How plants handle multiple stresses: hormonal interactions underlying responses to abiotic stress and insect herbivory

Duy Nguyen1 · Ivo Rieu1 · Celestina Mariani1 · Nicole M. van Dam1,2,3

Received: 31 October 2015 / Accepted: 9 April 2016 / Published online: 19 April 2016
© The Author(s) 2016. This article is published with open access at Springerlink.com

Abstract Adaptive plant responses to specific abiotic stresses or biotic agents are fine-tuned by a network of hormonal signaling cascades, including abscisic acid (ABA), ethylene, jasmonic acid (JA) and salicylic acid. Moreover, hormonal cross-talk modulates plant responses to abiotic stresses and defenses against insect herbivores when they occur simultaneously. How such interactions affect plant responses under multiple stresses, however, is less understood, even though this may frequently occur in natural environments. Here, we review our current knowledge on how hormonal signaling regulates abiotic stress responses and defenses against insects, and discuss the few recent studies that attempted to dissect hormonal interactions occurring under simultaneous abiotic stress and herbivory. Based on this we hypothesize that drought stress enhances insect resistance due to synergistic interactions between JA and ABA signaling. Responses to flooding or waterlogging involve ethylene signaling, which likely reduces plant resistance to chewing herbivores due to its negative cross-talk with JA. However, the outcome of interactions between biotic and abiotic stress signaling is often plant and/or insect species-dependent and cannot simply be predicted based on general knowledge on the involvement of signaling pathways in single stress responses. More experimental data on non-model plant and insect species are needed to reveal general patterns and better understand the molecular mechanisms allowing plants to optimize their responses in complex environments.

Keywords Drought · Flooding · Herbivory · Hormonal cross-talk · Induced resistance · Stress responses

Abbreviations

| Abbreviation | Description                                      |
|--------------|--------------------------------------------------|
| ABF          | ABA-responsive element binding factor             |
| AP2/ERF      | Apetala2/ethylene response factor                |
| COI1         | Coronatine insensitive1                           |
| CTR1         | Constitutive triple response1                     |
| EAR          | ERF-associated amphiphilic repression             |
| EBF          | EIN3-binding F-box protein                        |
| EIL1         | EIN3-like protein1                                |
| EIN2         | Ethylene insensitive2                             |
| EIN3         | Ethylene insensitive3                             |
| JAZ          | Jasmonate-ZIM domain corepressor                 |
| LAP          | Leucine aminopeptidase                           |
| LOX          | Lipoxygenase                                      |
| NINJA        | Novel interactor of JAZ                           |
| PDF1.2       | Plant defensin                                    |
| PP2C         | Type 2C protein phosphatase                       |
| PR           | Pathogenesis-related                              |
| PYR/PYL/RCAR | Pyrabactin resistance1/PYR-like/regulated component of ABA receptor |
| SCF          | Skp, Cullin, F-box containing                     |
| SnRK2        | Sucrose non-fermenting1-related protein kinase2 protein |
| TPL          | Groucho/Tup1-type co-repressor                    |
| TPR          | TPL-related protein                               |
| VSP          | Vegetative storage protein                        |

1 Molecular Plant Physiology, Institute for Water and Wetland Research (IWW), Radboud University, PO Box 9010, 6500 GL Nijmegen, The Netherlands
2 German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany
3 Institute of Ecology, Friedrich Schiller University Jena, Dornburger-Str. 159, 07743 Jena, Germany
Introduction

Plants have to constantly cope with a suite of biotic and abiotic stress factors. Their performance thus depends on the ability to quickly perceive changes in the environment and to express an adaptive response. Much effort has been made to understand the molecular mechanisms underlying plant adaptive responses because of their potential to improve agricultural production under adverse conditions.

Plant molecular responses to single abiotic stresses, such as drought, soil flooding, high or low temperatures, as well as to biotic interactions, such as insect herbivory and pathogen attacks, have been gradually elucidated. These responses are modulated by a complicated network of signaling pathways induced by a variety of small molecules, including Ca^{2+} signaling (Seybold et al. 2014), reactive oxygen and nitrogen species (Wang et al. 2013; Baxter et al. 2014) and phytohormones (Peleg and Blumwald 2011; Pieterse et al. 2012; De Vleesschauwer et al. 2014; Kazan 2015). Hormones and hormonal cross-talk play an important role in the molecular mechanisms that optimize plant responses to stresses which commonly occur simultaneously in the environment, such as abiotic stresses and herbivory. Over the years several reviews have discussed cross-talk between defense-related hormonal pathways in plants challenged by different herbivores, different pathogens or combinations thereof (e.g. Pieterse et al. 2002; Erb et al. 2008; De Vleesschauwer et al. 2014). Independently, ecophysiologists acquired substantial knowledge on the role of hormonal signaling pathways in responses to abiotic stresses, such as drought, flooding and shading (e.g. Peleg and Blumwald 2011; Voesenek and Bailey-Serres 2015). Since long, several ecological studies revealed that (induced) resistance to herbivores can be affected by simultaneously occurring abiotic stresses, such as drought (English-Loeb et al. 1997; Huberty and Denno 2004; Khan et al. 2010; Gutbrod et al. 2011; Tariq et al. 2013). However, only recently there has been an increased interest to identify the molecular mechanisms underlying these interactive effects (Lu et al. 2015; Davila Olivas et al. 2016; Foyer et al. 2016; Nguyen et al. 2016). For this reason, this a good moment for merging the knowledge on hormonal signaling in abiotic and biotic induced responses with the aim to come to a unified conceptual framework of how the signaling pathways induced by different stresses may interact. Thereby, we focus on the interactions between herbivore induced responses and water related stresses, specifically drought and flooding. Both drought and soil flooding or waterlogging are common phenomena in natural and agricultural ecosystems, and the frequency of their occurrence is expected to increase due to climate change (IPCC 2013). Here, we first review the most recent knowledge on how hormonal pathways regulate plant responses to single stresses. Then we discuss how interactions between these pathways may modulate defense responses in plants under combined stress conditions, considering that hormonal cross-talk may serve to optimize plant performance in complex environments. Finally, we will specify which testable hypotheses follow from our current knowledge that may help to better understand the role of signaling interactions in plants under multiple stresses.

Regulation of induced plant responses to insect herbivores

In natural habitats, plants have to defend themselves against herbivorous insects with different feeding strategies, including, but not limited to, leaf chewing beetles or caterpillars, piercing-sucking thrips or spider mites, and phloem-sucking aphids or whiteflies. Plant defense mechanisms may vary from morphological (e.g. trichomes, waxes) to chemical defenses [e.g. alkaloids, glucosinolates (GS), protease inhibitors (PIs)], which are often induced upon herbivory (Schaller 2008). When insects are feeding on plants, herbivore associated molecular patterns (HAMPs) and endogenous damage associated molecular patterns (DAMPs) are released (Acevedo et al. 2015). Upon perception of these cues, phytohormones, including jasmonic acid (JA), abscisic acid (ABA) and ethylene (ET), accumulate to activate signaling cascades that regulate...
downstream transcriptional responses (summarized in Fig. 1a–c). Among them, JA and particularly its most active isoleucine conjugate (JA-Ile), are generally accepted as the core inducers of many herbivore-induced defenses (Howe and Schaller 2008; Tytgat et al. 2013; Wasternack and Hause 2013). JA-insensitive or deficient mutants, therefore, exhibit very low levels of resistance to a wide range of herbivorous insects from different orders (Thaler et al. 2002; Bodenhausen and Reymond 2007; Schweizer et al. 2013).

