Jasmonic Acid for Sustainable Plant Growth and Production Under Adverse Environmental Conditions

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Abbreviations

ACX1	Acyl-CoA oxidase
AD	Activation domain
ARF	Auxin response factor
AUX/IAA	Auxin/indole acetic acid
BD	DNA binding domain
EAR	Ethylene-responsive element binding factor-associated amphiphilic repression
HAD19	Histone deacetylase 19
HDA6	Histone deacetylase 6
IAA	Indole acetic acid

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JA   Jasmonic acid
Jas   C-terminal JA-associated domain
JAV1   JA-associated VQ motif gene 1
KAT   L-3-ketoacylCoAthiolase
NINJA   Novel interactor of JAZ
OPDA   12-oxo-phytodienoic acid
OPR   Oxo-phytodienoate reductase
PLT   PLETHORA
TPL   TOPLESS

1   Introduction

The current climate change conditions arose due to the unsustainable and erratic use
of fossil fuel by humans, which has created a global threat to living systems (Mehta
et al. 2020; Mehta et al. 2021; Wuebbles et al. 2017; Singh et al. 2019; Rahman
et al. 2019; Mehta et al. 2019a). The adverse conditions like increased atmospheric
temperature and carbon dioxide concentration are imposing various stresses on vari-
ous ecosystems (Bharti et al. 2021). Plants, being sessile, cannot run away from
different stresses that prevail in their environment (Sahil et al. 2021). They undergo
different stresses caused due to biotic and abiotic factors (Dilawari et al. 2021;
Yadav et al. 2021; Rajput et al. 2021; Anamika et al. 2019; Mehta et al. 2019b).
Among the two categories, abiotic stresses are the most prevalent that affects the
productivity heavily and include temperature, light, salt, water, carbon dioxide,
ozone, and nutrient availability (Bharti et al. 2021; Husen 2010; Husen et al. 2014,
2016, 2017; Getnet et al. 2015; Embiale et al. 2016; Hussein et al. 2017; Lal et al.
2018; Isah 2019). All these stresses result in drastic changes in the normal physio-
logical behavior of the plants (Mehta et al. 2020; Sharma et al. 2021). They modify
their physiological and developmental conditions to adapt to these adversities by
producing certain compounds including phytohormones (Ashraf et al. 2010; Javid
et al. 2011; Liu et al. 2019a).

   In accordance with multiple studies published in the literature so far, the most
prominent way to tackle these stressful conditions is to focus on various endoge-
nously produced phytohormones. These plant hormones like auxins, cytokinins,
gibberellins, salicylic acids, jasmonic acids, etc. play a crucial part in sensing the
external stresses and also in signal transduction so that the plants can respond to
them (Lymperopoulos et al. 2018). Jasmonates, the collection of JA and its deriva-
tives (for example, methyl jasmonate and jasmonate isoleucine conjugate), are the
modifications of fatty acids (Viswanath et al. 2020; Ruan et al. 2019). Jasmonates
are found in all the higher plants in the reproductive parts and flowers at higher
concentrations and in the mature plant parts such as leaves at relatively lower con-
centration (Wasternack and Hause 2013; Dar et al. 2015). There are different roles
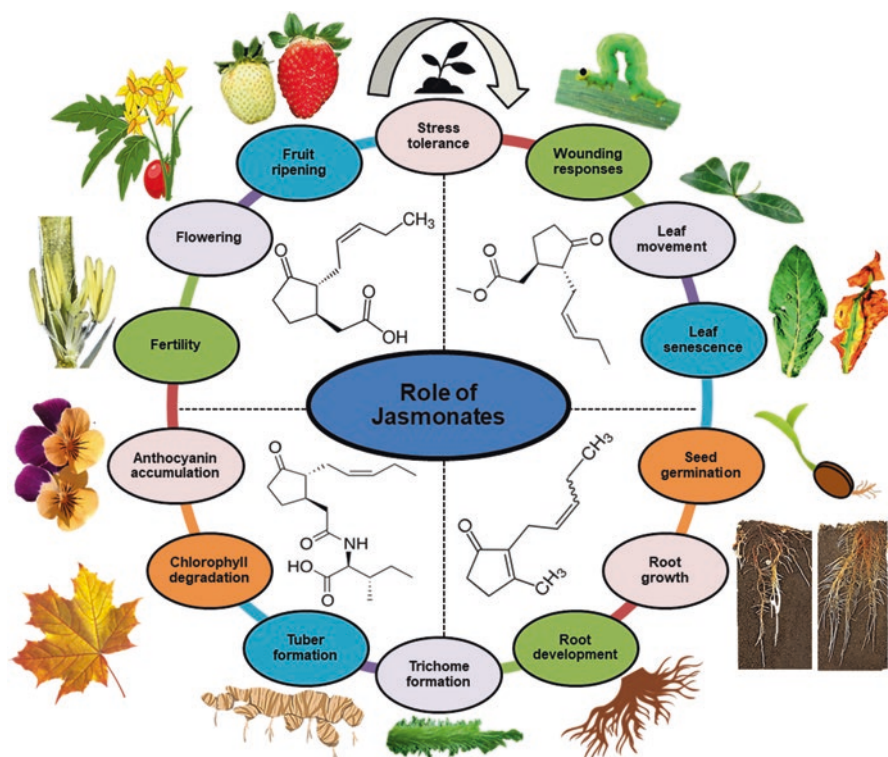played by jasmonates in plants in various processes like seed germination, trichome

Fig. 1 Different roles played by jasmonates in plants

formation, root growth, gravitropism, sex determination, seedling development, anthocyanin accumulation, chlorophyll degradation, leaf movement, leaf senescence, fertility, and tuber formation (Wasternack and Hause 2002; Wasternack 2014; Wu et al. 2019; Siddiqi and Husen 2019; Viswanath et al. 2020; Fig. 1). Jasmonates also function in providing tolerance against different stresses like salt, heavy metal, temperature, etc. by modifying certain gene expression (Li et al. 2018; Fig. 1). This chapter deals in detail about JA, its biosynthesis, its role in plants' response to various stresses, and its interaction with other phytohormones involved in the tolerance to these stresses.

