Abscisic Acid-Induced Stomatal Closure: An Important Component of Plant Defense Against Abiotic and Biotic Stress

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Abscisic acid (ABA) is a stress hormone that accumulates under different abiotic and biotic stresses. A typical effect of ABA on leaves is to reduce transpirational water loss by closing stomata and parallelly defend against microbes by restricting their entry through stomatal pores. ABA can also promote the accumulation of polyamines, sphingolipids, and even proline. Stomatal closure by compounds other than ABA also helps plant defense against both abiotic and biotic stress factors. Further, ABA can interact with other hormones, such as methyl jasmonate (MJ) and salicylic acid (SA). Such cross-talk can be an additional factor in plant adaptations against environmental stresses and microbial pathogens. The present review highlights the recent progress in understanding ABA's multifaceted role under stress conditions, particularly stomatal closure. We point out the importance of reactive oxygen species (ROS), reactive carbonyl species (RCS), nitric oxide (NO), and Ca^{2+} in guard cells as key signaling components during the ABA-mediated short-term plant defense reactions. The rise in ROS, RCS, NO, and intracellular Ca^{2+} triggered by ABA can promote additional events involved in long-term adaptive measures, including gene expression, accumulation of compatible solutes to protect the cell, hypersensitive response (HR), and programmed cell death (PCD). Several pathogens can counteract and try to reopen stomata. Similarly, pathogens attempt to trigger PCD of host tissue to their benefit. Yet, ABA-induced effects independent of stomatal closure can delay the pathogen spread and infection within leaves. Stomatal closure and other ABA influences can be among the early steps of defense and a crucial component of plants' innate immunity response. Stomatal guard cells are quite sensitive to environmental stress and are considered good model systems for signal transduction studies. Further research on the ABA-induced stomatal closure mechanism can help us design strategies for plant/crop adaptations to stress.

Keywords: pathogen resistance, water use, stress adaptation, guard cells, signaling components

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INTRODUCTION: ABA AND PLANT DEFENSE

Plants need to respond quickly to diverse stress conditions, as they cannot move away. Stress can be due to abiotic (e.g., drought, salinity, chilling, and high-temperature) or biotic factors (e.g., pathogens, insects, herbivores) (Zhu, 2016; Lamers et al., 2020). Plants developed various adaptation strategies to cope up with these situations. A typical example is the stomatal closure, limiting the water loss and restricting pathogen entry into the leaves (Melotto et al., 2008; Gudesblat et al., 2009a; Sussmilch and McAdam, 2017; Agurla et al., 2018a). Plants accumulate hormones [e.g., abscisic acid (ABA) or salicylic acid (SA) or methyl jasmonate (MJ)] under abiotic stress conditions and elicitors [e.g., flagellin 22 (flg22)] under pathogen attack. Among the hormones, ABA is involved in several abiotic and biotic stress conditions and is therefore considered an essential and versatile compound. In contrast, SA, MJ, and ethylene (ET) help in resistance against biotic stress. Under drought, salinity, or cold stress, ABA accumulation causes stomatal closure to conserve water while up-regulating genes to promote osmotic adjustment in leaves (Lim et al., 2015; Zhao et al., 2017; Niu et al., 2018). The enhanced ABA levels in plants mediate the cross-adaptation against drought and pathogens besides insect herbivores (Lee and Luan, 2012; Nguyen et al., 2016).

Several compounds other than ABA also accumulated in plants in response to different stresses (**Table 1**). These compounds can close stomata and, in many instances, improve plants' resistance to pathogens. The plant hormones and elicitors can further regulate transcription factors and induce pathogenesis-related (PR) genes (Bielach et al., 2017; Breen et al., 2017). There can also be a cross-talk between the factors involved in abiotic and biotic stress signaling (Nejat and Mantri, 2017; Saijo and Loo, 2020). However, these compounds either require ABA for their action or interact with ABA to activate defense responses.

Since its discovery, studies on ABA (a sesquiterpene) and its role in plant processes were studied extensively. Plant processes such as seed dormancy, seed development, promotion of desiccation tolerance, abscission, and, most importantly, stomatal closure were all regulated by ABA (Lim et al., 2015). Further, ABA can be crucial in also non-stress conditions (Yoshida et al., 2019). The action of ABA was complemented by hormones, such as SA (Robert-Seilaniantz et al., 2011; Wang H.Q. et al., 2020). Similarly, some of the secondary messengers triggered by ABA can also participate in plants' adaptation to abiotic and biotic stress. Examples are reactive oxygen species (ROS), nitric oxide (NO), and cytosolic free Ca^{2+} (León et al., 2014; Huang et al., 2019). Several compounds like polyamines (PAs), hydrogen sulfide (H_2S), and brassinosteroids (BRs) promote drought tolerance by regulating ABA synthesis and *vice versa* (Jin et al., 2013; Ha et al., 2014; Adamipour et al., 2020).

Readers interested in ABA and its role in plants may refer to some recent reviews (Kumar et al., 2019; Chen K. et al., 2020; Gietler et al., 2020; McAdam and Sussmilch, 2020). Our review emphasizes the role of ABA's stomatal closure as an adaptive measure against both abiotic and biotic stresses. We have also

TABLE 1 | A spectrum of compounds that accumulate in plant cells along with ABA during biotic/abiotic stress and can promote stomatal closure.

Hormone/ compound	Type of stress	References	Reason of closure
ABA	Drought, cold, salinity and heat	Nakashima et al., 2014	Increased ABA levels
Allyl isothiocyanate (AITC)	Wounding, insect, herbivore (biotic)	Khokon M.A. et al., 2011	Production of ROS and NO. elevated Ca^{2+} levels
Ethylene (ET)	Drought, ozone	Wilkinson and Davies, 2010	Mediated H_2O_2 production in ABA signaling
Hydrogen sulfide (H_2S)	Drought	Jin et al., 2013	H_2S affected ABA responses and ABA increased H_2S levels
Inositol 1,4,5-trisphosphate (IP_3)	Drought and salt stress	Jia et al., 2019	Stimulated Ca^{2+} release in the cell and ABA responses
Methyl jasmonate (MJ)	Wounding (biotic)	Förster et al., 2019	Signaling events overlap with ABA action
	Pathogen, insects (biotic)	Verma et al., 2016	Marked interaction with ABA and SA
Phosphatidic acid (PA)	Heavy metal (Arsenic) stress	Armendariz et al., 2016	Induced accumulation of PLD and PA, are due to ABA
Polyamines (PAs)	Drought	Adamipour et al., 2020	ROS and NO production. ABA caused accumulation of PAs
	PEG-induced osmotic stress, chilling	Pál et al., 2018	Increased PAs stimulated ABA accumulation
Proline and G-substances	Drought	Raghavendra and Reddy, 1987	Decreased proton efflux and K^+ content, as in case of ABA
Salicylic acid (SA)	Bacterial invasion (biotic)	Melotto et al., 2006	SA-action overlapped with ABA signaling
Sphingosine-1-phosphate (S1P)	Drought	Ng et al., 2001	Mobilized Ca^{2+} and mediated stomatal closure by ABA
Strigolactone (SL)	Drought and salt stress	Ha et al., 2014	ABA and SL cross-talk positively regulated stomatal closure
Sulfate (in xylem sap)	Drought	Malcheska et al., 2017	Promoted ABA synthesis in guard cell

The compounds are arranged in alphabetical order. The abbreviations are listed in the ***Appendix*** *(last page).*

discussed other compounds that can improve plant adaptations, still involving ABA. The stomatal closure by ABA follows a typical scheme of signal transduction. The interactions of these signaling components with others to synergize the plant's adaptation against pathogen attacks are described. To limit the length of

our article, reviews were cited when available. In some instances, original articles were referred, due to their classic importance.

INCREASED ABA LEVELS UNDER DIFFERENT STRESS CONDITIONS

When plants were exposed to water stress (drought), an increase in ABA was typical due to either synthesis or degradation of ABA or both (Ma et al., 2018; Chen K. et al., 2020; Gietler et al., 2020). The soil-water deficit could be perceived as a signal by roots to trigger ABA's *de novo* synthesis (Jiang and Hartung, 2008; Fang and Xiong, 2015; Qi et al., 2018). The increase in ABA of roots in response to drought was correlated with an increase in foliar-ABA concentrations, suggesting drought-induced ABA played a significant role in controlling leaf water potential (Zegada-Lizarazu and Monti, 2019). ABA accumulated in roots was transported to trigger stomatal closure in leaves and limit transpirational water-loss (Haworth et al., 2018). An increase in ABA could also occur in response to temperature-stress (high or low) (Tao et al., 2016; Karimi, 2019) or a newly discovered small peptide, CLE25 (Takahashi et al., 2018). Sato et al. (2018) found that NCED3 could be the trigger to enhance ABA biosynthesis in *Arabidopsis* under drought stress. Under these conditions, increased ABA and stomatal closure could limit the water-loss and restrict pathogen entry (Wu et al., 2007; Alazem and Lin, 2015). This phenomenon was complemented with additional steps of ABA transport from roots to shoots, conversion of bound ABA into free form to mobilize ABA within leaf (Hewage et al., 2020; Xylogiannis et al., 2020).

An increase in endogenous levels of ABA was also observed when plants were infected with pathogens, for e.g., *Phaseolus* by *Colletotrichum* (Dunn et al., 1990), flax by *Fusarium* (Boba et al., 2020), and *nced5* mutant of Arabidopsis by *Alternaria* (Fan et al., 2009). Similarly, the clonal variation of chestnut susceptibility or resistance to *Fusarium* was related to ABA levels under infection (Camisón et al., 2019). The exact relationship between endogenous ABA levels and disease susceptibility of plants appeared to be complex, as the relationship depended on the duration of infection, other stresses, and the type of pathogen (Asselbergh et al., 2008). During the early stages of pathogen infection, the increased ABA levels helped in resistance, while at later stages, high levels of ABA made the plants susceptible to pathogens (Maksimov, 2009). The differential effects of ABA on the modulation of pathogen sensitivity need to be examined further, particularly in relation to the predisposition of plant tissue. Readers interested in ABA accumulation mode may refer to relevant articles for further details (Maksimov, 2009; Finkelstein, 2013; Ali et al., 2020; Chen K. et al., 2020).

