processes, and different hormones converge to co-regulate specific stress and developmental responses. As such, phytohormones are indispensable for coordinating plant growth, development, and defense mechanisms against both biotic and abiotic stresses (Riemann et al., 2015). Consequently, the strategic manipulation of phytohormonal signaling represents a promising avenue for enhancing stress resilience and sustainability in horticultural production systems. Under saline conditions, osmotic stress induces rapid calcium influx, which is further exacerbated by ionic stress resulting from excessive sodium accumulation. Sodium ions primarily enter plant cells through non-selective cation channels located in the plasma membrane (Kaya et al., 2009). Comparative analyses of salt-tolerant and salt-sensitive grapevine cell lines have demonstrated that effective salt adaptation is closely associated with rapid intracellular Na⁺ compartmentalization, indicating that concurrent increases in cytosolic calcium and sodium concentrations act as key early signals triggering adaptive responses. The Salt Overly Sensitive (SOS) signaling pathway integrates these cytosolic Na⁺ and Ca²⁺ signals and activates Na⁺ efflux mechanisms to re-establish ion homeostasis. Although salt and drought stresses share several adaptive responses, such as osmolyte accumulation and stomatal closure, salt stress also induces distinct, ion-specific mechanisms. These include sodium extrusion via the plasma membrane SOS1 Na⁺/H⁺ antiporter and vacuolar sequestration through tonoplast NHX exchangers, which together contribute to the restoration of cellular turgor and facilitate growth recovery under saline conditions (Sadeghipour, 2017).

Salt stress induces a substantial accumulation of endogenous JA in plant tissues, particularly in leaves, and increasing evidence indicates that this elevation plays a protective role against salinity-induced damage. Exogenous JA application mitigates salt-induced reductions in carbon fixation and protein synthesis in pea and alleviates growth inhibition in rice (Tang et al., 2020). Similarly, foliar JA application markedly reduces visible salt toxicity symptoms and improves seedling vigor in soybean. Proteomic analyses of JA-treated rice seedling roots have revealed the upregulation of several defense-related proteins, including cationic peroxidases, pathogenesis-related proteins (PR-1 and PR-10), and other salt-responsive proteins, collectively contributing to enhanced salt tolerance. In pea plants, JA treatment alleviates salt toxicity by sustaining CO₂ assimilation, maintaining metabolic activity, and preserving photosystem II efficiency, as reflected by stable Fv/Fm ratios.

Exogenous JA application further enhances potassium uptake and retention under saline conditions while simultaneously stimulating antioxidant enzyme activity and reducing membrane lipid peroxidation. In soybean, JA treatment modulates nutrient partitioning by promoting nitrogen uptake in roots, which is associated with reduced seed protein content but increased sulfur accumulation in foliage (Labiad et al., 2021). JA also activates the shikimate biosynthetic pathway, leading to increased accumulation of sulfur-containing amino acids (methionine and cysteine) and aromatic amino acids (phenylalanine and tyrosine) in seeds. Recent studies demonstrate that foliar JA application under salinity significantly increases total oil content and enhances the conversion of oleic acid to polyunsaturated fatty acids, such as linoleic and linolenic acids, via activation of lipoxygenase pathways. This shift elevates the fatty acid unsaturation index and improves the nutritional quality of soybean oil (Hassini et al., 2017). At the cellular level, foliar JA application enhances vacuolar H⁺-ATPase activity in root tonoplasts, thereby facilitating Na⁺ sequestration into vacuoles and reducing cytosolic sodium concentrations in soybean plants. Likewise, MeJA application to salt-stressed pea plants alleviates ionic toxicity, restores photosystem II efficiency (Fv/Fm), and recovers photosynthetic carbon assimilation rates (Aghdam and Bodbodak, 2013).