2 Biosynthesis of JA

Biosynthesis of JA is not simple straightforward chemistry but actually involves three compartments within a cell, i.e., chloroplast, peroxisome, and cytosol. The α-linolenic acid, an immediate precursor of JA, gets converted into 12-oxo-phytodienoic acid (OPDA) inside the chloroplast with the help of allene oxide

synthase along with two more enzymes, lipoxygenase, and allene oxide cyclase. The final product is then transported into peroxisome by an ABC class of transporter COMATOSE (CTS). Oxo-phytodienoate reductase (OPR) is a peroxisomal enzyme that triggers the reduction of cyclopentanone ring of OPDA. Three enzymes of ß-oxidation are required for the final formation of JA from the substrate, i.e., 3-oxo-2(2′[Z]-pentenyl)-cyclopentane-1-octanoate which are L-3-ketoacylCoAthiolase (KAT), Acyl-CoA oxidase (ACX1) and two multifunctional protein (MFP), i.e., 1-3-hydroxy acyl-CoA dehydrogenase, 2-*trans*-enoyl-CoA hydratase. Then it is exported to the cytosol for further modification (Wasternack and Hause 2002; Wasternack and Hause 2019; Fig. 2).
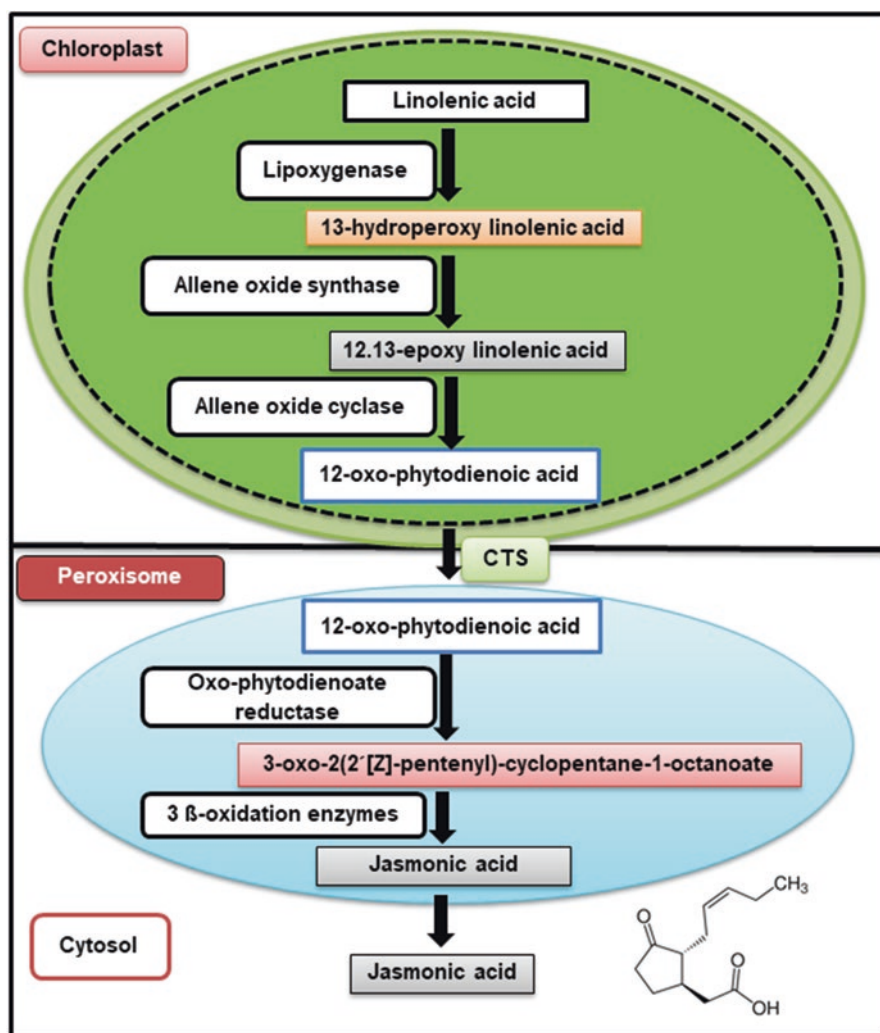

Fig. 2 Schematic illustration of the biosynthesis pathway of JA

3 Jasmonic Acid-Mediated Stress Responses

3.1 Biotic Stress

Jasmonic acid is a phytohormone which is well known to protect the plants against different harmful organisms (Mehta et al. 2021; Pieterse et al. 2012). It has also been identified to have a defensive role against wounding, pathogen attack, and herbivory (Rosahl and Feussner 2004). The *Arabidopsis* mutants with altered JA synthesis have revealed the role of JA in providing resistance to the plants against both the biotrophic and necrotrophic pathogens (Singh et al. 2017).

The JA responsive genes express as a result of E3 ubiquitin ligase mediated proteolysis of JAZ repressor protein involving JA-Ile (JA coupled with isoleucine). This E3 ubiquitin ligase complex is formed when F-box COI 1 protein, a receptor of JA, interacts with Skp1/Cullin counterparts (Thines et al. 2007). Hence, COI 1 is an important protein required for JA responsive gene expression which is also confirmed by studying *coi* 1 mutants where expression analysis revealed that >80% of JA responsive genes have a decline in expression (Xie et al. 1998; Devoto et al. 2005). In these mutants, this decline resulted in an increase in susceptibility to necrotrophic pathogens. Similarly, in the case of a *jar* 1-1mutant, the active enzyme involved in JA biosynthesis is mutated making the mutant plant vulnerable to *Pythium irregulare* (Staswick et al. 1998, 2002). The plants with constitutive expression of JA conferred resistance against fungal pathogens like *Erysiphe cichoracearum* (Ellis and Turner 2001). These studies explain the involvement of JAs in providing resistance to plants against plant pathogens.

The importance of JA in the regulation of plant response during wounding and insect attack is also reported in tomato. Various studies have revealed that the expression of genes important in wounding and expression of proteinase inhibitors is modulated by exogenous JA (Farmer et al. 1992). The *def1* mutant of the tomato plant is found to be defective in the octadecanoid pathway-mediated biosynthesis of wound-induced JA and hence has a lower accumulation of JA (Howe et al. 1996). This mutant also showed reduced resistance to tobacco hornworm, *Manduca sexta,* which correlates with the decrease in JA accumulation and reduction in proteinase inhibitor gene expression. This demonstrates that the octadecanoid signaling pathway is important for the protection of plants from different types of harmful organisms like chewing insects and harmful fungi. An exogenous application of JA to potato plants resulted in local and systemic defense in those plants against different pathogen attacks (Cohen et al. 1993). JA is found to accumulate in potato infected with *Pseudomonas syringae* pv. *Maculicola,* (Landgraf et al. 2002; Halim et al. 2004). However, JA accumulation against *P. syringae* is not observed in susceptible plants (Weber et al. 1999; Gobel et al. 2002) revealing that the cumulation of JA takes place in response to PAMP recognition and nonhost pathogen interaction.