STOMATAL CLOSURE: A FIRST LINE OF DEFENSE AGAINST DIVERSE STRESS CONDITIONS

Stomatal closure is one of the initial responses of plants to stress conditions to retain water status and provide innate immunity

against pathogens (McLachlan et al., 2014; Arnaud and Hwang, 2015; Agurla et al., 2018a). The physical barriers on the plant's outer surface, such as bark, cuticle, and cell wall, could protect against physical and biological factors. However, the microscopic pores on leaf surfaces called stomata are the accessible entrances to several microbes. Stomata form the gateways for transpiration, photosynthetic gas exchange as well as microbial entry into leaves. Stomatal guard cells are quite dynamic in sensing and responding to external microbial pathogens. Stomatal closure can be an essential strategy to defend against abiotic and biotic factors such as drought or pathogens (Lim et al., 2015; Melotto et al., 2017; Nejat and Mantri, 2017). Several instances of stomatal closure induced by plant pathogens are listed in **Table 2**. Stomatal closure was triggered by either elicitors or other compounds produced in the leaf in response to pathogens, such as SA, MJ, or PAs. Stomata can sense and respond to microbe-associated molecular patterns, including chitosan, flagellin, and harpin (Zhang L. et al., 2017; Klessig et al., 2018). The sensing of ABA or other compounds and the final response of stomatal closure follows a common signaling pathway involving receptors, protein kinases, secondary messengers, ion channels, ion efflux, and turgor loss in guard cells. Among kinases, OST1 is a primary activating factor NADPH oxidase and raises the ROS levels of guard cells.

During ABA-induced stomatal closure, an increase in OST1 kinase was followed by the activation of RBOH D/F, and increases in ROS/NO/Ca^{2+} levels. In turn, Ca^{2+} dependent CDPKs activated slow anion channel 1 (SLAC1), S-type anion channel 3 (SLAH3) and K^+out channels to promote ion efflux from guard cells and forced stomata to close. However, in presence of flg22 or yeast elicitor, the activity of OST1 did not increase (Montillet et al., 2013; Ye et al., 2015). Albeit in a resting stage, OST1 participated in stomatal closure by variety of signals including PAMPs (e.g., flg 22, yeast elicitor, chitosan) or environmental components, such as high CO_2 or high humidity (Melotto et al., 2006; Ye et al., 2015, 2020b; Ye and Murata, 2016; Pantin and Blatt, 2018). Besides its action through ROS/NO/Ca^{2+}, OST1 could directly modulate ion channels to cause stomatal closure (**Figure 1**). In a recent study, the events involving OST1/SnRK2s were studied in real-time using FRET sensors (Zhang et al., 2020). These experiments provided a visual evidence of the interaction of OST1 with signaling components of ABA and elevated CO_2. It is obvious that OST1 is an important point of convergence of signals from abiotic and biotic factors. It would be interesting to assess the mechanism by which OST1 keeps up such dual mode of activation and modulating downstream components, all converging to mediate stomatal closure.

There are reports indicating that stomatal closure can be induced by biotic and abiotic stresses in an "OST1-independent manner" (Hsu et al., 2018; Zheng et al., 2018). For e.g., plant elicitor peptides (Peps), a group of damage-associated molecular patterns, can trigger stomatal closure by activating SLAC1 and SLAH3 in an OST1-independent manner (Zheng et al., 2018). Similarly, elevated CO_2 can bypass OST1 kinase and activate SLAC1 (Hsu et al., 2018). SLACs may be activated without the involvement of OST1 but other kinases. For e.g., the signaling events in guard cells can utilize MAPK cascade to up-regulate SLAC1/SLAH3 (Jagodzik et al., 2018). MAP

TABLE 2 | Several compounds that induce stomatal closure can also promote pathogen resistance of plants.

Compound/Hormone	Effect on stomata	References	Response to Pathogen	References
ABA	Closure	Cummins et al., 1971	Increased callose deposition and enhanced resistance against *Leptosphaeria maculans* and *Pseudomonas syringae*	Oide et al., 2013
Allyl isothiocyanate (AITC)	Closure	Khokon M.A. et al., 2011	Required cooperative MJ-priming to evade pathogens	Khokon M.A. et al., 2011
Cerato-platanin	Closure	Baccelli et al., 2014	Increased ROS levels, and interaction with SA/ethylene for resistance against *Botrytis cinerea* and *P. syringae*	Baccelli et al., 2014
Chitin	Closure	Ye et al., 2020b	Converted to chitosan and caused guard cell death to restrict fungal pathogen invasion	Ye et al., 2020b
Chitosan	Closure	Srivastava et al., 2009	Immunity against *Fusarium* associated with stomatal closure	Narula et al., 2020
Cryptogein	Closure	Gayatri et al., 2017	Produced ROS and induced PCD for resistance against *Hyaloperonospora arabidopsidis*	Kurusu et al., 2018
Cyclodipeptides	Closure	Wu et al., 2017	Increased defense responses to *Phytophthora nicotianae* and *Tobacco mosaic virus*	Wu et al., 2017
Ethylene (ET)	Closure	Desikan et al., 2006	Promoted production of ROS accumulation and phytoalexin to boost resistance against *Magnaporthe oryzae*	Yang et al., 2017
Cytokinin	Closure	Novák et al., 2013	Induced HR-like response, cell death and activation of PR genes, in response to *Agrobacterium tumefaciens*	Novák et al., 2013
Methyl jasmonate (MJ)	Closure	Raghavendra and Reddy, 1987	Interacted with ethylene for resistance against *B. cinerea*	Song et al., 2014
PAMP-induced peptide (PIP1)	Closure	Hou et al., 2014	Stimulation of MAPK, ROS accumulation and callose deposition for resistance against *F. oxysporum* and *P. syringae*	Hou et al., 2014
Salicylic acid (SA)	Closure	Manthe et al., 1992	Promoted synthesis of catechin and proanthocyanidins to defend against *Melampsora larici-populina*	Ullah et al., 2019
Strigolactone (SL)	Closure	Lv et al., 2018	Down-regulated MYC2 and upregulated plant defense factor upon *Meloidogyne incognita* infection	Xu et al., 2019

*Further details of the mechanism of stomatal closure by several of these are indicated in **Table 3**. The abbreviations are listed in the **Appendix** (last page).*

kinases 3/6 participated upstream of NO during stomatal closure in darkness (Zhang T.Y. et al., 2017), while MPK 9/12 activated SLAC1 integrating with Ca^{2+}/CDPK system during the cross-talk of ABA and SA (Prodhan et al., 2018), though the exact mechanism is not known. When exposed to a small elicitor peptide, AtPeps, a two-kinase component of BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1 (BAK1)/BORTRYTIS-INDUCED KINASE 1 (BIK1)

was turned on to activate SLAC1 and SLAH3 in guard cells (Zheng et al., 2018). However, further experiments are necessary to identify the exact components involved in the activation of SLAC1 by MPK 9/12 or BAK1/BIK1.

There can be additional components of a leaf that can provide resistance to microbes as well as environmental stresses, e.g., callose or silicon deposition (Ellinger and Voigt, 2014; Alhousari and Greger, 2018; Islam W. et al., 2020), cuticular
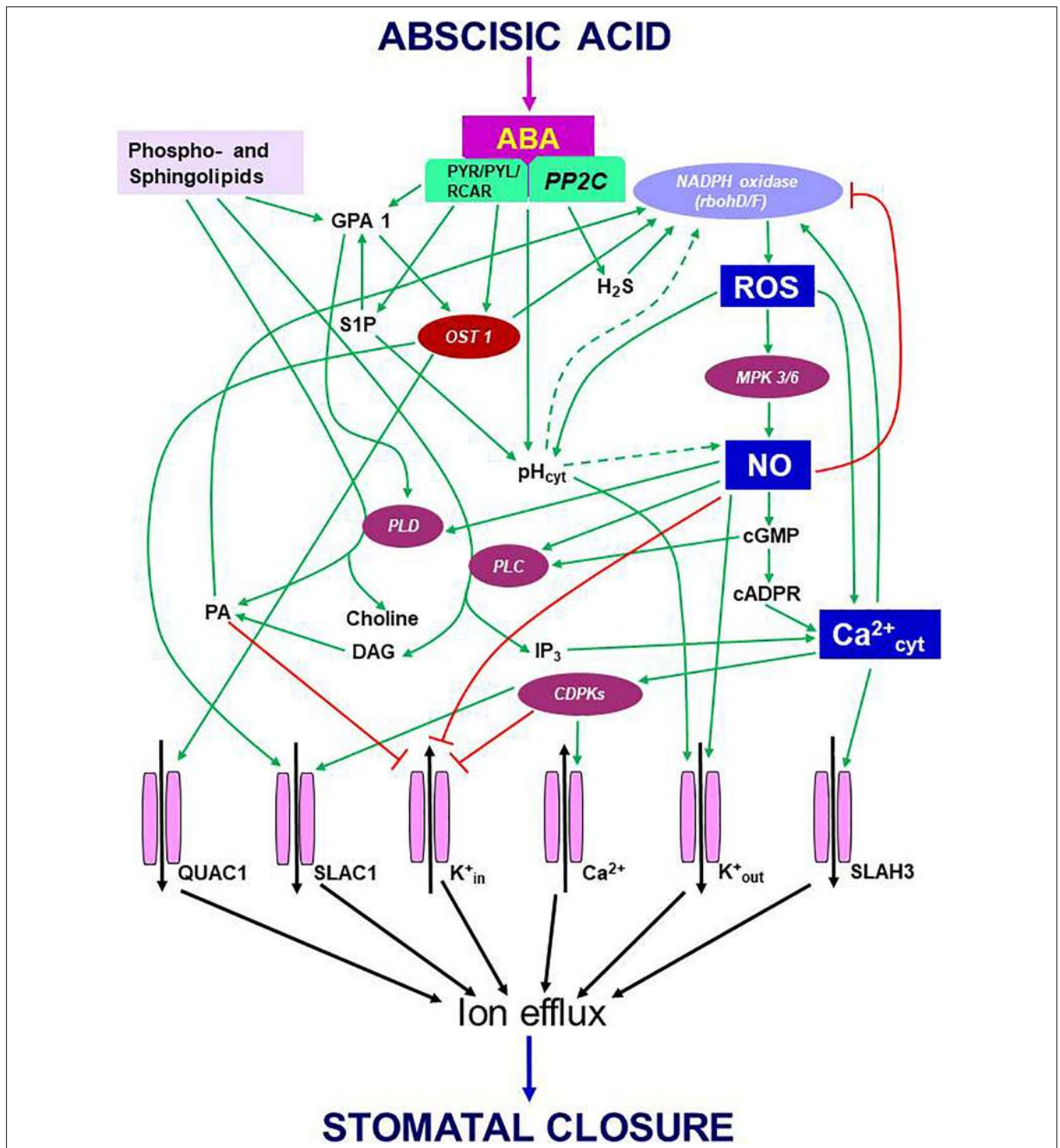
FIGURE 1 | Schematic representation of eventsm during signal transduction pathway induced by ABA leading to stomatal closure. Binding of ABA to its receptor (PYR/PYL/RCAR) blocks the function of PP2C. As a result, OST1, which stays phosphorylated, activates multiple components like NADPH oxidase (to generate ROS) and anion channels [quick anion channel 1 (QUAC1) and slow anion channel 1 (SLAC1)] to trigger anion efflux. The secondary messengers: ROS, NO, and cytosolic Ca^{2+}, exert multiple effects. The rise in cytosolic pH, another secondary messenger, appears to stimulate NADPH oxidase, but neither the origin nor the mode of pH action is understood. The high levels of ROS can promote NO production with the involvement of mitogen-activated protein kinases and elevate pH and Ca^{2+} in the cytosol. In turn, Ca^{2+} can activate RBOH-D/F and elevate ROS levels. The rise in NO downregulates K^+ inward channels and elevates cytosolic Ca^{2+} levels through cyclic guanosine monophosphate (cGMP) and cyclic ADP ribose (cADPR). An increase in Ca^{2+} can activate calcium-dependent protein kinases to facilitate a further influx of Ca^{2+} from outside. Ca^{2+}-activated calcium-dependent protein kinases stimulate SLAC1 and S-type anion channel 3 while inhibiting K+

