REVIEW

Jasmonate biosynthesis and signaling in monocots: a comparative overview

Rebecca Lyons · John M. Manners · Kemal Kazan

Abstract The plant hormone jasmonate (JA) fulfils essential roles in plant defense and development. While most of our current understanding of the JA pathway comes from the dicotyledonous model plant *Arabidopsis thaliana*, new studies in monocotyledonous plants are providing additional insights into this important hormone signaling pathway. In this review, we present a comparative overview of the JA biosynthetic and signaling pathways in monocots. We highlight recent studies that have revealed molecular mechanisms (mostly conserved but also diverged) underlying JA signaling and biosynthesis in the economically important plants: maize and rice. A better understanding of the JA pathway in monocots should lead to significant improvements in pest and pathogen resistance in cereal crops, which provide the bulk of the world's food and feed supply.

Keywords Arabidopsis · COI1 · Hormonal crosstalk · Gibberellin · Jasmonate · Jasmonate ZIM domain · Maize · Monocots · Plant defense signaling · Rice · Salicylates

Introduction

Jasmonates (JAs) are lipid-derived signaling molecules that regulate diverse developmental processes as well as

R. Lyons · J. M. Manners · K. Kazan (✉)
Commonwealth Scientific and Industrial Research Organization
(CSIRO) Plant Industry, Queensland Bioscience Precinct (QBP),
Brisbane, QLD 4067, Australia
e-mail: Kemal.Kazan@csiro.au

adaptive responses to biotic and abiotic stresses in plants. In recent years, significant progress has been made toward elucidating how JAs are produced and sensed in the model plant *Arabidopsis thaliana*. Complementary studies in model members of the Solanaceae family, namely tobacco (*Nicotiana* spp.) and tomato (*Lycopersicum esculentum*), have also contributed significantly to our understanding of the JA pathway while revealing interesting peculiarities. For instance, the peptide systemin involved in the expression of JA-, wound and insect-inducible proteinase inhibitors (PIs) is found in tomato but not in tobacco or Arabidopsis (reviewed by Sun et al. 2011). One of the ways by which important new insights into the signaling pathway of a plant hormone can be gained is through studying how the signaling pathway has evolved in diverse taxonomic groups. In this review, we present a comparative dicot-monocot overview of the JA signaling pathway. We highlight recent studies that have revealed novel insights into the biosynthesis and signaling pathway of this plant hormone, particularly in the monocot cereals maize (*Zea mays* L.) and rice (*Oryza sativa* L.).

JA biosynthesis and catabolism

Since the biosynthesis of JA has recently been reviewed elsewhere in both Arabidopsis (Wasternack 2007) and rice (Agrawal et al. 2004; Chehab et al. 2007), only a few recent highlights from monocots will be discussed here. Briefly, phospholipids such as linolenic (18:2) and α-linolenic (18:3) acid are liberated from chloroplast membranes through the action of phospholipases (PLDs). This provides substrates for the subsequent dioxygenation steps catalyzed by lipoxygenases (LOXs; 9-LOX and 13-LOX), leading to the formation of hydroperoxy octadecadienoic acids (e.g.,

13S-HPODE and 9S-HPODE). HPODEs are then converted into 12-oxo phytodienoic acid (12-OPDA) in the plastids via enzymatic reactions catalyzed first by allene oxide synthase (AOS) and subsequently by allene oxide cyclase (AOC). OPDA is then reduced/converted to jasmonic acid via the action of 12-oxo-phytodienoic acid reductase (OPR) followed by three cycles of β-oxidation in the peroxisome.

The following section details recent advances in our knowledge of key enzymatic and metabolic steps in the JA biosynthetic pathway with an emphasis on findings from monocots.

Phospholipases

The Arabidopsis phospholipase D alpha gene (*PLDα1*) has been implicated in wound-induced JA biosynthesis and JA-responsive gene expression (Wang et al. 2000), although more recent findings suggest that functional redundancy with other PLD family members may exist (Bargmann et al. 2009). Evidence toward the involvement of PLDs in JA production in rice has recently been shown. RNAi-mediated knockdown of *OsPLDα4* (Os06g0604200) and *OsPLDα5* (Os06g0604300) in rice resulted in reduced herbivory-induced JA levels and increased susceptibility to the rice striped stem borer (SSB) *Chilo suppressalis* and the rice brown planthopper (BPH) *Nilaparvata lugens* (Qi et al. 2011).

The Arabidopsis dongle (DGL) and defective in anther dehiscence (DAD1) genes encode plastidic galactolipases required for JA production during normal growth (Ellinger et al. 2010). A rice ortholog of DAD1, *OsPLA₁-Iβ1*, shows similar expression patterns to DAD1 (Singh et al. 2012), but a biological role for *OsPLA₁-Iβ1* is yet to be shown experimentally.

Lipoxygenases (LOX)

LOXs oxidize liberated phospholipids, providing substrates for other enzymes involved in JA biosynthesis, such as AOS and hydroperoxide lyase (HPL). Plant LOXs have traditionally been classified based on the specificity of the location at which they oxidize the hydrocarbon backbone of linolenic or linoleic acid: either at position C-9 (9 LOXs) or C-13 (13 LOXs). 'Non-conventional' LOX genes with dual C-9 and C-13 specificity have been reported mostly from monocots. For instance, ZmLOX1, OsLOX1 and the maize LOX known as TASSELSEED1 can generate both 9- and 13-hydroperoxides (HOX) (Kim et al. 2003; Wang et al. 2008; Acosta et al. 2009).