Although JA is well recognized for its role in regulating ion homeostasis under saline conditions, the precise molecular crosstalk between JA signaling and the Salt Overly Sensitive (SOS) pathway in horticultural crops remains poorly understood. Future research should focus on elucidating

how JA regulates key ion transporters, such as NHX and HKT family members, particularly in graft-compatible rootstocks used for vegetable production. Such insights could facilitate the development of grafted cultivars with enhanced salt exclusion capacity. In addition, a deeper understanding of the trade-offs between JA-mediated growth inhibition and salt tolerance mechanisms is essential to optimize JA-based strategies for practical, large-scale horticultural applications.

3.2. Jasmonic Acid and Drought

Drought represents a major constraint to global crop productivity, with particularly severe impacts when it occurs during reproductive development and grain-filling stages, commonly referred to as terminal drought. Terminal drought negatively affects grain set, grain-filling rate and duration, final yield, and quality attributes, with the extent of yield loss largely determined by the timing, duration, and severity of water deficit (Kondo, 2022). Consequently, the development of effective crop management strategies to enhance drought resilience requires a comprehensive understanding of the physiological and molecular responses associated with terminal drought stress. Recent advances in elucidating the molecular and physiological bases of drought responses have facilitated the development of drought-resilient wheat varieties. In particular, progress in high-throughput sequencing, molecular marker development, and genomic analysis has enabled the identification and manipulation of key components underlying drought tolerance.

Table 2. Physiological and molecular functions of jasmonates in enhancing horticultural crop performance and stress resilience.

Functions	References
Normalize stomatal progress	Munemasa et al., (2007)
Well-adjusted redox homeostasis	Zeng et al., (2024)
Cell extension and elongation	Gambetta et al., (2020)
Adjust seed germination	Pan et al., (2020)
Threatened photosynthetic scheme	Yu et al. (2022)
Upregulate antioxidant enzymes system	Admassie et al., (2022)
Flower and fruit progress	Pressman et al., (2002)
The improved mineral nutrient buildup	Jangid and Dwivedi., 2016
Adjust root architecture arrangement	Jing et al., (2022)
Boost abiotic stress tolerance	Raza et al., (2021)
Regulations in timely fruit ripening	Mesa et al., (2022)
Boosted secondary metabolites buildup	Hassini et al., (2017)

Drought-induced stomatal closure leads to sustained reductions in CO₂ uptake, representing a primary limitation to photosynthesis under water-deficit conditions (Wang et al., 2020a). Recent reviews have integrated hormonal regulation into stomatal signaling frameworks that operate during drought stress (Rhaman et al., 2025). Reduced gas exchange, coupled with degradation of photosynthetic pigments, collectively impairs plant growth and productivity. Although species-specific responses exist, drought universally restricts vegetative growth, developmental progression, biomass accumulation, and final yield. In rain-fed agricultural systems, enhanced root water extraction capacity and efficient hydraulic conductance from roots to shoots are strongly associated with improved drought tolerance and sustained biomass production (Fig. 3) (Gao et al., 2004). Plant water status under drought conditions is governed by the integration of multiple factors, including root system architecture, hydraulic conductivity, and stomatal regulation.

Carotenoids play multifaceted roles in drought tolerance by contributing to photoprotection, light harvesting, and antioxidant defense against drought-induced oxidative stress (Ali and Baek, 2020). In addition, abscisic acid serves as a central regulator of cellular and stomatal responses essential for drought adaptation. Despite extensive research, key questions remain

regarding how plants perceive drought signals, transmit these signals across cellular compartments, and precisely regulate ABA biosynthesis and accumulation to fine-tune stress tolerance while minimizing growth penalties (Chen et al., 2020). Membrane mechanical tension serves as the primary physical signal initiating drought stress perception. Osmotically induced turgor loss increases membrane tension, which is detected by mechanosensitive ion channels, an evolutionarily conserved sensing mechanism present in both prokaryotic and eukaryotic cells. Activation of mechanosensitive channels triggers rapid calcium influx in plant cells (Lim et al., 2015). Notably, this mechanosensing-calcium signaling mechanism is not

exclusive to osmotic stress but serves as a general stress perception system responsive to diverse stimuli, including mechanical touch, gravitropism, wounding, and cold stress. Until recently, the molecular identity of plant mechanosensitive channels remained elusive (Kouhen et al., 2023). The recent identification of OSCA1 (*Arabidopsis thaliana* osmotic stress-activated *thaliana* osmotic stress-activated calcium channel 1) as a hyperosmolarity-gated Ca²⁺ channel represents a major breakthrough in understanding membrane-based osmotic stress perception. Upon activation, Ca²⁺ influx triggers calcium-dependent protein kinases (CPKs/CDPKs),

