

Jasmonate

Subjects: Plant Sciences

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Temperature is a critical environmental factor that plays a vital role in plant growth and development. Temperatures below or above the optimum ranges lead to cold or heat stress, respectively. Temperature stress retards plant growth and development, and it reduces crop yields. Jasmonates (JAs) are a class of oxylipin phytohormones that play various roles in growth, development, and stress response.

Keywords: heat stress ; temperature stress ; jasmonates

1. Introduction

Plants are unable to move and thus have to cope with various adverse environmental factors, such as extreme temperatures, drought, salinity, and heavy metal toxicity ^{[1][2]}. Being a critical environmental factor, temperature plays a dominant role in plant growth and development ^[3], and it determines the geographical distribution of plant species ^[4]. As global climate change intensifies, the magnitude and frequency of extreme temperatures are increasing. Extreme temperatures cause various forms of damage at different stages during plant growth and development. The general consequences of heat and cold stress include impaired photosynthesis, excessive accumulation of reactive oxygen species, broken plasma membranes, and altered phytohormone levels ^{[5][6][7][8][9][10][11]}. Eventually, heat and cold stress inhibit plant growth and cause losses in crop yields, posing a serious threat to food security ^{[12][13][14][15]}. A survey showed that wheat, rice, maize, and soybean yields would decrease by 6.0%, 3.2%, 7.4%, and 3.1% on average, respectively, if the global temperature rises by 1 °C ^{[4][16]}. Low temperatures adversely affect plant growth and development and reduce crop production ^{[12][17][18][19]}. For instance, it has been estimated that in temperate and high-elevation regions, cold stress accounts for 30–40% of yield losses in rice ^{[4][20]}.

Unlike animals, plants are sessile organisms and thus are unable to escape unfavorable temperature conditions. Instead, plants have evolved a set of sophisticated strategies enabling them to survive under temperature stress. Plant hormones play a vital role in the initiation of temperature stress response by integrating temperature stimulus and endogenous signals. For instance, jasmonates (JAs), abscisic acid (ABA), and brassinosteroid (BR) positively regulate plant response to both heat and cold stress ^{[21][22][23][24][25][26]}. Jasmonates (JAs) are a typical class of phytohormones. The term “jasmonates” generally refers to jasmonic acid and its derivatives, typically including jasmonyl isoleucine (JA-Ile) and methyl jasmonate (MeJA) ^[27]. In addition to its well-known role in growth and development, and in defense against pathogen attack and insect herbivory ^{[28][29][30][31][32]}, a growing number of studies have highlighted the vital role of JA in the response to a variety of abiotic stresses, including drought, salinity, heat, and cold stress response ^{[33][34][35][36][37][38][39][40][41][42][43]}.

2. JA Biosynthesis and Signaling

The JA biosynthetic pathway and the major enzymes involved have been well characterized and extensively reviewed ^{[27][29][44][45][46][47][48]}. JA biosynthesis starts with polyunsaturated fatty acids released from plastid membranes through the action of phospholipase (PLA) ^[49]. Current evidence supports the assertion that JA is derived via the α -linolenic acid (α -LeA, C18:3) pathway and the hexadecatrienoic acid (HTA, C16:3) pathway ^[50]. As the α -LeA pathway is dominant in the biosynthesis of JA, researchers focus on this pathway to explain JA biosynthesis (**Figure 1A**). Overall, four major enzymes are engaged in JA biosynthesis from α -LeA, comprising lipoxygenase (LOX), allene oxide synthase (AOS), allene oxide cyclase (AOC), and oxophytodienoic acid reductase (OPR) ^{[51][52]}. In plastids, LOX catalyzes the first step of JA biosynthesis. α -LeA is converted to 13(S)-hydroperoxy-octadecatrienoic acid (13-HPOT) by LOXs. In Arabidopsis, four LOXs—LOX2, LOX3, LOX4, and LOX6—are able to oxygenate α -LeA ^[53]. Each LOX may function differentially depending on the types of external stimuli. For instance, LOX6 is predominantly involved in JA production upon wounding and drought stress ^{[54][55]}. Subsequently, 13-HPOT is catalyzed by AOS to produce 12,13(S)-epoxy-octadecatrienoic acid (12,13-EOT). AOS is a cytochrome P450 enzyme, which uses oxygenated fatty acid hydroperoxide substrates as oxygen