The functional analysis of two *LOX* genes, *ZmLOX8* and *ZmLOX10*, has provided additional insights into the operation of the LOX pathway in maize. ZmLOX10, a 13-LOX enzyme located in a yet unknown organelle, is the sole maize LOX known to generate green leaf volatile (GLV) production (GLVs are discussed further below). Given that five other functional 13-LOX enzymes are known in maize, it is not entirely clear what makes ZmLOX10 function specific to GLV biosynthesis. The function of ZmLOX8, a 13-LOX enzyme located in the chloroplast which is required for wound-induced JA accumulation, seems to be at least partly dependent on ZmLOX10. It was, therefore, proposed that signaling crosstalk is operational between ZmLOX8- and ZmLOX10-mediated signaling pathways in maize (Christensen et al. 2012).

Allene oxide synthase (AOS) hydroperoxide lyase (HPL) branches of the lox pathway

HPODEs are LOX-oxidized compounds which act as substrates for both AOS in the JA biosynthetic pathway, and for HPLs, which convert HPODEs into green leaf volatiles (GLV) in the aldehyde pathway (reviewed by Matsui 2006) (Fig. 1). Hence, AOS and HPL compete for the same substrate (Halitschke and Baldwin 2003; Halitschke et al. 2004; Chehab et al. 2006).

Three HPL-encoding genes, *OsHPL1*, *OsHPL2* and *OsHPL3*, have been identified in rice. Of these, only *OsHPL3*, which encodes a cytochrome P450 protein, is transcriptionally activated by wounding (Chehab et al. 2006), implying that this particular HPL isoform is associated with GLV biosynthesis. Indeed, the JA-overproducing rice mutant *cea62*, which contains a mutation in the *OsHPL3* gene, has provided experimental evidence for this hypothesis. In the *cea62* mutant, the levels of E-2-hexenal, a volatile involved in insect defense, were reduced, while JA levels and expression of *OsAOS* increased. Together, these data provide genetic evidence that the blockage of the pathway for aldehyde biosynthesis channels the substrates toward JA biosynthesis (Liu et al. 2012). Different effects of OsHPL3 on different types of insects are consistent with its differential regulatory roles on JAs and GLVs. OsHPL3 provides susceptibility to the insect pest SSB and the bacterial blight disease caused by *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), yet it is required for resistance against BPH. Based on the elevated expression of *OsAOS2* in the *hpl3-1* mutant, it has been suggested that OsHPL3 not only diverts substrates away from the JA pathway but also negatively affects the expression of genes involved in JA production (Tong et al. 2012). Overall, these findings are consistent with the view that AOS and HPL branches of the LOX pathway, which lead to the formation of JA and aldehydes, respectively, act in an antagonistic fashion in rice (Fig. 1).

Allene oxide cyclase (AOC)

AOC establishes the correct enantiomeric structure for naturally occurring jasmonates by cyclisation of the
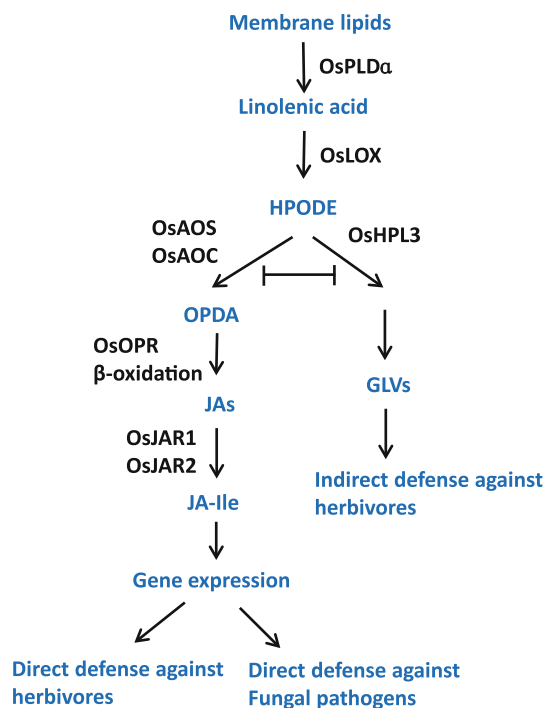
Membrane lipids

↓ **OsPLDα**

Linolenic acid

↓ **OsLOX**

HPODE

OsAOS
OsAOC **OsHPL3**

OPDA GLVs

OsOPR
β-oxidation ↓

JAs

OsJAR1
OsJAR2 ↓

JA-Ile Indirect defense against
herbivores

↓

Gene expression

Direct defense against Direct defense against
herbivores Fungal pathogens

Fig. 1 Production of jasmonates (JAs) and green leaf volatiles (GLVs) through different branches of the lipoxygenase (LOX) pathway in rice. Linolenic acid liberated from membrane lipids by phospholipases (PLD) is converted to hydroperoxy octadecadienoic acids (HPODE) by lipoxygenases (LOX). HPODEs are converted first to 12-oxo phytodienoic acid (OPDA) by allene oxide synthase (AOS) and allene oxide cyclase (AOS) and then to jasmonic acid by 12-oxo-phytodienoic acid reductase (OPR). JA is converted to bioactive JA-Ile by *jasmonate resistant 1* (*JAR1*) which encodes a jasmonate-amido synthetase. JAs activate a signaling cascade that leads to the activation of genes required for direct defense against phloem-feeding herbivores as well as fungal pathogens. HPODEs are also converted to green leaf volatiles (GLV) by hydroperoxide lyases (HPLs). GLVs emitted from plants under attack are involved in indirect defense by attracting natural enemies of chewing herbivores. Importantly, these two branches of the LOX pathway which compete for the same substrate can antagonize one another. See the text for details

unstable AOS-derived substrate. Arabidopsis contains multiple copies of AOS which seem to be functionally redundant since single or double knockouts lack JA-insensitivity phenotypes (Stenzel et al. 2012). In contrast, rice contains a single copy of AOC. Recently, the rice mutants *coleoptile photomorphogenesis 2* (*cpm2*) and *hebiba* were found to contain mutations in the *AOS* gene. As discussed below, both mutants show severely reduced levels of JAs and a number of other JA-related phenotypes (Riemann et al. 2013).