(Continued)

waxes (Lewandowska et al., 2020) and trichomes (Fürstenberg-Hägg et al., 2013). ABA was involved in some of these responses. Cuticular wax biosynthesis was ABA-dependent and mediated by MYB94 and MYB96 transcription factors (Lewandowska et al., 2020). A light-induced increase in trichome density and thick leaves was due to high ABA levels in the leaves (Escobar-Bravo et al., 2018). Furthermore, ABA promoted callose synthesis and deposition by negatively regulating callose degrading pathogenesis-related protein 2 (PR2) (Oide et al., 2013). Similarly, ABA up-regulated callose deposition and antiviral RNA silencing mechanism to evade virus attack (Alazem and Lin, 2020).

STOMATAL CLOSURE BY COMPOUNDS OTHER THAN ABA AND THEIR INTERACTIONS DURING STOMATA CLOSURE

Besides ABA, several other compounds increase when plants are exposed to stress, which close stomata and help plant defense responses. These compounds can be grouped into three categories: hormones, elicitors, and metabolites (**Table 3**). The hormones include MJ, SA, ET, and BRs. MJ was the most effective one and induced stomatal closure by elevating pH, ROS, NO, and Ca^{2+} leading to activation of anion channels, similar to ABA action (Munemasa et al., 2007; Gonugunta et al., 2009; Agurla and Raghavendra, 2016). Further studies in detail are needed to understand the effects of ET as well as BRs on closure.

Salicylic acid (SA) is considered a plant defense hormone with overlapping functions as an elicitor (Ding and Ding, 2020). SA-induced stomatal closure was mediated by ROS produced primarily through peroxidase (not NADPH oxidase, as in ABA). The other downstream events of NO production and ion channel modulation in guard cells were similar to ABA's action (Hao et al., 2010; Khokon A.R. et al., 2011; Khokon et al., 2017; Wang et al., 2018). Thus, there is an overlapping of signaling pathways mediated by SA and ABA to cause stomatal closure in Arabidopsis. Several microbial elicitors (chitosan, flg22, harpin, and cryptogein) promoted stomatal closure and prevented pathogens' entry. These elicitors produce NO and ROS via nitric oxide synthase (NOS) and NADPH oxidase, respectively (Klüsener et al., 2002; Melotto et al., 2006; Agurla and Raghavendra, 2016; Gayatri et al., 2017; Prodhan et al., 2020). The combined action of ROS and NO could be imparting pathogen resistance.

TABLE 3 | A spectrum of hormones (other than ABA)/elicitors/PAMPs and other metabolites capable of inducing stomatal closure and the basis of their action.

Compound	Effect on stomata	Plant	References
Allyl isothiocyanate (AITC)	Produces ROS and NO and elevates of cytosolic Ca^{2+}	*Arabidopsis thaliana*	Khokon M.A. et al., 2011
β-aminobutyric acid (BABA)	Triggers ABA accumulation under drought	*Triticum aestivum*	Du et al., 2012
Cerato-platanin (CP)	Produces ROS and closes stomata	*A. thaliana*	Baccelli et al., 2014
Chitin oligosaccharide (CTOS)	Elevates Ca^{2+} and activates SLAC1	*A. thaliana*	Ye et al., 2020b
Chitosan	Mediates the production of NO, ROS and Ca^{2+} levels	*Pisum sativum*	Srivastava et al., 2009
Cryptogein	Increases the levels of ROS and NO	*A. thaliana*	Gayatri et al., 2017
γ-aminobutyric acid (GABA)	Represses 14-3-3 proteins and influx of anions into the vacuole	*A. thaliana*	Mekonnen et al., 2016
Flagellin22 (flg22)	Accumulates ROS and activates SLAC	*A. thaliana*	Deger et al., 2015
Harpin	Increases the levels of ROS and NO	*A. thaliana*	Gayatri et al., 2017
Lipopolysaccharide (LPS)	Activates NOS and produces NO in guard cells	*A. thaliana*	Melotto et al., 2006
Methyl jasmonate (MJ)	Promotes H_2O_2 production and cytosolic alkalinization	*A. thaliana*	Suhita et al., 2004
Oligogalacturonic acid (OGA)	Increases cytosolic Ca^{2+} and ROS levels	*Lycopersicon esculentum*	Lee et al., 1999
PAMP induced peptide 1 (PIP1)	Activates Ca^{2+} channels and S-type anion channels	*A. thaliana*	Shen et al., 2020
Salicylic acid (SA)	Induce production of ROS, NO and cytosolic Ca^{2+}	*A. thaliana*	Khokon M.A. et al., 2011
Yeast elicitor (YEL)	Produces ROS and NO production	*A. thaliana*	Khokon et al., 2010

*The abbreviations are listed in the **Appendix** (last page).*

Allyl isothiocyanate (AITC), proline, and PAs are examples of metabolites that accumulate under stress. Despite accumulation

in large quantities, proline, a compatible osmolyte, caused only a partial closure (Raghavendra and Reddy, 1987). PAs (including putrescine, spermidine, and spermine) accumulated during water stress and pathogen attack (Alcázar et al., 2010; Hatmi et al., 2018). The oxidation of PAs by polyamine oxidase raised ROS levels, followed by NO to cause stomatal closure similar to ABA (Agurla et al., 2018b). Similarly, AITC promoted stomatal closure and defense responses against biotic components (Khokon M.A. et al., 2011; Ye et al., 2020a).

The hormones, elicitors, and metabolites described above interact markedly with ABA and act in tandem to promote abiotic stress tolerance (**Table 4**). ABA's interactions with SA or MJ to work together during stomatal closure and pathogen resistance are well-known (Koo et al., 2020; Wang J. et al., 2020). For e. g., MJ promoted ABA biosynthesis by inducing the AtNCED3 gene expression in Arabidopsis (Hossain et al., 2011). ABA was needed during SA-action on stomata (Wang et al., 2018). Conversely, elevated ABA triggered SA biosynthesis by activating SID2 and promoted stomatal closure (Prodhan et al., 2018). These reports confirm the synergy between MJ, SA, and ABA during stomatal closure.

An SA-receptor, NPR1, mediated chitosan signaling in guard cells (Prodhan et al., 2020). SA, chitosan, and ABA interacted during stomatal closure by activating MAP kinases (MPK9 and MPK12) (Salam et al., 2012; Khokon et al., 2017). Elevated levels of PAs stimulated biosynthesis of ABA (Yamasaki and Cohen, 2006; Alcázar et al., 2010). In turn, ABA stimulated oxidation of Pas to elevate H_2O_2 and NO, and stomatal closure (An et al., 2008; Konstantinos et al., 2010). Such interactions could fine-tune ABA's effects to strengthen the plant defense reactions against both abiotic and biotic stresses. The direct role of PAs and proline in pathogen resistance is not clear.

COUNTERMEASURES BY PATHOGENS

The stomatal closure by ABA cannot be a permanent strategy to prevent microbial entry, as pathogens, such as Puccinia, can enter leaves through places other than stomata (Mendgen et al., 1996; Solanki et al., 2019). Therefore, we do not mean to overemphasize the role of ABA-induced stomatal closure as the sole mode of adaptation. Also, stomata need to open subsequently to keep up the gas exchange and normal plant function. At the same time, microbial pathogens initiate counteractive measures to reopen stomata, by either effectors, (such as coronatine or fusicoccin, Schulze-Lefert and Robatzek, 2006; Gudesblat et al., 2009a; Melotto et al., 2017), locking the open-stomata (Prats et al., 2006) or even killing guard cells to prevent their closure (Ye et al., 2020b).

Some of the pathogens secrete a cocktail of cell wall digesting enzymes to facilitate the entry through the epidermis into the leaves (Mendgen et al., 1996). The pathogens can also restrict the biosynthesis/actions of ABA and related hormones (Zeng et al., 2010; Robert-Seilaniantz et al., 2011). Further, pathogens too can trigger programmed cell death

(PCD) of host tissue facilitating the spread of infection (Hofius et al., 2017; Huysmans et al., 2017). Despite the counteractive efforts by pathogens, ABA can still contribute to plant defense. It is known that ABA could initiate multifaceted measures involving hypersensitive response (HR) and long-term adaptation on its own or by synergetic interaction with other hormones, such as SA or MJ, to ensure improved resistance (described below).