Table 3. Summary of exogenous JA/MeJA applications enhancing abiotic stress tolerance across diverse horticultural crops.

Scientific Name	Stress Type	Key Physiological/Molecular Mechanisms	Reference
<i>Solanum lycopersicum</i>	Heat	Modulation of heat shock proteins (HSPs); protection of photosynthetic apparatus	He et al., (2025)
<i>Solanum lycopersicum</i>	Cold	Improved membrane stability; reduction of electrolyte leakage	Ding et al., (2022)
<i>Brassica oleracea var. italica</i>	Salinity	Upregulation of secondary metabolites; enhanced proline accumulation	Zaghoud et al., (2012)
<i>Capsicum annuum</i>	Drought	Promotion of root growth; stomatal regulation	Admassie et al., (2022)
<i>Capsicum annuum</i>	Cadmium	Chelation of metal ions; reduced translocation from root to shoot	Mozafariyan et al., (2014)
<i>Vitis vinifera</i>	Drought	Maintenance of cell turgor; modulation of aquaporin expression	Gambetta et al., (2020)
<i>Raphanus sativus</i>	Cadmium	Improvement of seed germination; DNA protection	Dentato et al., (2025)
<i>Lactuca sativa</i>	Salinity	Enhancement of nitrogen metabolism; increased chlorophyll content	Benito et al., (2024)
<i>Morus</i> spp.	Cadmium	Activation of phytochelatin synthesis; vacuolar sequestration of Cd	Fan et al., (2018)
<i>Ziziphus jujuba</i>	Salinity	Enhanced antioxidant enzyme activity; improved osmotic adjustment	Abudoukayoumu et al., (2025)
<i>Ziziphus</i> spp.	Salinity	Regulation of ion homeostasis; reduction of ROS accumulation	Singh et al., (2022)
<i>Brassica oleracea var. italica</i>	Salinity	Upregulation of secondary metabolites; enhanced proline accumulation	Zaghoud et al., (2012)