12-Oxophytodienoate reductase (OPR)

In rice, the involvement of OsOPR7 in JA biosynthesis is known based on both biochemical and genetic analyses. OsOPR7 but not OsOPR1 complements the male sterility

phenotypes of the Arabidopsis *opr3* mutant, suggesting that OsOPR7 is functionally equivalent to Arabidopsis OPR3 (Tani et al. 2008). The maize genome encodes multiple *OPR* genes and possible roles of two of these, *ZmOPR7* and *ZmOPR8*, in JA biosynthesis, have recently been investigated. While *opr7* and *opr8* single-maize mutants do not show JA deficiency or altered plant development, wound-induced JA levels were drastically reduced or abolished in the *opr7 opr8* double mutant, indicating the potential redundancy of these genes (Yan et al. 2012).

Metabolism of JA derivatives

Ja-Ile

Similarly to other hormones, jasmonic acid undergoes various biochemical modifications in plant cells. The *Arabidopsis JAR1* (*jasmonate resistant 1*) gene encodes a GH3 family amido synthetase which catalyzes the conjugation of JA to the amino acid isoleucine (JA-Ile), the bioactive form of JA recognized by COI1-JAZ (coronatine insensitive 1-jasmonate ZIM domain) co-receptor complexes (Staswick and Tiryaki 2004; Fonseca et al. 2009). In rice, two genes encoding JAR1-like GH3 enzymes, *Os-JAR1* and *OsJAR2,* are known. These two genes show different expression patterns in response to different stresses (Wakuta et al. 2011) and experimental evidence suggests that both OsJAR1 and OsJAR2 activities may be required for rapid biosynthesis of JA-Ile during wounding. However, only OsJAR1 activity seems to be required during defense against the blast fungus *Magnaporthe grisea*. As discussed below, the rice *osjar1* mutant also shows JA-related developmental alterations (Riemann et al. 2008). At least five GH3.1 enzyme-encoding genes have been isolated from maize, while in Brachypodium two GH3.1 enzyme-encoding genes are known (Wakuta et al. 2011). Possible roles of the *JAR1*-like genes in these species are currently unknown.

The catabolism of JA-Ile can also be a mechanism by which excessive stimulatory effects of JAs on downstream signaling components can be reduced (Koo and Howe 2012). In Arabidopsis, cytochrome P450 enzymes, CYP94C1 and in particular CYP94B3, were shown to be involved in the conversion of JA-Ile to 12COOH-JA-Ile and 12OH-JA-Ile, respectively (Heitz et al. 2012; Koo et al. 2011; Kitaoka et al. 2011). In tobacco (*Nicotiana attenuata*), the *JIH* gene encoding a jasmonyl-L-isoleucine hydrolase has also been associated with the hydrolysis of JA-Ile (Woldemariam et al. 2012). In rice, close homologs of these cytochrome P450s have been found (Koo et al. 2011) but currently no experimental evidence linking these genes to JA-Ile catabolism is available.

Methyl jasmonate

In Arabidopsis, jasmonic acid is also converted into the volatile signaling compound methyl jasmonate (MeJA) by the enzyme jasmonate-methyl transferase (JMT1) (Seo et al. 2001). Although *OsJMT1*, a putative rice homolog of *JMT1*, is induced in response to stress or MeJA in *AtJMT*-expressing rice plants, currently no experimental evidence implicating OsJMT1 in MeJA biosynthesis is available (Kim et al. 2009).

JA perception and signaling

The JA signaling pathway has also been extensively reviewed elsewhere (Kazan and Manners 2008, 2009, 2012; Howe 2010; Pauwels and Goossens 2011). Briefly, in the absence of stimulation, jasmonate ZIM domain (JAZ) proteins repress transcription of JA signaling components, such as the basic-helix–loop-helix (bHLH) master transcription factor MYC2 and its close homologs MYC3 and MYC4. JA-Ile (produced rapidly in response to biotic or abiotic stimuli) binds to coronatine insensitive 1 (COI1), which is a component of the Skp1-Cul-F-box protein (SCF) E3 ligase complex, and JAZ proteins are targeted for proteasome-mediated degradation, liberating MYC TFs from repression (Chini et al. 2007; Thines et al. 2007; Sheard et al. 2010; Xie et al. 1998). These MYC TFs then bind to G-box or G-box-like sequences found in the promoters of JA-responsive genes (Dombrecht et al. 2007; Fernández-Calvo et al. 2011) and interact with the MED25 subunit of the plant mediator complex (reviewed by Kidd et al. 2011) acting as a bridge between DNA-bound TFs and the RNA polymerase II transcription apparatus required for transcription (Çevik et al. 2012; Chen et al. 2012). In the following sections, we present a comparative overview of major players involved in JA signaling in monocots.

COI1-like genes

In contrast to Arabidopsis, which has a single copy of *COI1*, monocot species surveyed possess several *COI1*-like genes. In rice, three COI1-like genes, OsCOI1a (Os01g0853400), OsCOI1b (Os05g0449500) and OsCOI2 (Os03g0265500), have been found (Chico et al. 2008; Lee et al. 2013). The F-box proteins encoded by these genes share approximately 55 % amino acid sequence identity with COI1. RNAi-mediated knockdown of *OsCOI1a* and *OsCOI1b* produced mutants with reduced root and shoot sensitivity to JA, reduced JA-responsive activities of the trypsin protease inhibitor TrypPI and increased susceptibility to leaf folder (*Cnaphalocrocis medinalis*), a chewing insect (Ye

et al. 2012), implicating OsCOI1-like proteins in JA-perception in rice.