Due to herbivore-specific HAMPs (Acevedo et al. 2015; Xu et al. 2015), other signaling hormones in addition to JA are induced upon feeding to tailor the defenses against the attacker. The signal signature that is induced for a part is due to differences in herbivore feeding strategies. Piercing-sucking insects, such as aphids, have a ‘stealthy feeding strategy’ (De Vos et al. 2005) that avoids massive cell damage. On the other hand, the salivary sheet lining their mandibles contains specific enzymes that interact with the cells along the styler path (Foyer et al. 2016). Aphid feeding thus induces a significantly different set of signaling pathways and transcripts than chewing herbivores, that cause more cell damage and possess different elicitors in their saliva (De Vos et al. 2005; Bidart-Bouzat and Kliebenstein 2011). On the other hand, herbivore-induced signal signatures can also be species-specific within herbivore feeding guilds. For example, feeding by caterpillars of Manduca sexta induces the accumulation of JA and ET, whereas Spodoptera exigua caterpillars induce JA and salicylic acid (SA) in Nicotiana attenuata (Diezel et al. 2009). In contrast, S. exigua induces JA and ET accumulation in maize (Zea mays) and Arabidopsis thaliana (Schmelz et al. 2003; Rehrig et al. 2014), whereas Pieris rapae triggers JA and ABA levels in the latter species (Vos et al. 2013b). Simultaneous SA and JA accumulation also occurs upon herbivory by the Colorado potato beetle (Leptinotarsa decemlineata) and the mealy bug (Phenacoccus solenopsis) on tomato plants (Solanum lycopersicum) (Chung et al. 2013; Zhang et al. 2015a). Although not all hormones were measured in each study, this strongly suggests that plant hormonal responses to herbivores depend on the specific plant–insect interaction. Cross-talk between JA and other phytohormones has been proposed to fine-tune plant defense responses to specific attackers (Pierse et al. 2012; Erb et al. 2012).

ABA in defense regulation

ABA synthesis and signaling is required for plants, such as Arabidopsis, tomato and N. attenuata, to fully activate defenses and resistance against their herbivores; ABA deficiency increases plant susceptibility to herbivory (Thaler and Bostock 2004; Bodenhausen and Reymond 2007; Vos et al. 2013b; Dinh et al. 2013). Furthermore, ABA is involved in signaling process inducing JA-dependent defense responses in systemic tissues (Erb et al. 2009; Vos et al. 2013b). The synergistic interaction between JA and ABA can occur via the transcription factor (TF) MYC2 and its homologs MYC3 and MYC4 in Arabidopsis (Fig. 2). ABA induces COI-dependent expression of MYCs, which induce plant resistance to insects by regulating many wound/herbivore-responsive genes, e.g. VSPs, LOXs and glucosinolate biosynthetic genes (Lorenzo et al. 2004; Dombrecht et al. 2007; Schweizer et al. 2013). In tomato, the ABA/JA/wounding-responsive expression of LAP and the PI gene PIN2 are directly regulated by MYC2 orthologs, JAMYC2 and JAMYC10 (Pen˜a-Corte´s et al. 1995; Boter et al. 2004). However, due to the strong mutual antagonism between ABA and ET, and the fact that some JA-responsive defenses are mediated by ET (discussed below), logically ABA also negatively affects some JA/ET-dependent defenses, such as nicotine biosynthesis in tobacco plants (Nicotiana tabacum) (Lackman et al. 2011).

A key question is where in the signaling cascades interactions between JA and ABA occur. The requirement of normal ABA biosynthesis for JA production (Adie et al. 2007), the COI-dependency of the ABA-induced MYC2
expression (Lorenzo et al. 2004) and the fact that methyl-jasmonate (MeJA) still induces LAP and PIN2 in ABA-deficient mutants (Carrera and Prat 1998), suggest that the interaction occurs upstream of JA signaling. Indeed, JA and ABA mutually enhance their biosynthesis (Adie et al. 2007; Fan et al. 2009; Brossa et al. 2011). Mechanistic details on such interaction, however, are still lacking. Interestingly, it has been shown that interactions may also occur more downstream. A mechanism similar to the suppression of JA-induced TFs by JAZ–NINJA–TPL was identified for the ABA-dependent TF ABI5 (ABA insensitive5) in Arabidopsis. ABI5 binding proteins (AFPs) are NINJA homologs and contain the EAR motif to interact with the corepressors TPL or TPRs for ABI5 inactivation (Pauwels et al. 2010). Although the tested AFPs do not interact with JAZ1, this similarity nevertheless suggests that the JA–ABA interaction may exist at this JAZ–NINJA connection, downstream of JA biosynthesis, dependent on the binding specificity of different JAZs to NINJA or ABPs. This is supported by the recent finding that ZmJAZ14, a JAZ protein in maize, is involved in both JA and ABA signaling (Zhou et al. 2015).

**ET in defense regulation**

Like JA, ET signaling upon feeding by insect herbivores is common among plants. However, ET has very variable effects on defense regulation, acting more as a modulator of herbivore-induced responses than a direct elicitor (von Dahl and Baldwin 2007). Very few plant defenses are directly regulated by ET. One known case is the induction of defensive 1-cysteine protease (Mir1-CP) against both chewing Spodoptera frugiperda and phloem-feeding Rhopalosiphum maidis in maize. JA also induces Mir1-CP expression upon S. frugiperda feeding, which is dependent on ET signaling, since MeJA treatment had no effect on Mir1-CP induction in maize plants with blocked ET signaling (Ankala et al. 2009; Louis et al. 2015). In many cases, ET has been shown to modulate JA-mediated insect defenses, similar to the well-documented ET–JA synergism in regulating defensive genes induced upon infestation by necrotrophic pathogens, such as PDF1.2 and PR1, 4 and 5, via their co-regulation of the AP2/ERF TFs ERF1 and ORA59 (Lorenzo et al. 2003; Pré et al. 2008). For example, ET signaling contributes to the JA-mediated volatile emission upon S. exigua herbivory on maize or Bemisia tabaci infestation on Arabidopsis (Schmelz et al. 2003; Zhang et al. 2013). The wound-induced expression of tomato PIN2 requires both intact JA and ET pathways, but compromising ET signaling does not affect the M. sexta-increased PI transcript levels in N. attenuata (O’Donnell et al. 1996; Onkokesung et al. 2010a). The complex involvement of ET in modulating herbivore/JA-induced defense responses also shows in nicotine biosynthesis. Defective ET signaling in N. attenuata, in one case, resulted in reduced basal nicotine contents but enhanced inducibility of nicotine biosynthesis after M. sexta herbivory (von Dahl et al. 2007), but in other experiments, it did not affect basal levels and attenuated JA-induced nicotine response (Shoji et al. 2000; Winz and Baldwin 2001; Onkokesung et al. 2010a). Nevertheless, both maize and N. attenuata with compromised ET signaling are more susceptible to M. sexta and S. frugiperda, respectively, demonstrating the role of ET in fortifying plant defenses (Harfouche et al. 2006; Onkokesung et al. 2010a). On the other hand, ET signaling, via ERF1/ORA59 and their upstream TFs EIN3/EIL1 (Fig. 1c), also inhibits the JA/ABA-co-induced MYC2 and subsequently MYC2-mediated defense-related genes in Arabidopsis (Lorenzo et al. 2004; Zhu et al. 2011; Song et al. 2014a). Consequently, disruptions of ET perception and signaling in etr1, ein2-1 and ein3/eil1 mutants all increase Arabidopsis resistance to the generalist insects S. exigua and S. littoralis, whereas ET application results in plant susceptibility. ET signaling, however, does not influence the responses and resistance of Arabidopsis to the specialists Plutella xylostella and Pieris rapae (Stotz et al. 2000; Mewis et al. 2005; Bodenhausen and Reymond 2007; Song et al. 2014a).