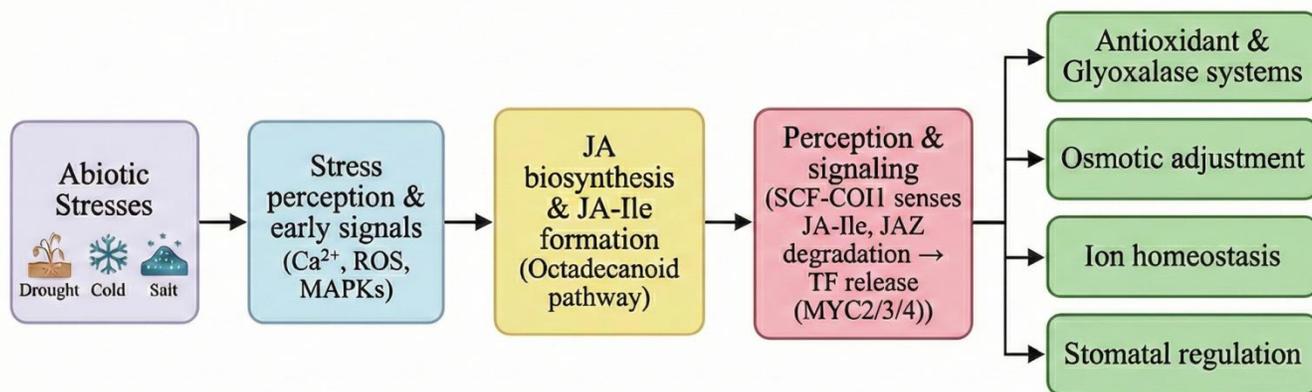


Fig. 2. Mechanistic overview of jasmonate-mediated abiotic stress tolerance in horticultural crops. Abiotic stresses induce early Ca²⁺/ROS/MAPK signals and activate JA biosynthesis (octadecanoid pathway) and JA-Ile formation. JA-Ile is perceived by the SCFCOII-JAZ core module, releasing transcription factors (e.g., MYC2/3/4) that regulate antioxidant/glyoxalase systems, osmotic adjustment, ion homeostasis, and stomatal regulation, ultimately improving stress tolerance, yield and quality.

which subsequently activate the NADPH oxidase RBOHD, leading to a transient oxidative burst and the production of apoplastic ROS, including superoxide and hydrogen peroxide (Takahashi et al., 2018). At the molecular level, drought adaptation involves the biosynthesis of compatible osmolytes such as proline, glycine betaine, and soluble sugars, which facilitate osmotic adjustment and turgor maintenance. In parallel, the accumulation of late embryogenesis abundant (LEA) proteins prevents protein aggregation and preserves cellular protein integrity under water-deficient conditions. At the

whole-plant scale, rapid abscisic acid mediated stomatal closure constitutes a critical water-conservation mechanism that minimizes transpirational water loss.

Beyond its role in stress responses, JA regulates a broad range of developmental processes across plant species, including tendril coiling in climbing plants, pollen development and viability, and fruit ripening and senescence (Mahajan and Tuteja, 2005). Phytohormones generally operate through complex regulatory networks characterized by extensive crosstalk at

multiple signaling levels. Such interconnected pathways allow plants to integrate environmental cues with intrinsic developmental programs, thereby coordinating adaptive responses to adverse conditions (Zheng et al., 2022). Jasmonates are synthesized via the oxidative degradation of membrane-derived polyunsaturated fatty acids, primarily α -linolenic acid, through the octadecanoid pathway. As ubiquitous plant growth regulators, JAs are widely distributed across diverse plant taxa (Anand et al., 2019). They interact both synergistically and antagonistically with other phytohormones, including ABA, SA, ethylene, and auxins, to fine-tune plant growth, development, and

stress responses. JAs also influence seed germination and dormancy through multiple regulatory mechanisms. Under water-stress conditions, exogenous JA application can inhibit seed germination in several species, including tomato, likely through modulation of the ABA-gibberellin (GA) hormonal balance. However, a comprehensive understanding of JA-mediated regulation of abiotic stress responses during distinct phases of seed germination remains incomplete and warrants further investigation (Liu et al., 2022). Recent work by Hoque et al., (2024) further emphasizes that exogenous phytohormone application enhances abiotic stress tolerance in crops by