Interestingly, although all three OsCOI proteins can physically interact with various OsJAZ proteins, only OsCOI1a and OsCOI1b could functionally complement the JA-related defects of the Arabidopsis *coi1* mutant, further suggesting that OsCOI1a and OsCOI1b may function as JA co-receptors in rice (Lee et al. 2013). Although OsCOI2 could not complement the Arabidopsis *coi1* mutant, the involvement of OsCOI2 in JA sensing cannot be completely ruled out. In fact, a single mutation that replaced the conserved His-391 residue of the OsCOI3 protein with a Tyr-enabled OsCOI2 to interact with a broader range of JAZ proteins (e.g., OsJAZ1, OsJAZ2, OsJAZ5-9 and OsJAZ11) and also to complement the *coi1* mutant (Lee et al. 2013).

In wheat, VIGS-mediated root-specific knockdown of two COI1 homologs, *TaCOI1* and *TaCOI2*, resulted in mutants with reduced root length, however, it is not known whether JA-sensitivity is altered in these plants (Bennypaul et al. 2012). It is also unclear whether TaCOI1 and TaCOI2 are encoded by the same ancestral gene located on different genomes or two related F-box proteins encoded by separate genes. In *Brachypodium distachyon*, three COI1-like proteins (LOC100829997; LOC100825916 and LOC100845226) with amino acid sequence identities of 59, 58 and 58 %, respectively, to Arabidopsis COI1 have been found. Again, possible functions of these genes in JA perception and/or signaling are currently unknown.

JAZ repressors

JAZ proteins in Arabidopsis and other dicotyledonous plants such as tobacco act as transcriptional repressors of JA responses and regulate hormonal crosstalk between JA and other signaling pathways (reviewed by Kazan and Manners 2012). Arabidopsis contains 12 JAZ proteins. According to a recent estimate, rice and Brachypodium each contains 15 while sorghum and maize contain 16 and 23 JAZ-encoding genes, respectively (Ye et al. 2009; Chung et al. 2010; Bai et al. 2011). In Arabidopsis, alternative splicing events that cause the retention of a conserved intron found in most JAZ genes generates JAZ variants with truncated Jas domains required for COI1 interaction. Some of these JAZ variants act as dominant repressors resistant to proteasome-mediated degradation during JA signaling. It was proposed that the reduced ability of some JAZ proteins to form complexes with COI1 can help fine-tune JA signaling to avoid any collateral damage occurring due to hyper-activation of the pathway. In rice and Brachypodium, the position of the Jas intron is conserved, suggesting that similar alternative splicing events may also affect JAZ-encoding genes in monocots (Chung et al. 2010).

Although roles of monocot JAZ proteins in JA signaling are still mostly unknown, in rice, the three OsCOI homologs interact with OsJAZs in a coronatine-dependent manner (Lee et al. 2013). Similar to its Arabidopsis counterpart, OsJAZ8 interacts with OsCOI1 homologs through its Jas domain (Yamada et al. 2012; Seo et al. 2011). OsJAZ8 is degraded in a JA-dependent manner, while transgenic overexpression of OsJAZ8 lacking the Jas domain resulted in JA-insensitivity phenotypes, suggesting that JA- and OsCOI1-mediated degradation of OsJAZ8 contributes to JA signaling activation in rice. OsJAZ8 also forms in vitro heterodimers with other OsJAZ proteins (Yamada et al. 2012). All these features are characteristic of Arabidopsis JAZ proteins and indicate that the JAZ function may be broadly conserved in monocots.

Transcriptional regulators of JA signaling

Mitogen activated protein (MAP) kinase pathways

MAP kinase signaling pathways play essential roles in the regulation of cellular signal transduction events in plants (Rasmussen et al. 2012). In rice, silencing of *OsMPK3* reduces basal as well as SSB-induced JA levels and reduces expression of JA biosynthesis genes such as *OsHI-LOX* and *OsAOS1* (Wang et al. 2013). In addition, the *OsMPK3*-silenced mutants (*ir-mpk3*) show reduced levels of trypsin protease inhibitors (TrypPIs) that are toxic to herbivores. Consequently, SSB larvae perform better on *ir-mpk3* plants than on non-transgenic controls (Wang et al. 2013). The role of OsMPK3 as a positive regulator of JA signaling in rice is in contrast to that of the Arabidopsis MPK3, which appears to regulate TFs (e.g., WRKYs) involved in other immunity-related responses (reviewed by Rasmussen et al. 2012).

MYC (bHLH) TFs

In Arabidopsis, MYC2 and related bHLH TFs MYC3 and MYC4 act as regulators of diverse JA responses (reviewed by Kazan and Manners 2013). Similar bHLH TFs are found in monocot genomes. For instance, the rice bHLH TF OsbHLH148 interacts with OsJAZ proteins to confer abiotic stress tolerance (Seo et al. 2011). Possible roles of monocot MYC homologs have recently been reviewed (Kazan and Manners 2013) and, therefore, will not be discussed in detail here.

AP2/ERFs

In Arabidopsis, JA and pathogen infection activate transcription of the B1 and B3 subclasses of apelata 2/ethylene response factor (AP2/ERF) transcription factors, which regulate the transcription of JA-responsive defense genes. In rice, the AP2/ERF TF OsERF3 positively regulates JA biosynthesis and signaling. *OsERF3* knockdown plants show reduced JA levels and reduced expression of JA-responsive genes *OsHI-LOX* and *OsOPR,* while *OsERF3* over-expressing plants show increased JA levels and increased expression of these genes. Knockdown and over-expression plants also show that OSERF3 positively regulates resistance to SSB but negatively regulates resistance to BPH (Lu et al. 2011). OsERF3 contains an EAR motif associated with transcriptional repression (reviewed by Kazan 2006), suggesting that OsERF3 may suppress yet unknown negative regulators to activate gene expression.

