



# Jasmonic Acid: A Versatile Phytohormone Regulating Growth, Physiology, and Biochemical Responses

Amit Kumar<sup>1,2</sup> · Mahinder Partap<sup>1</sup> · Ashish R. Warghat<sup>1,2</sup>

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## Abstract

Phytohormones are the key regulators of plant growth, development, and responses to environmental stressors. Among these, jasmonates (JAs) are particularly crucial, derived mainly from  $\alpha$ -linolenic acid ( $\alpha$ -LA). JAs govern various physiological processes like seed germination, root elongation, and apical hook formation, while also influencing secondary metabolite production and defense mechanisms. Interacting with enzymes, genes, and other growth regulators, JAs modulate intricate signaling pathways, activating metabolic responses in both normal and stressed conditions. Transcription factors such as MYB, WRKY, basic Helix-Loop-Helix (bHLH), and APETALA2/JA-responsive ethylene response factor (AP2/ERF) are central components to JA signaling pathways, impacting the synthesis of bioactive compounds of therapeutic potential. Additionally, JAs act as chemical elicitors, promoting secondary metabolite production *in vitro*, leveraging advancements in plant cell and tissue culture techniques. In this regard, the present review offers a comprehensive discussion on diverse roles of JAs in plant physiology and biochemistry, including its biosynthesis, and suggests strategies for large-scale bioactive compound production via plant cell and tissue culture methods.

**Keywords** Jasmonic acid · Secondary metabolites · Plant development · Phytohormones · Elicitation · Medicinal plants

## Introduction

Plants boast a rich repertoire of low molecular weight chemical compounds, spanning both primary and secondary metabolites. While primary metabolites are pivotal for plant growth and development, secondary metabolites play a vital role in mediating interactions between plants and their environment, empowering them to adapt and fend off threats (Afrin et al. 2015; Erb et al. 2020; Chen et al. 2022a, b). Synthesized across various plant tissues including roots, stems, and leaves, these bioactive compounds harbor therapeutic properties and have been harnessed for medicinal purposes since ancient times (Bhardwaj et al. 2021; Twajj

and Hasan 2022; Kumar et al. 2023). However, the reliance on natural plant sources for obtaining these bioactive compounds has raised concerns about the potential depletion of plant species due to overharvesting. Hence, exploring alternative approaches to produce these bioactive metabolites is imperative to meet the burgeoning market demand (Asigbaase et al. 2023). Chemical synthesis offers a viable avenue for generating significant quantities of bioactive compounds, reducing dependence on plant-derived extraction methods (Kumar et al. 2023). Nonetheless, the production of phytochemicals in plants is constrained and heavily dependent on the growth and developmental stage of the plant. In response, a diverse array of tissue culture techniques has been extensively employed to stimulate phytochemical biosynthesis. In recent years, among these methodologies, elicitation has emerged as a promising approach. Elicitation treatments effectively augment both biomass as well as the biosynthesis of bioactive molecules (Kandoudi and Németh-Zámboriné 2022; Jeyasri et al. 2023; Selwal et al. 2024). Jasmonic acid (JA) emerges as a potent elicitor, instrumental in the production and enhancement of secondary metabolites in numerous plant species. The literature review demonstrates that JA induces the production of bioactive metabolites in

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Handling Author: Mohammad Irfan.

✉ Ashish R. Warghat  
ashishwarghat@ihbt.res.in; ashishwarghat@hotmail.com

<sup>1</sup> Biotechnology Division, CSIR-Institute of Himalayan Bioresource Technology, Palampur 176061, Himachal Pradesh, India

<sup>2</sup> Academy of Scientific and Innovative Research (AcSIR), Ghaziabad 201002, India

various plants through tissue culture techniques, including callus culture, suspension culture, adventitious root culture, and hairy root culture of medicinal plants (Partap et al. 2020; Rattan et al. 2023; Selwal et al. 2024).

Jasmonates (JAs) encompass a group of compounds including cyclic precursors and derivatives like methyl jasmonate (MeJA) and jasmonyl isoleucine (JA-Ile). Initially derived from the extraction of *Jasminum grandiflorum* oil in 1962, these compounds, also known as oxylipins, originate from cyclopentanones and are categorized within the family of oxidized lipids (Demole et al. 1962; Wasternack and Feussner 2018). JAs, being lipid-derived biomolecules originating from  $\alpha$ -linolenic acid ( $\alpha$ -LA), are integral components of the oxidized lipids family. Oxylipins, as a class of signaling molecules, exert significant influence over various biological processes. They are synthesized through two primary pathways: the auto-oxidation of polyunsaturated fatty acids and the enzymatic activity of lipoxygenase and  $\alpha$ -dioxygenase enzymes. Within plants, JAs play crucial roles in diverse physiological activities such as stamen and trichome development, stomatal regulation, leaf expansion, apical hook formation, and glucose transport (Wasternack 2007; Yoshida et al. 2009; Ghorbel et al. 2021; Sood 2023).

The signaling cascade in plants is influenced by numerous plant growth regulators, transcription factors (TFs), and enzymes (Checker et al. 2018). These components are fundamental to biological processes, and their interaction is pivotal for plant growth and development. Additionally, various TFs, such as MYB, WRKY, bHLH, and AP2/ERF, play a significant role in modulating hormonal signaling pathways, thereby promoting the accumulation of pharmacologically active bioactive compounds in diverse medicinally important plant species (Zheng et al. 2023). Recent notable studies have focused on the role of JAs in various aspects of plant growth, defense, and the production of specialized bioactive compounds (Yan and Xie 2015; Nguyen et al. 2022a, b; Jeyasri et al. 2023). This comprehensive review article provides a detailed literature review of the mechanisms underlying the action of JAs in plant growth and development, as well as their cross-talk with other plant growth regulators. Furthermore, the review delves into their involvement in promoting the biosynthesis of secondary metabolites in plant species that are medicinally important.

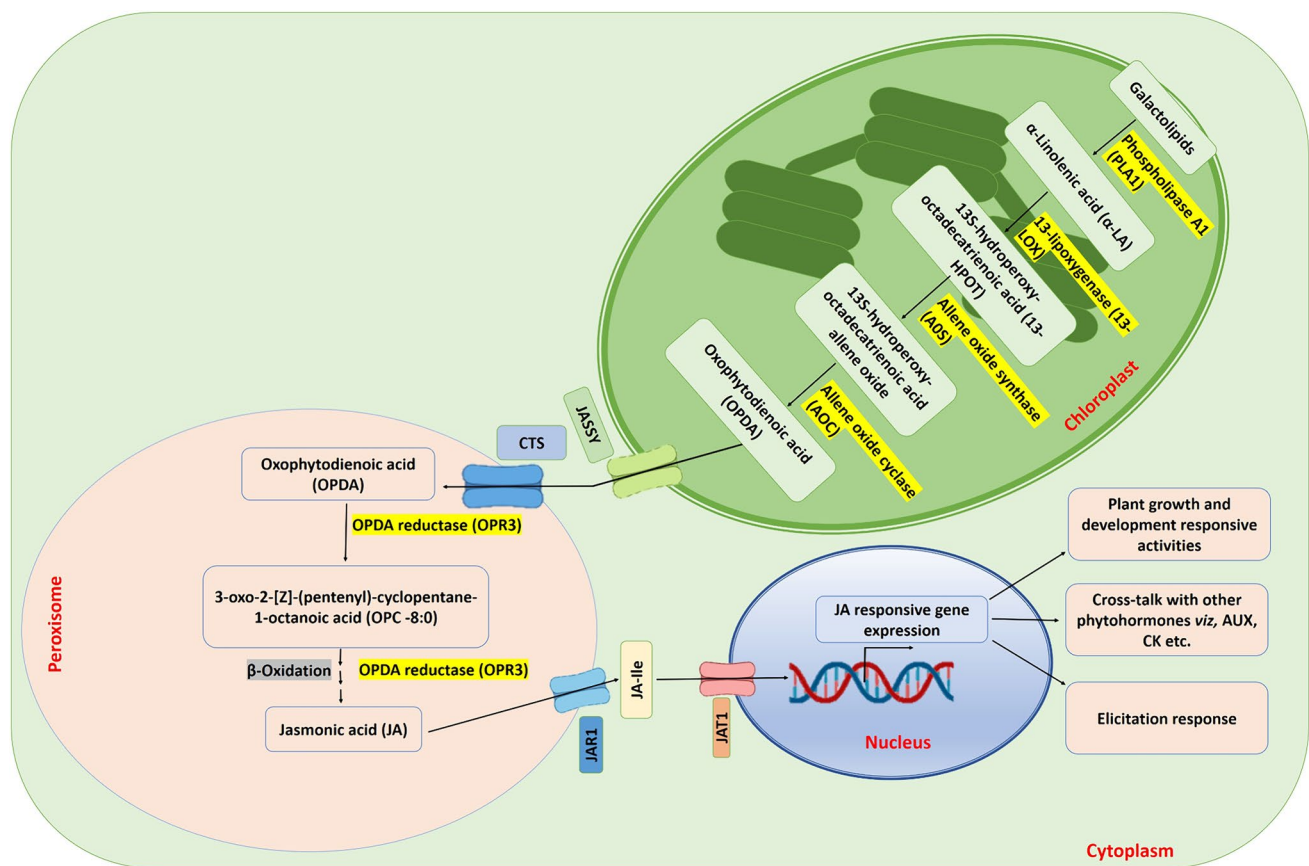
## Biosynthesis of JA

Enzymes responsible for the biosynthesis of Jasmonates (JAs) are ubiquitously present in the plant kingdom. JAs are derived from polyunsaturated fatty acids and synthesized through the octadecanoid pathway (Kupper et al. 2009; Kombrink and Wasternack 2010). The biosynthesis of JA commences with an 18-carbon fatty acid called  $\alpha$ -linolenic acid ( $\alpha$ -LA) (Lalotra

et al. 2020). Previous research has indicated that the activation of phospholipase enzymes aids in the release of  $\alpha$ -LA from the plasma membrane, correlating with an increase in JA levels in injured tissues (Canonne et al. 2011). Additionally, the acyl hydroxylase enzyme contributes to acids from plant lipids. The JA biosynthesis proceeds in two distinct stages; the formation of an intermediate compound called oxophytodienoic acid (OPDA) takes place in chloroplast, followed by the subsequent synthesis of JA and their derivatives in peroxisomes. All enzymes required for OPDA synthesis are localized in the chloroplast. The process begins with the release of  $\alpha$ -LA from galactolipids in chloroplast membranes, facilitated by phospholipase A1 (PLA1). Subsequently,  $\alpha$ -LA is oxygenated to form 13S-hydroperoxy-octadecatrienoic acid (13-HPOT) by chloroplast membrane-bound 13-lipoxygenase (13-LOX) enzyme (Wasternack and Strnad 2018). Further, it is followed by enzymatic conversion of 13-HPOT into an intermediary compound known as 13-HPOT allene oxide by *allene oxide synthase* (AOS), and then transformed into OPDA by *allene oxide cyclase* (AOC). The latter half of JA biosynthesis occurs in peroxisomes. Transport of plastid-synthesized OPDA into peroxisomes is facilitated by a protein called JASSY, reported by Guan et al. (2019). JASSY contains a steroid acute regulatory protein-related lipid transfer (START) domain. In plants with JASSY mutations, OPDA synthesis remains normal, but its export from the chloroplasts is impaired. The membrane-localized COMATOSE (CTS), an ATP-dependent Binding Cassette protein (ABC), assists in the entry of OPDA across the peroxisomal membrane (Theodoulou et al. 2005). In the peroxisome, OPDA undergoes reduction by OPDA reductase (OPR3) to become 3-oxo-2-[Z]-(pentenyl)-cyclopentane-1-octanoic acid (OPC-8:0). After this within peroxisomes, OPC-8:0 is further reduced to JA by OPR3 through 3 cycles of  $\beta$ -oxidation (Andersson et al. 2006; Lu et al. 2014; Sohn et al. 2022). Subsequently, JA is transferred to the cytoplasm where it combines with isoleucine (Ile) to create JA-Ile, which is regarded as the most potent JA conjugate. This process is facilitated by jasmonate resistance-1 (JAR1), an enzyme responsible for synthesizing JA-Ile. Ultimately, JA-Ile is conveyed into the nucleus via the jasmonate transporter1 (JAT1), where it engages in the afterward phases of the JA signaling cascade (Li et al. 2017). Once synthesized, JA is distributed throughout the plant, including the vascular bundles phloem and xylem, facilitated by the protein transporter glucosinolate transporter-1 (GTR1) (Matsui et al. 2017) (Fig. 1).

## Regulation of JA Biosynthesis

External stimuli trigger the release of  $\alpha$ -LA from plastid membranes, serving as a crucial substrate in JA biosynthesis. The regulatory mechanisms governing JA biosynthesis revolve around three key concepts: (i) the necessity for  $\alpha$ -LA



**Fig. 1** Biosynthesis of jasmonic acid (JA) in plants. This synthesis occurs in the chloroplast, and peroxisome. JA is produced by the octadecanoid pathway and the process initiates with the liberation of  $\alpha$ -linolenic acid ( $\alpha$ -LA) from galactolipids in the membranes of chloroplasts, aided by phospholipase A1 (PLA1) enzyme. The 13-lipoxygenase (13-LOX) enzyme present in the chloroplast is responsible for catalyzing the conversion of  $\alpha$ -LA to 13S-hydroperoxy-octadecatrienoic acid (13-HPOT). This 13-HPOT is then further transformed to 13-HPOT allene oxide and oxophytodienoic acid (OPDA) by the catalytic activities of *allene oxide synthase* (AOS), and *allene oxide cyclase* (AOC), enzymes respectively. The entry of OPDA into the

peroxisome is aided by JASSY and in COMATOSE (CTS) in chloroplast and peroxisomal membrane, respectively. In peroxisome, OPDA is reduced by OPDA reductase (OPR3) to convert 3-oxo-2-[Z]-(pentenyl)-cyclopentane-1-octanoic acid (OPC-8:0) and finally OPC-8:0 reduced by OPR3 through 3 cycles of  $\beta$ -oxidation to JA. Jasmonate resistance1 (JAR1) transports and catalyzes the conversion of JA and Isoleucine into JA-Ile. The transportation of the JA-Ile complex across the nuclear membrane is facilitated by a jasmonate transporter1 (JAT1) transfer protein, which in turn controls the expression of JA-responsive genes (Concept adapted from Sohn et al. 2022)

release prompted by external factors, (ii) feedback regulation of JA production genes by JA genes, and (iii) tissue-specificity (Wasternack 2007; Schaller and Stintzi 2009; Wasternack and Hause 2013). Furthermore, additional regulatory factors include (i) coordinated activity between the Allene Oxide Synthase (AOS) and hydroperoxide lyase (HPL) branches, (ii) negative regulation by Jasmonate ZIM-domain proteins (JAZs), (iii) post-translational modifications such as those involving OPR3, (iv) heteromerization, exemplified by Arabidopsis Allene Oxide Cyclases (AOCs) (Otto et al. 2016), (v) Calcium ion ( $\text{Ca}^{2+}$ ) signaling, and involvement of the mitogen-activated protein kinase (MAPK) pathway (Wasternack and Hause 2013). Expression of JA biosynthesis genes is up-regulated in response to various environmental stresses, with notable examples including injuries to

plant tissue (Wasternack 2007; Schaller and Stintzi 2009). Regulation via  $\text{Ca}^{2+}$  modulation of 13-lipoxygenase (13-LOX) activity has also been identified.

## Physiological and Developmental Role of JA in Plants

The JA molecule exhibits synergistic as well as antagonistic interactions with endogenous phytohormones to modulate plant growth, development, and resistance mechanisms in response to external stimuli. In recent years, numerous research has been conducted to find the effect of JA on plant growth and regulation. JA is involved in several plant physiological processes, including seed germination, growth

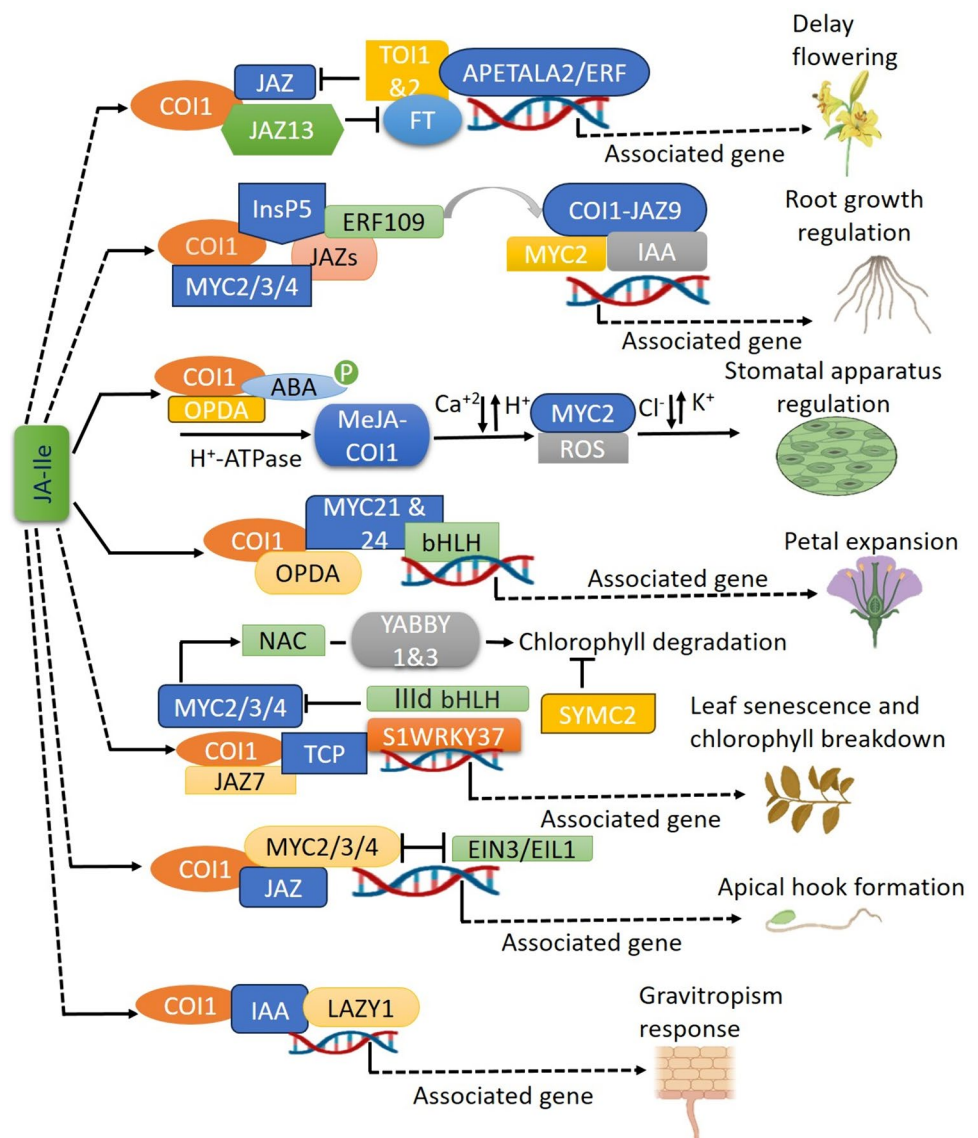
inhibition, regulation of stomatal closure, and reproductive maturation (Sohn et al. 2022; Sood 2023) (Fig. 2).