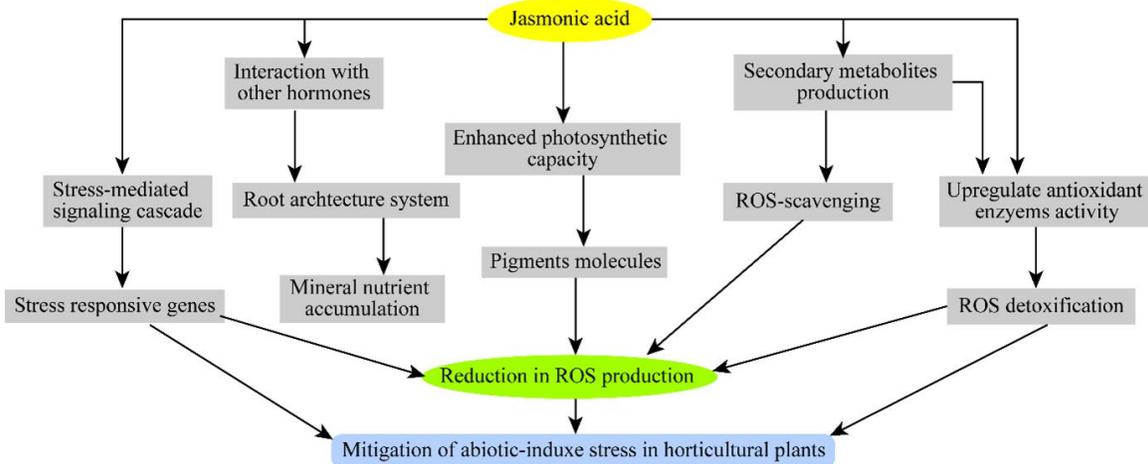


Fig. 3. JA-mediated regulatory networks enhancing abiotic stress tolerance in horticultural crops. JA biosynthesis, signaling cascade, and downstream physiological responses, including antioxidant activation, osmotic adjustment, and stress-responsive gene expression.

improving photosynthetic performance, increasing antioxidant enzyme activities, reducing oxidative damage, and regulating stress-responsive gene expression, thereby reinforcing multiple physiological and biochemical pathways that sustain growth under adverse conditions.

Current understanding of JA function in drought stress has largely focused on its role in regulating stomatal closure. However, the involvement of JA in modulating root hydraulic conductivity and root system architecture (RSA) plasticity under terminal drought conditions remains insufficiently explored. Future research should prioritize the identification of JA-responsive transcription factors that regulate deep-rooting traits, particularly in perennial fruit crops. In addition, potential interactions between JA signaling and hydraulic signaling components, such as CLE peptides, merit detailed investigation to better understand how plants coordinate above- and below-ground drought adaptation mechanisms.

3.3. Jasmonic Acid and Temperature

Extreme temperatures, including both heat and cold stress, represent major abiotic constraints that substantially reduce crop productivity in agricultural systems worldwide. Rising global temperatures pose serious risks to agricultural sustainability, with documented yield losses in numerous horticultural crops threatening global food and nutritional security (Wong et al., 2015). Climate projections indicate that tropical and subtropical regions will experience the most severe impacts of heat stress, as temperature increases are expected to exceed the thermal tolerance thresholds of many crops. Heat stress triggers extensive transcriptional reprogramming, activating multiple stress-responsive pathways, most notably the induction of heat shock proteins (HSPs). These specialized molecular chaperones prevent protein denaturation and aggregation, and their accumulation represents a primary mechanism underlying plant thermotolerance (Lastochkina et al., 2022). This evolutionarily conserved heat shock response has been documented across diverse plant species, underscoring its fundamental role in heat stress adaptation.

Studies in *Arabidopsis* and other plant systems have identified JA signaling as a critical component of heat tolerance mechanisms. Heat stress

induces rapid JA biosynthesis, which subsequently activates downstream protective responses (Venkatachalam and Meenune, 2015). Electrolyte leakage assays demonstrate that foliar application of low concentrations of JA helps maintain membrane integrity and cellular viability in heat-stressed plants (Jin et al., 2009). Moreover, exogenous JA modulates the expression of heat-responsive genes, including those encoding HSPs, thereby enhancing plant thermotolerance (Table 4). In contrast, horticultural crops originating from tropical and subtropical regions are particularly susceptible to chilling injury (CI) during cold storage, posing major postharvest challenges (Shi et al., 2019). CI symptoms in tropical fruits commonly include surface pitting and browning, abnormal firmness, off-flavor development, and accelerated senescence. Exogenous application of MeJA has been shown to effectively mitigate CI symptoms in a range of tropical fruits, including papaya, mango, avocado, bell pepper, and pineapple. JA-mediated protection involves the induction of multiple defense-related compounds, such as proteinase inhibitors, antimicrobial phytoalexins, antioxidant enzymes, pathogenesis-related (PR) proteins, and transcription factors associated with detoxification and ion homeostasis (Ding et al., 2002). In pineapple, MeJA application at concentrations of 0.3 and 0.6 mM significantly reduces CI incidence and electrolyte leakage compared with untreated controls.