Recent findings also shed light on the mechanism of how these hormonal cascades interact (Fig. 2). Several JA signaling repressor JAZs bind to and inactivate EIN3/EIL1 and recruit HDA6 (histone deacetylase6) to repress EIN3/ EIL1-dependent transcription (Zhu et al. 2011). Upon herbivore-induced ET and JA accumulation, ET signaling stabilizes EIN3/EIL1 while JA removal by JA signaling dissociates HDA6-EIN3/EIL1 and activates EIN3/EIL1 to transcribe downstream ERF1/ORA59. Interestingly, the ABA-inducible MYCs also physically interact with EIN3/ EIL1, which mutually inhibits their function. Moreover, MYC2 indirectly promotes proteasomal degradation of EIN3 by enhancing EBF1 expression (Song et al. 2014a; Zhang et al. 2014). This illustrates how the balance between ABA and ET signaling fine-tunes JA-mediated defenses induced by insect herbivory.

**SA antagonizes herbivore-induced defenses**

SA signaling mediates defense responses to hemi-biotrophic pathogens (Derksen et al. 2013). This is achieved via its receptor and regulator NPR1 (nonexpressor of PR genes1) and the action of two NPR1 homologs, NPR3 and NPR4, which are also SA receptors and mediate NPR1 degradation in SA-concentration-dependent manners (Kuai et al. 2015). In some cases, SA-induced defense
responses are effective against sedentary sucking insects, such as aphids (Klingler et al. 2009; Zhang et al. 2015b). SA accumulation in host plants can be induced by HAMPs and can also be exploited by insects to suppress JA-mediated defenses (Thaler et al. 2012; Caarls et al. 2015). Glucose oxidase in *S. exigua* oral secretion induces an SA burst in *N. attenuata*, which suppresses JA and ET accumulation (Diezel et al. 2009). Moreover, several insects carry viruses or microbes that trigger SA accumulation. *Tomato spotted wilt virus* transmitted by thrips feeding increases SA concentrations in *Arabidopsis*, resulting in increased performance and preference of thrips for infected plants (Abe et al. 2012). Flagellin from *Pseudomonas* sp. present on the mouth parts of *L. decemlineata* can induce SA accumulation in tomato leaves upon feeding, thereby suppressing JA-dependent defenses, such as PIs and polyphenol oxidases, and herbivore-induced resistance (Chung and Felton 2011; Chung et al. 2013).

The SA antagonism of JA-dependent defenses occurs downstream of JA biosynthesis and independently of the COI1-JAZs pathway. It inhibits defenses mediated by both ABA and ET signaling (Fig. 2). Disruption of SA accumulation or NPR1 function thus increases resistance to several chewing and sucking insects (Stotz et al. 2002; Mewis et al. 2005; Zarate et al. 2007). Cytosolic NPR1 activity is also a mediator of the SA–JA antagonism, which, however, is bypassed if herbivores also induce ET accumulation (Spoel et al. 2003; Leon-Reyes et al. 2009; Van der Does et al. 2013). Moreover, SA leads to degradation of the JA/ET-responsive ORA59 and suppresses JA/ET-responsive GCC-box-containing genes, including ORA59, by recruiting the SA-induced GRX480 (Glutaredoxin480) to their promoters. This inhibits the positive transcription regulators class II TGAs thereby repressing JA/ET-induced responses (Zander et al. 2012, 2014; Van der Does et al. 2013). Less is known about how SA inhibits JA/ABA-responsive defenses. Potential points of convergence in this interaction are WRKY TFs. WRKY62 and WRKY70 regulate the SA–JA antagonism in defense responses and ABA-responsive defense genes (Li et al. 2004; Mao et al. 2007), whereas WRKY18, WRKY40 and WRKY60 are ABA-responsive and blocked by SA (Xu et al. 2006; Chen et al. 2010).

### Growth hormones in defense regulation

Recently, phytohormones such as gibberellins (GAs), brassinosteroids (BRs), auxins (AUXs) and cytokinins (CKs) have also been shown to modulate JA-mediated responses to herbivores (Figs. 2, 3), besides their involvement in regulating defenses against pathogens (Naseem and Dandekar 2012; Denancé et al. 2013; De Bruyne et al. 2014). For example, GA signaling interacts with JA signaling via the negative regulators DELLAs. DELLAs and JAZs directly bind and deactivate each other (Fig. 2; Hou et al. 2013; Song et al. 2014b). In the presence of GA, DELLAs are degraded via the 26S proteasome, releasing JAZs to suppress MYC2 (Hou et al. 2010; Wild et al. 2012). On the other hand, DELLAs are necessary to attenuate *S. exigua*-induced JA accumulation in *Arabidopsis*, and consequently GA can promote JA biosynthesis (Cheng et al. 2009; Lan et al. 2014). Moreover, the DELLA protein RGA (repressor of GA1-3), binds to MYC2; its removal thus increases MYC2 activity (Hong et al. 2012). Another DELLA, RGL3 (RGA-like3), whose expression is enhanced by JA in a MYC2-dependent manner, can competitively bind to JAZs and further increase MYC2 activity (Wild et al. 2012). This JA-GA synergistic interaction plays a role in trichome initiation and sesquiterpene biosynthesis (Hong et al. 2012; Qi et al. 2014). Similarly, BRs, AUXs and CKs influence JA signaling both positively and negatively in regulating responses to herbivores (Dervinis et al. 2010; Yang et al. 2011; Meldau et al. 2011). In conclusion, interactions between hormonal signaling cascades help plants to fine-tune their defenses against a specific attacker. Conversely, insects may have the ability to interfere with these hormonal interactions to suppress defense responses to their benefit.

### Hormonal regulation of plant responses to abiotic stresses

Due to its involvement in many developmental processes, such as shoot growth inhibition, stomatal movement, leaf senescence and primary root growth, ABA is considered as a master regulator of responses to abiotic stresses, such as drought, salt, heat and high light intensity (Fig. 3; Sharp et al. 2004; Daszkowska-Golec and Szarejko 2013; Liang et al. 2014). JA, SA and BRs also interact with ABA to promote stomatal closure, prevent water loss during osmotic stresses, and induce leaf senescence for resource remobilization (Hossain et al. 2011; Miura et al. 2012; Qi et al. 2015). Stomatal opening, on the other hand, is promoted by CKs and AUXs, while leaf senescence is inhibited by GAs, CKs and AUXs (Daszkowska-Golec and Szarejko 2013; Jibran et al. 2013). ET is also considered as a major inducer of leaf senescence (Kim et al. 2015), whereas ABA and ET show a clear antagonism in regulating stomatal movement (Tanaka et al. 2005) and shoot and root growth under drought (Fig. 3; Sharp and LeNoble 2002; Sharp et al. 2004; Yin et al. 2015). Similarly, ABA antagonizes ET in controlling flooding responses, such as shoot elongation, leaf hyponasty and adventitious root
formation (Voesenek and Bailey-Serres 2015). The ET-mediated responses to flooding as well as shading, on the other hand, are synergistically regulated by GAs, BRs and AUXs (Cox et al. 2006; Gommers et al. 2013; van Veen et al. 2013; Pierik and Testerink 2014; Ayano et al. 2014). These insights demonstrate that plant responses to abiotic stresses and defense responses are controlled by the same interactive hormonal network.