Another gene JAV1, JA-associated VQ motif gene 1, negatively regulates the JA-mediated defense against insect and pathogen attack (Hu et al. 2013). JA-COI 1 signaling complex is a part of the degradation system responsible for the

degradation of this negative regulator, JAV1, through 26S proteasome, thereby contributing to the activation of defense-related genes and protection against pathogens. When there is no such attack by pathogens, active JAV1 is not degraded and interacts with the WRKY transcription factor leading to inactivation of its active functions. Once there is a pathogen attack, JAV1 gets degraded resulting in the activation of a downstream signaling pathway that results in the development of plant defense against these pathogens. This negative regulation by JAV1 helps a damaged plant to mediate their JA-mediated defense response to establish a harmony between growth and defense during stress.

Genetically engineered rice plants with AOS2 expression, allene oxide synthase (plays role in JA synthesis), have induced expression of antipathogenic proteins (like PR3, PR5, etc.) and enhanced resistance against pathogenic fungi (Mei et al. 2006). The two rice *osjar1* mutants having lower JA Ile (product of JAR 1) production are susceptible to blast fungi in contrast to the nonmutants (Shimizu et al. 2013), revealing the function of JA Ile in mediating defense mechanisms in rice against blast fungus. Also, the complete silencing of OsCOI 1 enhanced the susceptibility of rice plants against chewing insects that correlated with the downregulation of various genes encoding trypsin protease inhibitor, polyphenol oxidase (converts phenols to toxic quinones), and peroxidase.

The exogenous treatment of MeJA to *Arachis hypogea* has shown to increase the level of antioxidant enzymes, thereby reducing growth and development of *Helicoverpa armigera* (War et al. 2015), whereas in *Vigna mungo*, methyl jasmonate (MeJA) is found to protect the plant from *Mungbean yellow mosaic India virus* through the restoration of membrane stability and maintenance of reactive oxygen species homeostasis (Chakraborty and Basak 2019). In *Solanum lycopersicum,* external treatment with methyl jasmonate provides tolerance against *Helicoverpa zea* by inducing defense gene expression (Tian et al. 2014). The external treatment of MeJA to *Phaseolus vulgaris* and *Panax notoginseng* provided resistance against *Sclerotinia sclerotiorum* and *Fusarium solani*, respectively (Oliveira et al. 2015; Liu et al. 2019b), as shown in Table 1.

3.2   Abiotic Stress

JA is a crucial plant-hormone that protects against different stresses like cold stress, heat stress, etc. and its role against various abiotic stresses has been studied already in various crops (Acharya and Assmann 2009; Karpets et al. 2014; Wasternack 2014; Siddiqi and Husen 2019). The use of exogenous JA can protect the plants from various abiotic stresses.

Table 1 Review of literature highlighting the role of exogenous JA in both biological and nonbiological stresses

S. no	Stress type	Plant species	Exogenous JA concentration	Plant response	References
Abiotic stresses					
1	Heat stress	*Vitis vinifera* L.	50 µM JA	Increased activities of antioxidant enzymes	Chen et al. (2006)
		Arabidopsis thaliana (L.) Heynh.	5 µM MeJA	Stabilized membrane, induced JA pathway	Clarke et al. (2009)
2	Cold stress	*Prunus persica* (L.) Batsch	1 µM L^{-1} MeJA	Increased activities of phenylalanine ammonia lyase, superoxide dismutase, Polygalacturonase decreased activities of polyphenol oxidase, peroxidase, alleviated chilling injury	Jin et al. (2009)
		Punica granatum L.	0.01 and 0.1 mM MeJA	Increased total phenolics and anthocyanins, enhanced antioxidant activity, alleviated chilling injury	Sayyari et al. (2011)
		Solanum lycopersicum L.	0.05 mM MeJA	Modified arginine catabolism, improved post-harvest chilling tolerance	Zhang et al. (2012)
		Eriobotrya japonica (Thunb.) Lindl.	16 µmol L^{-1} MeJA	Increased antioxidant enzyme activity, decreased lignin content, mitigated harmful effects of freezing injury	Jin et al. (2014)
		Vigna sinensis (L.) Walp.	0.5, 1, 2, 4, and 8 µM MeJA	1 µM MeJA reduced chilling injury, increased malondialdehyde content, chlorophyll, and ascorbic acid, induced antioxidant activity	Fan et al. (2016)

(continued)

Table 1 (continued)

S. no	Stress type	Plant species	Exogenous JA concentration	Plant response	References
3	Heavy metal stress	*Cajanus cajan* (L.) Millsp.	1 μM, 1 nM, and 1 pM MeJA	Increased chlorophyll and carotenoids, enhanced antioxidant enzyme activity, mitigates copper (Cu) toxicity	Poonam et al. (2013)
		Capsicum frutescens L.	0.1–1 mM MeJA	Increased antioxidant enzyme activity and enhanced chlorophyll levels	Yan et al. (2013)
		Kandelia obovata Sheue, Liu and Yong	0.01 mM MeJA	Reduced Cd content, increased ascorbic acid content, mitigation of oxidative damage by increased concentration of antioxidant enzymes	Chen et al. (2014)
		Solanum nigrum L.	0.01 μM MeJA	Reduced Cd toxicity, decreased malondialdehyde, improved activities of antioxidant enzymes	Yan et al. (2015)
		Brassica napus L.	0.1–1 mM MeJA	Reduced arsenic stress, increased antioxidants, and secondary metabolites	Farooq et al. (2016)
4	Salt stress	*Brassica oleracea* L.	10 μM MeJA	Increased chlorophyll, relative water content, net photosynthesis rate, and abscisic acid level, induced antioxidant system	Wu et al. (2012)
		Matricaria chamomilla L.	75 μM MeJA	Increased proline content, enhanced photosynthetic rate, increased K^+ concentration and decreased Na^+ concentration, induced antioxidant system	Salimi et al. (2016)
		Robinia pseudoacacia L.	100 μM MeJA	Increased antioxidant enzyme activity and decreased levels of hydrogen peroxide and superoxide radicals	Jiang et al. (2016)
		Vigna unguiculata (L.) Walp.	50 μM MeJA	Enhanced net photosynthetic rate, increased total soluble proteins, sugars, and phenolics	Sadeghipour (2017)
		Brassica napus L.	100 μM MeJA	Increased photosynthetic rate, relative water content, and soluble sugar content	Ahmadi et al. (2018)

Table 1 (continued)