Chilling-induced browning in fruits is largely attributed to the oxidation of accumulated phenolic compounds by polyphenol oxidase (PPO). MeJA treatment modulates phenolic metabolism and suppresses PPO activity, thereby preventing enzymatic browning and preserving fruit visual quality (Sangprayoon et al., 2019). Similar protective effects of MeJA against chilling injury have also been reported in mango fruit (Rohwer and Erwin, 2008). For heat stress, a key research priority is to elucidate the synergistic interactions between JA signaling and established thermotolerance regulators, particularly Heat Shock Factors (HSFs), to better understand how JA integrates into core heat stress transcriptional networks. With respect to cold stress especially chilling injury in tropical and subtropical fruits future studies should focus on optimizing the timing and dosage of exogenous JA application to maximize stress “priming” effects without inadvertently accelerating fruit senescence. Determining species-specific concentration thresholds that balance enhanced cold tolerance with maintenance of fruit

quality remains a critical challenge for the practical implementation of JA-based postharvest management strategies.

3.4. Jasmonic Acid and Heavy Metals

Certain heavy metal ions, including iron (Fe), copper (Cu), zinc (Zn), and manganese (Mn), are essential micronutrients required in trace amounts for fundamental metabolic processes such as respiration, photosynthesis, and enzyme catalysis. Soil pH, organic matter, and metal speciation largely determine how readily metals are taken up by plants and whether they have beneficial or toxic effects. Excessive accumulation of heavy metals results in pronounced phytotoxicity, manifested as growth inhibition, premature senescence, chlorosis, impaired photosynthesis, and oxidative stress (Chen et al., 2021).

Cadmium and copper toxicity have been shown to induce JA accumulation in *Arabidopsis thaliana* through the upregulation of lipoxygenase (LOX) activity, a key rate-limiting enzyme in JA biosynthesis. Low-dose MeJA application enhances the biosynthesis of phenolic antioxidants and stimulates antioxidant enzyme activities, including superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), thereby mitigating aluminum-induced oxidative damage (Maksymiec, 2007). Foliar MeJA treatment improves aluminum tolerance via multiple mechanisms, such as promoting lignin deposition in cell walls (thus physically limiting Al³⁺ entry), reducing oxidative stress through enhanced antioxidant defenses, and increasing cell wall-associated peroxidase activity.

Similarly, foliar JA application under cadmium stress significantly reduces membrane lipid peroxidation, as indicated by decreased malondialdehyde (MDA) content, enhances antioxidant enzyme activities (SOD, CAT, POD, and APX), and alleviates overall Cd toxicity in soybean (Maksymiec et al., 2005). Low-dose JA application also protects plants against copper toxicity by maintaining chlorophyll content and stabilizing the integrity of the photosynthetic apparatus. MeJA treatment has been reported

to mitigate boron toxicity through enhanced antioxidant enzyme activities that scavenge boron-induced ROS. In addition, JA application effectively alleviates arsenic stress by increasing biomass accumulation, maintaining photosystem II efficiency (Fv/Fm), reducing lipid peroxidation, and suppressing ROS accumulation. Seed priming with JA further enhances copper stress tolerance in seedlings by pre-activating antioxidant defense systems and protecting chlorophyll biosynthesis pathways (Yu et al., 2018). In chili seedlings, treatment with 0.1 μM MeJA effectively mitigates Cd-induced damage by preserving chlorophyll content and upregulating antioxidant enzymes, particularly CAT and APX. The protective effects are associated with reduced Cd uptake and root-to-shoot translocation, elevated ascorbic acid levels, and enhanced antioxidant enzyme activities (Fig. 4) (Noor et al., 2022). Comparable protective responses have been observed in mangrove seedlings, where MeJA application (μM L⁻¹ range) confers Cd stress tolerance by activating Cd-responsive genes, upregulating glutathione (GSH) biosynthetic activating Cd-responsive genes, upregulating glutathione (GSH) biosynthetic pathways, and increasing GSH accumulation to chelate and detoxify Cd ions. Moreover, MeJA induces phytochelatin (PC) biosynthesis, facilitating the formation of PC-metal complexes that are sequestered into vacuoles, thereby reducing the cytotoxicity of Cu and Cd (Akula and Ravishankar, 2011).