NAC TFs

NAC (NAM/ATAF/CUC) domain containing TFs regulate diverse biological processes in plants. Two JA-responsive NAC domain containing transcription factors, ANACC019 and ANACC055, act downstream of MYC2 to regulate JA defense responses in Arabidopsis (Bu et al. 2008). In rice, a similar role has been ascribed to the NAC domain containing transcription factor RIM1 (rice dwarf virus multiplication 1; Os03g0119966). The *rim1* mutant shows up-regulation of basal *LOX*, *AOS2* and *OPR7* transcripts and accumulates increased levels of JAs in response to wounding (Yoshii et al. 2010). Further supporting a repressor-like role for RIM1 in JA signaling, the RIM1 protein is degraded in JA-dependent manner. The absence of any detectable physical interaction between OsCOI1 and RIM1 has led to the conclusion that OsCOI1 is probably not involved in the JA-mediated degradation of RIM1 (Yoshii et al. 2010).

Other JA-responsive NAC transcription factors such as ONAC122 (Os11g03300) and ONAC131 (Os12g03040) identified in rice were recently shown to positively regulate *OsLOX* expression and resistance to rice blast disease caused by *Magnaporthae grisea*, suggesting that these TFs might be involved in JA biosynthesis or signaling (Sun et al. 2013). JA-responsive NAC TFs have recently been identified in barley and wheat (Christiansen et al. 2012; Xia et al. 2010) but possible roles of these TFs in JA signaling are currently unknown.

WRKY TFs

WRKYs are most commonly associated with SA signaling in Arabidopsis. By contrast, rice WRKY TFs often show strong JA responsiveness (Wang et al. 2007; Liu et al. 2005, 2007) and specific roles for a number of WRKYs in JA signaling have been reported in monocots (Wang et al. 2007; Qiu et al. 2007). An allelic TF pair encoded by OsWRKY45-2 and OsWRKY45-1 positively regulates JA

accumulation and resistance to the rice blast fungus *M. grisea*, but differentially regulates SA accumulation and resistance to the bacterial pathogen *Xanthomonas oryzae* pv. *oryzae* (*Xoo*) (Tao et al. 2009). Over-expression of another rice WRKY TF, OsWRKY30, activates the expression of *LOX*, *AOS2*, *PR3* and *PR10* genes, increases endogenous JA levels and confers resistance to the rice fungal pathogens *Rhizoctonia solani* and *M. grisea* (Peng et al. 2012).

Other TFs

In addition to the major families of TFs discussed above, a number of other TFs are possibly involved in JA signaling in both dicots and monocots. For instance, the rice *JAmyb* gene encoding a JA-responsive MYB TF (Lee et al. 2001) activates JA-responsive stress-associated genes when transgenically expressed in Arabidopsis (Yokotani et al. 2013) and a C3H-type zinc finger TF positively regulates JA signaling and resistance to *Xoo* (Deng et al. 2012). LBD20, a member of the lateral organ boundaries (LBD) domain transcription factor, has recently been implicated in JA signaling in Arabidopsis (Thatcher et al. 2012). However, possible roles of the members of this TF gene family in monocots are currently unknown.

The Mediator complex

In Arabidopsis, the MEDIATOR25 (MED25) subunit of the plant Mediator complex (also known as phytochorome and flowering time 1 or PFT1) plays an important role in transmitting signals from DNA-bound JA-responsive transcriptional activators to the RNA Polymerase II transcription apparatus (Kidd et al. 2009; Çevik et al. 2012; Chen et al. 2012; reviewed by Kidd et al. 2011). MED25 is a conserved protein in all eukaryotes and MED25 homologs can readily be identified in monocots. TaPFT1, a PFT1/MED25 homolog from wheat, complements the Arabidopsis *pft1/med25* mutant, suggesting that the MED25 function may also be conserved in monocots (Kidd et al. 2009). Functional characterization of *TaPFT1* mutants recently identified in wheat (Fitzgerald et al. 2010) may reveal additional clues regarding the involvement of TaPFT1 in JA signaling in wheat.

JA-mediated pest and pathogen resistance

In Arabidopsis, pioneering studies have established that the JA pathway is important for resistance against multiple pests and pathogens. The specific effect of JA signaling-mediated resistance seems to be dependent on the type of pest or pathogen. For example, despite the importance of COI1 for resistance to necrotrophic pathogens such as *Botryris cinerea* and *Alternaria brassicicola* (Thomma et al. 1998), COI1 seems to promote susceptibility and symptom development against the root infecting fungal pathogens *Fusarium oxysporum* and *Verticillium longispoirides* (Thatcher et al. 2009; Ralhan et al. 2012). Similar to the *coi1* mutant, the maize *lox3-4* mutant (which contains a disruption in the 9-LOX encoded by *ZmLOX3*) shows increased susceptibility to the fungal necrotrophic pathogen *Aspergillus* (Gao et al. 2009) but increased resistance to the hemibiotrophs *Fusarium*, *Colletotrichum*, *Cochliobolus*, and *Exserohilum* spp. (Gao et al. 2007). The maize *opr7 opr8* double mutant, which has extremely reduced JA levels, was unable to survive when grown in non-sterile potting mix or in the field. This was possibly a consequence of hypersensitivity to infections caused by soil pathogens such as the oomycete pathogen *Phytium* spp. the causative agent of the damping off disease (Yan et al. 2012). A similar (e.g., differential) effect of the JA pathway on different herbivores was also observed. For instance, OsHI-LOX is required for increased resistance to chewing herbivores but increased susceptibility to phloem feeders in rice (Zhou et al. 2009).