## Effect of JA on Root Physiology

In plants, JAs inhibits the growth of seedlings, roots, and stems. The genes *MYC2/3/4* are primarily expressed in the tip of the primary root, where they play a role in suppressing primary root development in response to JA. Mosblech et al. (2011) propose that inositol pentakis-phosphate (InsP5) enhances the interaction between Coronatine-Insensitive-1 (COI1) and JAZ9, thereby mitigating JA's effect on root growth. Coronatine-O-methylxime acts as a competitive antagonist of JA, effectively counteracting the adverse effects of coronatine on primary root growth by inhibiting the interaction between COI1 and JAZs (Monte et al.

2019). Under conditions of salinity stress, mutants of rice with impaired JA production exhibit less pronounced inhibition of root growth compared to the wild type (Hazman et al. 2015). In unripened fruits, JA accelerates chlorophyll breakdown while suppressing anthocyanin production (Horbowicz et al. 2011). Moreover, even at lower concentrations, JA and methyl Jasmonate (MeJA) have been found to inhibit kinetin-induced soybean callus induction and meristematic culture of potatoes (Kamińska 2021). In Arabidopsis wild-type seedlings, low micromolar doses of JA inhibit primary root growth while promoting lateral root production simultaneously (Raya-González et al. 2012). JA influences the production of lateral and adventitious roots differently. In Arabidopsis, JA induces lateral root formation by upregulating the expression of JA-responsive ethylene response factor 109 (ERF109) (Cai et al. 2014; Sun et al. 2009). Conversely, JA suppresses the development of adventitious

**Fig. 2** Jasmonic acid and isoleucine (JA-Ile) complex, and its signaling on growth, physiology, and development of the plant. JA-Ile complex involves many TFs including COI1-JAZ-MYC2, and AP2/ERF signaling cascade plays a vital role in the regulation of flowering, root growth, closing and opening of stomata, petal expansion, leaf and chlorophyll breakdown, apical hook formation and gravitropism response in plants (Concept adapted from Sohn et al. 2022)





roots in *Arabidopsis* through the COI1 and MYC2/3/4 signaling pathways (Gutierrez et al. 2012). However, in *petunia*, JA stimulates the production of adventitious roots (AR) (Lischweski et al. 2015), indicating species-specific regulation of AR production by JA. Recently, Sharma et al. (2022a, b, c) demonstrated that the JA signaling pathway interacts with light, glucose, and auxin to regulate the branching angle of lateral root development in *Arabidopsis*.

## Regulation of Stomatal Closing

Stomata in plants play a vital role in regulating gas exchange, transpiration rates, and defending against pathogens. JAs also contribute to the regulation of stomatal closure in plants. MeJA acting through the COI1 pathway stimulates an H<sup>+</sup>-ATPase in the cell membrane. This process leads to membrane depolarization, causing the influx of calcium ions (Ca<sup>2+</sup>) and the efflux of hydrogen ions (H<sup>+</sup>) (Yin et al. 2016). The interaction of MeJA with COI1 triggers the stimulation of reactive oxygen species (ROS), activating chloride (Cl<sup>-</sup>) channels and promoting outward potassium (K<sup>+</sup>) channels. Collectively, these events cause guard cells to lose turgor pressure, resulting in stomatal closure (Yan et al. 2015). Additionally, Yin et al. (2016) demonstrated that the combined action of JA with abscisic acid (ABA) facilitates stomatal closure in *Arabidopsis* via the protein kinase OPEN STOMATA1. Moreover, under drought conditions, plants undergo a shift in the production of JA intermediates, favoring OPDA over JA. It has been observed that OPDA exhibits greater efficacy compared to JA, particularly in its synergistic interaction with ABA to promote stomatal closure in *Arabidopsis*. Recently, Zhao et al. (2022) observed that MYC2 plays a pivotal role in regulating stomatal closure in tomato plants under drought stress. This regulatory mechanism is mediated through the inhibition of two genes, namely *SIPP2C1* and *SIRR26*, by MYC2.

## Effect of JA on Flowering

In plants, JAs play a vital role in regulating flowering and senescence. COI1 and JAZ interaction inhibits flowering (Zhai et al. 2015). The COI1 defective and *JAZ1Δ3A* transgenic plants show premature blooming. Moreover, flowering in plants is regulated by *TARGET OF EAT TFs* (*TOE1* and *TOE2*), which are AP2/ERF domain TFs. Indeed, their interaction with the JAZ protein inhibits flowering by transcriptional suppression of the *FLOWERING LOCUS T* (*FT*) gene. The repression of the early blooming phenotype of *coi1* is achieved through the upregulation of *TOE1* and *TOE2* (Zhai et al. 2015). Decreased expression of *HDA19* by anti-sense RNA technology and mutant phenotype of *HDA19* leads

to delayed blooming in long-day circumstances (Gorham et al. 2018; Ning et al. 2019). The late blooming phenotype in *Chrysanthemum morifolium* is observed when there is an upregulation of a *chrysanthemum* jasmonate zim domain (*CmJAZ1-LIKE*) gene that lacks the JAZ domain (Guan et al. 2021).

## Retardation of Petal Expansion in Model Plant

JA regulates the growth of petals by modulating the COI1 pathway. Indeed, COI1 defective exhibits larger petals at anthesis than natural plants (Reeves et al. 2012). JA suppresses MYB21 and MYB24 proteins during reproductive organ development, limiting petal growth and indicating that these proteins are necessary for petal growth. Additionally, AOS and COI1 plants have higher levels of MYB21 expression in their petals, resulting in persistent petal elongation which leads to enlarged petals. In addition, *opr3* plants exhibit an elevated bHLH TF BIGPETALp expression. This TF promotes post-mitotic cell development leading to enlarged petals (Brioudes et al. 2009).

## Effect on Leaf Senescence/Chlorophyll Breakdown

JA triggers leaf senescence via a COI1-dependent pathway (Qi et al. 2015b). Moreover, Yu et al. (2016) proved that *JAZ7* inhibits leaf senescence in dark-grown seedlings. Numerous NAC (NAM, ATAF, and CUC) TFs (for example NAC019/055/072) act downstream of MYC2/3/4 to facilitate chlorophyll breakdown (Melotto et al. 2006). Subgroup IIIId bHLH TF suppresses leaf senescence by binding antagonistically to their target promoters and reducing MYC2/3/4 action. An interaction of protein YABBY1 and YABBY3 with JAZs to stimulate chlorophyll breakdown (Boter et al. 2015). However, many findings reported that during leaf senescence, JA and oxylipin derivatives are generated due to the breakdown of membranes and molecules (Seltmann et al. 2010; Zhu et al. 2015). In recent years, it was shown that miR319 affects the expression of transcription factors known as TEOSINTE BRANCHED/CYCLOIDEA/PCF (TCP) (Schommer et al. 2008). The TFs SIWRKY37 is tangled in both JA signaling and the modulator of tomato leaf senescence under dark-induced conditions (Wang et al. 2022). JA-induced leaf senescence is suppressed by silencing SIMYC2 through repression of chlorophyll breakdown and induction of photosynthetic carbon fixation, suggesting a beneficial impact of SIMYC2 in JA-induced leaf senescence (Ding et al. 2022).

## Retardation of Apical Hook Development in Arabidopsis

The COI1-JAZ-MYC2/3/4 pathway functions as an inhibitor of apical hook development in dark-grown Arabidopsis (Song et al. 2014). JA triggers the activation of MYC2/3/4, TFs that cooperate with and block the transcriptional action of Ethylene-insensitive3/ETHYLENE-INSENSITIVE3-like1 (EIN3/EIL1). This results in the down-regulation of the *HOOKLESS1* gene, which controls apical hook development, as well as the suppression of apical hook curvature (Song et al. 2014; Zhang et al. 2014). Furthermore, MYC2 promotes EIN3 BINDING F-BOX PROTEIN1 expression, which results in EIN3 breakdown (Zhang et al. 2014). Recently, Zhang et al. (2023) demonstrated JA exerts inhibitory effects on brassinosteroids (BRs) to modulate the process of apical hook growth in Arabidopsis.

## Gravitropism Response in Plant

Gravitropism has an impact on root and shoot development. In the root tip, JA influences lateral auxin relocation after gravity stimulation. It also inhibits the root gravitropic feedback in a COI1-mediated pathway (Sun et al. 2011). Tryptophan conjugates of JA and IAA impede the negative tropic root proliferation in a COI1-independent pathway (Staswick et al. 2009). JA concentrations are higher in the leaf portion and lesser in the root portion during the gravitropism action in rice (Staswick et al. 2009). *LAZY1* gene was discovered to be responsible for gravitropism in rice (Yoshihara 2007). Gravitropism is delayed

by JA administration, and the JA-deficient hebibba has a reduced gravitropism response. This indicates that JA is essential for proper gravitropic response in plants.

## Cross-Talks Between JA and Other Phytohormone Signaling Cascades

The interaction of JA and other endogenous phytohormones is fundamental for many plant and environmental responses. JA does not operate in isolation, but rather as an integral component of an intricate signaling network that encompasses other plant hormone signaling cascades (Checker et al. 2018; Rao et al. 2023a, b; Hewedy et al. 2023). The cross-talk among JA and other phytohormones is represented in Table 1.

## JA-Auxin Cross-Talk

Interactions between JAs and auxin (AUX) play a pivotal role in regulating various physiological processes in plants, including seed germination, root growth, flowering, seedling formation, tendril curling, cell proliferation, and senescence (Saniewski et al. 2002; Xu et al. 2020). Indole-3-acetic acid (IAA) is the primary form of auxin in plants. Critical components such as COI1, MYC2, and JAZ are essential for mediating the cross-talk between JA and IAA. The application of exogenous auxin triggers the activation of the Transport Inhibitor Response 1 (TIR1), auxin response factors (ARF), IAA-TIR-AUX/IAA-ARF signaling cascade, leading to increased JA synthesis. Conversely, JA promotes the expression of the *auxin synthase gene (ASA1)* and enhances auxin biosynthesis. Significantly, TF MYC2 suppresses the expressions of *PLETHORAs (PTL1 and PTL2)* and opposes

**Table 1** Summary of the crosstalk among phytohormones and their functions of plant growth regulation, development, defense against pathogens, and biotic or abiotic stress responses

Phytohormone cross-talk	Function and response	Components involved
JA-IAA	Growth, development, and leaf senescence	JAZ, MYC2, TIR1, AUX, IAA, <i>PTL1</i> , <i>PTL2</i> , ARF6, ARF8, <i>ASA1</i> , COI1, MYB21, MYB24, IAA29, WRKY57
JA-GA	Plant defense and photomorphogenesis	JAZ, GID1, DELLAs, MYC2, PIF3, <i>DAD1</i> , <i>LOX</i>
JA-ET	Environmental stress response and plant resistance against pathogens	CTR1, COI1, <i>ERF1</i> , <i>AP2</i> , <i>ORA59</i> , JAZ, MYC2, EIN2, EIN3, EIL1, <i>VSP2</i> , <i>PDF1.2</i>
JA-ABA	Defense against drought, heat, cold, salt stress, and closure of stomata	JAZ, MYC2, AOC1, PYLs, <i>VSP2</i> , MED25, <i>PTL1</i> , <i>PTL2</i> , WRKY72, PeOST1
JA-SA	Defense against pathogens and biotic stress response	MAPK, COI1, MYC2, <i>PDF 1.2</i> , GRX, <i>NPRI</i> , ICS1, WRKY70, NAC, <i>PDF 1.2.</i> , GRX480, PR, <i>VSP2</i>
JA-CK	Growth and development, and Xylem differentiation	COI1, JAZ, MYC2, <i>ERF115</i> , AHP6
JA-BR	BR response and defense response	COI1, <i>OsD11</i> , <i>DWARF1</i> , BAK1, BRI1, MED25, <i>VSP2</i> , <i>BES1</i> , <i>BZR1</i> , COI1, MYC2

the auxin-TIR-AUX/IAA-ARF signaling pathway to control root growth. Additionally, ERF109 modulates lateral root growth in Arabidopsis by facilitating JA-IAA cross-talk. During JA signaling, the interaction between COI1 and JAZ forms a network, consequently, the degradation of JAZ leads to the activation of auxin response factors 6 and 8 (ARF6 and ARF8), which in turn affect the growth and development of floral organs. ARF6 and ARF8 promote the growth of floral organs by regulating the transcription factors MYB21 and MYB24, which are responsive to JA (Jang et al. 2017; Yang et al. 2019). Furthermore, both JA and IAA are implicated in leaf senescence. While auxin acts as a suppressor of leaf senescence, JA induces this process, leading to characteristic signs such as reduced chlorophyll concentration, increased leaf yellowness, and enhanced cell mortality (Hu et al. 2017). Additionally, IAA29-IAA inhibitors positively regulate senescence, whereas JAZ4, JAZ8, and WRKY57 have negative effects on this process (Jiang et al. 2014) (Fig. 3A).

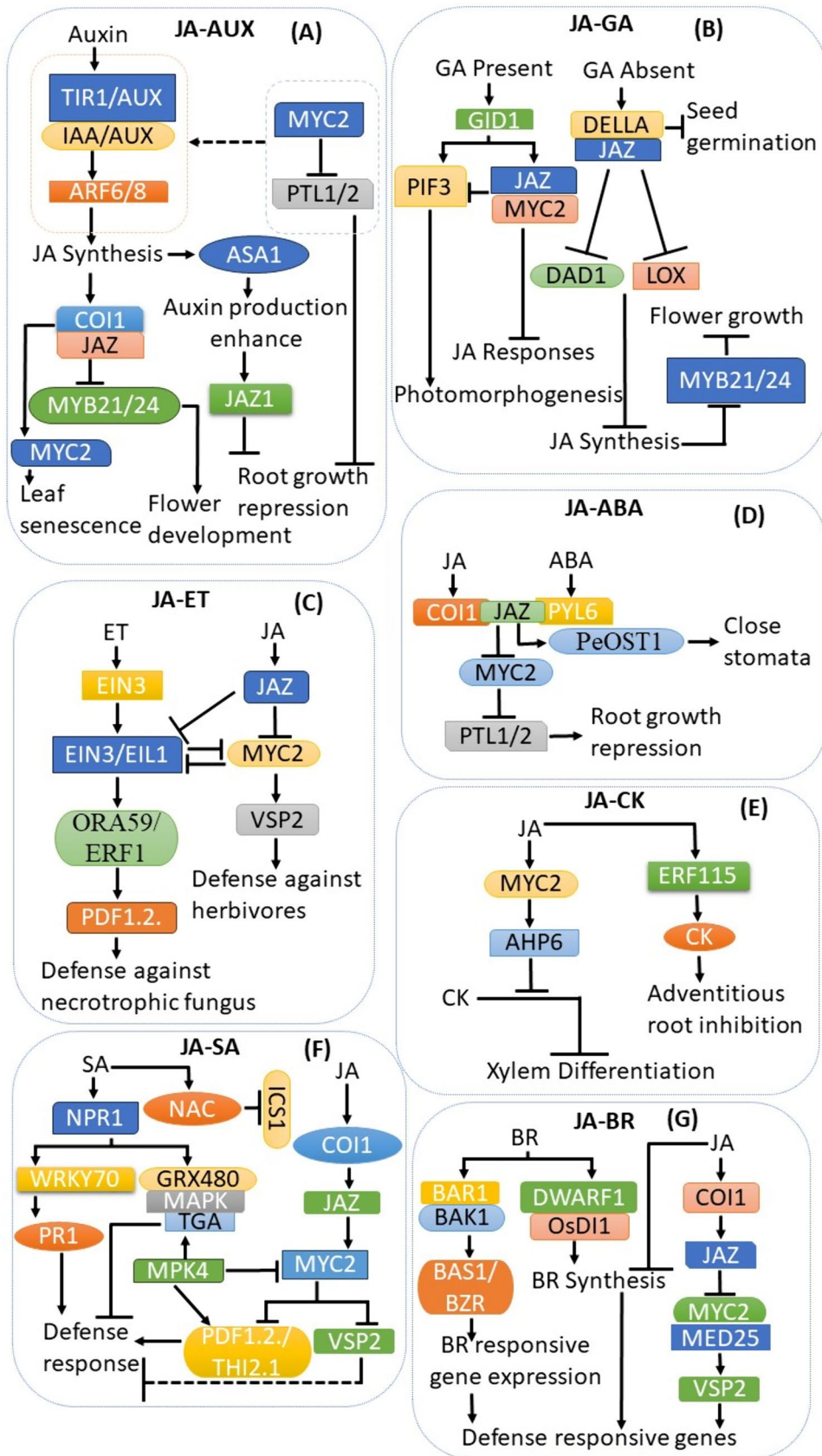
### JA-Gibberellic Acid Cross-Talk

Gibberellic acid (GA) represents a vital group of phytohormones that exert a significant influence on various physiological processes in plants, including plant growth, maturation, stem elongation, root development, flowering, and seed set (Hernández-García et al. 2021; Liu et al. 2021). The interaction between GA and JA manifests both synergistic and antagonistic responses depending on the specific activities they engage in. Together, these hormones collaborate to promote stamen growth. Extensive prior studies have demonstrated the antagonistic roles of GA and JA in coordinating plant growth under both normal and stressful conditions. This phenomenon is corroborated by the direct interplay between DELLA proteins, which inhibit GA signaling, and JAZ proteins, which impede JA signaling. GA displays an affinity for the GA INSENSITIVE DWARF1 (GID1) receptor, enhancing the interaction between GID1 and DELLA proteins. Subsequently, this triggers a ubiquitin–proteasome-driven cascade leading to the degradation of DELLA proteins (Sun 2011). Under normal conditions, GA synthesis prompts the breakdown of DELLA proteins. However, during chilling stress, GA signaling diminishes, hindering plant development while increasing DELLA protein concentration. The accumulated DELLA proteins then bind to JAZ proteins leading to inhibition of *delayed in anther dehiscence1* (*DAD1*) and LOX, which inhibits JA-associated genes along with MYC2 and MYC29, resulting in suppression of flowering. In rice, OsJAZ9 positively regulates GA but negatively regulates JA. Furthermore, GA stimulates PHYTOCHROME INTERACTING FACTOR3/4 (PIF3/PIF4) to control photomorphogenic response in plants.