ABA-INTERACTION WITH GASOTRANSMITTERS

The role of gasotransmitters in stomatal regulation requires special mention. In addition to NO, two more gaseous signaling molecules (gasotransmitters), hydrogen sulfide (H_2S), and carbon monoxide (CO) produced within plant cells are an integral part of ABA-dependent stomatal closure as well as other stress conditions. These three gasotransmitters interacted with ABA-signaling during drought (García-Mata and Lamattina, 2013; Yao et al., 2019; Gahir et al., 2020). Under abiotic stress, ABA could elevate the levels of NO as well as CO or H_2S. For e.g., ABA activated heme oxygenase (HO), thereby increased CO levels and caused stomatal closure (Cao et al., 2007; Wang and Liao, 2016). In turn, NO elevated the levels of H_2S by regulating H_2S producing enzymes (L/D-cysteine desulfhydrases) (Kolupaev et al., 2019; Gahir et al., 2020). Similarly, CO promoted both NO and ROS synthesis, facilitating stomatal closure during abiotic stress (Song et al., 2008; He and He, 2014). Thus, a triangular interaction appears to be operating in guard cells. These interactions and synergistic actions need to be examined further. We, however, feel that among the three gasotransmitters, NO could be the significant signaling molecule. Like in the case of ROS, the production of NO can also be triggered by microbial pathogens to activate defense-related genes (e.g., phenylalanine ammonia-lyase and pathogenesis-related protein-1) that play a significant role in acquired pathogen resistance (Romero-Puertas et al., 2004; Ma and Berkowitz, 2016). NO produced in response to lipopolysaccharide contributed towards resistance against *Pst* DC3000 (Melotto et al., 2006). The upregulation of H_2S production suggested a strong association between H_2S and plant defense (Shi et al., 2015; Gahir et al., 2020). Further studies on these protective abilities of gasotransmitters to improve pathogen resistance could help achieve plants' resilience.

Gasotransmitters exert their actions by mediating post-translational modifications (PTMs) such as S-nitrosylation, nitridation, and persulfidation of target proteins (Scuffi et al., 2016; Kolupaev et al., 2019; Gahir et al., 2020). These PTMs seem to exert different effects. Accumulation of H_2S by ABA mediates the persulfidation of SnRK2.6 to promote stomatal closure by ABA (Chen S. et al., 2020). S-nitrosylation, mediated by NO, inhibited OST1/SnRK2.6 kinase activity and limited stomatal closure (Fancy et al., 2017). Detailed experiments on such contrasting effects of NO and H_2S would unravel the mechanism of interaction between gasotransmitters and ABA during stomatal closure and plant defense against pathogens.

TABLE 4 | Interaction of ABA with other compounds during the stress responses that induce stomatal closure.

Hormone / Compound	Interaction with ABA	Stress / or HR response	Plant	References
Hormones				
Methyl-Jasmonate (MJ)	Common signaling components with ABA action	Drought	*Arabidopsis thaliana*	Suhita et al., 2004
Ethylene (ET)	Interacts with ABA signaling and inhibits stomatal closure	Drought	*A. thaliana*	Tanaka et al., 2005
Salicylic acid (SA)	Increases ABA signaling via MAPKs and CPKs	Abiotic/biotic stress	*A. thaliana*	Wang H.Q. et al., 2020
Brassinolide (active BR)	Promote and inhibit ABA-mediated stomatal closure	Drought	*A. thaliana*	Ha et al., 2016
Elicitors/PAMPs				
Chitosan	Rise in NO, ROS and cytosolic free Ca^{2+}, as in case of ABA	External elicitor application	*Pisum sativum*	Srivastava et al., 2009; Gonugunta et al., 2009
Yeast elicitor (YEL)	Regulates ABA action through MPK9 and MPK12 positively regulate ABA	External elicitor application	*A. thaliana*	Salam et al., 2013
12-oxo-phytodienoic acid (12-OPDA)	Functions together with ABA and controls stomatal aperture	Drought	*A. thaliana*	Savchenko et al., 2014
Flagellin	Merge with ABA at OST1kinase and activates SLAC1 and SLAH3	Bacterial infection	*A. thaliana*	Deger et al., 2015
Harpin	signaling merge at RBOH and induces ROS production	External application	*Nicotiana benthamiana*	Zhang et al., 2009
Lipopolysaccharide (LPS)	Produces rapid NO production via NOS	External application	*A. thaliana*	Melotto et al., 2006
Other factors				
Polyamines (PAs)	ABA increases PA biosynthesis	Polyethylene glycol-induced osmotic stress	*Triticum aestivum*	Pál et al., 2018
Strigolactone (SL)	Integrates with ABA signaling and enhances stomatal closure	Drought	*Oryza sativa*	Haider et al., 2018
Carbon dioxide (CO_2)	Enhances ABA signaling via MPKs	Elevated CO_2	*A. thaliana*	Töldsepp et al., 2018
Trehalose	Enhanced drought tolerance and ABA signaling	Drought	*Solanum lycopersicum*	Yu et al., 2019
Signaling components				
Cytosolic free Ca^{2+}	Cross-talk with H_2O_2 and NO during ABA action	Extra cellular Ca^{2+}	*A. thaliana*	Wang et al., 2012
Phospholipase D (PLDα and PLDδ)	Mediates ABA signaling in guard cells	Multiple abiotic stresses	*A. thaliana*	Uraji et al., 2012
Hydrogen sulfide (H_2S)	Regulates ABA signaling by persulfidation OST 1	Drought	*A. thaliana*	Chen S. et al., 2020
Phosphatidic acid (PA)	Gα subunit mediates ABA action in response to PA	Drought	*A. thaliana*	Mishra et al., 2006

*The abbreviations are listed in the **Appendix** (last page).*

SIGNALING COMPONENTS IN GUARD CELLS TRIGGERED BY ABA: ROLE IN STOMATAL CLOSURE AND PATHOGEN RESISTANCE

Stomatal closure is the result of turgor loss in guard cells because of increased cation/anion efflux. A well-defined transduction pathway mediates the events during stomatal closure by ABA or other compounds, as illustrated in **Figure 1**. Binding of ABA to its receptor inactivates protein phosphatase 2C resulting in the activation of OST1 kinase, which stimulates NADPH oxidase (due to phosphorylation) enzyme to generate ROS and then the production of NO. Both ROS and NO can elevate levels of cytosolic Ca^{2+}. The high levels of ROS, NO, and Ca^{2+} act either directly or together to activate anion/cation efflux channels while inhibiting the influx channels. The final result is the loss of cations/anions from guard cells, resulting in turgor loss and stomatal closure (Agurla et al., 2018a). These three secondary messengers (ROS, NO and Ca^{2+}) can also stimulate the production of other signaling components such as phospholipase C, phospholipase D, phosphatidic acid, and inositol 1,4,5-triphosphate besides raising cytosolic pH, all contributing to stomatal closure. Apart from well-known NO, other gasotransmitters, i.e., CO and H_2S, are also involved in ABA-induced stomatal closure.

In recent years, another signaling component, reactive carbonyl species (RCS) was found to play a significant role in stomatal closure. These RCS are products of lipid oxidation, produced and scavenged during various developmental processes, including PCD (Biswas and Mano, 2015). Montillet et al. (2013) suggested that RCS (also called oxylipins) played

TABLE 5 | List of Arabidopsis mutants deficient in ABA biosynthesis/signaling pathway and their susceptibility to pathogen attack.

Mutant	Deficiency	Response to pathogens	References
ABA biosynthesis / Reception			
aao3 and *aba2* (Abscisic aldehyde oxidase)	Impaired ABA biosynthesis	Susceptible to *Pythium irregulare*	Adie et al., 2007
aba3 (Abscisic acid)	Abscisic acid biosynthesis	Neither flg22 nor lipopolysaccharide (LPS), failed to induce closure	Melotto et al., 2006
ataf1 (NAC protein)	Increased ABA levels	Reduced resistance to biotrophic fungus	Wu et al., 2009
abi1 and *abi2* (ABA insensitive)	PP2C, needed for ABA signaling	Stomatal closure is absent in response to *Trichoderma* species	Contreras-Cornejo et al., 2015
coi1 (Coronatine-insensitive)	MeJA-induced stomatal closure	COR not able to prevent ABA-induced stomatal closure	Melotto et al., 2006
ABA-signaling components			
agb1 (Arabidopis G β-subunit)	G-protein β subunit, involved in GTPase activity	Stomata remained open and highly susceptible to *Pseudomonas* sps	Lee et al., 2013
cpk3-2 cpk6-1	Ca^{2+}-dependent protein kinases	SA and ABA-induced stomatal closure is impaired	Prodhan et al., 2018
gcn2 (General control non-derepressible 2)	GCN kinase activity	Less effective in closing stomata and resisting *P. syringae*	Liu et al., 2019
lcbk1 (Long-chain base kinase1)	Long-chain base kinase1	Susceptible to virulent pathogens and not able to close stomata	Gupta et al., 2020
mpk3 mpk6 and *mkk4 mkk5*	Mitogen-activated protein kinases	Unable to close stomata in response to PAMP or *Pst*	Su et al., 2017
ost1 (Open stomata1)	Reduced K^+ efflux	Stomatal closure is impaired in response to flg22	Deger et al., 2015
ost2 (open stomata2)	H^+-ATPase	ABA-insensitive and flg22/LPS unable to induce stomatal closure	Liu et al., 2009
rbohD (Respiratory burst oxidase homologue)	Impaired ROS production	Impaired flg22 responses and stomatal closure	Kadota et al., 2014
slac1 (Slow anion channel 1)	Slow anion channel	Hyposensitive to *Pst* and reduced stomatal closure	Shen et al., 2020
Other effectors			
era1 (Enhanced response to ABA1)	Farnesyl transferase β subunit	Hypersensitive to ABA and virulent pathogens	Jalakas et al., 2017
eds1 (Enhanced Disease Susceptibility)	Salicylic acid biosynthesis	Ability to close stomata in response to bacteria and LPS is compromised	Melotto et al., 2006
lox1 (Lipoxygenase)	Lipoxygenase activity	Compromised ability to close stomata in response to virulent and avirulent pathogens	Montillet et al., 2013
pip2;1 (Plasma membrane intrinsic protein)	Plasma membrane aquaporin	Impaired stomatal closure in response to ABA and flg22	Rodrigues et al., 2017
rpfF and *rpfC* (Regulation of pathogenicity factor)	Synthesis and perception of diffusible molecule	Stomatal closure is absent in response to *Xcc* and *Pst*	Gudesblat et al., 2009b