**Hormonal interactions regulate growth-defense tradeoffs**

The simultaneous roles of hormones in plant development and defense led to the view that they interact to prioritize resources towards growth or defense. This is a relevant concept when considering abiotic-biotic stress interaction, as abiotic stress usually severely impairs plant growth. The probability to survive under adverse conditions may increase if limited resources are efficiently allocated to tolerate abiotic stresses or to defend valuable tissues against herbivores (Van Dam and Baldwin 2001; Skirycz and Inzé 2010; Atkinson and Urwin 2012; Vos et al. 2013a). There is substantial evidence that this happens in case of pathogen attack (Denancé et al. 2013; Huot et al. 2014); and the regulation of the growth-defense tradeoff when plants are under combined abiotic stress and insect herbivory may also follow this strategy. The best illustrated hormonal interaction to regulate growth-defense tradeoffs is between JA and GA. Similar to their interaction in regulating defenses, JA also antagonizes GA-dependent growth responses via JAZs-DELLAs. In the absence of JA, *Arabidopsis JAZ9* binds the DELLA protein RGA, thereby preventing it from inhibiting the growth promoting TF *PIF3* (phytochrome-interacting factor3). Upon herbivory, JA induces JAZ degradation and delays GA-mediated DELLA degradation, allowing DELLA to inhibit GA-dependent plant growth responses (Yang et al. 2012). Furthermore, JA in concert with ET repress cell cycle processes and expansion of leaf cells by suppressing the cell expansion enhancers, AUXs. Conversely, AUXs were proposed as repressors of JA synthesis and JA/ET-dependent nicotine response. AUXs and JA, however, synergistically constrain *N. attenuata* regrowth after *M. sexta* herbivory (Shi et al. 2006; Onkokesung et al. 2010b; Noir et al. 2013; Machado et al. 2013). ABA and JA signaling also synergistically suppress plant growth and yield under drought stress (Kim et al. 2009; Harb et al. 2010). On the other hand, ABA signaling antagonizes nicotine biosynthesis in *N. tabacum* roots via *PYL4*, an ABA receptor that controls root metabolic responses to drought and drought resistance; whereas JA suppresses *PYL4* expression in roots but enhances it in leaves (Fig. 2; Lackman et al. 2011; Pizzio et al. 2013; González-Guzmán et al. 2014). These interactions suggest that hormone signaling can be finely tuned to accommodate the needs of plants under different environmental conditions.
examples show that the growth-defense balance is tightly regulated by a sophisticated network of hormonal cross-talk.

Furthermore, the growth-defense balance can also be controlled by master mediators that regulate multiple hormonal cascades. For example, the Arabidopsis CML42 (calmodulin-like protein42) suppresses both JA-dependent insect resistance and drought-responsive ABA accumulation; and the rice WRKY70 induces JA but represses GA biosynthesis and signaling (Vadassery et al. 2012; Li et al. 2015). However, the WRKY70-dependent prioritization of defenses over growth leads to resistance to the stem borer Chilo suppressalis but susceptibility to the brown planthopper Nilaparvata lugens, suggesting that defense prioritization is species-specific (Li et al. 2015).

Hormonal regulation of defense responses under combined stresses

Despite our extensive knowledge on hormonal regulatory pathways and their interactions, predicting plant responses and phenotypes under combined biotic and abiotic stress remains difficult. Hormonal cascades may interact in non-additive manners and the results may enhance plant tolerance/resistance to one stress but not to another (Atkinson and Urwin 2012; Stam et al. 2014; Suzuki et al. 2014; Foyer et al. 2016). Also at the transcriptional level, stress combinations evoke responses that are unique or unpredictable from the responses to single stresses even if the points of convergence are known (Rasmussen et al. 2013; Atkinson et al. 2013). Abiotic stresses, such as drought, salt, heat or flooding, have been found to exert both positive and negative influences on resistance to pathogens and insect herbivores (DeLucia et al. 2012; Suzuki et al. 2014; Ramegowda and Senthil-Kumar 2015). For example, the strong JA-ABA synergism in many stress responses suggests that drought may promote plant resistance to herbivores. However, drought increases defense responses and render plants resistant to insect herbivores in some cases, but reduces defenses and resistance in others (English-Loeb et al. 1997; Huberty and Denno 2004; Khan et al. 2010; Gutbrodt et al. 2011; Tariq et al. 2013; Nguyen et al. 2016).

Recently, a few studies have tried to dissect hormonal interactions occurring under simultaneous abiotic stress and herbivory. In Brassica oleracea plants, drought and Mamestra brassicae herbivory interactively regulate the emission of volatile organic compounds (VOCs) as an indirect defense (Weldegergis et al. 2015). While drought alone induces SA accumulation and reduces the emissions of several VOCs, it also reduces herbivore-induced JA accumulation and consequently alters the herbivore-induced emissions of these VOCs. This resulted in M. brassicae moth preference to lay eggs on drought-stressed plants but no differences in larval performance compared to those on well-watered plants. Interestingly, ABA accumulation was observed upon herbivory but not in drought-stressed plants, possibly due to the intermittent drought stress regime with recovery periods, during which ABA catabolism may be induced (Wang 2002; Fleta-Soriano et al. 2015). In contrast, drought enhanced resistance of Solanum dulcamara plants to S. exigua larvae (Nguyen et al. 2016). Both drought and herbivory induced ABA and JA accumulation in S. dulcamara. Transcriptomic analyses showed drought further enhanced several herbivore-induced defense-related responses, such as terpenoid biosynthesis and PIs (Nguyen et al. 2016). Similarly, drought increased leaf ABA and JA concentrations, JA-dependent defense and Medicago truncatula plant resistance to the pea aphids Acyrthosiphon pisum (Gou et al. 2016). Therefore, the synergistic interaction between ABA and JA signaling is suggested to play an important role in regulating plant defense under drought. This is supported by the finding that ABA signaling is required for the full activation of VOC emission and JA-responsive direct defenses in N. attenuata (Dinh et al. 2013). Silencing of an ABA catabolism suppressor, NaHER1 (herbivore elicitor-regulated1), in N. attenuata resulted in reduced levels of these defense responses upon herbivory by M. sexta as well as plant resistance. Moreover, NaHER1-silenced plants are also drought-sensitive, suggesting that NaHER1 serves as a connection between responses to the two stresses.

On the other hand, there may be mechanisms underlying plant increased resistance to herbivores under drought that are independent of the ABA-JA signaling interaction. In maize, drought and root herbivory by Diabrotica virgifera synergistically enhance levels of ABA and ABA-dependent defense gene transcripts in the leaves and resistance to the leaf herbivore Spodoptera littoralis (Erb et al. 2011). However, leaf water loss, but not the induced ABA level itself, was strongly correlated to the resistance. Therefore, hydraulic changes induced by drought and root herbivory were suggested to play a role in inducing ABA/JA-independent signaling that increases resistance to above-ground herbivores.

Interestingly, there is much less knowledge on the effect of soil flooding on herbivore resistance, possibly because most model plants are crops and drought is more commonly recognized as a problem in production systems around the world than flooding or waterlogging. Only recently Lu et al. (2015) studied the hormonal interaction between flooding and root herbivory in rice. The study showed, however, that hormonal responses to root herbivory or artificial wounding was not altered by flooding. In S. dulcamara, soil flooding increased ABA, but not JA, levels in the leaves and suppressed many transcriptional
responses involved in primary and secondary metabolism, including defense-related responses. These changes, however, did not affect the plant resistance to S. exigua larvae (Nguyen et al. 2016).