S. no	Stress type	Plant species	Exogenous JA concentration	Plant response	References
5	Drought stress	*Triticum aestivum* L.	250 mM MeJA	Reduced malonaldehyde content, decreased oxidative damage because of enhance antioxidant enzymes, increase of compensation irradiance	Ma et al. (2014)
		Solanum nigrum L.	0.01 mM MeJA	Increased antioxidant enzyme activity, decreased malondialdehyde content	Yan et al. (2015)
		Triticum aestivum L.	500 mM MeJA	Increased grain yield and productivity	Anjum et al. (2016)
		Glycine max (L.) Merr.	200 μM MeJA	Increased growth, and photosynthetic pigments, induced antioxidant enzymes, enhanced unsaturated fatty acids, and flavonoids	Mohamed and Latif (2017)
		Satureja hortensis L.	75 mM MeJA	Increased growth parameters, and proline content, enhanced antioxidant activity, and oil content	Miranshahi and Sayyari (2018)
Biotic stresses					
6	Insect feeding	*Arachis hypogaea* L.	1 mM JA	Induces the activity of antioxidative enzyme, therefore, reducing growth and development of *Helicoverpa armigera*	War et al. (2015)
		Solanum lycopersicum L.	2.5 mM MeJA	Exogenous MeJA application found to be effective against *Helicoverpa zea* through inducing defense gene expression, and increased density of glandular trichome	Tian et al. (2014)
7	Viral disease	*Vigna mungo* L.	0.01 mM, 0.1 mM, 1 mM and 10 mM MeJA	Methyl jasmonate (MeJA) found to be effective for *Mungbean yellow mosaic India virus* tolerance in *Vigna mungo* (L.) through restoration of membrane stability, maintenance of reactive oxygen species homeostasis and by reducing the expression of virus coat-protein encoding genes. 0.1 mM has been found to be most effective dose	Chakraborty and Basak (2019)

Table 1 (continued)

S. no	Stress type	Plant species	Exogenous JA concentration	Plant response	References
8	Fungal disease	*Phaseolus vulgaris* L.	10 μM MeJA	Foliar application of MeJA induces systemic defense against *Sclerotinia sclerotiorum* in dry bean plants by increasing the transcripts level that encode pathogenicity related proteins	Oliveira et al. (2015)
		Panax notoginseng (Burkill) F.H. Chen	100 μM MeJA	Resistance of *Panax notoginseng* found to be triggered by methyl jasmonate (MeJA) against *Fusarium solani* ultimately helping in disease resistance	Liu et al. (2019b)

3.2.1 Salinity Stress

Salinity stress contributes to huge crop losses every year (Munns and Tester 2008). Na^+ and Cl^- are the primary salts contributing to salt stress. The prime sources of accumulation of salts in agricultural lands are irrigation water having relatively high salt contents and chemical pesticides/insecticides used for crop protection (Munns and Tester 2008). Salinity hinders various processes such as uptake of nutrients, chlorophyll degradation, etc., and the evolution of ROS is observed under severe salinity conditions. This in turn leads to oxidative damage to various proteins and DNA as well (Farhangi-Abriz and Torabian 2017).

Salt treatment to different plants such as *Lycopersicon esculentum*, *Solanum tuberosum,* and *Arabidopsis thaliana* resulted in enhanced endogenous JA in these plants (Pedranzani et al. 2013; Ellouzi et al. 2013; De Domenico et al. 2019). Sweet potato under salt stress is found to have increased levels of JA as per the transcript profile (Zhang et al. 2017). The immediate increase in JA content is observed in salt-sensitive plants under salt stress whereas this increase is minimal in salt-tolerant plants (De Domenico et al. 2019). In rice, the accumulation of JA resulted in reducing the negative effects of salt stress on biomass production (Kang et al. 2005). The application of JA to safflower leaves growing under salt stress resulted in enhanced yield, and physiological performance (Ghassemi-Golezani and Hosseinzadeh-Mahootchi 2015). The external treatment of JA to salt stress exposed plants has shown better potassium content, lower lipid peroxidation, and higher antioxidant activity (Farhangi-Abriz and Ghassemi-Golezani 2018). The external treatment of JA to different plants like *Brassica oleracea, Matricaria chamomilla, Robinia pseudoacacia, Vigna unguiculate*, and *Brassica napus* have shown to increase antioxidant enzyme activity and net photosynthetic rate, thereby alleviating negative effects of salt stress (Wu et al. 2012; Salimi et al. 2016; Jiang et al. 2016; Sadeghipour 2017; Ahmadi et al. 2018).

3.2.2　Drought Stress

Drought stress is responsible for extensive crop losses every year. Various changes in plants are observed during drought, which has serious repercussions on their growth and yield (Pandey et al. 2017). There are various negative impacts of drought stress on different physiological processes of plants including the decrease in turgor pressure, reduction in photosynthetic rates, increase in leaf senescence, and ion toxicity.

As compared to the different stresses, there is little information related to the functions of JA in drought stress. Jasmonic acid can regulate the opening and closing of stomata, thereby reducing the rate of water loss during water-deficient conditions (Savchenko et al. 2014). The endogenous JA levels were increased when different plants such as A. *thaliana* (Balbi and Devoto 2008) and *Citrus* spp. (De Ollas et al. 2013) were subjected to water-deficient conditions, but JA concentration was declined to basal level upon prolonged exposure. The different components of JA signaling pathways are involved in making plants tolerant to the shortage of water. The negative regulator or a repressor of the JA signaling pathway termed jasmonate ZIM-domain proteins (JAZ) are found to negatively regulate the rice tolerance to water-deficient conditions (Fu et al. 2017).

The external employment of various plant hormones to plants growing under particular stress has proved to be an effective method to reduce harmful outcomes of the stress on plants, the same is with JA and drought stress. This strategy has been found to increase crop production under drought stress by increasing antioxidant enzyme activities. The exogenous application of JA to maize plants growing under drought stress resulted in an escalated amount of antioxidant enzymes that lower the damage done by the increased ROS (Abdelgawad et al. 2014). Also, the lipid peroxidation decreased in peanut grown under water-deficient conditions by the exogenous supply of JA that resulted in decreased oxidative stress because of the increased antioxidant enzyme production (Kumari et al. 2006). It is found that the synthesis of antioxidant enzymes like glutathione peroxidase, catalase, etc. is enhanced upon foliar application of JA in *Brassica* that in turn leads to an alleviation of damage caused by increased ROS (Alam et al. 2014). The exact mechanism of induction of these antioxidant enzymes by the JA application is still not known very well. Additionally, the external application of MeJA to different plants like *Solanum nigrum, Triticum aestivum, Glycine max,* and summer savory has shown to increase growth and decrease oxidative stress when subjected to stress conditions (Yan et al. 2015; Anjum et al. 2016; Mohamed and Latif 2017; Ma et al. 2014; Miranshahi and Sayyari 2018).