donors. There is only one AOS gene in Arabidopsis, and mutation in AOS leads to disrupted JA biosynthesis in response to wounding [56]. 12,13-EOT is further converted to 12-oxo-phytodienoic acid (12-OPDA), catalyzed by AOC. Four AOC genes have been identified and found to act redundantly in the biosynthesis of JA in Arabidopsis [57]. Next, 12-OPDA is translocated by the transporter COMATOSE (CTS1) to the peroxisome [58]. In the peroxisome, OPDA is reduced by OPDA reductase (OPR) to produce OPC-8:0. OPRs are encoded by six *OPR* genes in the Arabidopsis genome; however, only OPR3 acts on OPDA. OPC-8:0 is then subjected to three rounds of β -oxidation by acyl-CoA oxidase (ACX), L-3-KETOACYLCOA THIOLASE (KAT), and multifunctional protein (MFP) [59]. Finally, JasmonoylCoA, which is generated through β -oxidation reaction, can be further cleaved by THIOESTERASE (TE) to produce (+)-7-*iso*-JA, which is then transported to the cytoplasm. In the cytoplasm, various JA derivatives are formed, including methyl jasmonate (MeJA) and JA-isoleucine (JA-Ile) [60][61]. The conjugation of (+)-7-*iso*-JA with isoleucine produces JA-Ile, and the reaction is catalyzed by jasmonate-amido synthetase (JAR1). The *jar1* mutant was identified as the first JA-insensitive mutant, and the JA-Ile level in mutant plants is severely reduced [62]. The methylation of JA forms MeJA, with catalysis by jasmonate methyl transferase (JMT). JA-Ile and MeJA are active forms of JA, and they can be converted to inactive 12-OH-JA by jasmonate-induced oxygenases (JO) and jasmonic acid oxidases (JAO) [63][64].

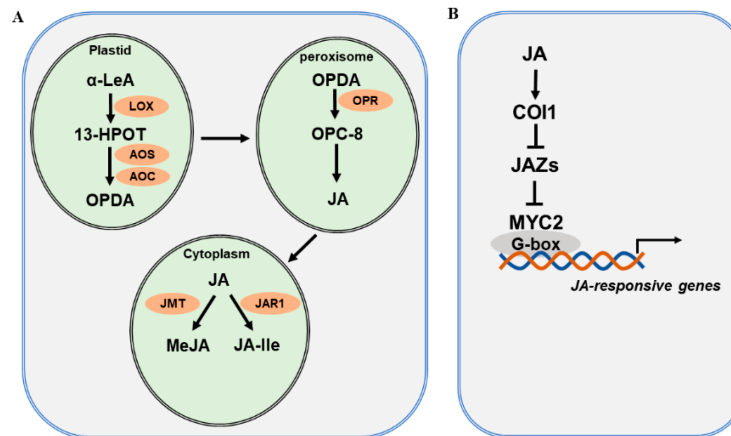


Figure 1. JA biosynthesis and signaling pathway. **(A)** A simplified JA biosynthesis pathway from α -linolenic acid (α -LeA). JA and its derivatives are produced from α -LeA through several sequential steps, which are catalyzed by lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase (AOC) in plastids; OPDA reductase (OPR) in peroxisomes; and jasmonate-amido synthetase (JAR1) and jasmonate methyl transferase (JMT) in the cytoplasm. **(B)** A simplified JA signaling pathway. Three main components are involved in JA signaling: the COI receptor, the JAZ repressor, and the MYC2 transcription factor.