*A few other instances of mutants altered in stomatal closure and pathogen sensitivity are also included. The abbreviations are listed in the **Appendix** (last page).*

a dominant role during stomatal closure by biotic factors (e.g., elicitors from pathogens), compared to ROS during the action of ABA (typical of abiotic stress factor). Soon, detailed reports appeared that RCS could function downstream of ROS production during closure by ABA and MJ in *Nicotiana tabacum* and *Arabidopsis thaliana* (Islam et al., 2016, 2019; Islam M.M. et al., 2020). Recently, RCS was found to activate CPK6, promote the elevation of Ca^{2+} and activate SLAC1, leading to stomatal closure (Islam M.M. et al., 2020). These observations imply that RCS and ABA could enable guard cells to respond to both biotic and abiotic stress conditions. Several authors had reviewed the details of the ABA-induced signal transduction pathway (Raghavendra et al., 2010; Munemasa et al., 2015; Sierla et al., 2016; Agurla et al., 2018a; Kolbert et al., 2019; Saito and Uozumi, 2019; Sun et al., 2019).

Several of the signaling components during ABA-induced stomatal closure can protect against pathogens (**Table 2**). The three major secondary messengers, triggered by ABA

(namely ROS, NO, and Ca^{2+}) can initiate defense processes such as stomatal closure and PCD (Sewelam et al., 2016; Suzuki and Katano, 2018). ABA-induced NO can act as a signaling molecule to initiate adaptive responses against abiotic (UV, drought, and salinity) or biotic factors (pathogens or elicitors). The reaction products of ROS and NO (like peroxynitrite) and NO-mediated post-translational modifications can all act together to initiate defense responses (Bellin et al., 2013; León et al., 2014; Arnaud and Hwang, 2015). The rise in cytosolic Ca^{2+} was often required to induce HR as a plant immunity response (e.g., against microbial pathogens). Other compounds involved in ABA signaling, like phospholipase D and phosphatidic acid, were also associated with plants' defense against pathogens (Li and Wang, 2019; Moeder et al., 2019). The ability of H_2S, a gasotransmitter, to impart resistance against typical plant pathogen (*Pseudomonas syringae*) suggests a link between stomatal closure and adaptation to plant pathogens (Shi et al., 2015; Gahir et al., 2020). The promotion or inhibition of

ROS and NO production by gasotransmitters can be a significant factor during plant defense.

Arabidopsis thaliana had been an excellent model to study and validate the components/mechanisms of plant function. Several mutants of *A. thaliana* were employed to establish ABA's signaling components (**Table 5**). These mutants fall under three groups: those with altered ABA biosynthesis/reception or deficient in signaling compounds or those with altered stomatal response independent of ABA. The mutants who cannot close their stomata also lose their ability to resist pathogens, becoming hypersensitive to pathogens. These observations emphasize the strong association of stomatal closure by ABA or related compounds with altered pathogen resistance.

Other Points to Be Considered

Evidence is emerging that ABA may not always impart resistance but increase plants' susceptibility to abiotic or biotic factors by compromising defense responses (Gietler et al., 2020). For e.g., ABA can act differently depending on the pathogen status: pre-entry or post-entry phases. During the early stages, induction of stomatal closure along with stimulation of wax and callose synthesis could reinforce the plant's defense. However, in the post-invasion stage, ABA can be antagonistic and increase susceptibility to microbes (Alazem and Lin, 2015; Arnaud and Hwang, 2015). Accumulation of ABA at infection site repressed events involving disease resistance against *Cercospora* in beetroot (Schmidt et al., 2008). Elevated ABA levels promoted sugar transport to fungi and enhanced the infection of wheat by *Puccinia striiformis* sp. *tritici* (pst) (Huai et al., 2019). Furthermore, increased ABA levels antagonized plant's defense responses by suppressing SA or MJ induced defense gene expression, callose deposition, and basal resistance against *Fusarium oxysporum* or *Magnaporthe grisea* (Anderson et al., 2004; Jiang et al., 2010; Lim et al., 2015; Ulferts et al., 2015).

We believe that ABA could play a significant role in restricting or at least delaying the pathogen entry and subsequent infections, at least in the case of bacteria (**Table 5** and description below). We acknowledge that the role of stomata should not be generalized, as the experiments done on pathogen infection with Arabidopsis (non-host) may not be all applicable with typical host species, such as wheat or barley.

SUBSEQUENT EFFECTS OF ABA BESIDES STOMATAL CLOSURE TOWARDS ADAPTIVE RESPONSES: PRE-ENTRY AND POST-ENTRY PHENOMENA

Pathogen resistance cannot be entirely due to stomatal closure, and the action of ABA needs to continue beyond stomata. Often during infection, an increase in ABA levels led to multiple events that help against abiotic stress and disease resistance (Shafiei et al., 2007). Even if pathogens manage to enter the intercellular spaces, elevated ABA can initiate a spectrum of events that restrict the multiplication and spread of plant pathogens inside
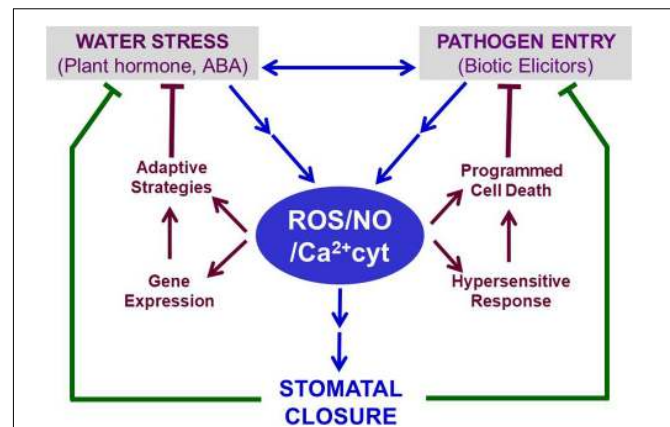

FIGURE 2 | Stomatal closure induced under conditions of abiotic (e.g., drought) or biotic (e.g., pathogens) stress serves as a common defense mechanism. In guard cells, ABA typically raises the levels of ROS, NO, and Ca^{2+}. These three secondary messengers bring out stomatal closure through a series of signaling events (as illustrated in **Figure 1**). The retention of water within leaves, when stomata are closed, helps to relieve water stress. In parallel, the closed stomata restrict microbial pathogens' entry into leaves. The trio of ROS, NO, and Ca^{2+} parallelly induce adaptive events to mitigate water stress and limit pathogen spread by triggering HR and PCD. Thus, ROS, NO, and Ca^{2+} can be considered vital regulators, participating in ABA-induced defense against abiotic and biotic stress. Further details are described in the text. Abbreviations used here are listed in the **Appendix**.

leaves. For e.g., ABA can raise the levels of ROS, NO, and Ca^{2+} (Wendehenne et al., 2004; Moeder et al., 2019; Sadhu et al., 2019). An important consequence of elevated ROS, NO, and Ca^{2+} is HR response, leading to PCD in several crop species while protecting against pathogens. The HR may also include callose deposition in cell walls, increased cuticular biosynthesis (Luna et al., 2011; Lewandowska et al., 2020), and blocking of plasmodesmata (Huysmans et al., 2017). Further, the modulation by ABA of miRNA can restrict viral replication and the viral movement due to blocked plasmodesmata, thus causing antiviral silencing (Staiger et al., 2013; Alazem and Lin, 2017).

Other ABA-promoted events include the activation of genes involved in either accumulation of compatible solutes for osmotic adaptation or PCD to restrict the spread of pathogens within leaves or enhanced secondary metabolites production (**Figure 2**). For example, ABRE-binding proteins (AREBs) and ABRE-binding factors (ABFs) up-regulate stress-responsive genes, involved in short-term and long term adaptations to abiotic stresses, including drought, cold, and heat (Verma et al., 2016; Vishwakarma et al., 2017). The accumulation of proline on exposure to water stress or ABA (Stewart, 1980; Planchet et al., 2014) can serve the dual purpose of providing compatible solute for osmotic adjustments in leaves and causing partial stomatal closure in the epidermis (Raghavendra and Reddy, 1987). Elevated proline levels due to ABA can further offer the plant defense against pathogens (Qamar et al., 2015; Christgen and Becker, 2019). There have been claims that proline accumulation is not all ABA-dependent (Savouré et al., 1997). It is not clear if ABA is the master regulator of proline accumulation or a consequence of stomatal closure. ABA and proline's

combined action can be beneficial under hypoxic stress (Cao et al., 2020). Similarly, ABA, proline, and PAs can help together during plant adaptation to osmotic stress (Pál et al., 2018).

Several ABA responses are beneficial during biotic stress, as well. ABA and SA promoted the accumulation of anti-microbial flavan-3-ols, enhancing the plant defense against rust infection in two popular trees, Poplar and Malus (Lu et al., 2017; Ullah et al., 2019). Similarly, the ABA-activated MYC2 transcription factor was essential for defense against *Meloidogyne incognita* (Xu et al., 2019). PCD is a controlled process and is a consequence of high ROS and NO levels typically up-regulated by ABA (Petrov et al., 2015; You and Chan, 2015). In plants, PCD is often an adaptive response during abiotic/biotic stress (Fagundes et al., 2015; Burke et al., 2020). However, PCD can also aggravate plant disease (Huysmans et al., 2017). ABA was involved in the induction of cell death around the wounded site (Cui et al., 2013). Further experiments are needed to establish if the process of PCD is incidentally associated with ABA or if ABA is the causal factor.