Additionally, DELLA proteins inhibit germination, with RGA-LIKE2 (RGL2) being the most crucial member in Arabidopsis among the five known DELLA proteins. RGL2 plays a significant regulatory role during seed formation (Piskurewicz and Lopez-Molina 2009). Exogenously administered OPDA primarily stimulates ABA production by upregulating RGL2 and ABA1 expression, leading to the inhibition of seed germination. GA promotes embryo development by alleviating DELLA inhibition on LEAFY COTYLEDON 1, resulting in an increase in auxin concentration beneficial for embryo growth (Hu et al. 2018a, b). Recently, Wang et al. (2023) reported that GA suppresses cellular competence in response to JA under potassium deficiency stress, thereby regulating root growth in tomatoes. Due to its antagonist interaction with GA, it can be inferred that JA serves as a pivotal hormone regulating plant growth and development, particularly in adverse environmental conditions (Fig. 3B).

### JA-Ethylene Cross-Talk

According to Zhang et al. (2021, 2022), more JA functions have recently been identified that can improve plant regeneration. Various studies suggest that JA and Ethylene (ET) can potentially exhibit either antagonistic or synergistic effects in regulating plant stressful responses (Zhu and Lee 2015). TFs like MYC2, EIN3-like 1 (EIL1), and ET INSENSITIVE3 (EIN3), have been participated during JA-ET interaction (Zhang et al. 2014). When plants get infected with necrotrophic fungus and pathogen JA-ET signaling is triggered to modulate the stressful effect on plants. Additionally, JA increases the breakdown of JAZ, therefore MYC2 is triggered to control octadecanoid-responsive Arabidopsis 59/Ethylene responsive factor1 (ORA59/ERF1) expression and *VEGETATIVE STORAGE PROTEIN 2* (*VSP2*), a wound-response gene to respond to the herbivorous pathogen (Yang et al. 2019). In addition, JAZ suppresses the EIL2/EIN3 in the ET signaling and promotes the transcription of ORA59/ERF1, which targets the promoter of *PLANT DEFENSIN 1.2* (*PDF1.2*) and promotes its expression, protecting against necrotrophic fungus (Pieterse et al. 2012). These findings suggest an antagonism relationship between JA and ET signaling which controls plant defense against pathogens. Increased JA causes JAZs to be degraded, which reduces the association between HDA6 and EIN3/EIL1 and increases the transcription action of associated genes. Surprisingly, JA shortage is often characterized by male sterility in plants. Liu et al. (2022) discovered repression of the pollen tube development by exogenous JA and MeJA at 1.0 mM treatment. Recently it was observed that JA-ET signaling controls leaf senescence in tomatoes. SIERF.F5 (Ethylene signaling), by its interaction with *SIMYC2* (JA signaling), integrates





**Fig. 3** The cross-talks between different signaling pathways of the jasmonic acid (JA) and other phytohormones in plant growth, development, and stress responses are mediated by the JASMONATE ZIM DOMAIN PROTEIN (JAZ). **A** The intricate interplay between the JA and auxin (AUX) signaling pathways, JA and AUX signaling pathways work together to control floral development and leaf senescence by altering the levels of JA, on the other hand, JA and auxin counteract each other to inhibit root growth through the JAZ-MYC2 pathway. **B** The complex cross-talk between the JA and gibberellic acid (GA) involves the many transcription factors (TFs) and proteins such as JAZ-MYC2-DELLA-PIF signaling molecules to modulate JA biosynthesis and photomorphogenesis response in plants. Furthermore, several TFs including MYC3, MYC4, MYB21, and MYB24 can interact with DELLAs, suggesting a potential synergistic effect between JA-GA signaling. **C** JA and ethylene (ET) cross-talk co-ordinately controls defense against necrotrophic or hemibiotrophic fungi and pathogens by interacting with JAZ-MYC2, EIN3/EIL1, octadecanoid-responsive Arabidopsis 59/Ethylene responsive factor1 (ORA59/ERF1) pathways. **D** Cross-talk of JA and abscisic acid (ABA) involves PYRABACTIN RESISTANCE1-Like protein (PYL6) and COI1-JAZ-MYC2 components to regulate the equilibrium between plant development and growth. **E** The JA and cytokinin (CK) signaling pathway in plants regulates xylem differentiation and several physiological responses, including the involvement of MYC2 and ERF115 TFs. **F** The complicated crosstalk between JA and salicylic acid (SA) signaling pathways. Cross-talk involves JAZ-COII, NONEXPRESSOR OF PR GENES1 (NPR1), WRKY70, *PLANT DEFENSIN 1.2* (*PDF 1.2*) and *pathogenesis-related (PR)* genes and TFs to modulate defense and resistance response against pathogens. **G** The interaction between JA and Brassinosteroids (BR) includes BR receptor1 (BRI1), BR-related kinase (BAK1), (BR signaling), and COI1-JAZ-MYC2 (JA signaling) TFs to regulate plant development and defense resistance (Concept adapted from Yang et al. 2019)

signals from JA and ET, and as a result, controls senescence in tomato leaves Chen et al. (2022a, b) (Fig. 3C).

## JA-Abscisic Acid Crosstalk

Plants frequently respond to numerous biological challenges by interacting with the abscisic acid (ABA) and JA signaling pathways. The interaction of JA-ABA controls plant growth, resistance against many pathogens, and response to stressful environments (Hu et al. 2013; Wang et al. 2020a). For instance, under harmful abiotic stress conditions, MYC2 and *AOC1* primarily regulate the modulation of ABA-JA signaling pathways (Browse et al. 2009). In lower temperature conditions, *Zostera japonica* leaf raised the levels of ABA-JA (Li et al. 2018). Surprisingly, in salinity stress, the concentration of ABA raised along with the concentration of JA (Wang et al. 2001). Upon binding of ABA to PYRABACTIN RESISTANCE1-Like proteins (PYLs) receptors, type 2C protein phosphatases (PP2Cs) form a stable complex with receptors, which are typically associated and inhibited by PP2Cs. The downstream TFs are then phosphorylated by the activated SNF1-related protein kinase 2 (SnRK2s) to initiate ABA signaling.

In general, ABA-JA works synergistically as well as antagonistically in various physiological activities. In recent Aleman et al. (2016) demonstrated that ABA receptor PYL6 RCAR9 and MYC2 TFs interact with each other to modulate cellular activities in plants. In contrast, MYC2 has inhibitory effects on the expressions of *PTL1* and *PTL2*, along with suppressing the development of roots. Recently, Rao et al. (2023a, b) postulate that PeOST1 cooperates with MeJA to close stomata as part of a systemic defensive mechanism mediated by the JAZ factor. Wang et al. (2020a, b) have published an intriguing finding that JA plays a significant role in enhancing drought tolerance in wheat plants. This effect is observed to occur upstream of the action of ABA. Contrarily, JAs function in a downstream manner relative to ABA signaling, hence augmenting plant resilience against cold-induced stress (Wang et al. 2016). Hou et al. (2019), elucidated that WRKY72 functions as a repressor of *AOS1* activity, leading to the suppression of JA biosynthesis. Peian et al. (2021) observed that the application of exogenous ABA led to a suppression of endogenous jasmonic acid levels in strawberry plants infected with *Botrytis cinerea*. This suppression of jasmonic acid resulted in increased susceptibility to pathogen assault, which was attributed to the overexpression of two *pathogenesis-related (PR)* proteins. In an alternative scenario, the JA-ABA cross-talk hinders the process of rice seed formation by regulating the SAPK10-bZIP72-AOC biosynthetic mechanism. This regulation involves the phosphorylation of basic leucine zipper (bZIP72), which subsequently enhances the transcription of *AOC* (Wang et al. 2020a, b).

Recently, Pluskota et al. (2019), demonstrated that the expression levels of SINP24 and the gene responsible for encoding its possible upstream regulator TERF1 (ethylene response factor) exhibit a boost in response to MeJA in the process of germination in tomato seeds. Moreover, the application of exogenous JA resulted in an upregulation of genes associated with ABA synthesis. Concurrently, there was a notable increase in the expression levels of genes that encode WRKY TFs, MYC2, and bZIPs. This suggests that the combined action of ABA and JA may contribute to the up-regulation of transcription factors in the defense response of rice (Li et al. 2022). Hence, it can be observed that there exists both synergistic and antagonistic interaction between JA and ABA. However, the available literature on the antagonistic crosstalk is limited, indicating the necessity for future exploration in this domain (Fig. 3D).

## JA-Cytokinin Cross-Talk

Cytokinins (CKs) regulate various factors associated with the growth and maturation of plants to interact with other endogenous hormones. Zeatin is the most prevalent type of

CK in higher plants. The expression of CK gene response is influenced by JA and JA-associated stress-responsive genes (Argueso et al. 2009). JA suppresses callus proliferation triggered by CK in soybeans (Ueda and Kato 1982). As JA also suppresses the expression of genes involved in chlorophyll formation, it has an opposing effect on CK (Liu et al. 2016). The specific procambium response to CK administration is suppressed and xylem differentiation is positively regulated in Arabidopsis roots by JA, as shown by (Jang and Choi 2018). It is noteworthy that the MYC2 mutant did not exhibit any additional xylem development and Arabidopsis histidine phosphotransfer protein 6 (AHP6) expression, encoding a CK signaling repressor when exposed to external JA. Indicating that the JA-responsive MYC2 transcription factor facilitates this process by enhancing AHP6 expression. When it comes to xylem differentiation in Arabidopsis roots, CK plays a negative regulatory role. However, previous studies have shown evidence that JA-CK interactions exhibit an antagonistic relationship between the plant's stimulation to circadian stresses (Nitschke et al. 2016). In addition, JA stimulates ERF115, a transcription factor that activates CK signaling by upregulating type-A response regulator (ARR5 and ARR7), and CK biosynthesis by promoting the expression of ISOPENTENYL TRANSFERASE 3 (IPT3), encoding one of the rate-limiting enzymes in CK formation. By altering CK equilibrium via ERF115 activity, JA suppresses AR production (Lakehal et al. 2020). Furthermore, an investigation conducted by Liu et al. (2022) revealed that the application of exogenous MeJA and CK could potentially exert antagonistic effects on the regulation of lignin accumulation in tea plants. This regulatory mechanism appears to be mediated via the expression of the *CsHCT* gene in tea (Liu et al. 2023). The upregulation of JA production genes induced by CK-enhanced signaling results in a decrease in growth in the maize Hsf1 leaf through the inhibition of cell growth (Uyehara et al. 2019) (Fig. 3E).

## JA-Salicylic acid Cross-Talk

The interaction between the salicylic acid (SA) and JA signaling pathways was first documented in the context of the wound-induced reaction in tomato plants (Harms et al. 1998). Following the sensing of stress, JA quickly modulates the plant's gene defense mechanisms (Genva et al. 2019). SA plays a vital role in enhancing plant immunity against biotrophic and hemi-biotrophic fungi (Fu et al. 2012). The regulation of numerous NAC TF, including ANAC019/055/072, by JA signaling, serves to inhibit the production of SA. In short, when MYC2 and the promoters of several NACs come into direct contact, their transcription is turned on. According to Zheng et al. (2012), NAC TFs have been found to suppress the expression of a gene tangled in the production

known as *ISOCHORISMATE SYNTHASE 1 (ICS1)*. However, NAC TFs have been observed to enhance the transcriptional activity of a gene responsible for SA methylation, namely *BENZOIC ACID/SA CARBOXYL METHYLTRANSFERASE 1 (BSMT1)*. Furthermore, in JA and SA cross-talk a broad range of mediators participates. The components of the system consist of MAPK, redox regulators, specifically glutathione (GRX), thioredoxin (TRX), MYC2, TGACG-BINDING FACTORS (TGAs), and *PDF 1.2*. (Gatz 2013) and WRKY70 (Shim et al. 2013). The GRXs genes could inhibit the expression of TGA-dependent JA response genes, including ORA59, confirming the existence of an SA-JA antagonistic relationship (Zander et al. 2010, 2012). Mitogen-activated protein kinase 4 (MPK4) regulates GRX480 (SA signaling cascade) in a positive manner and regulates MYC2 (JA signaling cascade) in a negative manner (Wasternack and Hause 2013). When exposed to external SA, the NONEXPRESSOR OF PR GENES1 (NPR1) becomes active, leading to the activation of WRKY70. This activation stimulates the production of *PRI* and triggers a defense response. Upon stimulation of SA, the TRX enzyme facilitates the conversion of NPR1 polymers into monomers. The monomers, including GRX480, are conveyed to the nucleus where they selectively adhere to TGAs, and in turn, directly control the production of *PRI*.

SA has been identified as a key factor involved in the physiological response of plants to salt stress, light, and chilling stress (Gornik et al. 2014). Furthermore, it has been observed that the application of MeJA and Methyl Salicylate (MeSA) exhibits a beneficial effect in mitigating the occurrence of chilling damage in pomegranate (Sayyari et al. 2011). Both SA and JA have been found to play a role in plant adaptation to drought (Ilyas et al. 2017). Furthermore, previous research has shown that the administration of exogenous SA and JA resulted in a decrease in sodium ( $\text{Na}^+$ ) concentrations within soybean cells subjected to a variety of salinity stress. Additionally, it was observed that JA exhibited a greater impact on reducing  $\text{Na}^+$  levels compared to SA. In the context of *Nicotiana attenuata* plants, researchers have provided evidence to support the notion that MPK4 has two distinct functions in plant signal transduction. Indeed, in the context of light-induced conditions, this kinase functions as a suppressor within the SA signaling network, while assuming an activating role within the JA signaling cascade (Tuteja and Gill 2013). Hence, the involvement of MYC2 and MPK4 may be observed in the intercommunication between the JA-SA cross-talk. The MPK4 protein has been found to have a positive regulatory effect on GRX480 and a negative regulatory effect on MYC2. This negative regulation is crucial for the activation of JA-sensitive genes, specifically *PDF1.2* and *THI2.1*. SA and JA are recognized as crucial defense hormones that play significant roles in both basal and induced resistance mechanisms against a diverse

range of pests (Nguyen et al. 2022a, b; Qiong et al. 2022). The interaction of JA and SA regulates the plant's ability to withstand diseases caused by necrotrophic or hemi-biotrophic pests. SA triggers the activation of defense-related genes at the earliest stage in diseased plants. Several necrotrophic pests could inhibit plant resistance by modulating the SA signaling pathway, which in turn opposes the JA route. An instance of this phenomenon can be observed in the case of *Botrytis cinerea*, a necrotrophic fungus known for its ability to infect tomatoes. It has been found that *B. cinerea* can effectively inhibit the JA signaling pathway by generating an elicitor that activates the SA pathway (Hu et al. 2018a, b; Qiong et al. 2022). Conversely, JA increases the expression of defense-related genes at a later stage, particularly during the necrotrophic phase of necrotrophic or hemi-biotrophic diseases. Zhang et al. (2022), reported that hydrogen peroxide ( $H_2O_2$ ) plays a crucial role in both the JA and SA-mediated systemic cascade that are involved in the defense response against cotton bollworm feeding on tomato seedlings. The levels of both SA and JA were shown to be elevated in several poplar genotypes when exposed to the biotrophic rust fungus *Melampsora larici-populina*. Poplar trees that have been genetically modified to express elevated quantities of SA also exhibited heightened concentrations of JA and antimicrobial flavonoids. Furthermore, these modified poplar trees show enhanced protection against rust (Ullah et al. 2022). Recently, Zamora et al. (2021) indicated that ABA,  $CO_2$ , and light exert significant regulatory control over the fast-signaling process in guard cells. On the other hand, it is possible that JA and SA exhibit restricted participation in the broader stomatal reaction to external stimuli in *Arabidopsis* and Tomato (Fig. 3F).