In Arabidopsis, JAs and microbial pathogens are well-known inducers of secondary metabolites, including the phytoalexin camalexin. Similarly, in rice, both JA and the blast pathogen *M. oryzae* induce the major flavonoid phytoalexin sakuranetin by activating expression of *OsNOMT* (Shimizu et al. 2012), which encodes a naringenin 7-*O*-methyltransferase involved in sakuranetin biosynthesis (Rakwal et al. 2000). Indeed, *rice mutants cpm2* and *hebiba,* which are defective for OsAOC activity and JA production, show reduced sakuranetin levels and increased susceptibility to *M. oryzae*. Exogenous application of JA restores resistance to *M. oryzae* in these mutants suggesting that JAs are required for this response (Riemann et al. 2013).

In maize, JA induces the production of sesquiterpenoid phytoalexins named zealexins and the diterpenoid phytoalexins, both are also induced by pathogens and herbivores (Huffaker et al. 2011; Schmelz et al. 2011). Hence, although the type or general classes of phytoalexins may differ between dicots and monocots, the effect of JAs on the production of these defensive compounds appears to be largely conserved.

The Arabidopsis gene *PDF1.2* encodes a JA inducible plant defensin that is widely used as a marker gene to follow the activation of JA responses as well as the crosstalk between JA and other signaling pathways, particularly the SA signaling pathway (Penninckx et al. 1996). So far, a *PDF1.2* ortholog that would serve as a marker for the activation of the monocot JA pathway has not been

identified, despite the presence of small cysteine rich defensin-like peptides in rice and possibly other monocots (Silverstein et al. 2007). Interestingly, when transgenically expressed in rice, RsAFP2, a radish defensin peptide and a close homolog of PDF1.2, protects rice plants from pathogen attack (Jha and Chattoo 2010).

JAs, fertility and floral development

An intriguing aspect of the JA pathway in Arabidopsis is its effect on flower development and fertility. Arabidopsis mutants defective in JA biosynthesis and/or signaling show abnormalities that mainly affect male reproductive organs (Stintzi and Browse 2000; Sanders et al. 2000; Ishiguro et al. 2001; Park et al. 2002; Caldelari et al. 2011). The coi1 mutant lacks fertile pollen, but the coi1 female flower tissue functions normally and the mutant can produce seed when pollinated with fertile pollen. Intriguingly, tomato mutants containing a defective copy of the COI1 homolog have viable pollen but show reduced fertility due to impaired seed maturation (Li et al. 2004). In rice, no sterility phenotype was reported for OsCOI1 RNAi lines (Yang et al. 2012), however, a recent study has shown that expression of OsCOI1a or OsCOI1b in the coi1 background can restore fertility defects in Arabidopsis (Lee et al. 2013). Osjar-1 mutants display an 'open husk' phenotype which impairs normal seed set (Riemann et al. 2008), while the JA-deficient rice mutants cpm2 and hebiba (see above) also show reduced fertility and altered flower morphology, suggesting that JAs play a role in flower development and fertility (Riemann et al. 2013). Interestingly, these rice mutants as well as the cpm1 mutant defective for OsAOS activity flower earlier than wild-type plants (Haga and Iino 2004; Riemann et al. 2013).

In contrast to Arabidopsis in which JAs affect male fertility, in maize, defects in JA signaling and biosynthesis affect female fertility and sex determination. In monoecious plants such as Arabidopsis and rice, every flower contains both male and female organs, whereas in dioecious plants such as maize, male and female flowers are physically separated. The male inflorescence called the tassel is located at the apex of the stem while female inflorescences (ears) form along the stem and are the site of seed formation. Interestingly, mutations called tassel-seeds (ts) can lead to the formation of seeds on tassels by promoting female floral structures in a process called "feminization". The discovery that the inactivation of the ZmLOX8/TS1 gene, which results in JA deficiency in maize, is responsible for the ts1 phenotype, strongly suggested a role for JA in sex determination. Confirming the requirement of JA for normal sex determination, exogenous JA treatment alleviates the effects of the ts1 mutation

on fertility (Acosta et al. 2009). The suppression of male flower but promotion of female flower features, manifested by the formation of tassels containing seeds, has also been observed in the recently characterized opr7 opr8 double maize mutant (Yan et al. 2012), further implicating JAs in sex determination in maize.

Hormonal crosstalk between JA and other phytohormone signaling pathways

Hormonal crosstalk is one of the mechanisms plants employ to manage their response to the environmental cues. The interplay between JA and other hormone signaling pathways enables the plant to achieve optimal growth while defending itself from a multitude of potentially life-threatening pests and pathogens. In the following sections, we briefly discuss recent studies that have reported how the JA signaling pathway interacts with signaling pathways of other plant hormones in monocots.

JA-salicylic acid (SA) crosstalk

In Arabidopsis, one of the most intriguing examples of hormonal crosstalk occurs between the signaling pathways of SA and JA, implicated in conferring resistance to biotrophic and necrotrophic pathogens, respectively (see Thaler et al. 2012 for a recent review). The antagonistic interaction between these two pathways seems to be conserved in monocots. For instance, SA suppresses the JA-inducibility of both RSOsPR10, which encodes a root-specific homolog of the rice PR protein OsPR10, and the OsERF1 gene, a proposed regulator of RSOsPR10 (Takeuchi et al. 2011).

In Arabidopsis, nonexpressor of pathogenesis related1 (NPR1) positively and negatively regulates the SA and JA signaling pathways, respectively (Spoel et al. 2003). In rice, OsNPR1 functions similarly to the Arabidopsis NPR1 in negative regulation of the JA pathway (Yuan et al. 2007). OsNPR1 antisense rice plants display elevated JA levels and increased insect-inducibility of the JA-responsive genes OsLOX2 and OsACS2 (Li et al. 2012).

Although it is evident from these examples that the SA and JA pathways act antagonistically in rice, in the Oshlp3-1 mutant (Tong et al. 2012) and antisense OsPLD plants (Qi et al. 2011) discussed above, both SA and JA levels are elevated, suggesting that the interactions between these pathways are indeed complex. Further research is required to determine which mechanisms are operational in this phenomenon.