The JA signaling pathway has been well defined primarily in Arabidopsis and tomato. In brief, it consists of the receptor CORONATINE INSENSITIVE 1 (COI1), the repressors JASMONATE ZIM-DOMAIN PROTEIN (JAZs), and the master transcription factors MYCs (**Figure 1B**). Early genetic screens identified *coronatine insensitive 1* (*coi1*), which is insensitive to the functional homolog of JA-Ile, coronatine. Later studies confirmed that COI1 acts as a receptor that perceives active JA [65][66]. COI1 is an F-box protein [67] that is able to associate with SKP1 and CULLIN1 to form an E3 ubiquitin ligase complex, SCF^{COI1}. In search of the substrate for SCF^{COI1}, researchers from three independent laboratories discovered JASMONATE ZIM-DOMAIN (JAZ) proteins, which are repressors of JA signaling [68][69][70]. JAZs belong to the plant-specific TIFY family, possessing a core TIF[F/Y]XG motif within the ZIM (ZN-FINGER PROTEIN EXPRESSED IN INFLORESCENCE MERISTEM) protein domain. There are 12 JAZ proteins that have been identified in Arabidopsis [68][69][71]. These JAZs are distinct from other proteins in the TIFY family as they contain a C-terminal Jas motif, SLX2FX2KRX2RX5PY [70][72][73]. The interaction of COI1 with the Jas domain of JAZ proteins forms the co-receptor complex [74][75]. TOPLESS (TPL) and TPL-related proteins (TPRs) are corepressors that interact with JAZ proteins through the ETHYLENE RESPONSE FACTOR (ERF)-ASSOCIATED AMPHIPHILIC REPRESSION (EAR) motif. MYC2, a bHLH transcription factor, is the master regulator of JA signaling and mediates a variety of biological processes. MYC2 is repressed by JAZ proteins and is released following the degradation of JAZs [69][75][76]. Eventually, MYC2 activates various downstream JA-responsive genes [44][77][78][79]. MYC2 plays multifaceted roles in growth and development, defense against biotic stress, abiotic stress response, and regulation of secondary metabolite biosynthesis. MYC3 and MYC4 are two close homologs of MYC2. MYC2 forms dimers with MYC3 and MYC4 to modulate the transcription of various target genes by binding to the G-box or its variants within the promoters [80][81].

3. The Role of JA in Cold Stress Response

Cold stress generally refers to two types of stresses: chilling stress, with a temperature ranging from 0 °C to 15 °C, and freezing stress, with a temperature below 0 °C. Cold stress is one of the most severe environmental stresses in plants. Cold stress inhibits plant growth and development and threatens crop productivity. To cope with cold stress, plants have evolved a wide variety of mechanisms. JA, a classical phytohormone, positively mediates plant cold response. Plenty of studies have shown that JA production is increased in plants in response to cold stress, which implies the potential role of JA in the response to cold stress. For instance, upon cold stress, JA accumulation is markedly enhanced in *Arabidopsis*, tomato, and rice [82][93][94][95]. Consistent with increased JA accumulation, the expression of JA biosynthesis genes is induced by low temperatures. As observed in rice, cold stress triggers the expression of *OsLOX2*, *OsAOC*, *OsAOS1*, and *OsAOS2* and promotes endogenous JA levels [85]. Similarly, in *Artemisia annua*, higher levels of JA and increased expression of JA biosynthesis genes were observed following cold treatment [35]. Furthermore, the application of exogenous MeJA potentiates cold tolerance in a variety of species, including banana, tomato, loquat, orange, guava, mango, and peach [24][86][87][88][89][90]. All these results support the assertion that JA is involved in plant cold stress response.

The role of JA in cold response is further substantiated by mutant or transgenic plants with altered JA biosynthesis. *Arabidopsis* plants with mutations in *AOS* and *LOX2* show impaired JA biosynthesis, and these plants are hypersensitive to low temperatures [82]. Another study showed that *MaLBD5* (lateral-organ boundaries domain) is associated with the JA-mediated cold response in banana fruits. *MaLBD5* promotes JA biosynthesis by transactivating the expression of *MaAOC2* [91]. Furthermore, a genetic study showed that *HAN1*, a rice gene that encodes an oxidase that catalyzes the active form JA-Ile to the inactive form 12OH-JA-Ile, negatively regulates cold tolerance [92]. In addition, transgenic *Arabidopsis* plants overexpressing *GLR1.2* (glutamate-like receptor) and *GLR1.3* display enhanced accumulation of JA by activating the expression of JA biosynthesis genes and increased cold tolerance [93].