### JA-Brassinosteroids Cross-Talk

JA has been shown to hinder plant growth, whereas brassinosteroids (BR) have been found to stimulate above-surface plant growth. The synergistic interaction of the JA-BR cross-talk is important for regulating the delicate equilibrium between plant development and defensive mechanisms (Yang et al. 2019). For instance, high levels of BR trigger BR signaling pathways involving BR receptor (BRI1), BR-related kinase (BAK1), and BR-related TFs. This leads to the activation of numerous genes such as PhyB Activation-tagged Suppressor1 (BES1) and BRASSINAZOLE-RESISTANT 1 family proteins (BZR1), which play a role in regulating BR signaling. The lower quantity of BR stimulates the production of *OsDII* and *OsDWARF* during both the initial and final phases of BR synthesis thus, in turn, triggering the activation of the defensive response (Yang et al. 2019). Additionally, the *DWARF4* gene encodes an essential enzyme involved in the production of BR. A partial

loss-of-function mutation in *DWARF4* resulted in the restoration of JA sensitivity in the *coi1* mutant context, while also causing a greater susceptibility to JA in the wild-type environment. Moreover, the expression of *DWARF4* was suppressed by JA in a COI1-dependent manner, and the inhibitory effects of JA on root growth were mitigated by external BR administration. (Ren et al. 2009). JA triggers the formation of a complex between JAZ and COI, whereas MYC2 facilitates the upregulation of *VSP2* expression through the involvement of mediator transcriptional regulation complex 2 (MED2), thereby providing resistance against herbivorous insects. Both JA and BR biosynthesis are suppressed when there is a surplus of either compound in the tissue (Choudhary et al. 2012). Recently, Zhang et al. (2023) suggested that JA has a dual role in regulating BR biosynthesis and signaling during apical hook formation. JAs not only suppress the expression of the BR biosynthetic gene *DWF4* but also play a crucial role in attenuating BR signaling. This attenuation occurs through the inhibition of the transcriptional activation of BZR1 by MYC2. Hence, the interaction between the production of JA and BR may have a role in regulating the equilibrium between plant development and protection mechanisms (Fig. 3G).

### JA-Based Elicitation Strategies of Secondary Metabolites in Medicinal Plants

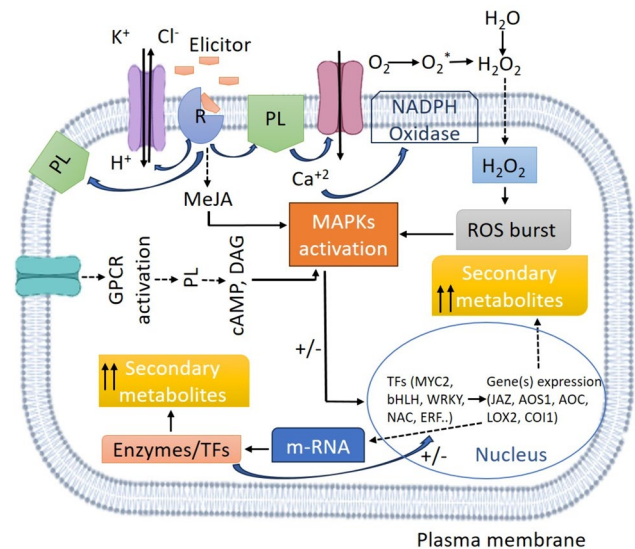
In addition to aiding in plant growth and development, JAs derivatives are a significant elicitor for the increase of bioactive metabolites. Among the different types of JAs, MeJA is a highly reported and widely employed phytohormone elicitor (Nadir and Alwan 2022; Jeyasri et al. 2023; Albayrak et al. 2024; Selwal et al. 2024). The varied effects of elicitors on physiological processes in plant systems include transcription, protein translation, environment adjustment, secondary metabolites production, and gene expression patterns. The growth and enhanced production of bioactive compounds in plants during elicitation is influenced by various parameters, such as the dosage of the elicitor, duration of treatment, nature of the elicitor, and growth phase of the plant (Dhiman et al. 2018; Halder et al. 2019). The multitude of biochemical and physiological reactions that transpire within a cellular entity as a reaction to a stimulus or elicitor. The cellular receptor located on the plasma membrane is responsible for detecting the elicitor, subsequently initiating a cascade of intracellular events. These events involve the reversible phosphorylation and dephosphorylation of proteins found in both the plasma membrane and cytosol. Additionally, there is an observed elevation in the concentration of cytosolic calcium, as well as the efflux of  $Cl^-$  and  $K^+$  ions. Furthermore, there is an influx of  $H^+$ , leading to extracellular



alkalinization and cytoplasmic acidification (Anjum et al. 2019; Guru et al. 2022). These modifications elicit many signaling cascades, including the MAPK pathway activating G proteins, tyrosine kinases, phospholipase (PL) mediating  $\text{Ca}^{2+}$  signaling, and activating pathways facilitated by diacylglycerol (DAG), or cyclic adenosine monophosphate (cAMP), resulting in the induction of NADPH (Nicotinamide adenine dinucleotide phosphate hydrogen) oxidase, an enzyme responsible for generating ROS and reactive nitrogen species (RNS) (Nabi et al. 2021; Guru et al. 2022). In addition, this mechanism triggers the activation of TFs such as MYC2, BHLH, and WRKY, the activation of early defense genes, the synthesis of JAs, and the subsequent activation of defensive response genes. Ultimately, this leads to the enhancement of the activation of genes/transcription factors responsible for secondary metabolites and increases the accumulation of secondary metabolites. Many past studies, suggested that MeJA affects the accumulation of secondary metabolites in various tissue culture techniques, including micro-propagated plants, adventitious root culture, callus culture, cell suspension culture, and hairy root culture (Fig. 4).

### Effect of JA in Micropropagation

In *Rauvolfia serpentina*, it has been observed that the application of 1.5 mg/L and 2 mg/L of MeJA under in vitro cultivated roots results in elevated levels of reserpine (0.456%) and ajmalicine (0.261%) content, respectively (Dey et al. 2020). In *Bacopa monnieri*, 1 mg/L JA dose increases the total Bacosides content in shoot culture (Sharma et al. 2013; Jauhari et al. 2019). A synergistic combination of 25  $\mu\text{M}$  of salicylic acid and MeJA increase Bacoside A3, Bacopaside II, Jujubogenin (an isomer of bacopasaponin C), and bacopasaponin C content in shoot culture of *B. monnieri* (Largia et al. 2015). In *Podophyllum hexandrum* Sharma et al. (2022a, b, c) reported a higher podophyllotoxin (POTX) content (0.33% w/w) when in vitro root treated with 1 mM MeJA elicitor. The addition of 1.5 mg/L MeJA enhances reserpine content (0.45% reserpine) in *Rauvolfia serpentina* in comparison to the control (0.40% reserpine) under tissue culture-raised plants (Dey et al. 2020). A concentration of 50  $\mu\text{M}$  MeJA leads to a maximum accumulation of apigenin content in *Salvia tebesana* (Shoja et al. 2022). In *Maytenus ilicifolia* root culture Santos et al. (2022) demonstrated that MeJA triggered an upsurge in the amounts of the alkaloids ilicifoliunine A and aquifoliunine E-I after 7 and 28 days, respectively. In *Dioscorea membranacea* a dose of 100  $\mu\text{M}$  JA exhibited the maximum amount of dioscorealide B under in vitro shoot culture (Jirakiattikul et al. 2020).



**Fig. 4** Schematic representation of the mode of the action of cells to elicitation. R receptor, PL phospholipase, MAPKs mitogen-activated protein kinases, ROS reactive oxygen species, RNS reactive nitrogen species, TFs transcription factors,  $\text{H}_2\text{O}_2$  Hydrogen peroxide, cAMP cyclic adenosine monophosphate, DAG diacylglycerol, GPCR G protein-coupled receptor, bHLH Basic helix loop helix

### Effect of JA in Callus Culture

In *Arnebia euchroma*, Hao et al. (2014) reported that 3.67  $\mu\text{M}$  MeJA enhances naphthoquinone and shikonin content in callus culture. The application of MeJA at a concentration of 0.03 mM resulted in a significantly increased rutin content of (5.606 mg/gm) compared to the control (1.569 mg/gm) in *Abutilon hirtum* callus culture (Nadir and Alwan 2022). Yazdani et al. (2022) reported the maximum anthocyanin content (8.99  $\mu\text{mol g}^{-1}$  fresh weight) (FW) was observed with a dose of 25  $\mu\text{M}$  of MeJA in *Allium jesdianum*. Suryawanshi et al. (2022) described that in the callus culture, of *Mucuna imbricata* concentration of 1 mM MeJA resulted in the maximum content of L-DOPA (4.3  $\pm$  0.4%).

### Effect of JA in Cell Suspension Culture

The utilization of elicitation has demonstrated its efficacy as a strategic approach to enhance the synthesis of specific metabolites across several cell culture systems. Recently, Rattan et al. (2023), shown that the application of a 100  $\mu\text{M}$  dose of MeJA elicitation leads to increased levels of salidroside (1.85 mg/g DW) and rosavin (0.67 mg/g DW) in the cell culture of *Rhodiola imbricata*. A concentration of 100  $\mu\text{M}$  JA induces salidroside (5.25 mg/g DW) accumulation in *R. imbricata* cell suspension culture (Kapoor et al. 2019). Krishnan et al. (2019) reported that MS media fortified with 100  $\mu\text{M}$  concentration of MeJA increased the Asiatic



acid content by 1.9-fold in the cell suspension culture of *Centella asiatica*. A synergistic effect of SA and MeJA has been found to have a considerable positive impact on the accumulation of ginkgolid, and bilobalide in *Ginkgo biloba* (Sukito and Tachibana 2016). Numerous research studies have documented that the administration of MeJA leads to an increased accumulation of POTX in *Podophyllum hexandrum* (Hazra et al. 2017; Bhattacharyya et al. 2012). According to Wang et al. (2014), the application of a 5  $\mu\text{M}$  dosage of MeJA in *Arnebia euchroma* resulted in an increase in shikonofuran derivatives and rosmarinic acid concentration in cell culture. Recently, Bisht et al. (2023) reported that a dose of 100  $\mu\text{M}$  MeJA in *Berberis lyceum*, leads to an elevated level of callus biomass and production of phytochemicals. In *Taraxacum officinale*, a notable enhancement in the taraxasterol level was found when MeJA was given at a dose of 0.2 mM (Sharma et al. 2016). In *Coriandrum sativum*, the supplementation of 150  $\mu\text{M}$  MeJA resulted in an increase in the production of essential oil in embryogenic cultures (Ali et al. 2019). The highest accumulation of verbascoside was observed after the process of elicitation at a concentration of 50  $\mu\text{M}$ , resulting in a yield of 4.97  $\text{g/L}^{-1}$  in *Buddleja cordata* (Arano-Varela et al. 2020).

### Effect of JA in Adventitious and Hairy Root Culture

In *Centella asiatica*, MeJA enhances triterpenoid accumulation in diploid and tetraploid hairy root cultures (Nguyen et al. 2019). Similarly, a significant amount of asiaticoside was produced when 0.1 mM MeJA was used in the growing medium for 21 days (7.12 mg/gm DW) (Kim et al. 2007). Furthermore, Baek et al. (2022) demonstrated that hairy root cultures of *C. asiatica* subjected to treatment with 400  $\mu\text{M}$  MeJA exhibited the most substantial concentration of triterpenoids (60.25 mg/g DW). In a recent study conducted by Zhao and Tang (2020), it has been shown that the application of MeJA results in a substantially increased level of valtrate content (3.63 times) compared to the control cultures in *Valeriana jatamansi*. The application of 0.6 mg/L MeJA in *Ajuga bracteosa* resulted in a significantly greater dry biomass accumulation of (8.88 g/L DW) after 32 days of log phase (Saeed et al. 2017). After being treated with 100  $\mu\text{M}$  MeJA, *Swertia chirayita* showed a 1.80-fold rise in swerchirin content and a sixfold increase in 1,2,5,6-tetrahydroxyanthrone content compared to the control (Mahendran et al. 2022). At 7 days post-elicitation, valerenic acid production was increased sixfold in *Valeriana officinalis* when treated with MeJA 100  $\mu\text{M}$  compared to untreated culture (Torkamani et al. 2014). In *Withania somnifera* a combination of 0.5 mM  $\beta$ -cyclodextrin( $\beta$ -CD) + 100  $\mu\text{M}$  MeJA results in a 6.84-fold increase in withaferin A content, whereas 5.0 mM

$\beta$ -CD + 100  $\mu\text{M}$  MeJA results in a 12.46-fold increase withaferin A content as compare to non-treated culture (Karami et al. 2023). In *Scutellaria bornmuelleri*, the addition of 100  $\mu\text{M}$  MeJA enhances monoterpene content (Gharari et al. 2023). The application of MeJA results in a substantial increase in the content of rosmarinic acid, with levels reaching 55.44  $\mu\text{g g}^{-1}\text{DW}$  after 6 h of exposure to the elicitor. This represents an approximately 11.84-fold increase compared to the control culture in *Mentha spicata* (Yousefian et al. 2020). A 13-fold rise in zerumbone concentration was observed after collaborative elicitation with 400  $\mu\text{M}$  MeJA and 400  $\mu\text{M}$  SA, whereas a 4.3-fold rise in  $\alpha$ -humulene concentration was observed after treatment with 400  $\mu\text{M}$  MeJA and 600  $\mu\text{M}$  SA in *Zingiber zerumbet* adventitious root culture (Alwakil et al. 2022). In *Talinum paniculatum* adventitious root culture an elicitation of 0.2 mM MeJA for a duration of 15 days leads to a 1.5-fold rise in saponin content (Faizal et al. 2019). The effect of JA and MeJA elicitors is used for the enhancement of specialized metabolites in medicinal plants. The concentration of elicitor and enhanced metabolites are listed in Table 2.

### Effect of JA on Antioxidant Activity in Tissue Culture

In the case of *Ajuga bracteosa*, the application of MeJA at doses of 0.6 mg/L and 1.2 mg/L resulted in elevated levels of total phenolic compounds (TPC) in the root cultures during the log phase (3.6 mg gallic acid equivalents/g DW) (GAE) and stationary phase (3.7 mg GAE/g DW), respectively (Saeed et al. 2017). Likewise, the concentration of 100  $\mu\text{M}$  MeJA has been seen to result in an elevation in both total phenolic and flavonoid content in *Rhodiola imbricata* cell culture. In *Paris polyphylla*, a concentration of 50  $\mu\text{M}$  MeJA leads to an increased level of total phenol, flavonoids, and tannin content under in vitro conditions (Rawat et al. 2023). In *Nardostachys jatamansi*, a 6  $\mu\text{M}$  concentration of MeJA enhances total phenolic, flavonoid, and tannin and increases overall antioxidant activity in callus culture (Rawat et al. 2020). The phenolic content was negatively impacted by an increase in MeJA concentration. In *Ruta graveolens* the maximum value of 44.33 mg GAE  $\text{g}^{-1}\text{FW}$  was achieved on the fifth day after elicitation with MJ, resulting in a 4.4-fold enhancement compared to the control (Joshi et al. 2023). The addition of 1  $\mu\text{M}$  MeJA and exposure to blue light leads to a substantial increase in the content of phenolic content in *Glycyrrhiza glabra* under in vitro conditions (Emami et al. 2023). In the shoot culture of *Ocimum sanctum* a supplementation of 100  $\mu\text{M}$ , MeJA enhances total phenols and flavonoid content (Autajamsripon et al. 2023). It is important to acknowledge that the application of 20 mg/L MeJA resulted in the maximum flavonoid concentration in *Moringa*

**Table 2** Secondary metabolites enhancement in the in vitro cultures of medicinal plants in response to JA/MeJA elicitor treatment

Plant species	Type of culture	Enhanced metabolites	JA/MeJA concentration	References
<i>Ocimum sanctum</i>	Shoot culture	Eugenol	100 $\mu$ M	Autajamsripon et al. (2023)
<i>Ganoderma applanatum</i>	Suspension culture	Triterpene	150 $\mu$ M	Sułkowska-Ziaja et al. (2023)
<i>Mentha piperata</i>	Cell suspension cultures	Rosmarinic acid	100 $\mu$ M	Krzyzanowska et al. (2012)
<i>Gymnema sylvestre</i>	Cell suspension cultures	Gymnemic acid	150 $\mu$ M	Chodisetti et al. (2015)
<i>Catharanthus roseus</i>	Hairy root culture	Vinblastine	50 $\mu$ M	Vu et al. (2022)
<i>Echinacea purpurea</i>	Cell suspension culture	Chicoric acid	7.5 mg/L	Ravazzolo et al. (2022)
<i>Prunella vulgaris</i>	Hairy root culture	Rosmarinic acid	100 $\mu$ M	Ru et al. (2022)
<i>Hyoscyamus muticus</i>	Cell suspension culture	Atropine	100 $\mu$ M	Abdelazeez et al. (2022)
<i>Dioscorea membranacea</i>	Shoot culture	Dioscorealide B	100 $\mu$ M	Jirakiattikul et al. (2020)
<i>Rhodiola imbricata</i>	Cell suspension culture	Salidroside and rosavin	100 $\mu$ M	Rattan et al. (2023)
<i>Sinopodophyllum hexandrum</i>	In vitro culture	Podophyllotoxin	1.0 mM	Sharma et al. (2022a, b, c)
<i>Taxus species</i>	Hairy root culture	Triterpenoid and steroids	100 $\mu$ M	Syklowska-Baranek et al. (2022)
<i>Senna obtusifolia</i>	Hairy root culture	Betulinic acid	100 $\mu$ M	Kowalczyk et al. (2021)
<i>Calendula officinalis</i>	Hairy root culture	Oleanolic acid	100 $\mu$ M	Alsoufi et al. (2019)
<i>Vernonia anthelmintica</i>	Cell suspension culture	Rhamnetin	0.8 mM	Rajan et al. (2020)
<i>Isatis tinctoria</i>	Hairy root culture	Flavonoids	179.54 $\mu$ M	Gai et al. (2019)

*Oleifera* callus culture (Abed et al. 2023). A synergistic combination of Cu (25  $\mu$ M) and MeJA (5  $\mu$ M) enhances antioxidant activity and total phenolic compound in *Ocimum basilicum* under in vitro conditions (Górski et al. 2023). In *Allium jesdianum* and *Hibiscus sabdariffa* a maximum amount of total phenolics, flavonoids, and flavonols was found under treatment of 50  $\mu$ M and 100  $\mu$ M MeJA doses, respectively (Yazdaniyan et al. 2022; Jirakiattikul et al. 2021). Treatment with 100  $\mu$ M MeJA increased total phenolic and flavonoid content in *Prunella vulgaris* hairy root culture (Ru et al. 2022). In the cell suspension culture of the *vetia peruviana* application to 3  $\mu$ M MeJA increased phenolic compounds, antioxidant activity, and flavonoid content by 1.49, 1.66, and 2.55-fold, respectively, as compared to untreated cultures (Pablo Arias et al. 2018). The callus cultures that were treated to a concentration of 150  $\mu$ M JA for a duration of 20 days exhibited the highest levels of phenolic and flavonoids content in comparison to the non-treated culture of *Givotia moluccana* (Woch et al. 2023).