Enhanced production of secondary metabolites is another defense mechanism of plants against stress (Kumar and Sharma, 2018; Khare et al., 2020). Abscisic acid itself is a secondary metabolite produced during stress and can play a significant role in secondary metabolite production when plants encounter abiotic or biotic stress factors (Murcia et al., 2017). ABA-induced increase in flavonoids and other metabolites served as a defensive measure against UV-B radiation (Mazid et al., 2011). *Trichoderma harzianum* infection increased ABA levels, which helped in osmotic adaptation under drought by restricting water loss and increasing osmolytes, like proline (Mona et al., 2017). Such interactions between ABA and secondary metabolite production are quite exciting and need to be examined in detail.

CONCLUSION

Based on the extensive literature available, we tried to emphasize the role of ABA-induced stomatal closure as an essential component of plant defense against both limited water and pathogens (**Figure 2**). ABA's role is complemented further by the cross-talk and interaction of ABA with other hormones, microbial elicitors, and metabolites. We, therefore, emphasize ABA can play either a direct role or an indirect role as well. The stomatal closure by ABA can be considered a quick short-term response. However, the three vital secondary messengers involved in ABA-signaling, namely ROS, NO, and cytosolic free Ca^{2+}, can promote events, such as osmolyte accumulation, up-regulation of adaptive genes, HR and PCD. These events

facilitate the long-term adaptation of plants against abiotic stress as well as pathogens. ABA's ability to induce stomatal closure may not always be due to changes occurring in guard cells' secondary messengers. For e.g., chitosan, a microbial elicitor, can cause the death of guard cells (Ye et al., 2020b), likely to make them non-functional. This aspect is thought-provoking and needs to be examined further using ABA or other hormones, such as SA or MJ.

There are emerging areas that are related to the role of ABA and stomatal closure in plant defense. ABA's ability to induce priming could help plants tolerate heat or drought stress occurring later (Zhang et al., 2019; Wang X. et al., 2020). Similarly, plants could have a transcriptional memory of ABA and MJ that can be useful for long-term adaptations (Avramova, 2019). Because of the well-documented importance, there had been recurring attempts to discover ABA-analogs or ABA-agonists. Stomatal closure and signaling components in guard cells can be excellent model systems to monitor such compounds. A few ABA-analogs were found, which mimic ABA to induce stomatal closure (Puli and Raghavendra, 2012; Vaidya et al., 2019). An extension of such work would open up an exciting possibility of exploiting ABA-analogs to improve plants/crops' water-use efficiency. There were reports that ABA and or stomatal closure may not be crucial, particularly during fungal pathogen infection of crops, e.g., barley and wheat. A few experiments on mutants of such crop plants deficient in ABA or ability to close stomata may help us clarify the exact situation. Plants are indeed known to employ more than one strategy to overcome stress conditions or to optimize metabolism. ABA-induced stomatal closure is one of the approaches, while plants/pathogens could evoke other strategies, as well.

AUTHOR CONTRIBUTIONS

AR conceived the idea and developed the outline. All authors reviewed the literature and wrote the article. AR edited the final draft of the review. All authors approved the final version.

FUNDING

REFERENCES

Adamipour, N., Khosh-Khui, M., Salehi, H., Razi, H., Karami, A., and Moghadam, A. (2020). Role of genes and metabolites involved in polyamines synthesis pathways and nitric oxide synthase in stomatal closure on *Rosa damascena* Mill. under drought stress. *Plant Physiol. Biochem.* 148, 53–61. doi: 10.1016/j.plaphy.2019.12.033

Adie, B. A., Pérez-Pérez, J., Pérez-Pérez, M. M., Godoy, M., Sánchez-Serrano, J. J., Schmelz, E. A., et al. (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

Agurla, S., Gahir, S., Munemasa, S., Murata, Y., and Raghavendra, A. S. (2018a). Mechanism of stomatal closure in plants exposed to drought and cold stress. *Adv. Exp. Med. Biol.* 1081, 215–232. doi: 10.1007/978-981-13-1244-1_12

Agurla, S., Gayatri, G., and Raghavendra, A. S. (2018b). Polyamines increase nitric oxide and reactive oxygen species in guard cells of *Arabidopsis thaliana* during stomatal closure. *Protoplasma* 255, 153–162. doi: 10.1007/s00709-017-1139-3

Agurla, S., and Raghavendra, A. S. (2016). Convergence and divergence of signaling events in guard cells during stomatal closure by plant hormones or microbial elicitors. *Front. Plant Sci.* 7:1332. doi: 10.3389/fpls.2016.01332

Alazem, M., and Lin, N. S. (2015). Roles of plant hormones in the regulation of host-virus interactions. *Mol. Plant Pathol.* 16, 529–540. doi: 10.1111/mpp.12204

Alazem, M., and Lin, N. S. (2017). Antiviral roles of abscisic acid in plants. *Front. Plant Sci.* 8:1760. doi: 10.3389/fpls.2017.01760

Alazem, M., and Lin, N. S. (2020). Interplay between ABA signaling and RNA silencing in plant viral resistance. *Curr. Opin. Virol.* 42, 1–7. doi: 10.1016/j.coviro.2020.02.002

Alcázar, R., Altabella, T., Marco, F., Bortolotti, C., Reymond, M., Koncz, C., et al. (2010). Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. *Planta* 231, 1237–1249. doi: 10.1007/s00425-010-1130-0

Alhousari, F., and Greger, M. (2018). Silicon and mechanisms of plant resistance to insect pests. *Plants* 7, 33. doi: 10.3390/plants7020033

Ali, A., Pardo, J. M., and Yun, D. J. (2020). Desensitization of ABA-signaling: the swing from activation to degradation. *Front. Plant Sci.* 11:379. doi: 10.3389/fpls.2020.00379

An, Z., Jing, W., Liu, Y., and Zhang, W. (2008). Hydrogen peroxide generated by copper amine oxidase is involved in abscisic acid-induced stomatal closure in *Vicia faba. J. Exp. Bot.* 59, 815–825. doi: 10.1093/jxb/erm370

Anderson, J. P., Badruzsaufari, E., Schenk, P. M., Manners, J. M., Desmond, O. J., Ehlert, C., et al. (2004). Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in *Arabidopsis. Plant Cell* 16, 3460–3479. doi: 10.1105/tpc.104.025833

Armendariz, A. L., Talano, M. A., Villasuso, A. L., Travaglia, C., Racagni, G. E., Reinoso, H., et al. (2016). Arsenic stress induces changes in lipid signalling and evokes the stomata closure in soybean. *Plant Physiol. Biochem.* 103, 45–52. doi: 10.1016/j.plaphy.2016.02.041

Arnaud, D., and Hwang, I. (2015). A sophisticated network of signaling pathways regulates stomatal defenses to bacterial pathogens. *Mol. Plant.* 8, 566–581. doi: 10.1016/j.molp.2014.10.012

Asselbergh, B., De Vleesschauwer, D., and Höfte, M. (2008). Global switches and fine-tuning-ABA modulates plant pathogen defense. *Mol. Plant Microbe Interact.* 21, 709–719. doi: 10.1094/MPMI-21-6-0709

Avramova, Z. (2019). Defence-related priming and responses to recurring drought: two manifestations of plant transcriptional memory mediated by the ABA and JA signalling pathways. *Plant Cell Environ.* 42, 983–997. doi: 10.1111/pce.13458

Baccelli, I., Lombardi, L., Luti, S., Bernardi, R., Picciarelli, P., Scala, A., et al. (2014). Cerato-platanin induces resistance in *Arabidopsis* leaves through stomatal perception, overexpression of salicylic acid- and ethylene-signalling genes and camalexin biosynthesis. *PLoS One* 9:e100959. doi: 10.1371/journal.pone.0100959

Bellin, D., Asai, S., Delledonne, M., and Yoshioka, H. (2013). Nitric oxide as a mediator for defense responses. *Mol. Plant Microbe Interact.* 26, 271–277. doi: 10.1094/MPMI-09-12-0214-CR

Bielach, A., Hrtyan, M., and Tognetti, V. B. (2017). Plants under stress: involvement of auxin and cytokinin. *Int. J. Mol. Sci.* 18:1427. doi: 10.3390/ijms18071427

Biswas, M. S., and Mano, J. (2015). Lipid peroxide-derived short-chain carbonyls mediate hydrogen peroxide-induced and salt-induced programmed cell death in plants. *Plant Physiol.* 168, 885–898. doi: 10.1104/pp.115.256834

Boba, A., Kostyn, K., Kozak, B., Wojtasik, W., Preisner, M., Prescha, A., et al. (2020). Fusarium oxysporum infection activates the plastidial branch of the terpenoid biosynthesis pathway in flax, leading to increased ABA synthesis. *Planta* 251:50. doi: 10.1007/s00425-020-03339-9

Breen, S., Williams, S. J., Outram, M., Kobe, B., and Solomon, P. S. (2017). Emerging insights into the functions of pathogenesis-related protein 1. *Trends Plant Sci.* 22, 871–879. doi: 10.1016/j.tplants.2017.06.013

Burke, R., Schwarze, J., Sherwood, O. L., Jnaid, Y., McCabe, P. F., and Kacprzyk, J. (2020). Stressed to death: The role of transcription factors in plant programmed cell death induced by abiotic and biotic stimuli. *Front. Plant Sci.* 11:1235. doi: 10.3389/fpls.2020.01235

Camisón, Á, Martín, M. Á, Sánchez-Bel, P., Flors, V., Alcaide, F., Morcuende, D., et al. (2019). Hormone and secondary metabolite profiling in chestnut during susceptible and resistant interactions with *Phytophthora cinnamomi. J. Plant Physiol.* 241:153030. doi: 10.1016/j.jplph.2019.153030

Cao, X., Wu, L., Wu, M., Zhu, C., Jin, Q., and Zhang, J. (2020). Abscisic acid mediated proline biosynthesis and antioxidant ability in roots of two different rice genotypes under hypoxic stress. *BMC Plant Biol.* 20:198. doi: 10.1186/s12870-020-02414-3