In an attempt to understand the underlying mechanisms of JA-mediated cold tolerance, numerous studies have revealed that major components of the JA signaling pathway play a critical role in cold tolerance in plants. Being the master regulator of JA signaling, *MYC2* is of great importance in cold response. In *Poncirus trifoliata*, *MYC2* targets a betaine aldehyde dehydrogenase gene (*PtBADH-I*) and directly upregulates it, thereby increasing the production of glycine betaine. A high level of glycine betaine confers cold tolerance in *Poncirus trifoliata* [94]. In tomato, *MYC2* targets and upregulates *ADC1*, which is a putrescine biosynthesis gene, leading to enhanced putrescine accumulation and decreased cold damage [83]. Under cold conditions, *MYC2* directly stimulates the expression of *SIGSTU24*, a JA-responsive glutathione S-transferase gene, and consequently alleviates cold-induced oxidative stress [84]. These results indicate that JA positively regulates cold response by promoting the production of antioxidant enzymes and non-enzymatic cryoprotective compounds through *MYC2*.

The module ICE (inducer of CBF expression)-DREB1/CBF (dehydration-response element-binding protein 1/C-repeat binding factors) plays a vital role in cold response in plants [95][96]. DREB1/CBFs are AP2/ERF (APETALA2/ETHYLENE-RESPONSIVE FACTOR)-type transcription factors capable of binding to DREs (dehydration-responsive element) in the promoters of target genes and acting as key regulators of COR (cold-regulated) genes [97][98][99]. Previous studies have identified three DREB1/CBF genes: *DREB1A/CBF3*, *DREB1B/CBF1*, and *DREB1C/CBF2* [98][100]. Cold stress leads to rapid induction of these genes, and mutations in them severely impair cold tolerance [101][102]. Overexpression of *CBF* genes induces the expression of numerous cold-inducible genes and confers cold tolerance [103][104]. ICE1 is an MYC-like basic helix–loop–helix transcription factor that acts as a master regulator in the DREB1/CBF pathway. In the past two decades, a large number of studies have established the role of ICE1 in the expression of *DREB1/CBF*. However, recently, it has been reported that repression of *CBF3* in *ice1-1* mutant plants is due to DNA-methylation-mediated gene silencing caused by inserted T-DNA, not by ICE1 mutation, and that ICE1 is not associated with *CBF3* expression [105][106][107].

JAZs, the repressors of JA signaling, are important for the JA-mediated cold response, and the ICE-CBF module is involved in this process. In *Arabidopsis*, JAZs interact with ICEs to repress the expression of *CBFs*. Upon cold treatment, JA accumulation is increased, promoting the degradation of JAZs, thus releasing ICEs. ICEs then activate *CBFs*, conferring cold tolerance in *Arabidopsis* [82]. In apple, *MdJAZ1* and *MdJAZ2* interact with the transcription factor *BBX37* and suppress the transcription of *MdCBF1* and *MdCBF4*. In response to cold stress, increased JA leads to the degradation of *MdJAZ1* and *MdJAZ2*, allowing *BBX37* to activate *MdCBF1* and *MdCBF4* [108]. Interestingly, under cold stress, the expression of *MaMYC2a* and *MaMYC2b* is tremendously induced in banana, and *MaMYC2* physically interacts with *MaICE1*, thus triggering the expression of *MaCBF1* and *MaCBF2* [87]. In *Arabidopsis*, *SFR6* (SENSITIVE TO FREEZING 6) controls the expression of cold-regulated genes by acting on the CBF module [109][110][111]. Meanwhile,

SFR6 is also involved in the regulation of JA responses ^{[112][113]}. These studies highlight the role of JA in cold response via the induction of CBFs.

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