## Molecular Regulation of JA Action

Over the past decade, researchers have integrated elicitation investigations with gene expression analyses using molecular biology techniques to validate the molecular machinery behind elicitation treatment. In the hairy roots of *Salvia przewalskii*, the application of 400  $\mu$ M MeJA resulted in a significant enhancement in the production of salvianolic acid B and rosmarinic acid, with an increase of 8.14-fold and 1.78-fold, respectively. This improvement was mostly attributed

to the regulation of gene expression, specifically *copalyl diphosphate synthase (CPS)*, *cytochrome P450-dependent monooxygenase (CYP76AH1)*, and *entkaurene synthase like (KSL)* genes (Li et al. 2020). The co-stimulation of MeJA with putrescine in the shoot culture of *Catharanthus roseus* led to the increased expression of genes responsible for alkaloid production and signal transduction (Khataee et al. 2019). Zhou et al. (2021) also discovered another MeJA-associated TF gene, namely *SmMYB1*, in *S. miltiorrhiza*. This gene enhances the expression of *CYP98A14* by specifically binds to cis-element located in the promoter region. Additionally, *SmMYB1* exhibits a positive correlation with *SmMYC2*, thereby enhancing the accumulation of anthocyanin production and phenolic compounds. The application of MeJA induces an upregulation in the expression of pivotal genes involved in the rosmarinic acid, namely *phenylalanine ammonia-lyase (PAL)*, *4-coumarate CoA ligase (4CL)*, and *rosmarinic acid synthase (RAS)*, in two *Salvia* species (Kianersi et al. 2023).

TFs are attractive candidates for metabolic engineering because they have the capacity to control the transcription of numerous genes involved in biosynthetic pathways. Elicitation leads to the stimulation of TFs that control transcription and translation by specifically binding to cis-acting regions in the promoters of target genes. This ultimately leads to the buildup of bioactive compounds generated by JAs. Conversely, several TFs including WRKY, bZIP, bHLH, COI1, AP2/ERF, and MYB2/3 participate in the MeJA signaling pathway and regulate bioactive metabolites production and accumulation in plants. Additionally, MeJA regulates the activity

of WRKY TFs, which are essential for the biosynthesis of secondary metabolites in therapeutically valuable plant species. The WRKY TFs are responsible for regulating the accumulations of medicinally important bioactive compounds, such as taxol in *Taxus chinensis* and artemisinin in *Artemisia annua*.

In the cell suspension culture of *R. imbricata*, Rattan et al. (2023) showed that the synergistic effect of SA and MeJA resulted in an increased expression of the phenylethanoids, and phenylpropanoids pathways genes led to the higher accumulation of salidroside and rosavin metabolites. In a hairy root culture investigation, Yousefian et al. (2020) reported that the application of MeJA increased the accumulation of phenolic compounds as well as the relative expression levels of *MsPAL*, *MsC4H*, *Ms4CL*, and *MsHPPR* gene in *Mentha spicata*. A significant upregulation in the comparative transcript expression of *superoxide dismutase (SOD)*, *catalase (CAT)*, *peroxidase (POD)*, and *ascorbate peroxidase (APX)* was seen in callus cultures of *Givotia moluccana* when treated with a dose range of 100–200  $\mu\text{M}$  JA (Woch et al. 2023). Recently Fang et al. (2023), reported that TFs SbWRKY75 exert direct control over the expression of the flavonoid biosynthetic gene *SbCLL-7*. Additionally, SbWRKY41 was shown to directly regulate the expression of two other flavonoid biosynthetic genes, namely *SbF6H* and *SbUGT*, hence controlling the production of baicalin in *Scutellaria baicalensis*. The application of MeJA in *Taxus baccata* was seen to enhance the transcription of specific genes *10-deacetylbaccatin III-10- $\beta$ -O-acetyltransferase (DBAT)*, *baccatin III-13-O-(3-amino3-phenyl propyl) transferase (BAPT)*, and *taxadiene synthase (TS)* associated with the taxol biosynthesis pathway, resulting in a higher level of taxol biosynthesis (Zhouliideh et al. 2022).

Caretto et al. (2011) reported that a concentration of 22  $\mu\text{M}$  MeJA resulted in a threefold augmentation in artemisinin synthesis after around 30 min, while a concentration of 200  $\mu\text{M}$  miconazole led to a 2.5-fold increase in artemisinin production after 24 h, but had detrimental effects on the survival of the cells. The application of MeJA resulted in an increase in the expression of *CYP71AV1*, whereas the application of miconazole led to an increase in the expression of *cytochrome P450 reductase (CPR)* and *artemisinic aldehyde  $\Delta 11(13)$  reductase (DBR2)* genes in the suspension culture of *A. annua*. There is evidence indicating that plants employ regulatory mechanisms TFs to manage signaling cascades, which can counteract the detrimental effects of biotic and abiotic stress. In the last few years recommended research done on transgenic plants has uncovered the crucial involvement of TFs and gene expression. These pathways play a vital role in safeguarding plants against

various stresses and promoting the synthesis of secondary metabolites. In addition, Table 3 provides a brief overview of the effect of elicitor treatment in response to gene expression and secondary metabolite accumulation in medicinally valuable plants.

## Conclusion and Prospects

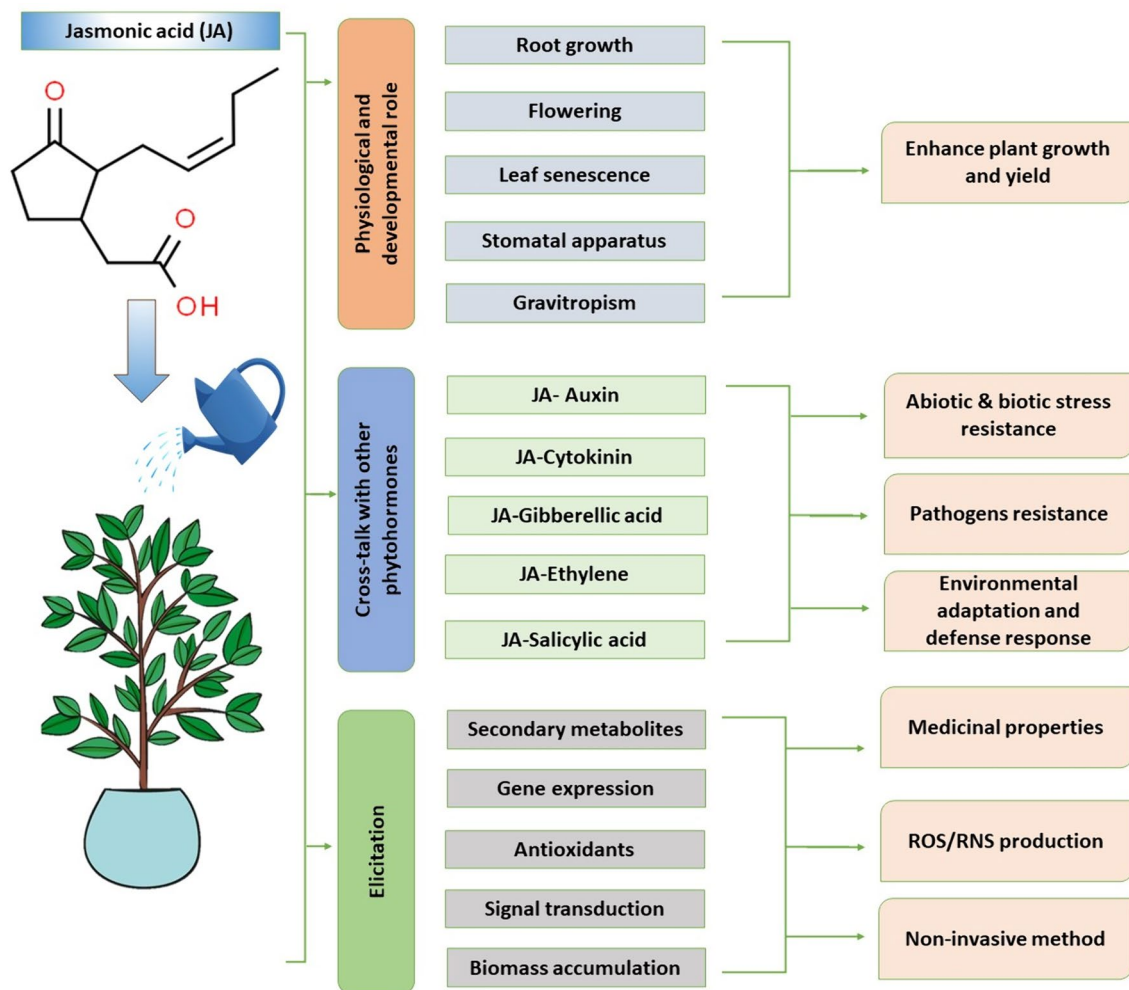
In recent years, numerous research studies have highlighted the multifaceted role of JA as a phytohormone, functioning as a defense signal while impacting various facets of plant growth, development, and defense systems (Ghorbel et al. 2021; Hewedy et al. 2023; Rao et al. 2023a, b). Advances in understanding JA's signaling and metabolic pathways, primarily through studies in model plants such as Arabidopsis and rice, provide crucial insights applicable to a broader spectrum of plant species. Key genes like *JAZ*, *AOS1*, *AOC*, *LOX2*, and *CO11*, alongside TFs like *MYC2* and *bHLH*, orchestrate the central JA signaling pathway, exerting both stimulating and inhibitory effects to regulate plant responses to environmental cues (Checker et al. 2018; Sohn et al. 2022; Rao et al. 2023a, b; Sood 2023). Medicinal plants, with their potential to produce pharmacologically important bioactive compounds, offer promising avenues for future natural medication development and various industrial applications. Elicitation strategies emerge as effective means to enhance the production of therapeutically valuable metabolites, necessitating further exploration of JA-mediated elicitation mechanisms across diverse plant systems amidst changing environmental conditions (Ueda et al. 2021; Kandoudi and Németh-Zámboriné 2022; Jeyasri et al. 2023; Selwal et al. 2024) (Fig. 5).

The burgeoning field of eliciting secondary metabolites from plant cell cultures holds promise for enhancing metabolite output and represents an area for further investigation. Literature suggests that the external application of JAs and MeJA regulates and impacts morphological characteristics, physiological processes, metabolic pathways, as well as yield and quality components of crops under varying environmental conditions (Jeyasri et al. 2023; Sood 2023). However, comprehensive future research is essential to fully uncover JA's potential role and its utility as a management tool for enhancing crop development, productivity, and resilience. Moreover, a more thorough investigation into the complex interplay between JA and other phytohormones across diverse growth and physiological scenarios is necessary for a holistic comprehension of plant hormone dynamics.

**Table 3** Effect of elicitor treatment in response to molecular regulation and secondary metabolite accumulation in medicinally valuable plants

Plant species	Types of culture	Metabolites	Gene expression	Elicitors concentration	References
<i>Prunella vulgaris</i>	Hairy root culture	Rosmarinic acid	Upregulation of expression of <i>PvPAL</i> , <i>PvHPPR</i> , <i>PvC4H</i> , <i>Pv4CL1</i> , <i>Pv4CL2</i> , and <i>PvCYP98A101</i> genes	100 $\mu$ M MeJA	Ru et al. (2022)
<i>Salvia przewalskii</i>	Hairy root culture	Cryptotanshinone, tanshinone IIA, rosmarinic acid, and salvianolic acid B	Enhanced production of <i>CPS</i> , <i>CYP76AH1</i> , and <i>KSL</i> genes	400 $\mu$ M MeJA	Li et al. (2020)
<i>Catharanthus roseus</i>	Shoot culture	Alkaloid production	Increased expression levels of <i>STR</i> , <i>GS</i> , <i>DAT</i> , and <i>PRX1</i> genes	100 $\mu$ M MeJA along with 1 mM of putrescine	Khataee et al. (2019)
<i>Salvia miltiorrhiza</i>	Hairy root culture	Anthocyanin and phenolic compounds	Higher expression of the <i>CYP98A14</i> gene leads to a higher production of secondary metabolites	50 $\mu$ M MeJA and 10 mg/L SA	Zhou et al. (2021)
<i>Rhodiola imbricata</i>	Cell suspension culture	Salidroside and Rosavin	Higher expression of the aromatic-L-amino-acid decarboxylase ( <i>TDC</i> ), Uridine 5' -diphosphoglucuronosyltransferase ( <i>UGT 73 C</i> ), cinnamyl alcohol dehydrogenase ( <i>CAD</i> ) and cinnamoyl-CoA reductase ( <i>CCR</i> ) genes	50 $\mu$ M SA and 100 $\mu$ M MeJA	Rattan et al. (2023)
<i>Mentha spicata</i>	Hairy root culture	Rosmarinic acid, caffeic acid, chlorogenic acid, and cinnamic acid	MeJA increases relative expression levels of <i>MsPAL</i> , <i>MsC4H</i> , <i>Ms4CL</i> , and <i>MsHPPR</i> genes	MeJA 100 $\mu$ M	Yousefian et al. (2020)
<i>Givotia moluccana</i>	Callus culture	Enhanced Phenolics and flavonoids accumulation	Significant upregulation in the comparative transcript expression of <i>SOD</i> , <i>CAT</i> , <i>POD</i> , and <i>APX</i> genes	100–200 $\mu$ M JA	Woch et al. (2023)
<i>Valeriana officinalis</i>	Hairy root culture	Increased the activity of catalase enzymes and proline content	The <i>VtPS6</i> gene was the most highly expressed	MeJA 100 $\mu$ M and L-leucine 1 mM	Madami et al. (2021)
<i>Taxus baccata</i>	Cell suspension culture	Taxol and baccatin III	Higher expression of taxadiene synthase ( <i>TXS</i> ) and baccatin III 13-O-(3-amino-3-phenylpropenyl) transferase ( <i>BAPT</i> ) genes	MeJA 100 $\mu$ M	Miriam et al. (2010)
<i>Castilleja tenuiflora</i>	In vitro plants	Iridoid glycosides and phenolic compounds	Enhanced metabolite biosynthesis-related genes such as <i>Cte-PAL1</i> , <i>Cte-CHSI</i> , <i>Cte-DXS1</i> , and <i>Cte-G10H</i>	100 $\mu$ M MeJA	Rubio-Rodriguez et al. (2021)





**Fig. 5** Pictorial representations of the effect of jasmonic acid (JA) on physiological and developmental biology, interaction with other phytohormones and elicitation

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical Approval** This article followed the ethical standards of the institute.