Cao, Z. Y., Huang, B. K., Wang, Q. Y., Xuan, W., Ling, T. F., and Zhang, B. (2007). Involvement of carbon monoxide produced by heme oxygenase in ABA-induced stomatal closure in Vicia faba and its proposed signal transduction pathway. *Chin. Sci. Bull.* 52, 2365–2373. doi: 10.1007/s11434-007-0358-y

Chen, K., Li, G. J., Bressan, R. A., Song, C. P., Zhu, J. K., and Zhao, Y. (2020). Abscisic acid dynamics, signaling, and functions in plants. *J. Integr. Plant Biol.* 62, 25–54. doi: 10.1111/jipb.12899

Chen, S., Jia, H., Wang, X., Shi, C., Wang, X., Ma, P., et al. (2020). Hydrogen sulfide positively regulates abscisic acid signaling through persulfidation of SnRK2.6 in guard cells. *Mol. Plant.* 13, 732–744. doi: 10.1016/j.molp.2020.01.004

Christgen, S. L., and Becker, D. F. (2019). Role of proline in pathogen and host interactions. *Antioxid. Redox Signal.* 30, 683–709. doi: 10.1089/ars.2017.7335

Contreras-Cornejo, H. A., Macías-Rodríguez, L., Vergara, A. G., and López-Bucio, J. (2015). Trichoderma modulates stomatal aperture and leaf transpiration through an abscisic acid-dependent mechanism in Arabidopsis. *J. Plant Growth Regul.* 34, 425–432. doi: 10.1007/s00344-014-9471-8

Cui, F., Brosché, M., Sipari, N., Tang, S., and Overmyer, K. (2013). Regulation of ABA dependent wound induced spreading cell death by MYB108. *New Phytol.* 200, 634–640. doi: 10.1111/nph.12456

Cummins, W. R., Kende, H., and Raschke, K. (1971). Specificity and reversibility of the rapid stomatal response to abscisic acid. *Planta* 99, 347–351. doi: 10.1007/BF00385826

Deger, A. G., Scherzer, S., Nuhkat, M., Kedzierska, J., Kollist, H., Brosché, M., et al. (2015). Guard cell SLAC1−type anion channels mediate flagellin−induced stomatal closure. *New Phytol.* 208, 162–173. doi: 10.1111/nph.13435

Desikan, R., Last, K., Harrett-Williams, R., Tagliavia, C., Harter, K., Hooley, R., et al. (2006). Ethylene-induced stomatal closure in *Arabidopsis* occurs via AtrbohF-mediated hydrogen peroxide synthesis. *Plant J.* 47, 907–916.

Ding, P., and Ding, Y. (2020). Stories of salicylic acid: a plant defense hormone. *Trends Plant Sci.* 25, 549–565. doi: 10.1016/j.tplants.2020.01.004

Du, Y. L., Wang, Z. Y., Fan, J. W., Turner, N. C., Wang, T., and Li, F. M. (2012). β-Aminobutyric acid increases abscisic acid accumulation and desiccation tolerance and decreases water use but fails to improve grain yield in two spring wheat cultivars under soil drying. *J. Exp. Bot.* 63, 4849–4860. doi: 10.1093/jxb/ers164

Dunn, R. M., Hedden, P., and Bailey, J. A. (1990). A physiologically-induced resistance of Phaseolus vulgaris to a compatible race of *Colletotrichum lindemuthianum* is associated with increases in ABA content. *Physiol. Mol. Plant Pathol.* 36, 339–349. doi: 10.1016/0885-5765(90)90063-4

Ellinger, D., and Voigt, C. A. (2014). Callose biosynthesis in *Arabidopsis* with a focus on pathogen response: what we have learned within the last decade. *Ann. Bot.* 114, 1349–1358. doi: 10.1093/aob/mcu120

Escobar-Bravo, R., Ruijgrok, J., Kim, H. K., Grosser, K., Van Dam, N. M., Klinkhamer, P., et al. (2018). Light intensity-mediated induction of trichome-associated allelochemicals increases resistance against thrips in tomato. *Plant Cell Physiol.* 59, 2462–2475. doi: 10.1093/pcp/pcy166

Fagundes, D., Bohn, B., Cabreira, C., Leipelt, F., Dias, N., Bodanese-Zanettini, M. H., et al. (2015). Caspases in plants: metacaspase gene family in plant stress responses. *Funct. Integr. Genomics* 15, 639–649. doi: 10.1007/s10142-015-0459-7

Fan, J., Hill, L., Crooks, C., Doerner, P., and 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

Fancy, N. N., Bahlmann, A. K., and Loake, G. J. (2017). Nitric oxide function in plant abiotic stress. *Plant Cell Environ.* 40, 462–472. doi: 10.1111/pce.12707

Fang, Y., and Xiong, L. (2015). General mechanisms of drought response and their application in drought resistance improvement in plants. *Cell Mol. Life Sci.* 72, 673–689. doi: 10.1007/s00018-014-1767-0

Finkelstein, R. (2013). Abscisic acid synthesis and response. *Arabidopsis Book* 11:e0166. doi: 10.1199/tab.0166

Förster, S., Schmidt, L. K., Kopic, E., Anschütz, U., Huang, S., Schlücking, K., et al. (2019). Wounding-induced stomatal closure requires jasmonate-mediated activation of GORK K+ channels by a Ca2+ sensor-kinase CBL1-CIPK5 complex. *Dev. Cell* 48, 87–99. doi: 10.1016/j.devcel.2018.11.014

Fürstenberg-Hägg, J., Zagrobelny, M., and Bak, S. (2013). Plant defense against insect herbivores. *Int. J. Mol. Sci.* 14, 10242–10297. doi: 10.3390/ijms140510242

Gahir, S., Bharath, P., and Raghavendra, A. S. (2020). The role of gasotransmitters in movement of stomata: mechanisms of action and importance for plant immunity. *Biol. Plant.* 64, 623–632. doi: 10.32615/bp.2020.071

García-Mata, C., and Lamattina, L. (2013). Gasotransmitters are emerging as new guard cell signaling molecules and regulators of leaf gas exchange. *Plant Sci.* 201-202, 66–73. doi: 10.1016/j.plantsci.2012.11.007

Gayatri, G., Agurla, S., Kuchitsu, K., Anil, K., Podile, A. R., and Raghavendra, A. S. (2017). Stomatal closure and rise in ROS/NO of *Arabidopsis* guard cells by Tobacco microbial elicitors: Cryptogein and Harpin. *Front. Plant Sci.* 8:1096. doi: 10.3389/fpls.2017.01096

Gietler, M., Fidler, J., Labudda, M., and Nykiel, M. (2020). Abscisic acid-enemy or savior in the response of cereals to abiotic and biotic stresses? *Int. J. Mol. Sci.* 21:4607. doi: 10.3390/ijms21134607

Gonugunta, V. K., Srivastava, N., and Raghavendra, A. S. (2009). Cytosolic alkalinization is a common and early messenger preceding the production of ROS and NO during stomatal closure by variable signals, including abscisic acid, methyl jasmonate and chitosan. *Plant Signal Behav.* 4, 561–564. doi: 10.4161/psb.4.6.8847

Gudesblat, G. E., Torres, P. S., and Vojnov, A. A. (2009a). Stomata and pathogens: warfare at the gates. *Plant Signal Behav.* 4, 1114–1116. doi: 10.4161/psb.4.12.10062

Gudesblat, G. E., Torres, P. S., and Vojnov, A. A. (2009b). Xanthomonas campestris overcomes *Arabidopsis stomatal* innate immunity through a DSF cell-to-cell signal-regulated virulence factor. *Plant Physiol.* 149, 1017–1027. doi: 10.1104/pp.108.126870

Gupta, P., Roy, S., and Nandi, A. K. (2020). MEDEA-interacting protein LONG-CHAIN BASE KINASE 1 promotes pattern-triggered immunity in *Arabidopsis thaliana*. *Plant Mol. Biol.* 103, 173–184. doi: 10.1007/s11103-020-00982-4

Ha, C. V., Leyva-González, M. A., Osakabe, Y., Tran, U. T., Nishiyama, R., Watanabe, Y., et al. (2014). Positive regulatory role of strigolactone in plant responses to drought and salt stress. *Proc. Natl. Acad. Sci. U.S.A.* 111, 851–856. doi: 10.1073/pnas.1322135111

Ha, Y., Shang, Y., and Nam, K. H. (2016). Brassinosteroids modulate ABA-induced stomatal closure in *Arabidopsis*. *J. Exp. Bot.* 67, 6297–6308. doi: 10.1093/jxb/erw385

Haider, I., Andreo-Jimenez, B., Bruno, M., Bimbo, A., Floková, K., Abuauf, H., et al. (2018). The interaction of strigolactones with abscisic acid during the drought response in rice. *J. Exp. Bot.* 69, 2403–2414. doi: 10.1093/jxb/ery089

Hao, F., Zhao, S., Dong, H., Zhang, H., Sun, L., and Miao, C. (2010). Nia1 and Nia2 are involved in exogenous salicylic acid-induced nitric oxide generation and stomatal closure in *Arabidopsis*. *J. Integr. Plant Biol.* 52, 298–307. doi: 10.1111/j.1744-7909.2010.00920.x

Hatmi, S., Villaume, S., Trotel-Aziz, P., Barka, E. A., Clément, C., and Aziz, A. (2018). Osmotic stress and ABA affect immune response and susceptibility of grapevine berries to gray mold by priming polyamine accumulation. *Front. Plant Sci.* 9:1010. doi: 10.3389/fpls.2018.01010

Haworth, M., Marino, G., Cosentino, S. L., Brunetti, C., De Carlo, A., Avola, G., et al. (2018). Increased free abscisic acid during drought enhances stomatal sensitivity and modifies stomatal behaviour in fast growing giant reed (*Arundo donax* L.). *Environ. Exp. Bot.* 147, 116–124. doi: 10.1016/j.envexpbot.2017.11.002

He, H., and He, L. (2014). The role of carbon monoxide signaling in the responses of plants to abiotic stresses. *Nitric Oxide* 42, 40–43. doi: 10.1016/j.niox.2014.08.011

Hewage, K. A. H., Yang, J. F., Wang, D., Hao, G. F., Yang, G. F., and Zhu, J. K. (2020). Chemical manipulation of abscisic acid signaling: a new approach to abiotic and biotic stress management in agriculture. *Adv. Sci.* 7:2001265. doi: 10.1002/advs.202001265