Although JA application effectively reduces heavy metal uptake and translocation, the long-term implications of JA-mediated metal accumulation in the edible tissues of horticultural crops require rigorous evaluation from a food safety perspective (Table 4). Future research should aim to identify specific JA-regulated metal transporters and vacuolar sequestration mechanisms that govern detoxification processes. Furthermore, integrating JA application with microbial remediation strategies such as the use of JA-producing plant growth-promoting rhizobacteria (PGPR) represents a promising, sustainable approach that warrants validation under field-scale conditions.

Table 4. The role of exogenous phytohormones against abiotic stresses in horticultural crops production.

Stress types	JA concentrations	Crop types	Main impacts	References
Drought	2.4 and 4.8 mM	Sweet basil	Under 40% field capacity, JA spraying at 4.8 mM produced high yields of oil with good quantity and quality in both seasons.	Sorial et al., (2010)
Drought	13 μM L ⁻¹	Sweet potatoes	MeJA enriched growth, yield, and quality attributes of sweet potato	Yoshida et al., (2020)
Salinity	10, 20, 30, 40, 50, 60 μM MeJA	Tomato	50 mM NaCl for 38 days disturbed the antioxidant defense system. So, improved plant growth and yield by modulation of physiological responses were recorded through MeJA	Manan et al., (2016)
Heat	0.1 mmol L ⁻¹	Pear	5 °C increase for 21 days disturbed the antioxidant defense system and resulted in poor yield and quality. So, MeJA improved plant growth and yield by modulation of physiological responses	Wang et al., (2020b)
Heat	0.01 and 0.1 mM MeJA	Pomegranate	2 °C increased for 84 days resulting in poor yield and quality by disturbance in plant physiological processes. So, MeJA improved plant growth and yield by modulation of physiological and biochemical processes	Sayyari et al., (2011)
Toxic metals	1 mM L ⁻¹	Pepper	Electrolyte leakage, MDA, and lipid peroxidation were enhanced due to toxic metals. However, MeJA is effective to reduce the production of MDA and lipid peroxidation	Yan et al., (2013)