## References

- Abdelazez WMA, Anatolievna KY, Zavdetovna KL, Damirovna AG, Abou El-Dis GR, Arnoldovna TO (2022) Enhanced productivity of atropine in cell suspension culture of *Hyoscyamus muticus* L. *In Vitro Cell Dev Biol Plant* 58(4):593–605
- Abed AS, Ismail EN, Majeed DM, Al-Jibouri AMJ (2023) Increasing amounts of secondary metabolites and medicinal compounds in callus culture of *Moringa Oleifera* (Lam.) using abiotic elicitors. *Iraqi J Sci*. <https://doi.org/10.24996/ij.s.2023.64.8.17>
- Afrin S, Huang JJ, Luo ZY (2015) JA-mediated transcriptional regulation of secondary metabolism in medicinal plants. *Sci Bull* 60:121062–121072
- Albayrak İ, Demirci T, Baydar NG (2024) Enhancement of *in vitro* production of tropane alkaloids and phenolic compounds in *Hyoscyamus niger* by culture types and elicitor treatments. *Plant Cell Tissue Organ Cult* 156(3):72
- Aleman F, Yazaki J, Lee M, Takahashi Y, Kim AY, Li Z, Kinoshita T, Ecker JR, Schroeder JI (2016) An ABA-increased interaction of the PYL6 ABA receptor with MYC2 transcription factor: a putative link of ABA and JA signalling. *Sci Rep* 6(1):28941
- Ali M, Mujib A, Gulzar B, Zafar N (2019) Essential oil yield estimation by Gas chromatography–mass spectrometry (GC–MS) after Methyl jasmonate (MeJA) elicitation in *in vitro* cultivated tissues of *Coriandrum sativum* L. *3 Biotech*. <https://doi.org/10.1007/s13205-019-1936-9>
- Alsoufi ASM, Pączkowski C, Szakiel A, Długosz M (2019) Effect of jasmonic acid and chitosan on triterpenoid production in *Calendula officinalis* hairy root cultures. *Phytochem Lett* 31:5–11
- Alwakil NH, Mohamad Annuar MS, Jalil M (2022) Synergistic effects of plant growth regulators and elicitors on  $\alpha$ -humulene and zerumbone production in *Zingiber zerumbet* Smith adventitious root cultures. *Molecules* 27(15):4744
- Andersson MX, Hamberg M, Kourtchenko O, Brunnstro Å, McPhail KL, Gerwick WH, Go C, Feussner I, Ellerstro M (2006) Oxylin profiling of the hypersensitive response in *Arabidopsis thaliana*: formation of a novel oxo-phytodienoic acid-containing galactolipid, arabidopside E World. *J Biol Chem* 281(42):31528–31537
- Anjum S, Anjum I, Hano C, Kousar S (2019) Advances in nanomaterials as novel elicitors of pharmacologically active plant specialized metabolites: current status and future outlooks. *RSC Adv* 9(69):40404–40423
- Arano-Varela H, Cruz-Sosa F, Estrada-Zúñiga ME, Fernández FJ (2020) Effects of phenylalanine and methyl jasmonate on verbascoside production in *Buddleja cordata* Kunth cell suspension cultures. *S Afr J Bot* 135:41–49
- Argueso CT, Ferreira FJ, Kieber JJ (2009) Environmental perception avenues: the interaction of cytokinin and environmental response pathways. *Plant Cell Environ* 32(9):1147–1160
- Asigbaase M, Adusu D, Anaba L, Abugre S, Kang-Milung S, Acheamfour SA, Adamu I, Ackah DK (2023) Conservation and economic benefits of medicinal plants: Insights from forest-fringe communities of Southwestern Ghana. *Trees for People* 14:100462
- Autajamsripon J, Jirakiattikul Y, Rithichai P, Itharat A (2023) Effect of phenylalanine and methyl jasmonate on secondary metabolite production by shoot cultures of holy basil, purple-type (*Ocimum sanctum* L.). *Sci Technology Asia* 28:229–239
- Baek S, Han JE, Ho TT, Park SY (2022) Development of hairy root cultures for biomass and triterpenoid production in *Centella asiatica*. *Plants* 11(2):148
- Bhardwaj K, Silva AS, Atanassova M, Sharma R, Nepovimova E, Musilek K, Sharma R, Alghuthaymi MA, Dhanjal DS, Nicoletti M, Sharma B (2021) Conifers phytochemicals: a valuable forest with therapeutic potential. *Molecules* 26(10):3005
- Bhattacharyya D, Sinha R, Ghanta S, Chakraborty A, Hazra S, Chattopadhyay S (2012) Proteins differentially expressed in elicited cell suspension culture of *Podophyllum hexandrum* with enhanced podophyllotoxin content. *Proteome Sci* 10:1–12
- Bisht A, Singh L, Pandey A, Pandey V, Dasila K, Bhatt ID, Pande V (2023) Elicitor-induced phytochemicals production in *Berberis lycium* Royle. *Ind Crops Prod*. <https://doi.org/10.1016/j.indcrop.2023.116735>
- Boter M, Golz JF, Giménez-Ibañez S, Fernandez-Barbero G, Franco-Zorrilla JM, Solano R (2015) FILAMENTOUS FLOWER is a direct target of JAZ3 and modulates responses to jasmonate. *Plant Cell* 27(11):3160–3174
- Brioudes F, Joly C, Szécsi J, Varaud E, Leroux J, Bellvert F, Bertrand C, Bendahmane M (2009) Jasmonate controls late development stages of petal growth in *Arabidopsis thaliana*. *Plant* 160(6):1070–1080
- Browse J (2009) Jasmonate passes muster: a receptor and targets for the defense hormone. *Annu Rev Plant Biol* 60:183–205
- Cai XT, Xu P, Zhao PX, Liu R, Yu LH, Xiang CB (2014) Arabidopsis ERF109 mediates cross-talk between jasmonic acid and auxin biosynthesis during lateral root formation. *Nat Commun* 5(1):5833
- Canonne J, Froidure Nicolas S, Rivas S (2011) Phospholipases in action during plant defense signaling. *Plant Signal Behav* 6(1):13–18
- Caretto S, Quarta A, Durante M, Nisi R, De Paolis A, Blando F, Mita G (2011) Methyl jasmonate and miconazole differently affect artemisinin production and gene expression in *Artemisia annua* suspension cultures. *Plant Biol* 13(1):51–58
- Checker VG, Kushwaha HR, Kumari P, Yadav S (2018) Role of phytohormones in plant defense: signaling and cross talk. *Molecular aspects of plant-pathogen interaction*, pp 159–184
- Chen Y, Feng P, Tang B, Hu Z, Xie Q, Zhou S, Chen G (2022a) The AP2/ERF transcription factor SIERF. F5 functions in leaf senescence in tomato. *Plant Cell Rep* 41(5):1181–1195
- Chen D, Mubeen B, Hasnain A, Rizwan M, Adrees M, Naqvi SAH, Iqbal S, Kamran M, El-Sabroun AM, Elansary HO, Mahmoud EA (2022b) Role of promising secondary metabolites to confer resistance against environmental stresses in crop plants: Current scenario and future perspectives. *Front Plant Sci* 13:881032
- Chodisetti B, Rao K, Gandhi S, Giri A (2015) Gymnemic acid enhancement in the suspension cultures of *Gymnema sylvestre* by using the signaling molecules—methyl jasmonate and salicylic acid. *In Vitro Cell Dev Biol Plant* 51:88–92
- Choudhary SP, Yu JQ, Yamaguchi-Shinozaki K, Shinozaki K, Tran LSP (2012) Benefits of brassinosteroid crosstalk. *Trends Plant Sci* 17(10):594–605
- Demole E, Lederer E, Mercier D (1962) Isolement et détermination de la structure du jasmonate de méthyle, constituant odorant caractéristique de l'essence de jasmin. *Helv Chim Acta* 45(2):675–685
- Dey A, Nandy S, Nongdam P, Tikendra L, Mukherjee A, Mukherjee S, Pandey DK (2020) Methyl jasmonate and salicylic acid elicit indole alkaloid production and modulate antioxidant defence and biocidal properties in *Rauvolfia serpentina* Benth. *Ex Kurz*. *S Afr J Sci* 135:1–17
- Dhiman N, Patial V, Bhattacharya A (2018) The current status and future applications of hairy root cultures. *Biotechnol Approaches Med Aromatic: Plants Conserv, Genetic Improv Utilization*. [https://doi.org/10.1007/978-981-13-0535-1\\_5](https://doi.org/10.1007/978-981-13-0535-1_5)
- Ding F, Wang C, Xu N, Zhang S, Wang M (2022) SIMYC2 mediates jasmonate-induced tomato leaf senescence by promoting chlorophyll degradation and repressing carbon fixation. *Plant Physiol Biochem* 180:27–34

- Emami M, Estaji A, Ghanbari A, Khazaei Z, Ghorbani Ghouzhdhi H (2023) The effect of methyl jasmonate and light on licorice secondary metabolites (*Glycyrrhiza glabra* L.) under in vitro condition. *J Plant Process Funct* 12(54):91–104
- Erb M, Kliebenstein DJ (2020) Plant secondary metabolites as defenses, regulators, and primary metabolites: the blurred functional trichotomy. *Plant Physiol* 184(1):39–52
- Faizal A, Sari AV (2019) Enhancement of saponin accumulation in adventitious root culture of Javanese ginseng (*Talinum paniculatum* Gaertn.) through methyl jasmonate and salicylic acid elicitation. *AJB* 18(6):130–135
- Fang S, Zhang C, Qiu S, Xiao Y, Chen K, Lv Z, Chen W (2023) SbWRKY75- and SbWRKY41-mediated jasmonic acid signaling regulates baicalin biosynthesis. *Front Plant Sci* 14:1213662
- Fu ZQ, Yan S, Saleh A, Wang W, Ruble J, Oka N, Mohan R, Spoel SH, Tada Y, Zheng N, Dong X (2012) NPR3 and NPR4 are receptors for the immune signal salicylic acid in plants. *Nature* 486(7402):228–232
- Gai QY, Jiao J, Wang X, Zang YP, Niu LL, Fu YJ (2019) Elicitation of *Isatis tinctoria* L. hairy root cultures by salicylic acid and methyl jasmonate for the enhanced production of pharmacologically active alkaloids and flavonoids. *Plant Cell Tissue Organ Cult* 137:77–86
- Gatz C (2013) From pioneers to team players: TGA transcription factors provide a molecular link between different stress pathways. *Mol Plant-Microbe Interact* 26(2):151–159
- Genva M, Obounou Akong F, Andersson MX, Deleu M, Lins L, Faconnier ML (2019) New insights into the biosynthesis of esterified oxylipins and their involvement in plant defense and developmental mechanisms. *Phytochem Rev* 18:343–358
- Gharari Z, Bagheri K, Sharafi A (2023) Enhanced terpenoids production of elicited hairy root cultures of *Scutellaria bornmuelleri*. *Braz Arch Biol Technol* 66:23210435
- Ghorbel M, Brini F, Sharma A, Landi M (2021) Role of jasmonic acid in plants: the molecular point of view. *Plant Cell Rep* 40:1471–1494
- Gill SS, Anjum NA, Hasanuzzaman M, Gill R, Trivedi DK, Ahmad I, Pereira E, Tuteja N (2013) Glutathione and glutathione reductase: a boon in disguise for plant abiotic stress defense operations. *Plant Physiol Biochem* 70:204–212
- Gorham SR, Weiner AI, Yamadi M, Krogan NT (2018) HISTONE DEACETYLASE 19 and the flowering time gene *FD* maintain reproductive meristem identity in an age-dependent manner. *J Exp Bot* 69(20):4757–4771
- Gornik K, Badowiec A, Weidner S (2014) The effect of seed conditioning, short-term heat shock and salicylic, jasmonic acid or brassinolide on sunflower (*Helianthus annuus* L.) chilling resistance and polysome formation. *Acta Physiol Plant* 36:2547–2554
- Górski F, Gerotti GM, Gonçalves JE, Gazim ZC, Magalhães HM (2023) Methyl jasmonate and copper activate volatiles and antioxidant mechanisms in ‘Grecco a Palla’ basil produced in vitro. *J Crop Sci Biotechnol* 26(5):615–629
- Guan L, Denkert N, Eisa A, Lehmann M, Sjuts I, Weiberg A, Soll J, Meinecke M, Schwenkert S (2019) JASSY a chloroplast outer membrane protein required for jasmonate biosynthesis. *Proc Acad Sci* 116(21):10568–10575
- Guan Y, Ding L, Jiang J, Shentu Y, Zhao W, Zhao K, Zhang X, Song A, Chen S, Chen F (2021) Overexpression of the CmJAZ1-like gene delays flowering in *Chrysanthemum morifolium*. *Hortic Res*. <https://doi.org/10.1038/s41438-021-00525-y>
- Guru A, Dwivedi P, Kaur P, Pandey DK (2022) Exploring the role of elicitors in enhancing medicinal values of plants under *in vitro* condition. *S Afr J Bot* 149:1029–1043
- Gutierrez L, Mongelard G, Floková K, Păcurar DI, Novák O, Staswick P, Kowalczyk M, Păcurar M, Demailly H, Geiss G, Bellini C (2012) Auxin controls arabidopsis adventitious root initiation by regulating jasmonic acid homeostasis. *Plant Cell* 24(6):2515–2527
- Halder M, Sarkar S, Jha S (2019) Elicitation: a biotechnological tool for enhanced production of secondary metabolites in hairy root cultures. *Eng Life Sci* 19(12):880–895
- Hao H, Lei C, Dong Q, Shen Y, Chi J, Ye H, Wang H (2014) Effects of exogenous methyl jasmonate on the biosynthesis of shikonin derivatives in callus tissues of *Arnebia euchroma*. *Appl Biochem Biotechnol* 173:2198–2210
- Harms K, Ramirez I, Pena-Cortés H (1998) Inhibition of wound-induced accumulation of allene oxide synthase transcripts in flax leaves by aspirin and salicylic acid. *Plant Physiol* 118(3):1057–1065
- Hazman M, Hause B, Eiche E, Nick P, Riemann M (2015) Increased tolerance to salt stress in OPDA-deficient rice ALLENE OXIDE CYCLASE mutants is linked to an increased ROS-scavenging activity. *J Exp Bot* 66(11):3339–3352
- Hazra S, Bhattacharyya D, Chattopadhyay S (2017) Methyl jasmonate regulates podophyllotoxin accumulation in *Podophyllum hexandrum* by altering the ROS-responsive podophyllotoxin pathway gene expression additionally through the down regulation of few interfering miRNAs. *Front Plant Sci* 8:164
- Hernández-García J, Briones-Moreno A, Blázquez MA (2021) Origin and evolution of gibberellin signaling and metabolism in plants. *Seminars in cell & developmental biology*, vol 109. Academic Press, pp 46–54
- Hewedy OA, Elsheery NI, Karkour AM, Elhamouly N, Arafa RA, Mahmoud GAE, Dawood MFA, Hussein WE, Mansour A, Amin DH, Allakhverdiev SI (2023) Jasmonic acid regulates plant development and orchestrates stress response during tough times. *Environ Exp Bot* 208:105260
- Horbowicz M, Wiczowski W, Koczkodaj D, Saniewski M (2011) Effects of methyl jasmonate on accumulation of flavonoids in seedlings of common buckwheat (*Fagopyrum esculentum* Moench). *Acta Biol Hung* 62:265–278
- Hou Y, Wang Y, Tang L, Tong X, Wang L, Liu L, Huang S, Zhang J (2019) SAPK10-mediated phosphorylation on WRKY72 releases its suppression on jasmonic acid biosynthesis and bacterial blight resistance. *Iscience* 16:499–510
- Hu Y, Jiang L, Wang F, Yu D (2013) Jasmonate regulates the inducer of CBF expression—c-repeat binding factor/DRE binding factor1 cascade and freezing tolerance in arabidopsis. *Plant Cell* 25(8):2907–2924
- Hu Y, Jiang Y, Han X, Wang H, Pan J, Yu D (2017) Jasmonate regulates leaf senescence and tolerance to cold stress: crosstalk with other phytohormones. *J Exp Bot* 68(6):1361–1369
- Hu J, Israeli A, Ori N, Sun TP (2018a) The interaction between DELLA and ARF/IAA mediates crosstalk between gibberellin and auxin signaling to control fruit initiation in tomato. *Plant Cell* 30(8):1710–1728
- Hu Z, Shao S, Zheng C, Sun Z, Shi J, Yu J, Qi Z, Shi K (2018b) Induction of systemic resistance in tomato against *Botrytis cinerea* by N-decanoyl-homoserine lactone via jasmonic acid signaling. *Planta* 247:1217–1227
- Ilyas N, Gull R, Mazhar R, Saeed M, Kanwal S, Shabir S, Bibi F (2017) Influence of salicylic acid and jasmonic acid on wheat under drought stress. *Commun Soil Sci Plant Anal* 48(22):2715–2723
- Jang G, Choi YD (2018) Drought stress promotes xylem differentiation by modulating the interaction between cytokinin and jasmonic acid. *Plant Signal Behav* 13:e1451707
- Jang G, Chang SH, Um TY, Lee S, Kim JK, Choi YD (2017) Antagonistic interaction between jasmonic acid and cytokinin in xylem development. *Sci Rep* 7(1):10212
- Jauhari N, Bharadwaj R, Sharma N, Bharadwaja N (2019) Assessment of bacoside production, total phenol content and antioxidant