3.2.3　Heat Stress

The changes in temperature above and below the limits of ambient temperature decrease crop productivity drastically (Zandalinas et al. 2018). The overall rise in temperature because of the greenhouse effect is termed as heat stress. This type of

stress has various adverse effects on plants including the protein denaturation, lowering of enzymatic activity, etc. When exposed to heat stress, plants regulate gene expression, thereby producing essential proteins or controlling signaling pathways. One of the important proteins with excessive production during heat stress is heat-shock protein (HSP). HSPs protect different proteins from heat stress along with some major roles in many other processes.

Jasmonic acid has many protective functions against stress and can also produce different secondary metabolites as well as heat-shock proteins (Creelman and Mullet 1995; Balfagón et al. 2019). JA signaling functions in providing tolerance to *Arabidopsis* against heat stress (Clarke et al. 2009). The increased concentration of JA in plants growing under heat stress contributes to plant defense against stressful conditions (Hasanuzzaman et al. 2013). The foliar treatment of JA to barley enhances the production of heat-shock proteins by changes in gene expression (Mueller-Uri et al. 1988; Aghdam et al. 2013). A counterview has been proposed by many other scientists stating that the modification in plant phenolic components was responsible for increased production of HSPs, thereby protecting plants from heat stress (Saltveit 2000). The application of JA results in an increase in abscisic acid which led to the induction of stomatal closure and reduced transpiration for maintaining plant temperature (Lehmann et al. 1995; Creelman and Mullet 1997; Acharya and Assmann 2009). JA also regulates water potential in a plant cell resulting in the preservation of water.

3.2.4 Cold Stress

Since a long time, cold stress is considered as harmful for the overall growth of the plant that can be further categorized into freezing stress and chilling stress based on temperature either below 0 °C or above 0 °C, respectively (Huang et al. 2014; Trischuk et al. 2014; Sharma et al. 2020). The major effects of cold stress in plants include ice crystal formation inside the cells and cellular dehydration. Various other changes like the molecular and the biochemical changes along with physiological changes are observed in plants during cold stress that results in the synthesis of cold stress-induced proteins, essential amino acids, and soluble proteins (Hincha and Zuther 2014; Ritonga and Chen 2020).

Different plant hormones are demonstrated to be involved in plant protection against cold stress (Kosova et al. 2012; Wasternack 2014). In plants, during low-temperature stress, an increase in the concentration of JA is observed (Kosova et al. 2012). Also, when the *Pinus pinaster* plants suffered two different stresses, water stress and cold stress, a rise in JA content of leaves is observed (Pedranzani et al. 2007). The transcription of different genes like allene oxide cyclase (AOC), lipoxygenase 2, and allene oxide synthase 1 (AOS) increased as a result of cold stress and all these genes are found to contribute to JA biosynthesis. Jasmonates can alleviate chilling stress by inducing the production of proteinase inhibitors, antioxidants, abscisic acid, cryoprotectants, and polyamines (Cao et al. 2009; Zhao et al. 2013). The JA application to chilled rice in a low dosage enhances their survival ratio (Lee

et al. 1997). Methyl jasmonate has been used on plants like *Prunus persica, Punica granatum Solanum lycopersicum, Eriobotrya japonica*, and *Vigna sinensis*, resulting in enhanced antioxidant enzyme activity, decreased oxidative damage, and mitigation of cold stress (Jin et al. 2009; Sayyari et al. 2011; Zhang et al. 2012; Fan et al. 2016).

3.2.5 Heavy Metal Stress

This type of abiotic stress is highly prevalent in agricultural lands because of the usage of chemical fertilizers and pesticides, weathering of rocks, etc. Heavy metal stress has various ill effects on plant growth, which could lead to increased leaf senescence and decreased photosynthetic rates (Maksymiec 2007; Berni et al. 2019).

Heavy metal toxicity like cadmium and copper toxicity can increase the concentration of endogenous JA in *Arabidopsis thaliana* plants (Xiang and Oliver 1998). The exogenous application of JA to *Glycine max* seedlings before $NiCl_2$ stress increased plant survival in Ni^{2+} stress (Sirhindi et al. 2015). Heijari et al. (2008) determined that the external use of methyl jasmonate in lower doses alleviates the adverse effects of aluminum toxicity by elevating the enzymatic and nonenzymatic antioxidants. JA also reduced lipid peroxidation by enhancing the production of glutathione or ascorbate antioxidants (Noriega et al. 2012). The application of jasmonates to soybean leaves growing under cadmium stress alleviated cadmium stress by lowering lipid peroxidation, ROS, and enhancing antioxidant activity (Keramat et al. 2009). The external employment of jasmonates in low dosage to plants under copper toxicity protected plants by modifying photosynthetic pigments (Poonam et al. 2013). The use of MeJA externally can prevent oxidative damage and mitigate heavy metal stress in various plants including *Cajanus cajan*, *Capsicum frutescens, Kandelia obovate, Solanum nigrum*, and *Brassica napus* (Poonam et al. 2013; Yan et al. 2013, 2015; Chen et al. 2014; Farooq et al. 2016). Hence, it can be known from different observations that jasmonates are involved in the reduction of harmful impacts of heavy metal stress.

4 JA Signaling

4.1 In the Absence of JA

The synthesis of JA involves three compartments, chloroplast, peroxisome, and cytosol. JA is then transferred to the cytoplasm/cytosol (Wasternack and Hause 2002; Ruan et al. 2019). In the cytoplasm, JA-Ile was found to be the most bioactive form. In response to different stresses, JA moved to the nucleus and apoplast through a transporter protein known as jasmonic acid transfer protein 1 (JAT1).
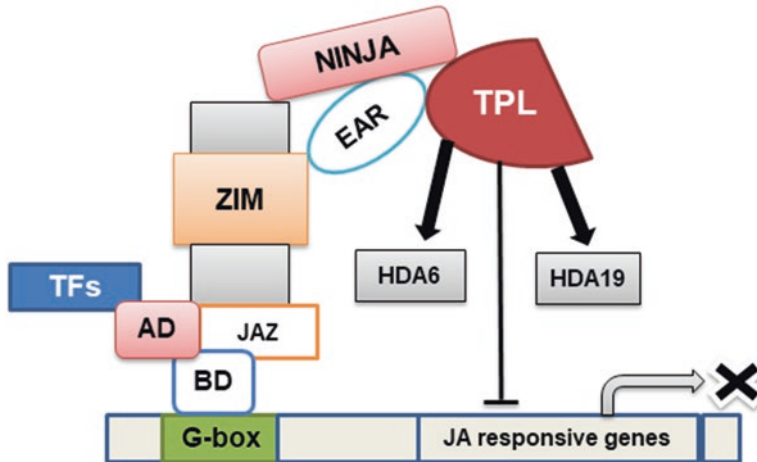
Fig. 3 JA signaling pathway in the absence of JA