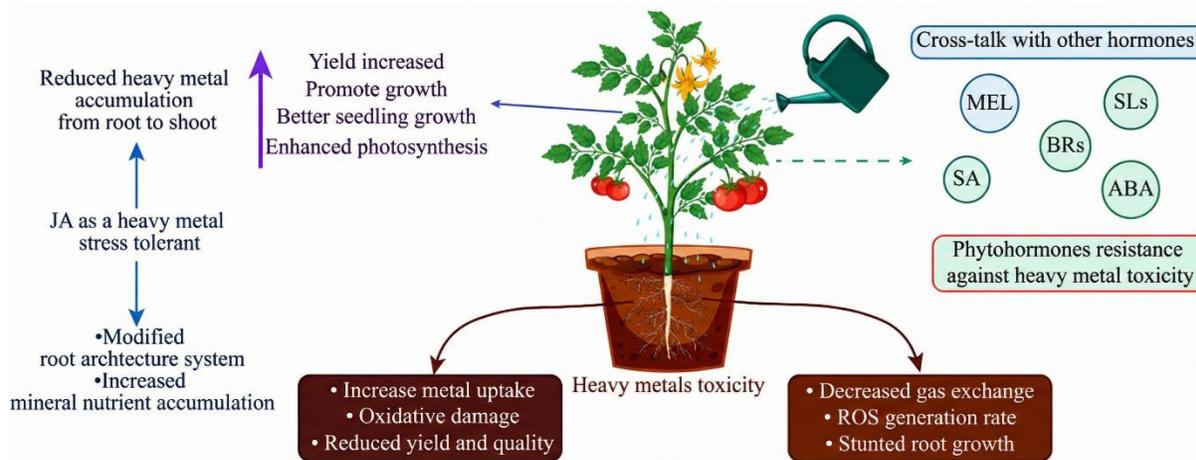


Fig. 4. Mechanisms of JA-mediated reduction of heavy metal accumulation and toxicity in horticultural plants. JA-regulated processes include reduced metal uptake and translocation, Enhanced antioxidant defense systems, Phytochelatin and metallothionein induction for metal chelation, Vacuolar sequestration, and Maintenance of photosynthetic apparatus integrity.

4. Conclusion and Future Prospective

Jasmonates, including jasmonic acid (JA) and its derivative MeJA, function as central regulators of stress resilience in horticultural crops through a suite of interconnected molecular and physiological mechanisms. At the molecular level, jasmonates orchestrate large-scale transcriptional reprogramming that activates stress-responsive genes encoding antioxidant enzymes, heat shock proteins, osmolyte biosynthetic enzymes, and metal-chelating proteins. At the physiological level, JA signaling modulates stomatal conductance, photosynthetic efficiency, osmotic adjustment, and membrane stability. Exogenous application of jasmonates has consistently demonstrated effectiveness across a broad range of abiotic stress conditions, including salinity, drought, temperature extremes, and heavy metal toxicity, by reinforcing endogenous defense systems and maintaining cellular homeostasis. Collectively, these pleiotropic protective effects position jasmonates as promising, economically viable, and environmentally sustainable tools for advancing climate-smart horticulture. Despite these advantages, the effectiveness of jasmonate-based interventions is highly context-dependent. Field-scale validation of optimal application parameters, including concentration thresholds, timing, formulation chemistry, and delivery methods, remains limited and requires systematic evaluation across diverse horticultural crops and environments. Current application technologies are often limited by restricted foliar penetration, rapid ultraviolet degradation, and inconsistent uptake efficiency, underscoring the need for advanced delivery strategies, such as nanoencapsulation, to enhance stability and bioavailability. Moreover, the intrinsic chemical instability of jasmonates under field conditions presents additional formulation challenges that must be addressed through protective chemistries or stabilized analogs. In parallel, heterogeneous regulatory frameworks governing plant hormone-based products across regions introduce further uncertainty for large-scale commercial deployment.

Addressing these challenges will require coordinated, multidisciplinary research efforts. Systems biology approaches integrating transcriptomics, metabolomics, and phosphoproteomics under realistic field conditions are essential for resolving the multilayered regulatory networks that govern jasmonate responses under combined stress scenarios. Precision agriculture tools, including stress-responsive biosensors and decision-support algorithms, can facilitate site-specific jasmonate application strategies that maximize efficacy while minimizing input costs. In parallel, molecular

breeding programs integrating genomic selection with CRISPR-based editing of key negative regulators, such as JAZ repressors and MYC2-associated inhibitors, offer promising pathways for developing inherently climate-resilient cultivars. Additionally, microbiome engineering approaches that exploit jasmonate-modulating plant growth-promoting rhizobacterial consortia provide complementary, biologically based strategies to enhance crop stress tolerance. Finally, identifying synergistic combinations of jasmonates with other stress-mitigating agents, such as silicon, polyamines, and osmoprotectants, will be critical for developing integrated crop protection systems capable of conferring broad-spectrum, multi-stress resilience. Comprehensive techno-economic assessments are ultimately required to evaluate the scalability, cost-effectiveness, and commercial feasibility of jasmonate-based technologies, thereby supporting their informed adoption into mainstream horticultural production systems.

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SH designed and wrote the original article; XZ and YD analyzed the data and created figures; JZ, CN, and YC reviewed and edited the manuscript. All authors read and approved the manuscript.

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The authors have no relevant financial or non-financial interests to disclose.

Data availability

No data was used for the research described in the article.

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