These insights, though not always as expected beforehand, are invaluable to understand how plants fine-tune their responses to specific combinations of stress conditions. Based on what we know about the interactions between hormones and a few experimental studies, we suggest that drought in general may enhance resistance because of the synergistic effect of ABA and JA signaling. Drought and herbivory both significantly reduce plant performance but when a drought period is followed by herbivory, the negative effect is more than additive (Davila Olivas et al. 2016). Thus it may be functional for a drought-stressed plant to reduce additional damage by increasing herbivore defenses. It should be stressed that the resulting effect on the herbivore may differ, depending on its level of host plant specialization or feeding strategy (Foyer et al. 2016). On the other hand, flooding or waterlogging elicits the production of ET. The interaction of ET with herbivore-induced responses is not as uniform as that found for ABA. Hence it can be expected that flooding has a neutral or negative effect on plant resistance. It is likely that plants surrounded by water (temporarily) do not receive as many herbivores as a plant on dry land. Therefore, it is conceivable that flooded plants may increase their performance more if they invest in overcoming the negative effects of hypoxia, for example by producing aerenchymous adventitious roots (Dawood et al. 2016).

Conclusions

Simultaneously occurring stresses may compromise plant hormonal homeostasis. If this leads to a misregulation of stress responses, it may result in lower plant survival or yield reduction. Therefore, a better understanding of these hormonal interactions is essential to attain resilient and ‘multitasking’ crop plants that can perform well in adverse and variable environments. However, hormonal interactions under combined stresses cannot be simply inferred from experiments applying single stresses. Thus, more studies on plants responses to multiple and simultaneous stresses, especially abiotic stresses and insect herbivory, are needed to gain insights on how hormones truly interact under such—more natural—conditions. Furthermore, downstream changes induced by multiple stresses should be investigated by untargeted high-throughput approaches, such as transcriptomics, proteomics or metabolomics to obtain a broad and precise view of the regulatory and phenotypic consequences of hormonal interactions. Finally, plant performance or resistance should be assessed to validate the ecological effects of these molecular interactions. Given the common co-occurrence of abiotic and biotic stresses, the response to stress combination is likely to be under strong natural selection. Thus, we argue that the seemingly low level of conservation in the effect of abiotic stress on herbivore defenses, depending on plant and insect species, does not represent random output of the signaling network. Rather, it may be the consequence of divergent choices in prioritization and thus resource allocation that only appear upon combined stress application. Recognition of general patterns then requires availability of a larger set of data. Preferably, experiments should be carried out using plant species thriving in both wet and dry habitats as well as with a diverse natural herbivore community. This will allow us to ‘learn from nature’ whether plants can be selected to handle multiple stresses at the same time while maintaining a high performance.

Acknowledgments This project is funded by a grant (844.10.001) in the ALW-Ecogenomics program from the Netherlands Organisation for Scientific Research (NWO). NMV gratefully acknowledges the support of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118).

Authors contribution Duy Nguyen took the lead in writing this review, with active contributions of Nicole M. van Dam, Ivo Rieu, and Celestina Mariani during the writing process.

Open Access This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

References

Abe H, Tomitaka Y, Shimoda T, Sego S, Sakurai T, Kugimiya S, Tsuda S, Kobayashi M (2012) Antagonistic plant defense system regulated by phytohormones assists interactions among vector insect, thrips and a tospovirus. Plant Cell Physiol 53:204–212. doi:10.1093/pchp/pcr173

Acevedo FE, Rivera-Vega LJ, Chung SH, Ray S, Felton GW (2015) Cues from chewing insects—the intersection of DAMPs, HAMPs, MAMPs and effectors. Curr Opin Plant Biol 26:80–86. doi:10.1016/j.pbi.2015.05.029

Adie BAT, Pérez-Pérez J, Pérez-Pérez MM, Godoy M, Sánchez-Serrano J-J, Schmelz EA, Solano R (2007) ABA is an essential signal for plant resistance to pathogens affecting JA biosynthesis and the activation of defenses in Arabidopsis. Plant Cell 19:1665–1681. doi:10.1105/tpc.106.048041

Ankala A, Lathe DS, Williams WP, Wilkinson JR (2009) Integration of ethylene and jasmonic acid signaling pathways in the expression of maize defense protein Mir1-CP. Mol Plant Microbe Interact 22:1555–1564. doi:10.1094/MPMI-22-12-1555

Atkinson NJ, Urwin PE (2012) The interaction of plant biotic and abiotic stresses: from genes to the field. J Exp Bot 63:3523–3543. doi:10.1093/jxb/ers100
Erb M, Meldau S, Howe GA (2012) Role of phytohormones in insect-specific plant reactions. Trends Plant Sci 17:250–259. doi: 10.1016/j.tplants.2012.01.003

Fan J, Hill L, Crooks C, Doerner P, Lamb C (2009) Abscisic acid has a key role in modulating diverse plant-pathogen interactions. Plant Physiol 150:1750–1761. doi:10.1104/pp.109.137943

Fleta-Soriano E, Pintó-Marijuan M, Munné-Bosch S (2015) Evidence of drought stress memory in the facultative CAM, Aiptasia cordofolia: possible role of phytohormones. PLoS ONE 10:e0135391. doi:10.1371/journal.pone.0135391

Foyer CH, Rasool B, Davey JW, Hancock RD (2016) Cross-tolerance to biotic and abiotic stresses in plants: a focus on resistance to aphid infestation. J Exp Bot 67:2025–2037. doi:10.1093/jxb/erw079

Gomers CMM, Visser EJW, St Onge KR, Voesenek LACJ, Pierik R (2013) Shade tolerance: when growing tall is not an option. Trends Plant Sci 18:65–71. doi:10.1016/j.tplants.2012.09.008

González-Guzmán M, Rodríguez L, Lorenzo-Orts L, Pons C, Sarrión-Perdiguones A, Fernández MA, Peirats-Llobet M, Forment J, Moreno-Alvero M, Cutler SR, Albert A, Granell A, Rodríguez PL (2014) Tomato PYR/PYL/RCAR abscisic acid receptors show high expression in root, differential sensitivity to the abscisic acid agonist quinabactin, and the capability to enhance plant drought resistance. J Exp Bot 65:4451–4464. doi:10.1093/jxb/eru219

Guo H, Sun Y, Peng X, Wang Q, Harris M, Ge F (2016) Up-regulation of abscisic acid signaling pathway facilitates aphid xylem absorption and osmoregulation under drought stress. J Exp Bot 67:681–693. doi:10.1093/jxb/erv481

Guthrodt B, Mody K, Dorn S (2011) Drought changes plant chemistry and causes contrasting responses in lepidopteran herbivores. Oikos 120:1732–1740. doi:10.1111/j.0030-1299.2011.19558.x

Harb A, Krishnan A, Ambavaram MMR, Pereira A (2010) Molecular and physiological stress patterns in plant stress. Arabidopsis reveals early responses leading to acclimation in plant growth. Plant Physiol 154:1254–1271. doi:10.1104/pp.110.161752

Harfouche AL, Shivaji R, Stocker R, Williams PW, Luthe DS (2006) Ethylene signaling mediates a maize defense response to insect herbivory. Mol Plant Microbe Interact 19:189–199. doi:10.1094/MPMI-19-0189

Hong G-J, Xue X-Y, Mao Y-B, Wang L-J, Chen X-Y (2012) Arabidopsis MYC2 interacts with DELLA proteins in regulating sesquiterpene synthase gene expression. Plant Cell 24:2635–2648. doi:10.1105/tpc.112.098749

Hossain MA, Munemasa S, Uraji M, Nakamura Y, Mori IC, Murata Y (2013) Shade tolerance: when growing tall is not an option. Trends Plant Sci 18:65–71. doi:10.1016/j.tplants.2012.09.008

Hou X, Lee LYC, Xia K, Yan Y, Yu H (2010) DELLA modulate jasmonate signaling via competitive binding to JAZs. Dev Cell 19:884–904. doi:10.1016/j.devcel.2010.10.024