Under normal conditions, various transcription factors are unable to activate promoters of jasmonate-responsive genes because of very little concentration of JA-Ile. The coronatine insensitive 1 (COI1) and JAZ co-receptors together are a part of the jasmonate receptor. It was reported that the COI1-JAZ co-receptor has >100-fold greater affinity for the ligand than either COI1 or JAZ alone (Sheard et al. 2010). The F-box protein, COI1, associates with Skp/cullin to establish an E3 ubiquitin ligase complex, i.e., SCF^{COI1}. JAZ proteins are the repressors of jasmonate signaling. JAZ proteins have conserved Jas and ZIM/TIFY domains. Both these domains have different functions like Jas domain interacts with COI1 and MYC2 proteins whereas the ZIM domains cause dimerization and association with JAZ proteins and NINJA (Chung and Howe 2009). The NINJA [having an EAR motif] communicates with TOPLESS (TPL). NINJA, TOPLESS along with JAZ proteins form a complex having a role in the repression of transcription (Fig. 3). Through the participation of histone deacetylase 6 (HDA6) and HDA19, this complex aims at inhibiting the jasmonate-responsive genes expression by the formation of a closed complex from an open one (Pauwels et al. 2010; Causier et al. 2012; Acosta et al. 2013; Chini et al. 2016; Wasternack and Song 2017).

4.2   In the Presence of JA

After the plant perceives any kind of abiotic stress, it starts elevating the production of JA-Ile and it is recognized by COI1. In the nucleus, JA-Ile promotes interaction between JAZ and COI1 (Xie et al. 1998; Zhai et al. 2015; Ali and Baek 2020). This JA-Ile, COI1, and JAZ interaction facilitate the ubiquitin-dependent degradation of JAZ proteins by 26S proteasome which serves as a repressor of jasmonate signaling.
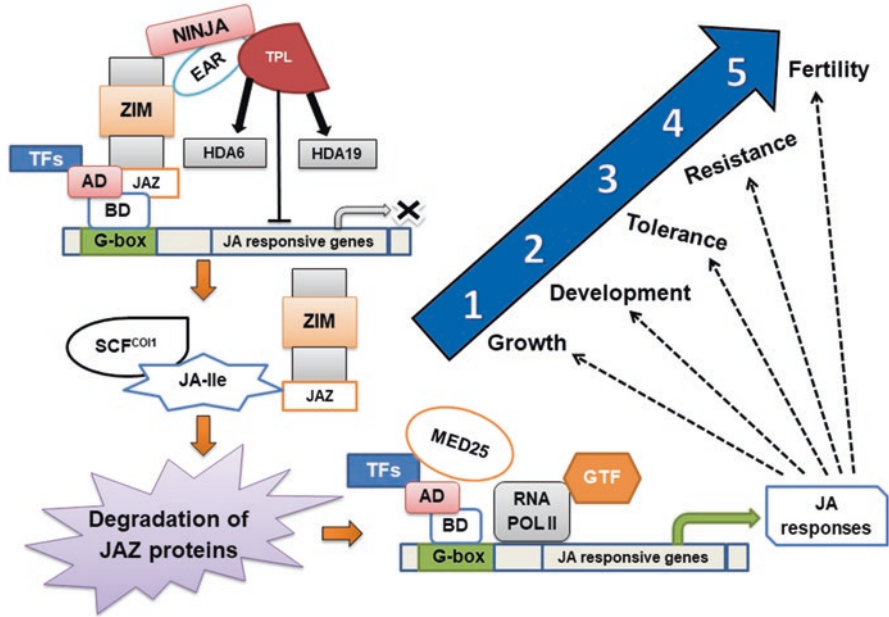
Fig. 4 JA signaling pathway in the presence of JA

Degradation of repressor permits transcriptional activation of different jasmonate-responsive genes by the activity of various transcription factors (Fig. 4). In *Arabidopsis*, Mediator 25 (MED25) (Bäckström et al. 2007) serves as a communicator between the general transcription factors (GTFs), RNA polymerase II, and the gene-specific TFs (Chen et al. 2012).

5 Interaction of JA with Other Phytohormone Signaling Pathways Under Stress Conditions

5.1 Interaction of JA with Auxins for Root Development

Cross talk can be visualized as two distinct pathways not independent of each other which can be negative or positive and can alter synthesis, transport, or signaling pathway of another hormone (Jang et al. 2020). For example, the growth of plant roots is being regulated by different hormonal pathways. Auxin plays a crucial role among them. It has been already reported that PLT genes that encode AP2 (APETALA2) class of TFs plays a crucial part in the patterning of SCN (Galinha et al. 2007). Auxin signaling pathway was reported by Dharmasiri et al. (2005), Kepinski and Leyser (2005), and Mockaitis and Estelle (2008), where it was demonstrated that TRANSPORT INHIBITOR RESPONSE1 (TIR1) which is an F-box

protein serves as auxin receptor. After attachment of auxin with TIR1, it facilitates the association of TIR1 with Aux/IAA substrates which serve as an inhibitor of auxin signaling. TIR1 is a component of SCF ubiquitin ligase complex SCF^{TIR1} leading to the ubiquitin-dependent proteolysis of Aux/IAA by 26S proteasome (Fig. 5). Degradation of repressor permits transcriptional activation by ARFs that promote the expression of different auxin-responsive genes including *PLT1* and *PLT2*.