- potential of elicited and non-elicited shoot cultures of (*Bacopa monnieri* L.). *Environmental Sustainability* 2:441–453
- Jeyasri R, Muthuramalingam P, Karthick K, Shin H, Choi SH, Ramesh M (2023) Methyl jasmonate and salicylic acid as powerful elicitors for enhancing the production of secondary metabolites in medicinal plants: an updated review. *Plant Cell Tissue Organ Cult* 153(3):447–458
- Jiang Y, Liang G, Yang S, Yu D (2014) *Arabidopsis* WRKY57 functions as a node of convergence for jasmonic acid–and auxin-mediated signaling in jasmonic acid–induced leaf senescence. *Plant Cell* 26(1):230–245
- Jirakiattikul Y, Rithichai P, Boonyeun T, Ruangnoo S, Itharat A (2020) Improvement of dioscorealide B production by elicitation in shoot cultures of *Dioscorea membranacea* Pierre ex Prain & Burkill. *Physiol Mol Biol Plants* 26:585–591
- Jirakiattikul Y, Rithichai P, Songsoem K, Itharat A (2021) Elicitation of salicylic acid on secondary metabolite production and antioxidant activity of in vitro *Musa acuminata* L. cv. ‘Gros Michel’ Shoots. *Curr Appl Sci* 21:569–578
- Joshi N, Agarwal K, Ghosh S (2023) Improved antioxidant metabolism in shoot cultures of *Ruta graveolens* (L.) in response to methyl jasmonate and abscisic acid. *Plant Cell Tissue Organ Cult* 153(2):367–376
- Kamińska M (2021) Role and activity of jasmonates in plants under in vitro conditions. *Plant Tissue Cult Lett* 146(3):425–447
- Kandoudi W, Németh-Zámboriné É (2022) Stimulating secondary compound accumulation by elicitation: is it a realistic tool in medicinal plants in vivo. *Phytochem Rev* 21(6):2007–2025
- Kapoor S, Sharma A, Bhardwaj P, Sood H, Saxena S, Chaurasia OP (2019) Enhanced production of phenolic compounds in compact callus aggregate suspension cultures of *Rhodiola imbricata* Edgew. *Appl Biochem Biotechnol* 187:817–837
- Karami M, Naghavi MR, Nasiri J, Farzin N (2023) Methyl jasmonate and  $\beta$ -cyclodextrin shake hands to boost withaferin A production from the hairy root culture of *Withania somnifera*
- Khataee E, Karimi F, Razavi K (2019) Alkaloids production and antioxidant properties in *Catharanthus roseus* (L.) G. Don. Shoots and study of alkaloid biosynthesis-related gene expression levels in response to methyl jasmonate and putrescine treatments as eco-friendly elicitors. *Biologia Futura* 70:38–46
- Kianersi F, Amin Azarm D, Fatemi F, Jamshidi B, Pour-Aboughadareh A, Janda T (2023) The influence of methyl jasmonate on expression patterns of rosmarinic acid biosynthesis genes, and phenolic compounds in different species of *Salvia* subg. *Perovskia* Kar L. *Genes* 14(4):871
- Kim OT, Bang KH, Shin YS, Lee MJ, Jung SJ, Hyun DY, Kim YC, Seong NS, Cha SW, Hwang B (2007) Enhanced production of asiaticoside from hairy root cultures of *Centella asiatica* (L.) Urban elicited by methyl jasmonate. *Plant Cell Rep* 26:1941–1949
- Kowalczyk T, Sitarek P, Merez-Sadowska A, Szyposzyńska M, Szałwska A, Gorniak L, Bijak M, Śliwiński T (2021) Methyl jasmonate effect on betulinic acid content and biological properties of extract from *Senna obtusifolia* transgenic hairy roots. *Molecules* 26(20):6208
- Krishnan ML, Roy A, Bharadvaja N (2019) Elicitation effect on the production of asiaticoside and asiatic acid in shoot, callus, and cell suspension culture of *Centella asiatica*. *J Appl Pharm Sci* 9(6):067–074
- Krzyżanowska J, Czubačka A, Pecio L, Przybys M, Doroszeńska T, Stochmal A, Oleszek W (2012) The effects of jasmonic acid and methyl jasmonate on rosmarinic acid production in *Mentha piperita* cell suspension culture. *Plant Cell Tissue Organ Cult* 108:73–81
- Kumar A, Nirmal P, Kumar M, Jose A, Tomer V, Oz E, Proestos C, Zeng M, Elobeid T, Sneha K, Oz F (2023) Major phytochemicals: recent advances in health benefits and extraction method. *Molecules* 28(2):887
- Küpper FC, Gaquerel E, Cosse A, Adas F, Peters A, Müller DG, Kloareg B, Salaün JP, Potin P (2009) Free fatty acids and methyl jasmonate trigger defense reactions in *Laminaria digitata*. *Plant Cell Physiol* 50:4789–4800
- Lakehal A, Dob A, Rahnesan Z, Novák O, Escamez S, Alal-laq S, Strnad M, Tuominen H, Bellini C (2020) ETHYLENE RESPONSE FACTOR 115 integrates jasmonate and cytokinin signaling machineries to repress adventitious rooting in *Arabidopsis*. *New Phytol* 228(5):1611–1626
- Lalotra S, Hemantaranjan A, Yashu BR, Srivastava R, Kumar S (2020) Jasmonates: an emerging approach in biotic and abiotic stress tolerance. *Plant science-structure anatomy and physiology in plants cultured in vivo and in vitro*. IntechOpen
- Largia MJV, Pothiraj G, Shilpha J, Ramesh M (2015) Methyl jasmonate and salicylic acid synergism enhances bacoside A content in shoot cultures of *Bacopa monnieri* (L.). *Plant Cell Tissue Organ Cult* 122:9–20
- Li Q, Zheng J, Li S, Huang G, Skilling SJ, Wang L, Li L, Li M, Yuan L, Liu P (2017) Transporter-mediated nuclear entry of jasmonoyl-isoleucine is essential for jasmonate signaling. *Mol Plant* 10(5):695–708
- Li S, Yang Y, Zhang Q, Liu N, Xu Q, Hu L (2018) Differential physiological and metabolic response to low temperature in two zoysiagrass genotypes native to high and low latitude. *PLoS ONE* 13(6):0198885
- Li J, Li B, Luo L, Cao F, Yang B, Gao J, Yan Y, Zhang G, Peng L, Hu B (2020) Increased phenolic acid and tanshinone production and transcriptional responses of biosynthetic genes in hairy root cultures of *Salvia przewalskii* Maxim. Treated with methyl jasmonate and salicylic acid. *Mol Biol Rep* 47:8565–8578
- Li J, Chen L, Ding X, Fan W, Liu J (2022) Transcriptome analysis reveals crosstalk between the abscisic acid and jasmonic acid signaling pathways in rice-mediated defense against *Nilaparvata lugens*. *Int J Mol Sci* 23(11):6319
- Lischweski S, Muchow A, Guthörl D, Hause B (2015) Jasmonates act positively in adventitious root formation in petunia cuttings. *BMC Plant Biol* 15:1–10
- Liu L, Li H, Zeng H, Cai Q, Zhou X, Yin C (2016) Exogenous jasmonic acid and cytokinin antagonistically regulate rice flag leaf senescence by mediating chlorophyll degradation, membrane deterioration, and senescence-associated genes expression. *J Plant Growth Regul* 35:366–376
- Liu Y, Yin Q, Dai B, Wang KL, Lu L, Qaseem MF, Wang J, Li H, Wu AM (2021) The key physiology and molecular responses to potassium deficiency in *Neolamarckia cadamba* Ind Crops. *Prod* 162:113260
- Liu Y, Zhou J, Lu M, Yang J, Tan X (2022) The core jasmonic acid-signalling module CoCO11/CoJAZ1/CoMYC2 are involved in jas mediated growth of the pollen tube in *Camellia oleifera*. *Curr Issues Mol Biol* 44(11):5405–5415
- Liu CF, Yang N, Teng RM, Li JW, Chen Y, Hu ZH, Li T, Zhuang J (2023) Exogenous methyl jasmonate and cytokinin antagonistically regulate lignin biosynthesis by mediating CsHCT expression in *Camellia sinensis*. *Protoplasma* 260(3):869–884
- Lu G, Wang X, Liu J, Yu K, Gao Y, Liu H, Wang C, Wang W, Wang G, Liu M, Mao G (2014) Application of T-DNA activation tagging to identify glutamate receptor-like genes that enhance drought tolerance in plants. *Plant Cell Rep* 33:617–631
- Madani V, Zare N, Asgahri Zakaria R (2021) The effect of elicitors on the biochemical properties and expression of the genes involved in sesquiterpenes biosynthesis pathway in the hairy root cultures of medicinal plant *Valeriana officinalis* L. *IJPB* 12(4):19–42
- Mahendran G, Verma N, Singh M, Shanker K, Banerjee S, Kumar B, Rahman L (2022) Elicitation enhances swerchirin and 1, 2,



- 5, 6-tetrahydroxyxanthone production in hairy root cultures of *Swertia chirayita* (Roxb) H. Karst Ind Crops Prod 177:114488
- Matsui R, Amano N, Takahashi K, Taguchi Y, Saburi W, Mori H, Kondo N, Matsuda K, Matsuura H (2017) Elucidation of the biosynthetic pathway of cis-jasmone in *Lasiodiplodia theobromae*. Sci Rep 7(1):6688
- Melotto M, Underwood W, Koczan J, Nomura K, He SY (2006) Plant stomata function in innate immunity against bacterial invasion. Cell 126(5):969–980
- Miriam O, Moyano E, Bonfill M, Expósito O, Palazón J, Cusidó RM (2010) An approach to the molecular mechanism of methyl jasmonate and vanadyl sulphate elicitation in *Taxus baccata* cell cultures: the role of txs and bap1 gene expression. Biochem Eng J 53(1):104–111
- Monte I, Franco-Zorrilla JM, García-Casado G, Zamarreño AM, García-Mina JM, Nishihama R, Kohchi T, Solano R (2019) A single JAZ repressor controls the jasmonate pathway in *Marchantia polymorpha*. Mol Plant 12(2):185–198
- Mosblech A, Thurow C, Gatz C, Feussner I, Heilmann I (2011) Jasmonic acid perception by COI1 involves inositol polyphosphates in *Arabidopsis thaliana*. Plant J 65(6):949–957
- Nabi N, Singh S, Saffellah P (2021) Responses of *in vitro* cell cultures to elicitation: regulatory role of jasmonic acid and methyl jasmonate: a review. In Vitro Cell Dev Biol 57:341–355
- Nadir DS, Alwan AM (2022) Effect of abiotic elicitor methyl jasmonate on production of rutin in callus cultures of *Abutilon hirtum* L. J Appl Nat Sci 14(4):1493–1499
- Nguyen KV, Pongkitwitoon B, Pathomwichaiwat T, Viboonjun U, Prathanturug S (2019) Effects of methyl jasmonate on the growth and triterpenoid production of diploid and tetraploid *Centella asiatica* (L.) Urb. hairy root cultures. Sci Rep 9(1):18665
- Nguyen TH, Goossens A, Lacchini E (2022a) Jasmonate: a hormone of primary importance for plant metabolism. Curr Opin Plant Biol 67:102197
- Nguyen TN, Tuan PA, Ayele BT (2022b) Jasmonate regulates seed dormancy in wheat via modulating the balance between gibberellin and abscisic acid. J Exp Bot 73(8):2434–2453
- Ning YQ, Chen Q, Lin RN, Li YQ, Li L, Chen S, He XJ (2019) The HDA 19 histone deacetylase complex is involved in the regulation of flowering time in a photoperiod-dependent manner. Plant J 98(3):448–464
- Nitschke S, Cortleven A, Iven T, Feussner I, Havaux M, Riefler M, Schmölling T (2016) Circadian stress regimes affect the circadian clock and cause jasmonic acid-dependent cell death in cytokinin-deficient *Arabidopsis* plants. Plant Cell 28(7):1616–1639
- Otto M, Naumann C, Brandt W, Wasternack C, Hause B (2016) Activity regulation by heteromerization of *Arabidopsis* allene oxide cyclase family members. Plants 5(1):3
- Pablo Arias J, Mendoza D, Penuela M, Arias M (2018) Cardiac glycoside production in plant cell suspension culture of *Thevetia peruviana* at bench bioreactor scale. Vitro Cell Dev Biol, vol 54. Springer, NY, pp s47–s47
- Partap M, Kumar P, Kumar A, Joshi R, Kumar D, Warghat AR (2020) Effect of elicitors on morpho-physiological performance and metabolites enrichment in *Valeriana Jatamansi* cultivated under aeroponic conditions. Front Plant Sci 11:01263
- Peian Z, Haifeng J, Peijie G, Sadeghnezhad E, Qianqian P, Tianyu D, Teng L, Huanchun J, Jinggui F (2021) Chitosan induces jasmonic acid production leading to resistance of ripened fruit against *Botrytis cinerea* infection. Food Chem 337:127772
- Pieterse CM, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees SC (2012) Hormonal modulation of plant immunity. Annu Rev Cell Dev Biol 28:489–521
- Piskurewicz U, Lopez-Molina L (2009) The GA-signaling repressor RGL3 represses testa rupture in response to changes in GA and ABA levels. Plant Signal Behav 4(1):63–65
- Pluskota WE, Pupel P, Głowacka K, Okorska SB, Jerzmanowski A, Nonogaki H, Górecki RJ (2019) Jasmonic acid and ethylene are involved in the accumulation of osmotin in germinating tomato seeds. J Plant Physiol 232:74–81
- Qiong TA, Zheng XD, Jun GU, Ting YU (2022) Tomato SlPTi5 plays a regulative role in the plant immune response against *Botrytis cinerea* through modulation of ROS system and hormone pathways. J Integr Agric 21(3):697–709
- Qiu K, Li Z, Yang Z, Chen J, Wu S, Zhu X, Gao S, Gao J, Ren G, Kuai B, Zhou X (2015) EIN3 and ORE1 accelerate degreening during ethylene-mediated leaf senescence by directly activating chlorophyll catabolic genes in *Arabidopsis*. PLoS Genet 11(7):1005399
- Rajan M, Feba KS, Chandran V, Shahena S, Mathew L (2020) Enhancement of rhamnetin production in *Vernonia anthelmintica* (L.) Willd. Cell suspension cultures by eliciting with methyl jasmonate and salicylic acid. Physiol Mol Biol Plants 26:1531–1539
- Rao S, Tian Y, Zhang C, Qin Y, Liu M, Niu S, Li Y, Chen J (2023a) The JASMONATE ZIM-domain–OPEN STOMATA1 cascade integrates jasmonic acid and abscisic acid signaling to regulate drought tolerance by mediating stomatal closure in poplar. J Exp Bot 74(1):443–457
- Rao Y, Peng T, Xue S (2023b) Mechanisms of plant saline-alkaline tolerance. J Plant Physiol 281:153916
- Rattan S, Warghat AR (2023) Comparative analysis of salidroside and rosavin accumulation and expression analysis of biosynthetic genes in salicylic acid and methyl jasmonate elicited cell suspension culture of *Rhodiola imbricata* (Edgew.). Front Plant Sci 1:98116667
- Ravazzolo L, Ruperti B, Frigo M, Bertaiola O, Pressi G, Malagoli M, Quaggiotti S (2022) C3H expression is crucial for methyl jasmonate induction of chicoric acid production by *Echinacea purpurea* (L.) moench cell suspension cultures. Int J Mol Sci 23(19):11179
- Rawat V, Ghildiyal A, Singh L, Jugran AK, Bhatt ID, Nandi SK, Pande V (2020) Methyl jasmonate induced polyphenols and antioxidant production in callus suspension culture of *Nardostachys jatamansi*. Plant Biosyst-an Int J Dealing All Asp Plant Biol 154(6):851–859
- Rawat JM, Pandey S, Rawat B, Purohit S, Anand J, Negi AS, Thakur A, Mahmoud MH, El-Gazzar AM, Batiha GES (2023) *In vitro* production of steroidal saponin, total phenols and antioxidant activity in callus suspension culture of *Paris polyphylla* Smith: an important Himalayan medicinal plant. Front Plant Sci. <https://doi.org/10.3389/fpls.2023.1225612>
- Raya-González J, Pelagio-Flores R, López-Bucio J (2012) The jasmonate receptor COI1 plays a role in jasmonate-induced lateral root formation and lateral root positioning in *Arabidopsis thaliana*. J Plant Physiol 169:141348–141358
- Reeves PH, Ellis CM, Ploense SE, Wu MF, Yadav V, Tholl D, Chételat A, Haupt I, Kennerley BJ, Hodgens C, Farmer EE (2012) A regulatory network for coordinated flower maturation. PLoS Genet 8(2):1002506
- Ren C, Han C, Peng W, Huang Y, Peng Z, Xiong X, Zhu Q, Gao B, Xie D (2009) A leaky mutation in DWARF4 reveals an antagonistic role of brassinosteroid in the inhibition of root growth by jasmonate in *Arabidopsis*. Plant Physiol 151(3):1412–1420
- Ru M, Li Y, Guo M, Chen L, Tan Y, Peng L, Liang Z (2022) Increase in rosmarinic acid accumulation and transcriptional responses of synthetic genes in hairy root cultures of *Prunella vulgaris* induced by methyl jasmonate. Plant Cell Tissue Organ Cult 149:371–379
- Rubio-Rodríguez E, Vera-Reyes I, Sepúlveda-García EB, Ramos-Valdivia AC, Trejo-Tapia G (2021) Secondary metabolite production and related biosynthetic genes expression in response to methyl jasmonate in *Castilleja tenuiflora* Benth. in vitro plants. Plant Cell Tiss Org Cult 144(3):519–532