Hou X, Ding L, Yu H (2013) Crossstalk between GA and JA signaling mediates plant growth and defense. Plant Cell Rep 32:1067–1074. doi:10.1007/s00126-013-1423-4

Howe GA, Schaller A (2008) Direct defenses in plants and their induction by wounding and insect herbivores. In: Schaller A (ed) Induced plant resistance to herbivory. Springer, Dordrecht, pp 7–29

Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383–1398. doi:10.1890/03-0352

Huot B, Yao J, Montgomery BL, He SY (2014) Growth–defense tradeoffs in plants: a balancing act to optimize fitness. Mol Plant 7:1267–1287. doi:10.1093/mp/usp049

IPCC (2013) Summary for policymakers. In: Stocker TF, D Qin, G-K Plattner, M Tignor, KLI Allen, J Boschung, A Nauels, Y Xia, V Bex, PM Midgley (eds) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Jibran R, Hunter A, Dijkwel P (2013) Hormonal regulation of leaf senescence through integration of developmental and stress signals. Plant Mol Biol 82:547–561. doi:10.1007/s11103-013-0043-2

Kazan K (2015) Diverse roles of jasmonates and ethylene in abiotic stress tolerance. Trends Plant Sci 20:219–229. doi:10.1016/j.tplants.2015.02.001

Khan MAM, Ulrichs C, Mewis I (2010) Influence of water stress on the glucosinolate profile of Brassica oleracea var. italica and the performance of Brevicoryne brassicae and Myzus persicae. Entomol Exp Appl 137:229–236. doi:10.1111/j.1570-7458.2010.01059.x

Kim EH, Kim YS, Park SH, Koo YJ, Do Choi Y, Chung Y-Y, Lee J-I, Kim J-K (2009) Methyl jasmonate reduces grain yield by mediating stress signals to alter spikelet development in rice. Plant Physiol 149:1751–1760. doi:10.1104/pp.109.134684

Kim J, Chang C, Tucker ML (2015) To grow old: regulatory role of ethylene and jasmonic acid in senescence. Front Plant Sci 6:20. doi:10.3389/fpls.2015.00020

Klingler JP, Nair RM, Edwards OR, Singh KB (2009) A single gene, AIN, in Medicago truncatula mediates a hypersensitive response to both bluegreen aphid and pea aphid, but confers resistance only to bluegreen aphid. J Exp Bot 60:4115–4127. doi:10.1093/jxb/erp244

Kuai X, MacLeod BJ, Desprès C (2015) Integrating data on the Arabidopsis NPR1/NPR3/NPR4 salicylic acid receptors: a differentiating argument. Front Plant Sci 6:235. doi:10.3389/fpls.2015.00235

Lackman P, González-Guzmán M, Tillemans S, Carqueijeiro I, Pérez AC, Moses T, Seo M, Kannoy N, Häkkinen ST, Van Montagu MCE, Thevelein JM, Mahecho IM, Oksman-Calderney K-M, Rodriguez PL, Rischer H, Goossens A (2011) Jasmonate signaling involves the abscisic acid receptor PYL4 to regulate metabolic reprogramming in Arabidopsis and tobacco. Proc Natl Acad Sci USA 108:5891–5896. doi:10.1073/pnas.1103010108

Lan Z, Krosos S, Achard P, van Dam NM, Bede JC (2014) DELLA proteins modulate Arabidopsis defences induced in response to caterpillar herbivory. J Exp Bot 65:571–583. doi:10.1093/jxb/eru420

Leon-Reyes A, Spoel SH, De Lange ES, Abe H, Kobayashi M, Tsuda S, Milenarr FF, Welschen RM, Rietema T, Pieterse CMJ (2009) Ethylene modulates the role of NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1 in cross talk between salicylate and Jasmonate signaling. Plant Physiol 149:1797–1809. doi:10.1104/pp.108.133926

Li J, Brader G, Palva ET (2004) The WRKY70 transcription factor: a node of convergence for jasmonate-mediated and salicylate-mediated signals in plant defense. Plant Cell 16:319–331. doi:10.1105/tpc.016980

Li R, Zhang J, Li J, Zhou G, Wang Q, Bian W, Erb M, Lou Y (2015) Prioritizing plant defence over growth through WRKY regulation facilitates infestation by non-target herbivores. Elife 4:e04805. doi:10.7554/eLife.04805

Liang C, Wang Y, Zhu Y, Tang J, Hu B, Liu L, Ou S, Wu H, Sun X, Chu J, Chu C (2014) OsSNAP connects abscisic acid and leaf senescence by fine-tuning abscisic acid biosynthesis and directly targeting senescence-associated genes in rice. Proc Natl Acad Sci USA 111:10013–10018. doi:10.1073/pnas.1231568111

Lorenzo O, Piqueras R, Sánchez-Serrano JJ, Solano R (2003) ETHYLENE RESPONSE FACTOR1 integrates signals from ethylene and jasmonate pathways in plant defense. Plant Cell 15:165–178. doi:10.1105/tpc.007468
Lorenzo O, Chico JM, Salchez-Serrano JJ, Solano R (2004) JASMONATE-SENSITIVE1 Encodes a MYC transcription factor essential to discriminate between different jasmonate-regulated defense responses in Arabidopsis. Plant Cell 16:1938–1950. doi:10.1105/tpc.022319

Louis J, Basu S, Varsani S, Castano-Duque L, Jiang V, Williams WP, Felton GW, Luthe DS (2015) Ethylene contributes to maize insect resistance 1-mediated maize defense against the phloem sap-sucking corn leaf aphid. Plant Physiol 169:313–324. doi:10.1104/pp.15.00958

Lu J, Robert CAM, Riemann M, Cosme M, Mène-Saffrane L, Massana J, Stout MJ, Lou Y, Gershenzon J, Erb M (2015) Induced jasmonate signaling leads to contrasting effects on root damage and herbivore performance. Plant Physiol 167:1100–1116. doi:10.1104/pp.15.252700

Machado RAR, Ferrieri AP, Robert CAM, Glauser G, Kallenbach M, Baldwin IT, Erb M (2013) Leaf-herbivore attack reduces carbon reserves and regrowth from the roots via jasmonate and auxin signaling. New Phytol 200:1234–1246. doi:10.1111/nph.12438

Mao P, Duan M, Wei C, Li Y (2007) WRKY62 transcription factor mediates the wound-induced promoter activation of the gene encoding transcription factor essential to discriminate between different jasmonate-regulated defense responses in Arabidopsis. Plant Physiol 48:833–842. doi:10.1093/pch/pcm058

Meldau S, Baldwin IT, Wu J (2011) SGT1 regulates wounding- and herbivory-induced jasmonate acid accumulation and Nicotiana attenuata’s resistance to the specialist lepidopteran herbivore Manduca sexta. New Phytol 189:1143–1156. doi:10.1111/j.1469-8137.2010.03558.x

Mewis L, Appel HM, Hom A, Raina R, Schultz JC (2005) Major signaling pathways modulate Arabidopsis glucosinolate accumulation and resistance to both phloem-feeding and chewing insects. Plant Physiol 138:1149–1162. doi:10.1104/pp.105.053389

Miura K, Okamoto H, Okuma E, Shiba H, Kamada H, Hasegawa PM, Murata Y (2012) SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in Arabidopsis. Plant J. doi: 10.1111/j.1365-313X.2012.04713.x

Naseem M, Dandekar T (2012) The role of auxin-cytokinin antagonism in plant-pathogen interactions. PLoS Pathog 8:e1002720