Chen et al. (2011) observed that the expression levels of *PLT1 and PLT2* are downregulated by JA, which is reliant on the MYC2 transcription factor. Dombrecht et al. (2007) have reported that the preferable site of MYC2 binding is 5′-CACATG-3′ motif in the target genes. Chen et al. (2011) also reported the existence of this single motif in P1 region (−1609 to −1614 bp) whereas two motifs in P2 region (−940 to −945 and −1098 to −1103 bp) of PLT 1 promoter and also one same motif in P3 region (+288 to +293) of PLT2 promoter. Their study also revealed MYC2 TFs act upstream of PLT1 and PLT2 TFs in regulating SCN maintenance and root meristem activity. It has already been reported that transcription of PLT1 and PLT2 are being upregulated by auxin. SCN maintenance and meristem activity are also being positively regulated by auxin (Aida et al. 2004). As compared to this, the study of Chen
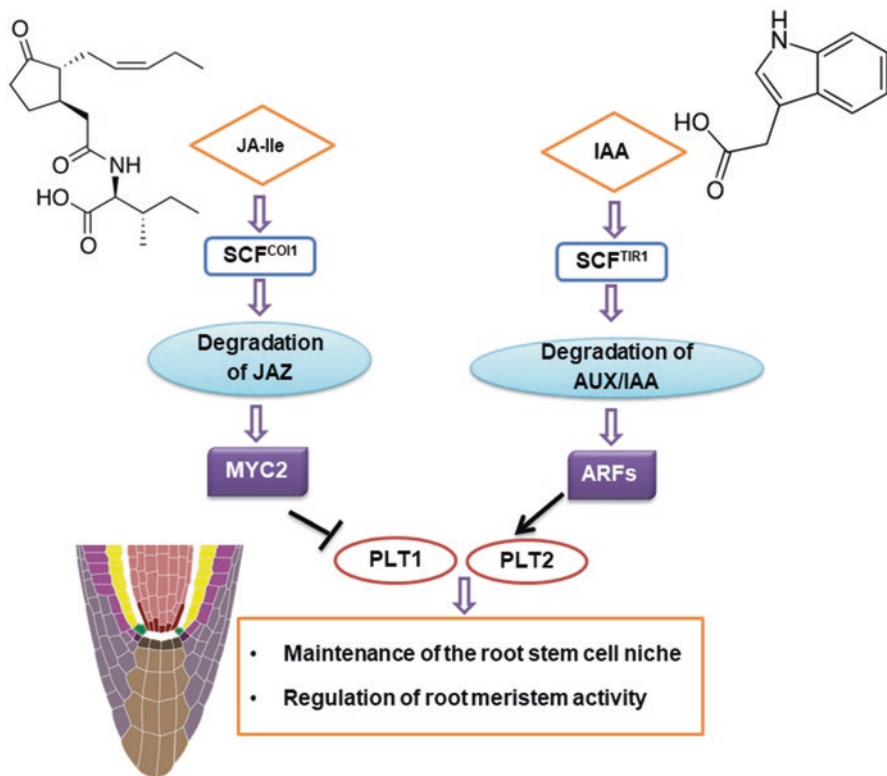

Fig. 5 Hormonal pathways showing an interplay between JA and auxin resulting in regulation of root meristem activity and root stem cell niche (SCN) maintenance

et al. (2011) focused on lowered *PLT1* and *PLT2* expression by JA and negative regulation of SCN maintenance and meristem activity, therefore, hints at the convergence of different JA and auxin signaling pathways in the modulation of maintenance of root SCN.

5.2   Interaction of JA with Ethylene in the Regulation of Apical Hook Formation

Various epigeal plants have developed an organ known as an apical hook during evolution to protect apical meristem and cotyledons from any sort of damage. It is already reported that formation of ethylene (ET) and gibberellins (GAs) contributes to apical hook formation whereas jasmonate (JA) and brassinosteroids discourage the apical hook formation (Vriezen et al. 2004; Li et al. 2004; De Grauwe et al. 2005). Lehman et al. (1996) reported that HOOKLESS1 (HLS1) is a key regulator of auxin distribution and responses at the time of apical hook formation of *Arabidopsis* seedlings. *HLS1* transcript accumulation is promoted by ET through ETHYLENE INSENSITIVE3 (EIN3) which binds directly to the promoter of *HLS1*.

Several ET receptors like ERS1, ERS2, ETHYLENE TRIPLE RESPONSE (ETR1), ETR2, and ETHYLENE INSENSITIVE4 (EIN4) have already been identified. In the absence of ET, the ET responses are negatively regulated by its receptors. CONSTITUTIVE TRIPLE RESPONSE1 (CTR1) is present downstream of the ET receptors and negatively regulates the ethylene response in the absence of ethylene. The binding of ethylene to its receptors promotes the deactivation of its receptors. EIN2 works downstream of CTR1 which gets inactive in the absence of ET because of ETP1 and ETP2 that are components of the ubiquitin ligase complex that targets EIN2 for proteolysis. In the presence of ethylene, ETP1 and ETP2 get degraded whereas the degradation of EIN2 gets halted leading to the activation of downstream signaling. EIN2 promotes the stabilization of EIN3 and EIL1 that are TFs binding at a particular site on the promoter of ERF1 termed as ethylene binding site (EBS). Another TF is encoded by ERF1 that modulates the transcription of ethylene-responsive genes including *HLS1*. During the unavailability of ET, EIN3 and EIL1 are degraded via ubiquitin-mediated proteolysis by F-box proteins, EBF1, and EBF2 (Fig. 6).

The activity of EIN3/EIL1 is repressed by the JA-activated transcription factor (MYC2) in the modulation of *HLS1* expression and hook development (Zhang et al. 2014). There are several pieces of evidence available that support the statement that EIN3/EIL1 degradation is being promoted by JA in a SCF[EBF1]-dependent manner. It can also be concluded that apical hook development is being governed by the antagonistic action of the JA-ET signaling pathway where these two hormones have opposite effects on the stability of EIN3/EIL1 protein. ET stabilizes the cumulation of EIN3/EIL1 whereas JA is responsible to foster their degradation.
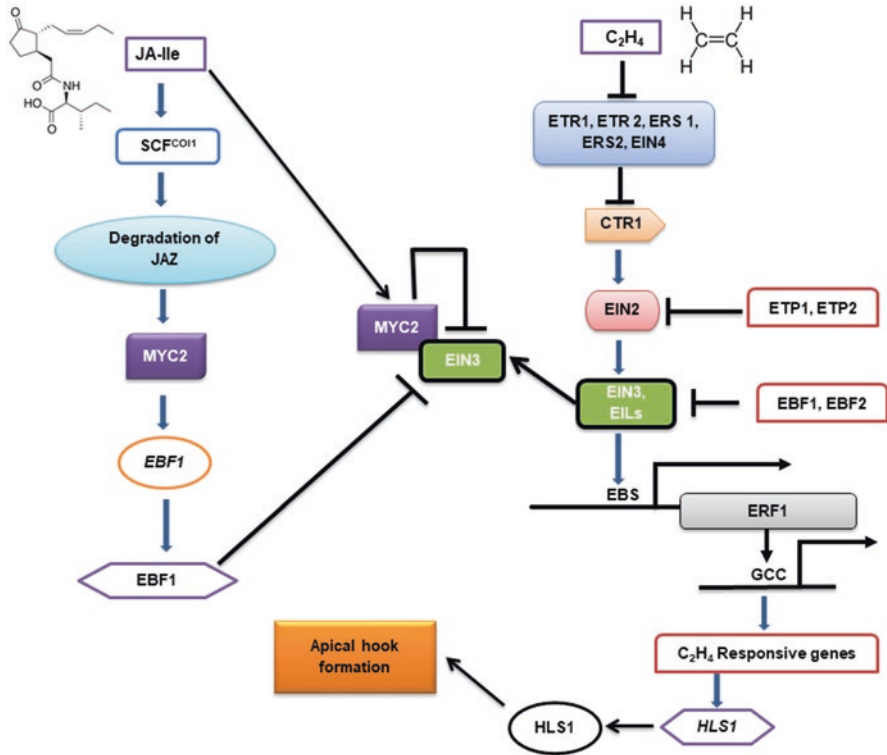
Fig. 6 Cross talk between ethylene and JA signaling pathway in the formation of the apical hook

5.3 JA and GA Cross talk for Stamen Development

Stamen is a male reproductive organ that produces pollen, crucial for the fertility of a plant. Different development stages of stamen development are governed by various environmental factors and hormonal signaling. JA and GA are the master regulators of stamen development.