JA-gibberellic acid (GA) crosstalk

JA and GA signaling act in a mutually antagonistic manner in Arabidopsis and other dicots such as tobacco (Heinrich

et al. 2013). Given the primary regulatory roles of JA and GA in plant defense and development, respectively, this antagonistic crosstalk enables the plant to allocate more resources either into growth or defense (reviewed in Kazan and Manners 2012). New evidence suggests that the antagonistic interaction between JA and GA signaling is conserved in rice. *OsCOI1* RNAi lines with reduced JA sensitivity show increased GA sensitivity and exhibit phenotypes reminiscent of GA over-producing mutants. It was proposed that JA interferes with the GA-mediated degradation of the growth-inhibiting DELLA protein SLR1, which acts as suppressor of the GA signaling pathway (Yang et al. 2012) (Fig. 2).

JA-ethylene (ETH) crosstalk

In Arabidopsis, JA and ETH signaling acts in a synergistic manner for the induction of the plant defensin gene *PDF1.2* (Penninckx et al. 1996). A similar cooperation between these two hormone signaling pathways was found in rice, in which both JA and ETH treatment lead to the expression of chitinases (Rakwal et al. 2004). In maize, both JA and ETH are required to induce expression of *mir1*, a gene encoding a 1-cysteine protease with defensive functions against insects (Ankala et al. 2009). Both JA and ETH levels were elevated in *PLD* antisense rice plants (Qi et al. 2011), the maize *opr7 opr8* double mutant (Yan et al. 2012) and in roots of the *lox3-4* maize mutant (Gao et al. 2008).
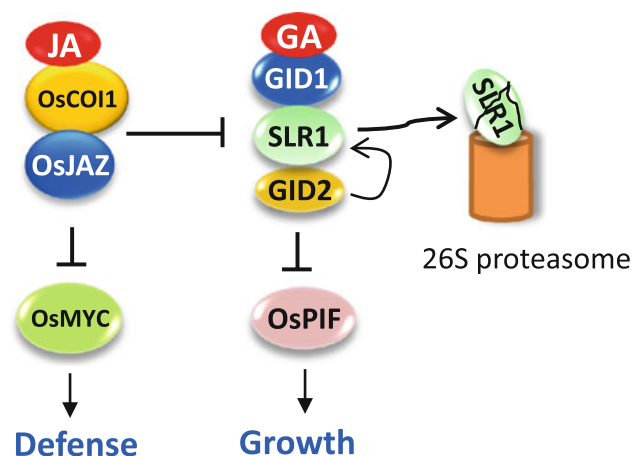

Fig. 2 JA antagonizes GA signaling in rice to promote defense at the expense of growth. In the absence of GA, plant growth is repressed by the DELLA repressor SLR1 (slender rice1). Upon binding of GA to the receptor protein GID1 (GA-insensitive dwarf1), SLR1 is degraded by the 26S proteasome through the action of the F-box protein GID2, the rice homolog of the Arabidopsis SLEEPY1 (SLY1). This relieves repression of OsPIFs, presumed orthologous of Arabidopsis phytochrome interacting factors (PIFs), a class of bHLH TFs with growth promoting properties. The OsCOI1-mediated JA signaling pathway antagonizes GA signaling by interfering with the SLR1 degradation

JA-abscisic acid (ABA) crosstalk

Antagonistic crosstalk between JA and ABA signaling has been shown in Arabidopsis (Anderson et al. 2004). In addition to SA- and JA-responsive genes, ABA-related genes are commonly induced in monocot plants challenged with fungal pathogens (Wang et al. 2012). A recent report showed that in rice, ABA promotes susceptibility to *M. oryzae* at the early stages of fungal infection (Yazawa et al. 2011). The disease promoting-effects of ABA in rice seem to be occurring through SA-ABA antagonism, as benzothioadozole (BTH, an SA analog)-mediated induction of WRKY45 and *OsNPR1* is suppressed by ABA (Jiang et al. 2010). ABA negatively regulates JA, ethylene and SA pathways, which are required for resistance against the migratory nematode *Hirschmanniella oryzae* in rice (Nahar et al. 2012). This suggests that the nature of interactions between these pathways can be complex and also attacker dependent.

JA-brassinosteroid (BR) crosstalk

Similar to JA-GA crosstalk, JA-BR crosstalk tailors the allocation of resources to development or defense depending on the requirements of the plant. A mutually antagonistic interaction between JA and the BR pathway has been proposed in rice. BRs seem to induce susceptibility to root knot nematode (*Meloidogyne graminicola*) at least partly through the suppression of the JA pathway (Nahar et al. 2013), which is required to confer resistance to these pests (Nahar et al. 2011). In a mutually antagonistic manner, JA appears to repress BR biosynthesis through negative regulation of the BR biosynthetic genes *OsD11* and *OsDWARF* in the roots, while BRs exert a negative effect on JA biosynthesis by downregulating *OsAOS2* expression (Nahar et al. 2013). Similarly, in Arabidopsis, JA negatively regulates *DWARF4* expression in a COI1-dependent manner while BR inhibits JA-dependent gene induction and root inhibition (Kim et al. 2013; Ren et al. 2009).

In Arabidopsis, interactions between JA and auxin pathways have also been identified (reviewed by Kazan and Manners 2009). In monocots, very little, if any, is known regarding JA-auxin crosstalk.