Nguyen D, D’Agostino N, Tuengerl TO, Sun P, Lortzing T, Visser EJM, Cristescu SM, Steppuhn A, Mariani C, van Dam NM, Rieu I (2016) Drought and flooding have distinct effects on herbivore-induced responses and resistance in Solanum dulcamara. Plant Cell Environ. doi: 10.1111/pce.12708

Noir S, Bömer M, Takahashi N, Ishida T, Tsui T-L, Balvi B, Shanahan H, Sugimoto K, Sugimoto T, Devoto A (2013) Jasmonate controls leaf growth by repressing cell proliferation and the onset of leaf senescence. Science 339:1242–1246. doi:10.1126/science.1223802

O’Donnell PJ, Calvert C, Atzorn R, Wasternack C, Leyser HMO, Van Pelt JA, van Loon LCM, Ton J, Van der Does D, Zamioudis C, Leon-Reyes A, Van Wees SCM (2012) Hormonal modulation of plant immunity. Annu Rev Cell Dev Biol 28:489–521. doi:10.1146/annurev-cellbio-092910-154055

Pérez MA, Atallah M, Champion A, De Vos M, Pieterse CMJ, Memelink J (2008) The AP2/ERF domain transcription factor ORA59 integrates jasmonic acid and ethylene signals in plant defense. Plant Physiol 147:1347–1357. doi:10.1104/pp.108.117523

Qi T, Huang H, Wu D, Yan J, Qi Y, Song S, Xie D (2014) Arabidopsis DELLA and IAA3 proteins bind the WD-repeat/bHLH/MBF complex to modulate gibberellin and jasmonate signaling synergy. Cell 161:1108–1123. doi:10.1016/j.cell.2015.01.032

Qi T, Wang J, Huang H, Liu B, Gao H, Liu Y, Song S, Xie D (2015) Regulation of jasmonate-induced leaf senescence by antagonism between bHLH subgroup IIIe and IIIId factors in Arabidopsis. Plant Cell 27:1634–1649. doi:10.1105/tpc.15.00110

Ramegowda V, Senthil-Kumar M (2015) The interactive effects of simultaneous biotic and abiotic stresses on plants: mechanistic understanding from drought and pathogen combination. J Plant Physiol 176:47–54. doi:10.1016/j.jplph.2014.11.008

Raschke L, Barah P, Suarez-Rodriguez MC, Bressendorff F, Friis P, Costantino P, Bones AM, Nielsen HB, Mundy J (2013) Transcriptome responses to combinations of stresses in Arabidopsis. Plant Physiol 161:1783–1794. doi:10.1104/pp.112.210773

Rehrig EM, Appel HM, Jones AD, Schultz JC (2014) Roles for jasmonate- and ethylene-induced transcription factors in the ability of Arabidopsis to respond differentially to damage caused by two insect herbivores. Front Plant Sci 5:407. doi:10.3389/fpls.2014.00407

Schaller A (2008) Induced plant resistance to herbivory. Springer, Dordrecht

Schmelz EA, Alborn HT, Banchio E, Tumlinson JH (2003) Quantitative relationships between induced jasmonic acid levels and volatile emission in Zea mays during Spodoptera exigua herbivory. Planta 216:665–673. doi:10.1007/s00425-002-0898-y

Schneider F, Fernández-Calvo P, Zander M, Diez-Díaz M, Fonseca S, Glauser G, Lewsey MG, Ecker JR, Solano R, Reymond P (2013) Arabidopsis basic helix-loop-helix transcription factors MYC2, MYC3, and MYC4 regulate glucosinolate biosynthesis, insect performance, and feeding behavior. Plant Cell 25:3117–3132. doi:10.1105/tpc.113.115139

Seybold H, Trempel F, Rafi S, Scheel D, Romeis T, Lee J (2014) Ca2+ signaling in plant immune response: from pattern
recognition receptors to Ca2+ decoding mechanisms. New Phytol 204:782–790. doi:10.1111/nph.13031

Sharp RE, Le Noble ME (2002) ABA, ethylene and the control of shoot and root growth under water stress. J Exp Bot 53:33–37

Sharp RE, Poroyko V, Hejlek LG, Spollen WG, Springer GK, Bohnert HJ, Nguyen HT (2004) Root growth maintenance during water deficits: physiology to functional genomics. J Exp Bot 55:2343–2351. doi:10.1093/jxb/erh276

Shi Q, Li C, Zhang F (2006) Nicotine synthesis in Nicotiana tabacum L. induced by mechanical wounding is regulated by auxin. J Exp Bot 57:2899–2907. doi:10.1093/jxb/erl051

Shoji T, Nakajima K, Hashimoto T (2000) Ethylene suppresses jasmonate-induced gene expression in nicotine biosynthesis. Plant Cell Physiol 41:1072–1076

Shyu C, Figueroa P, DePew CL, Cooke LB, Moreno JE, Katari L, Zheng N, Browse J, Howe GA (2012) JA Z8 lacks a canonical degron and has an EAR motif that mediates transcriptional repression of jasmonate responses in Arabidopsis. Plant Cell 24:536–550. doi:10.1105/tpc.111.093005

Skirycz A, Inzé D (2010) More from less: plant growth under limited water. Curr Opin Biotechnol 21:197–203. doi:10.1016/j.copbio.2010.03.002

Song S, Huang H, Gao H, Wang J, Wu D, Liu X, Yang S, Zhai Q, Li C, Qi T, Xie D (2014a) Interaction between MYC2 and ETHYLENE INSENSITIVE3 modulates antagonism between jasmonate and ethylene signaling in Arabidopsis. Plant Cell 26:263–279. doi:10.1105/tpc.113.120394

Song S, Qi T, Wasternack C, Xie D (2014b) Jasmonate signaling and cross-talk with gibberellin and ethylene. Curr Opin Plant Biol 21:112–119. doi:10.1016/j.opbi.2014.07.005

Spoel SH, Koomneef A, Claessens SMC, Korzelius JP, Van Pelt JA, Mueller MJ, Buchala AJ, Métraux J-P, Brown R, Kazan K, Van Loon LC, Dong X, Pieterse CMJ (2003) NPR1 modulates cross-talk between salicylate- and jasmonate-dependent defense pathways through a novel function in the cytosol. Plant Cell 15:760–770

Stam JM, Kroues A, Li Y, Gols R, van Loon JJA, Poelman EH, Dicke M (2014) Plant interactions with multiple insect herbivores: from community to genes. Annu Rev Plant Biol 65:689–713. doi:10.1146/annurev-plant-050213-035937

Storz HU, Pittendrigh BR, Kroymann J, Weniger K, Fritsche J, Bauke B, van Dam NM, Baldwin IT (2001) Competition mediates costs of jasmonate-induced defences, nitrogen acquisition and transgerational plasticity in Nicotiana attenuata. Funct Ecol 15:406–415. doi:10.1046/j.1365-2454.2001.00533.x

van der Does D, Leon-Reyes A, Koornneef A, Van Verk MC, Rodenburg N, Pauwels L, Goossens A, Körbes AP, Memelink J, Ritsema T, Van Wees SCM, Pieterse CMJ (2013) Salicylic acid suppresses jasmonic acid signaling downstream of SCF(C4D1–JAZ by targeting GCC promoter motifs via transcription factor ORA59. Plant Cell 12.108548. doi:10.1105/tpc.112.108548

van Veen H, Mustroph A, Bading GA, Vergeer-van Eijk M, Wilschen-Evertsten RM, Pedersen O, Visser EJW, Laarke CV, Pierik R, Bailey-Serres J, Voesenek LACJ, Sasidharan R (2013) Two Rumex species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. Plant Cell 25:4691–4707. doi:10.1105/tpc.113.119016

Voesenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73. doi:10.1111/nph.13209

von Dahl CC, Bailey-Serres J (2007) Deciphering the role of ethylene in plant–herbivore interactions. J Plant Growth Regul 26:201–209. doi:10.1007/s00344-007-0014-4

Wagner Z (2002) ABA is necessary for maize kernel development under water deficit at early endosperm development. Ann Bot 90:623–630. doi:10.1093/aob/mcf239

Wang Y, Loake GJ, Chu C (2013) Cross-talk of nitric oxide and reactive oxygen species in plant programmed cell death. Front Plant Sci 4:314. doi:10.3389/fpls.2013.00314

Winz RA, Kühnemann F, Gase K, Baldwin IT (2007) Tuning the herbivore-induced ethylene burst: the role of transcript accumulation and ethylene perception in Nicotiana attenuata. Plant Physiol 148(2):513–525. doi:10.1104/pp.107.108717

Woesenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73. doi:10.1111/nph.13209

von Dahl CC, Baldwin IT (2007) Deciphering the role of ethylene in plant–herbivore interactions. J Plant Growth Regul 26:201–209. doi:10.1007/s00344-007-0014-4

von Dahl CC, Winz RA, Halitschke R, Kühnemann F, C, Baldwin IT (2007) Tuning the herbivore-induced ethylene burst: the role of transcript accumulation and ethylene perception in Nicotiana attenuata. Plant Physiol 148(2):513–525. doi:10.1104/pp.107.108717

Woesenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73. doi:10.1111/nph.13209

Wagner Z (2002) ABA is necessary for maize kernel development under water deficit at early endosperm development. Ann Bot 90:623–630. doi:10.1093/aob/mcf239

Wang Y, Loake GJ, Chu C (2013) Cross-talk of nitric oxide and reactive oxygen species in plant programmed cell death. Front Plant Sci 4:314. doi:10.3389/fpls.2013.00314

Wasternack C, Hause B (2013) Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in Annals of Botany. Ann Bot 111:1021–1058. doi:10.1093/aob/mct067

Weldegergis BT, Zhu F, Poelman EH, Dicke M (2015) Drought stress affects plant metabolites and herbivore preference but not host location by its parasitoids. Oecologia 177:701–713. doi:10.1007/s00442-014-3129-x
Wild M, Davière J-M, Cheminant S, Regnault T, Baumberger N, Heintz D, Baltz G, Genschik P, Achard P (2012) The Arabidopsis DELLa RGA-LIKE3 is a direct target of MYC2 and modulates jasmonate signaling responses. Plant Cell 24:3307–3319. doi:10.1105/tpc.112.101428

Winz RA, Baldwin IT (2001) Molecular interactions between the specialist herbivore Manduca sexta (Lepidoptera, Sphingidae) and its natural host Nicotiana attenuata. IV. Insect-Induced ethylene reduces jasmonate-induced nicotine accumulation by regulating putrescine N-methyltransfer. Plant Physiol 125:2189–2202

Xu X, Chen C, Fan B, Chen Z (2006) Physical and functional interactions between pathogen-induced Arabidopsis WRKY18, WRKY40, and WRKY60 transcription factors. Plant Cell 18:1310–1326. doi:10.1105/tpc.105.037523

Xu S, Zhou W, Pottinger S, Baldwin IT (2015) Herbivore associated elicitor-induced defences are highly specific among closely related Nicotiana species. BMC Plant Biol 15:2. doi:10.1186/s12870-014-0406-0

Yang D-H, Hettenhausen C, Baldwin IT, Wu J (2011) BAK1 regulates the accumulation of jasmonic acid and the levels of trypsin proteinase inhibitors in Nicotiana attenuata’s responses to herbivory. J Exp Bot 62:641–652. doi:10.1093/jxb/erq298

Yang D-L, Yao J, Mei C-S, Tong X-H, Zeng L-J, Li Q, Xiao L-T, Sun T, Li J, Deng X-W, Lee CM, Thomashow MF, Yang Y, He Z, He SY (2012) Plant hormone jasmonate prioritizes defense over growth by interfering with gibberellin signaling cascade. Proc Natl Acad Sci USA 109:E1192–E1200. doi:10.1073/pnas.1201616109

Yin C-C, Ma B, Collinge DP, Pogson BJ, He S-J, Xiong Q, Duan K-X, Chen H, Yang C, Lu X, Wang Y-Q, Zhang W-K, Chu C-C, Sun X-H, Fang S, Chu J-F, Lu T-G, Chen S-Y, Zhang J-S (2015) Ethylene responses in rice roots and coleoptiles are differentially regulated by a carotenoid isomerase-mediated abscisic acid pathway. Plant Cell 27:1061–1081. doi:10.1105/tpc.15.00080

Zander M, Chen S, Imkampe J, Thurow C, Gatz C (2012) Repression of the Arabidopsis thaliana jasmonate/ethylene-induced defense pathway by TGA-interacting glutaredoxins depends on their C-terminal ALWL motif. Mol Plant 5:831–840. doi:10.1093/mp/ssr113

Zander M, Thurow C, Gatz C (2014) TGA transcription factors activate the salicylic acid-suppressible branch of the ethylene-induced defense program by regulating ORA59 expression. Plant Physiol 165:1671–1683. doi:10.1104/pp.114.243360

Zarate SI, Kempema LA, Walling LL (2007) Silverleaf whitefly induces jasmonic acid defenses and suppresses effectual jasmonic acid defenses. Plant Physiol 143:866–875. doi:10.1104/pp.106.090035

Zhang P-J, Broekgaarden C, Zheng S-J, Snoeren TAL, van Loon JJA, Gols R, Dicke M (2013) Jasmonate and ethylene signaling mediate whitefly-induced interference with indirect plant defense in Arabidopsis thaliana. New Phytol 197:1291–1299. doi:10.1111/nph.12106

Zhang X, Zhu Z, An F, Hao D, Li P, Song J, Yi C, Guo H (2014) Jasmonate-activated MYC2 represses ETHYLENE-SENSITIVE3 activity to antagonize ethylene-promoted apical hook formation in Arabidopsis. Plant Cell 26:1105–1117. doi:10.1105/tpc.113.122002

Zhang P-J, Huang F, Zhang J-M, Wei J-N, Lu Y-B (2015a) The mealybug Phenacoccus solenopsis suppresses plant defense responses by manipulating JA–SA crosstalk. Sci Rep 5:9354. doi:10.1038/srep09354

Zhang X, Xue M, Zhao H (2015b) Species-specific effects on salicylic acid content and subsequent Myzus persicae (Sulzer) performance by three phloem-sucking insects infesting Nicotiana tabacum L. Arthropod Plant Interact 9:383–391. doi:10.1007/s11829-015-9385-9

Zhou X, Yan S, Sun C, Li S, Li J, Xu M, Liu X, Zhang S, Zhao Q, Li Y, Fan Y, Chen R, Wang L (2015) A maize jasmonate Zim-domain protein, ZmJAZ14, associates with the 1A, ABA, and GA signaling pathways in transgenic Arabidopsis. PLoS ONE 10:e0121824. doi:10.1371/journal.pone.0121824

Zhu Z, An F, Feng Y, Li P, Xue L, Jiang Z, Kim J-M, To TK, Li W, Zhang X, Yu Q, Dong Z, Chen W-Q, Seki M, Zhou J-M, Guo H (2011) Derepression of ethylene-stabilized transcription factors (EIN3/EIL1) mediates jasmonate and ethylene signaling synergy in Arabidopsis. Proc Natl Acad Sci USA 108:12539–12544. doi:10.1073/pnas.1103959108