GIBBELELLINE INSENSITIVE DWARF1 (GID1) serves as a receptor in the GA signaling pathway. After binding of bioactive GA to GID1, a conformational switch in the GID1 ensures DELLA binding. This interaction in turn promotes transition in the GRAS domain of the DELLA protein for recognition of SKP, Cullin, and F-box proteins, SCF$^{SLY1/GID2}$ that results in ubiquitin-mediated proteolysis of DELLA protein. Degradation of DELLA promotes the transcription of different GA responsive genes. GA responses begin and SPINDLY (SPY) encodes an *N*-acetylglucosamine transferase that adds *N*-acetylglucosamine to DELLA for its activation and therefore serves as GA signaling repressor. EARLY FLOWERING 1 (EL1), a casein kinase in rice, may also phosphorylate and activate DELLA (Sun 2010; Qin et al. 2011).

Various studies revealed that JA promotes the transcription of R2R3 MYB TFs MYB21, MYB24, etc. crucial for stamen development (Cheng et al. 2009; Mandaokar and Browse 2009; Song et al. 2011). JAZ proteins act as a repressor of JA signaling where it inhibits the activity of MYB TFs MYB21, MYB24, etc. (Song et al. 2011). The bHLH-MYB complex formed as a result of an association between lle bHLH and MYB21, MYB24 regulates the stamen development (Qi et al. 2015). At the time plant perceives environmental cues it starts synthesizing JA. Interaction of JA to its co-receptor COI1 and JAZ facilitates JAZ to degrade through 26S proteasome, thereby releasing the bHLH-MYB complex that also modulates the downstream gene expression in mediating stamen development (Fig. 7). It was already reported that DELLA is involved in inhibition of JA biosynthesis gene expression in flowers that lead to altering the process of stamen development. Hong et al. (2012) demonstrated direct interaction of DELLA with MYC2 to repress its activity. Further, it remains an area of investigation to find out whether all the bHLH members (MYC2, MYC3, etc.) and MYB21 and MYB24 are targets of DELLA in inhibiting the transcription function of the bHLH-MYB complex for regulating stamen development.
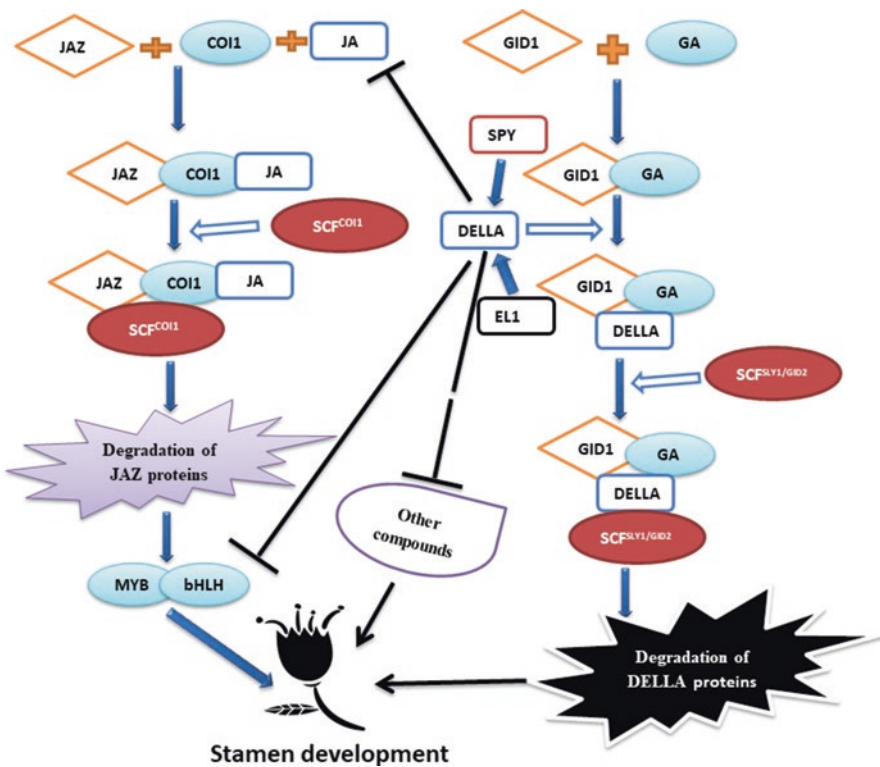

Fig. 7 Cross talk between JA and GA in the regulation of stamen development

6   Concluding remarks

While growing in nature, the green plants are often subjected to multiple abiotic and biotic stresses either in single or in combination. To tackle challenging conditions and support their growth, plants initiate a fine-tuning in their signaling networks as well as bring changes in the concentration of endogenous plant hormones. This makes it necessary to further investigate the cross talk of natural plant hormones in the balance warfare of growth and defense. One of such important phytohormone is jasmonic acid (JA). Due to the continuous research and parallel advancements in omics in recent years, the crucial roles of JA and its derivatives have been investigated from seed germination to plant's defense as well as tolerance. During the challenging various stresses, JAs induce antioxidative enzymes and other defensive compounds as well as modulate the nutrition uptake for combating the stresses.

At present, it has been deduced that the action mechanism of the core JA signaling pathway varies under every stress due to the diversity of both positive and negative interactions with numerous genes, regulatory TFs, small RNAs, hormones, elicitor, and treatments. However, so far, the data still fail to throw light on the highly complex molecular mechanism of JA signaling with changeable networks of other plant hormones in combinatorial stresses at a time. Furthermore, the identified components of hormone signaling are still very low as compared with the unidentified components. Moreover, there are very high chances of the variability in the data recorded in labs from those that actually occur in the farmer fields. Additionally, there is still no single report available in the literature that embarks the complete temporal analysis of plant hormone signaling networks starting from the seedling stage to senescence. So overall, we have to keep in mind that the current knowledge is limited as compared with a big list of related questions. As a result, in the future, systematic omics research on the interaction of JA signaling with each and every interacting factor will be done for broad application prospect, i.e., super tolerance in plants that do not compromise yield. In the future, the exact molecular mechanisms of both vascular and airborne transmission of the JA signal will also be elucidated. The light will be also given on how various environmental signals initiate the synthesis of JA.

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