JA-light/phytochrome crosstalk

As recently reviewed elsewhere (Kazan and Manners 2011), multiple instances of crosstalk between JA, light (e.g., Red/Far Red), phytochrome and circadian clock signaling exist in Arabidopsis (Robson et al. 2010). This seems to have been broadly conserved in monocots. In rice, mutants with altered JA biosynthesis such as *jar1*

(Riemann et al. 2003, 2008) *cpm2* and *kamakubi* (Svyatyna and Riemann 2012; Riemann et al. 2013) also display altered light responses. The JA-dependent accumulation of PR1 proteins was significantly reduced in *phyA phyB phyC* rice, whereas basal expression of JA biosynthetic genes *LOX2* and *AOS2* were reduced in the *phyA phyB phyC* mutant, suggesting that the phytochrome pathway is required for JA signaling in rice (Xie et al. 2011).

Conclusions and future perspectives

Recent studies highlighted here suggest that despite minor variations, the JA pathway plays a significant role in both monocots and dicots that diverged 200 million years ago. Ancestral plant forms such as algae contain a relatively primitive oxylipin signaling component but expansion of this hormone signaling pathway has likely occurred during the adaptation of plants into diverse land environments.

Despite the existence of multiple co-receptor proteins for most other hormones, so far only a single JA-co-receptor component, COI1, has been found in Arabidopsis. The recent identification of at least two related COI1-like F-box proteins from rice that could complement the Arabidopsis *coi1* mutant suggests that monocots might contain additional JA co-receptors. Each OsCOI1 homolog interacts with different subsets of OsJAZ proteins. For example, JAZ4 and JAZ7 interact with OsCOI1b, but not OsCOI1a, whereas JAZ11 interacts with OsCOI2 and OsCOI1a but not OsCOI1b (Lee et al. 2013). Increasing the number of possible COI-JAZ interactions may be a strategy employed by monocots to help fine-tune downstream JA signaling in response to specific stressors.

The discovery of JAZ repressors has significantly advanced our understanding of how the JA signaling pathway operates in Arabidopsis. The JAZ gene family is conserved in plants and there is every reason to believe that at least some members of this gene family are involved in JA signaling. It is intriguing that as many as 23 JAZ proteins exist in maize. Although maize is an ancient polyploid and expansion of gene families may be expected in this species, the presence of 23 potential JAZ repressors in this species seems a little extravagant, assuming most of these genes are functional and involved in JA signaling. Given that the number and the functionality of JAZ proteins can also be further expanded through alternative splicing, heterodimer formation between different JAZ proteins and differential interaction with potentially multiple copies of COI1 and downstream transcription factors, it is unclear why this repressor family has expanded. It is possible that some JAZ proteins may be involved in other hormone signaling pathways or even abiotic stress

tolerance. Future studies should reveal new clues about JAZ gene function(s) in monocots.

In Arabidopsis, forward genetic approaches (i.e., mutant analyses) have been instrumental for initial identification of genes encoding important components of JA biosynthesis and signaling (Browse 2009). So far, reverse genetic approaches aimed at testing the roles of monocot homologues of Arabidopsis genes have played a prominent role in monocots. It is obvious that research on model monocot species should also focus on the identification of new signaling components rather than simply testing whether functional homologs of Arabidopsis JA genes perform similarly in monocots. Differences in morphology and pathogen-host specificities between Arabidopsis and monocots suggest that JA biosynthetic or signaling components particular to economically important cereal crops may exist. For instance, the pistillate flowering phenotype in maize *ts1* and *ts2* mutants (first observed in an agricultural show in 1913; Emerson 1920) were found to be a result of disruptions in 13-LOX and short-chain alcohol-dehydrogenase-encoding genes, respectively (Delong et al. 1993; Acosta et al. 2009). Both mutant phenotypes could be rescued with exogenous JA suggesting that first, JA regulates pistil cell death and second, TS2 might represent a novel component of the JA biosynthetic pathway.

Novel findings from monocots can also be utilized to further understand JA signaling in Arabidopsis and other dicots. For example, the NAC TF RIM1, a negative regulator of JA signaling in rice (also identified using a forward genetic approach) was shown to be degraded by the 26S proteasome in response to JA. Functionality of RIM-like homolog(s) has not yet been ascribed in Arabidopsis, possibly due to functional redundancy. The function of this subclass of NAC TFs in JA signaling could, therefore, be specific to monocots or may represent another layer of complexity in the JA pathway yet to be discovered in Arabidopsis.

Genetic and genomic resources available in rice as well as maize are being increasingly utilized. Rice is not only a model organism, but also provides over 20 % of the world's calorific intake. Rice, therefore, provides fertile scope for the identification of novel signaling components as well as more immediate application to increasing global food production. In comparison to rice and maize, less is known about JA signaling and biosynthesis in wheat and barley. It is expected that in the near future, research on the model cereal Brachypodium will also start making new contributions to this area.

Rewiring of JA response networks were proposed for engineering of plant disease resistance (Grant et al. 2013). However, exploitation of the increasing knowledge of JA signaling in monocots to enhance biotic stress tolerance in the field should be exercised with caution. Although

manipulation of a particular component of the JA signaling pathway might increase resistance to one pathogen or pest, an unwanted side effect frequently observed when altering the hormonal signaling balance in plants is increased susceptibility to other pathogens or pests. This can occur via crosstalk with other hormone signaling pathways, or within the oxylipin pathway itself. In areas prone to particular insect or pathogen damage, utilization of specifically bred cultivars in conjunction with disease forecasting might be a useful strategy for disease control in the future. However, further work is required to determine how to achieve broad spectrum resistance to pathogens which either manipulate the JA pathway or are defended against using components of the JA signaling pathways in plants.

In conclusion, despite widespread conservation of processes in how JA is produced and sensed in monocots, recent studies briefly reviewed here have also uncovered unique complexities associated with this hormone pathway in monocots. Given the importance of the JA signaling pathway for biotic stress tolerance, better understanding of these complexities in monocot cereals that collectively provide the bulk of the world's food, feed and fuel supply will be an exciting and rewarding process for plant scientists in the years to come.

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