- Saeed S, Ali H, Khan T, Kayani W, Khan MA (2017) Impacts of methyl jasmonate and phenyl acetic acid on biomass accumulation and antioxidant potential in adventitious roots of *Ajuga bracteosa* Wall ex Benth., a high valued endangered medicinal plant. *Physiol Mol Biol Plants* 23:229–237
- Saniewski M, Ueda J, Miyamoto K (2002) Relationships between jasmonates and auxin in regulation of some physiological processes in higher plants. *Acta Physiol Plant* 24:211–220
- Santos VAD, Coppede JDS, Dias NB, Pereira AMS, Palma MS, Furlan M (2022) Proteome profiling of methyl jasmonate elicitation of *Maytenus ilicifolia* in vitro roots reveals insights into sesquiterpene pyridine alkaloids. *Plant Cell Tissue Organ Cult* 151(3):551–563
- Sayyari M, Babalar M, Kalantari S, Martínez-Romero D, Guillén F, Serrano M, Valero D (2011) Vapour treatments with methyl salicylate or methyl jasmonate alleviated chilling injury and enhanced antioxidant potential during postharvest storage of pomegranates. *Food Chem* 124(3):964–970
- Schaller A, Stintzi A (2009) Enzymes in jasmonate biosynthesis—structure, function, regulation. *Phytochem* 70(13–14):1532–1538
- Schommer C, Palatnik JF, Aggarwal P, Chételat A, Cubas P, Farmer EE, Nath U, Weigel D (2008) Control of jasmonate biosynthesis and senescence by miR319 targets. *PLoS Biol* 6(9):230
- Seltmann MA, Stingl NE, Lautenschlaeger JK, Krischke M, Mueller MJ, Berger S (2010) Differential impact of lipoxygenase 2 and jasmonates on natural and stress-induced senescence in *Arabidopsis*. *Plant Physiol* 152(4):1940–1950
- Selwal N, Goutam U, Akhtar N, Sood M, Kukreja S (2024) Elicitation: “A Trump Card” for enhancing secondary metabolites in plants. *J Plant Growth Regul.* <https://doi.org/10.1007/s00344-024-11294-y>
- Sharma K, Zafar R (2016) Optimization of methyl jasmonate and  $\beta$ -cyclodextrin for enhanced production of taraxerol and taraxasterol in (*Taraxacum officinale* Weber) cultures. *Plant Physiol Biochem* 103:24–30
- Sharma P, Yadav S, Srivastava A, Shrivastava N (2013) Methyl jasmonate mediates upregulation of bacoside A production in shoot cultures of *Bacopa monnieri*. *Biotechnol Lett* 35:1121–1125
- Sharma M, Sharma M, Jamsheer KM, Laxmi A (2022a) Jasmonic acid coordinates with light, glucose and auxin signalling in regulating branching angle of *Arabidopsis* lateral roots. *Plant Cell Environ* 45(5):1554–1572
- Sharma N, Thakur M, Sharma P, Dutt B, Sharma YP (2022b) In vitro propagation from seeds and enhanced synthesis of podophyllotoxin from root callus of *Sino Podophyllum hexandrum* Royle TS Ying (Himalayan Mayapple)—An endangered medicinal plant. *Ind Crops Prod* 186:115300
- Sharma N, Thakur M, Sharma P, Sharma YP, Dutt B (2022c) In vitro propagation from rhizomes, molecular evaluation and podophyllotoxin production in Himalayan May Apple (*Sinopodophyllum hexandrum* Royle TS Ying): an endangered medicinal plant. *Plant Cell Tissue Organ Cult* 149(1–2):159–173
- Shim JS, Jung C, Lee S, Min K, Lee YW, Choi Y, Lee JS, Song JT, Kim JK, Choi YD (2013) A tMYB 44 regulates WRKY 70 expression and modulates antagonistic interaction between salicylic acid and jasmonic acid signalling. *Plant J* 73(3):483–495
- Shoja AA, Çirak C, Ganjeali A, Cheniany M (2022) Stimulation of phenolic compounds accumulation and antioxidant activity in in vitro culture of *Salvia tebesana* Bunge in response to nano-TiO<sub>2</sub> and methyl jasmonate elicitors. *Plant Cell Tissue Organ Cult* 149(1–2):423–440
- Sohn SI, Pandian S, Rakkammal K, Largia MJV, Thamilarasan SK, Balaji S, Zoclanclounon YAB, Shilpha J, Ramesh M (2022) Jasmonates in plant growth and development and elicitation of secondary metabolites: an updated overview. *Front Plant Sci* 13:942789
- Song S, Huang H, Gao H, Wang J, Wu D, Liu X, Yang S, Zhai Q, Li C, Qi T, Xie D (2014) Interaction between MYC2 and ETHYLENE INSENSITIVE3 modulates antagonism between jasmonate and ethylene signaling in *Arabidopsis*. *Plant Cell* 26(1):263–279
- Sood M (2023) Jasmonates: “The Master Switch” for regulation of developmental and stress responses in plants. *J Plant Growth Regul* 42(8):5247–5265
- Staswick PE (2009) The tryptophan conjugates of jasmonic and indole-3-acetic acids are endogenous auxin inhibitors. *Plant Physiol* 150(3):1310–1321
- Sukito A, Tachibana S (2016) Effect of methyl jasmonate and salicylic acid synergism on enhancement of bilobalide and ginkgolide production by immobilized cell cultures of *Ginkgo biloba*. *Bioresour Bioprocess* 3(1):1–11
- Sułkowska-Ziaja K, Galanty A, Szweczyk A, Paśko P, Kała K, Apola A, Podolak I, Muszyńska B (2023) Effect of methyl jasmonate elicitation on triterpene production and evaluation of cytotoxic activity of mycelial culture extracts of *Ganoderma applanatum* (Pers) Pat. *Plants* 12(2):294
- Sun TP (2011) The molecular mechanism and evolution of the GA–GID1–DELLA signaling module in plants. *Curr Biol* 21(9):R338–R345
- Sun J, Xu Y, Ye S, Jiang H, Chen Q, Liu F, Zhou W, Chen R, Li X, Tietz O, Wu X (2009) *Arabidopsis* ASA1 is important for jasmonate-mediated regulation of auxin biosynthesis and transport during lateral root formation. *Plant Cell* 21(5):1495–1511
- Sun J, Chen Q, Qi L, Jiang H, Li S, Xu Y, Liu F, Zhou W, Pan J, Li X, Palme K (2011) Jasmonate modulates endocytosis and plasma membrane accumulation of the *Arabidopsis* PIN2 protein. *New Phytol* 191(2):360–375
- Suryawanshi S, Kshirsagar P, Kamble P, Bapat V, Jadhav J (2022) Systematic enhancement of l-DOPA and secondary metabolites from *Mucuna imbricata*: Implication of precursors and elicitors in callus culture. *S Afr J Bot* 144:419–429
- Syktowska-Baranek K, Kamińska M, Paćzkowski C, Pietrosiuk A, Szakiel A (2022) Metabolic modifications in terpenoid and steroid pathways triggered by methyl jasmonate in *Taxus media* hairy roots. *Plants* 11(9):1120
- Theodoulou FL, Job K, Slocombe SP, Footitt S, Holdsworth M, Baker A, Larson TR, Graham IA (2005) Jasmonic acid levels are reduced in COMATOSE ATP-binding cassette transporter mutants implications for transport of jasmonate precursors into peroxisomes. *Plant Physiol* 137(3):835–840
- Torkamani MRD, Abbaspour N, Jafari M, Samadi A (2014) Elicitation of valerenic acid in the hairy root cultures of *Valeriana officinalis* L (Valerianaceae). *Trop J Pharm Res* 13(6):943–949
- Twaij BM, Hasan MN (2022) Bioactive secondary metabolites from plant sources: types, synthesis, and their therapeutic uses. *Int J Plant Sci* 13(1):4–14
- Ueda J, Kato J (1982) Inhibition of cytokinin-induced plant growth by jasmonic acid and its methyl ester. *Physiol Plant* 54(3):249–252
- Ueda KZ, Haifeng J, Peijie G, Sadeghnezhad E, Qianqian P, Tianyu D, Teng L, Huanchun J, Jingui F (2021) Chitosan induces jasmonic acid production leading to resistance of ripened fruit against *Botrytis cinerea* infection. *Food Chem* 337:127772
- Ullah C, Schmidt A, Reichelt M, Tsai CJ, Gershenson J (2022) Lack of antagonism between salicylic acid and jasmonate signalling pathways in poplar. *New Phytol* 235(2):701–717
- Uyehara AN, Del Valle-Echevarria AR, Hunter CT, Nelissen H, Demuyneck K, Cahill JF, Jander G, Muszynski MG (2019) Cytokinin promotes jasmonic acid accumulation in the control of maize leaf growth. *Biorxiv* 221:760
- Vu PTB, Bui AL, Nguyen NN, Quach PND (2022) In vitro growth and content of vincristine and vinblastine of *Catharanthus roseus* L. hairy roots in response to precursors and elicitors. *Plant Sci Today* 9(1):21–28

- Wang Y, Mopper S, Hasenstein KH (2001) Effects of salinity on endogenous ABA, IAA, JA, and SA in *Iris hexagona*. *J Chem Ecol* 27:327–342
- Wang S, Guo LP, Xie T, Yang J, Tang JF, Li X, Wang X, Huang LQ (2014) Different secondary metabolic responses to MeJA treatment in shikonin-proficient and shikonin-deficient cell lines from *Arnebia euchroma* (Royle) Johnston. *Plant Cell Tissue Organ Cult* 119:587–598
- Wang F, Guo Z, Li H, Wang M, Onac E, Zhou J, Xia X, Shi K, Yu J, Zhou Y (2016) Phytochrome A and B function antagonistically to regulate cold tolerance via abscisic acid-dependent jasmonate signaling. *Plant Physiol* 170(1):459–471
- Wang J, Song L, Gong X, Xu J, Li M (2020a) Functions of jasmonic acid in plant regulation and response to abiotic stress. *Int J Mol Sci* 21(4):1446
- Wang Y, Hou Y, Qiu J, Wang H, Wang S, Tang L, Tong X, Zhang J (2020b) Abscisic acid promotes jasmonic acid biosynthesis via a ‘SAPK10-bZIP72-AOC’ pathway to synergistically inhibit seed germination in rice (*Oryza sativa*). *New Phytol* 228(4):1336–1353
- Wang Z, Gao M, Li Y, Zhang J, Su H, Cao M, Liu Z, Zhang X, Zhao B, Guo YD, Zhang N (2022) The transcription factor SIWRKY37 positively regulates jasmonic acid- and dark-induced leaf senescence in tomato. *J Exp Bot* 73(18):6207–6225
- Wang X, Luo JF, Liu R, Liu X, Jiang J (2023) Gibberellins regulate root growth by antagonizing the jasmonate pathway in tomato plants in response to potassium deficiency. *Sci Hortic* 309:111693
- Wasternack C (2007) Jasmonates: an update on biosynthesis, signal transduction and action in plant stress response, growth and development. *Ann Bot* 100(4):681–697
- Wasternack C, Feussner I (2018) The oxylipin pathways: biochemistry and function. *Annu Rev Plant Biol* 69:363–386
- Wasternack C, Hause B (2013) Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in *annals of botany*. *Ann Bot* 111(6):1021–1058
- Wasternack C, Kombrink E (2010) Jasmonates: structural requirements for lipid-derived signals active in plant stress responses and development. *ACS Chem Biol* 5(1):63–77
- Wasternack C, Strnad M (2018) Jasmonates: News on occurrence, biosynthesis, metabolism and action of an ancient group of signaling compounds. *Int J Mol Sci* 19(9):2539
- Woch N, Laha S, Gudipalli P (2023) Salicylic acid and jasmonic acid induced enhanced production of total phenolics, flavonoids, and antioxidant metabolism in callus cultures of *Givottia moluccana* (L.) Sreem. *In Vitro Cell Dev Biol Plant*. <https://doi.org/10.1007/s11627-023-10335-7>
- Xu P, Zhao PX, Cai XT, Mao JL, Miao ZQ, Xiang CB (2020) Integration of jasmonic acid and ethylene into auxin signaling in root development. *Front Plant Sci* 11:271
- Yan C, Xie D (2015) Jasmonate in plant defence: sentinel or double agent? *J Exp Bot* 13(9):1233–1240
- Yan S, McLamore ES, Dong S, Gao H, Taguchi M, Wang N, Zhang T, Su X, Shen Y (2015) The role of plasma membrane H<sup>+</sup>-ATPase in jasmonate-induced ion fluxes and stomatal closure in *Arabidopsis thaliana*. *Plant J* 83(4):638–649
- Yang J, Duan G, Li C, Liu L, Han G, Zhang Y, Wang C (2019) The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses. *Front Plant Sci* 10:1349
- Yazdani E, Golkar P, Vahabi MR, Taghizadeh M (2022) Elicitation effects on some secondary metabolites and antioxidant activity in callus cultures of *Allium jesdianum* Boiss. & Buhse.: methyl jasmonate and putrescine. *Appl Biochem Biotechnol* 194(2):601–619
- Yin Y, Adachi Y, Nakamura Y, Munemasa S, Mori IC, Murata Y (2016) Involvement of OST1 protein kinase and PYR/PYL/RCAR receptors in methyl jasmonate-induced stomatal closure in *Arabidopsis* guard cells. *Plant Cell Physiol* 57(8):1779–1790
- Yoshida Y, Sano R, Wada T, Takabayashi J, Okada K (2009) Jasmonic acid control of GLABRA3 links inducible defense and trichome patterning in *Arabidopsis*. *Development*. <https://doi.org/10.1242/dev.030585>
- Yoshihara T, Iino M (2007) Identification of the gravitropism-related rice gene LAZY1 and elucidation of LAZY1-dependent and-independent gravity signaling pathways. *Plant Physiol* 48(5):678–688
- Yousefian S, Lohrasebi T, Farhadpour M, Haghbeen K (2020) Effect of methyl jasmonate on phenolic acids accumulation and the expression profile of their biosynthesis-related genes in *Mentha spicata* hairy root cultures. *Plant Cell Tissue Organ Cult* 142(2):285–297
- Yu J, Zhang Y, Di C, Zhang Q, Zhang K, Wang C, You Q, Yan H, Dai SY, Yuan JS, Xu W (2016) JAZ7 negatively regulates dark-induced leaf senescence in *Arabidopsis*. *J Exp Bot* 67(3):751–762
- Zamora O, Schulze S, Azoulay-Shemer T, Parik H, Unt J, Brosché M, Schroeder JI, Yarmolinsky D, Kollist H (2021) Jasmonic acid and salicylic acid play minor roles in stomatal regulation by CO<sub>2</sub>, abscisic acid, darkness, vapor pressure deficit and ozone. *Plant J* 108(1):134–150
- Zander M, La Camera S, Lamotte O, Métraux JP, Gatz C (2010) *Arabidopsis thaliana* class-II TGA transcription factors are essential activators of jasmonic acid/ethylene-induced defense responses. *Plant J* 61(2):200–210
- Zander M, Chen S, Imkamp J, Thurow C, Gatz C (2012) Repression of the *Arabidopsis thaliana* jasmonic acid/ethylene-induced defense pathway by TGA-interacting glutaredoxins depends on their C-terminal ALWL motif. *Mol Plant* 5(4):831–840
- Zhai Q, Zhang X, Wu F, Feng H, Deng L, Xu L, Zhang M, Wang Q, Li C (2015) Transcriptional mechanism of jasmonate receptor COI1-mediated delay of flowering time in *Arabidopsis*. *Plant Cell* 27(10):2814–2828
- Zhang X, Zhu Z, An F, Hao D, Li P, Song J, Yi C, Guo H (2014) Jasmonate-activated MYC2 represses ETHYLENE INSENSITIVE3 activity to antagonize ethylene-promoted apical hook formation in *Arabidopsis*. *Plant Cell* 26(3):1105–1117
- Zhang M, Wang A, Qin M, Qin X, Yang S, Su S, Sun Y, Zhang L (2021) Direct and indirect somatic embryogenesis induction in *Camellia oleifera* (Abel). *Front Plant Sci* 12:644389
- Zhang Y, Zhou H, Tang Y, Luo Y, Zhang Z (2022) Hydrogen peroxide regulated salicylic acid- and jasmonic acid-dependent systemic defenses in tomato seedlings. *Food Sci Technol* 42:e54920
- Zhang J, Chen W, Li X, Shi H, Lv M, He L, Bai W, Cheng S, Chu J, He K, Gou X (2023) Jasmonates regulate apical hook development by repressing brassinosteroid biosynthesis and signaling. *Plant Physiol* 193(2):1561–1579
- Zhao S, Tang H (2020) Enhanced production of valtrate in hairy root cultures of *Valeriana jatamansi* Jones by methyl jasmonate, jasmonic acid and salicylic acid elicitors. *Not Bot Horti Agrobot Cluj Napoca* 48(2):839–848
- Zhao W, Huang H, Wang J, Wang X, Xu B, Yao X, Sun L, Yang R, Wang J, Sun A, Wang S (2022) Jasmonic acid enhances osmotic stress responses by MYC2-mediated inhibition of protein phosphatase 2C1 and response regulators 26 transcription factor in tomato. *Plant J* 113(3):546–561
- Zheng XY, Spivey NW, Zeng W, Liu PP, Fu ZQ, Klessig DF, He SY, Dong X (2012) Coronatine promotes *Pseudomonas syringae* virulence in plants by activating a signaling cascade that inhibits salicylic acid accumulation. *Cell Host Microbe* 11(6):587–596
- Zheng J, Xie X, Li C, Wang H, Yu Y, Huang B (2023) Regulation mechanism of plant response to heavy metal stress mediated

by endophytic fungi. *Int J Phytoremediation*. <https://doi.org/10.1080/15226514.2023.2176466>

- Zhou W, Shi M, Deng C, Lu S, Huang F, Wang Y, Kai G (2021) The methyl jasmonate-responsive transcription factor SmMYB1 promotes phenolic acid biosynthesis in *Salvia miltiorrhiza*. *Hortic Res*. <https://doi.org/10.1038/s41438-020-00443-5>
- Zhou Y, Mohammadi Y, Mashayekhi M (2022) Investigation of the methyl jasmonate effect on the Taxol biosynthetic pathway through the expression of DBAT, BAPT, and TS genes. *Sci for*. <https://doi.org/10.18671/scifor.v50.47>
- Zhu Z, Lee B (2015) Friends or foes: new insights in jasmonate and ethylene co-actions. *Plant Physiol* 56(3):414–420
- Zhu M, Li Y, Chen G, Ren L, Xie Q, Zhao Z, Hu Z (2015) Silencing SIELP2L, a tomato Elongator complex protein 2-like gene,

inhibits leaf growth, accelerates leaf, sepal senescence and produces dark-green fruit. *Sci Rep* 5(1):7693

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