Hofius, D., Li, L., Hafrén, A., and Coll, N. S. (2017). Autophagy as an emerging arena for plant-pathogen interactions. *Curr. Opin. Plant Biol.* 38, 117–123. doi: 10.1016/j.pbi.2017.04.017

Hossain, M. A., Munemasa, S., Uraji, M., Nakamura, Y., Mori, I. C., and Murata, Y. (2011). Involvement of endogenous abscisic acid in methyl jasmonate-induced stomatal closure in *Arabidopsis*. *Plant Physiol.* 156, 430–438. doi: 10.1104/pp.111.172254

Hou, S., Wang, X., Chen, D., Yang, X., Wang, M., Turrà, D., et al. (2014). The secreted peptide PIP1 amplifies immunity through receptor-like kinase 7. *PLoS Pathog.* 10:e1004331. doi: 10.1371/journal.ppat.1004331

Hsu, P. K., Takahashi, Y., Munemasa, S., Merilo, E., Laanemets, K., Waadt, R., et al. (2018). Abscisic acid-independent stomatal CO2 signal transduction pathway and convergence of CO2 and ABA signaling downstream of OST1 kinase. *Proc. Natl. Acad. Sci. U.S.A.* 115, E9971–E9980. doi: 10.1073/pnas.1809204115

Huai, B., Yang, Q., Qian, Y., Qian, W., Kang, Z., and Liu, J. (2019). ABA-induced sugar transporter TaSTP6 promotes wheat susceptibility to stripe rust. *Plant Physiol.* 181, 1328–1343. doi: 10.1104/pp.19.00632

Huang, H., Ullah, F., Zhou, D. X., Yi, M., and Zhao, Y. (2019). Mechanisms of ROS regulation of plant development and stress responses. *Front. Plant Sci.* 10:800. doi: 10.3389/fpls.2019.00800

Huysmans, M., Lema, A. S., Coll, N. S., and Nowack, M. K. (2017). Dying two deaths – programmed cell death regulation in development and disease. *Curr. Opin. Plant Biol.* 35, 37–44. doi: 10.1016/j.pbi.2016.11.005

Islam, M. M., Ye, W., Akter, F., Rhaman, M. S., Matsushima, D., Munemasa, S., et al. (2020). Reactive carbonyl species mediate methyl jasmonate-induced stomatal closure. *Plant Cell Physiol.* 61, 1788–1797. doi: 10.1093/pcp/pcaa107

Islam, M. M., Ye, W., Matsushima, D., Munemasa, S., Okuma, E., Nakamura, Y., et al. (2016). Reactive carbonyl species mediate ABA signaling in guard cells. *Plant Cell Physiol.* 57, 2552–2563. doi: 10.1093/pcp/pcw166

Islam, M. M., Ye, W., Matsushima, D., Rhaman, M. S., Munemasa, S., Okuma, E., et al. (2019). Reactive carbonyl species function as signal mediators downstream of H2O2 production and regulate [Ca2+]cyt elevation in ABA signal pathway in *Arabidopsis* guard cells. *Plant Cell Physiol.* 60, 1146–1159. doi: 10.1093/pcpo/pcz031

Islam, W., Tayyab, M., Khalil, F., Hua, Z., Huang, Z., and Chen, H. (2020). Silicon-mediated plant defense against pathogens and insect pests. *Pestic. Biochem. Physiol.* 168:104641. doi: 10.1016/j.pestbp.2020.104641

Jagodzik, P., Tajdel-Zielinska, M., Ciesla, A., Marczak, M., and Ludwikow, A. (2018). Mitogen-activated protein kinase cascades in plant hormone signaling. *Front. Plant Sci.* 9:1387. doi: 10.3389/fpls.2018.01387

Jalakas, P., Huang, Y. C., Yeh, Y. H., Zimmerli, L., Merilo, E., Kollist, H., et al. (2017). The role of ENHANCED RESPONSES TO ABA1 (ERA1) in *Arabidopsis stomatal* responses is beyond ABA signaling. *Plant Physiol.* 174, 665–671. doi: 10.1104/pp.17.00220

Jia, Q., Kong, D., Li, Q., Sun, S., Song, J., Zhu, Y., et al. (2019). The function of inositol phosphatases in plant tolerance to abiotic stress. *Int. J. Mol. Sci.* 20:3999. doi: 10.3390/ijms20163999

Jiang, C. J., Shimono, M., Sugano, S., Kojima, M., Yazawa, K., Yoshida, R., et al. (2010). Abscisic acid interacts antagonistically with salicylic acid signaling pathway in rice-*Magnaporthe grisea* interaction. *Mol. Plant Microbe Interact.* 23, 791–798. doi: 10.1094/MPMI-23-6-0791

Jiang, F., and Hartung, W. (2008). Long-distance signalling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal. *J. Exp. Bot.* 59, 37–43. doi: 10.1093/jxb/erm127

Jin, Z., Xue, S., Luo, Y., Tian, B., Fang, H., Li, H., et al. (2013). Hydrogen sulfide interacting with abscisic acid in stomatal regulation responses to drought stress in *Arabidopsis*. *Plant Physiol. Biochem.* 62, 41–46. doi: 10.1016/j.plaphy.2012.10.017

Kadota, Y., Sklenar, J., Derbyshire, P., Stransfeld, L., Asai, S., Ntoukakis, V., et al. (2014). Direct regulation of the NADPH oxidase RBOHD by the PRR-associated kinase BIK1 during plant immunity. *Mol. Cell* 54, 43–55. doi: 10.1016/j.molcel.2014.02.021

Karimi, R. (2019). Spring frost tolerance increase in *Sultana grapevine* by early season application of calcium sulfate and zinc sulfate. *J. Plant Nutr.* 42, 2666–2681.

Khare, S., Singh, N. B., Singh, A., Hussain, I., Niharika, K., Yadav, V., et al. (2020). Plant secondary metabolites synthesis and their regulations under biotic and abiotic constraints. *J. Plant Biol.* 63, 203–216. doi: 10.1007/s12374-020-09245-7

Khokon, A. R., Okuma, E., Hossain, M. A., Munemasa, S., Uraji, M., Nakamura, Y., et al. (2011). Involvement of extracellular oxidative burst in salicylic acid-induced stomatal closure in *Arabidopsis*. *Plant Cell Environ.* 34, 434–443.

Khokon, M., Salam, M. A., Jammes, F., Ye, W., Hossain, M. A., Okuma, E., et al. (2017). MPK9 and MPK12 function in SA-induced stomatal closure in *Arabidopsis thaliana*. *Biosci. Biotechnol. Biochem.* 81, 1394–1400. doi: 10.1080/09168451.2017.1308244

Khokon, M. A., Hossain, M. A., Munemasa, S., Uraji, M., Nakamura, Y., Mori, I. C., et al. (2010). Yeast elicitor-induced stomatal closure and peroxidase-mediated ROS production in *Arabidopsis. Plant Cell Physiol.* 51, 1915–1921. doi: 10.1093/pcp/pcq145

Khokon, M. A., Jahan, M. S., Rahman, T., Hossain, M. A., Muroyama, D., Minami, I., et al. (2011). Allyl isothiocyanate (AITC) induces stomatal closure in *Arabidopsis. Plant Cell Environ.* 34, 1900–1906.

Klessig, D. F., Choi, H. W., and Dempsey, D. A. (2018). Systemic acquired resistance and salicylic acid: past, present, and future. *Mol. Plant Microbe Interact.* 31, 871–888. doi: 10.1094/MPMI-03-18-0067-CR

Klüsener, B., Young, J. J., Murata, Y., Allen, G. J., Mori, I. C., Hugouvieux, V., et al. (2002). Convergence of calcium signaling pathways of pathogenic elicitors and abscisic acid in *Arabidopsis* guard cells. *Plant Physiol.* 130, 2152–2163. doi: 10.1104/pp.012187

Kolbert, Z., Feigl, G., Freschi, L., and Poór, P. (2019). Gasotransmitters in action: nitric oxide-ethylene crosstalk during plant growth and abiotic stress responses. *Antioxidants* 8:167. doi: 10.3390/antiox8060167

Kolupaev, Y. E., Karpets, Y. V., Beschasniy, S. P., and Dmitriev, A. P. (2019). Gasotransmitters and their role in adaptive reactions of plant cells. *Cytol. Genet.* 53, 392–406. doi: 10.3103/S0095452719050098

Konstantinos, P. A., Imene, T., Panagiotis, M. N., and Roubelakis-Angelakis, K. A. (2010). ABA-dependent amine oxidases-derived H2O2 affects stomata conductance. *Plant Signal Behav.* 5, 1153–1156. doi: 10.4161/psb.5.9.12679

Koo, Y. M., Heo, A. Y., and Choi, H. W. (2020). Salicylic acid as a safe plant protector and growth regulator. *Plant Pathol. J.* 36, 1–10. doi: 10.5423/PPJ.RW.12.2019.0295

Kumar, I., and Sharma, R. K. (2018). Production of secondary metabolites in plants under abiotic stress: an overview. *Significan. Bioeng. Biosci.* 2, 1–5. doi: 10.31031/SBB.2018.02.000545

Kumar, M., Kesawat, M. S., Ali, A., Lee, S. C., Gill, S. S., and Kim, A. (2019). Integration of abscisic acid signaling with other signaling pathways in plant stress responses and development. *Plants* 8:592. doi: 10.3390/plants8120592

Kurusu, T., Mitsuka, D., Yagi, C., Kitahata, N., Tsutsui, T., Ueda, T., et al. (2018). Involvement of S-type anion channels in disease resistance against an oomycete pathogen in *Arabidopsis* seedlings. *Commun. Integr. Biol.* 11, 1–6. doi: 10.1080/19420889.2018.1495007

Lamers, J., van der Meer, T., and Testerink, C. (2020). How plants sense and respond to stressful environments. *Plant Physiol.* 182, 1624–1635. doi: 10.1104/pp.19.01464

Lee, Choi, H., Suh, S., Doo, I. S., Oh, K. Y., Choi, E. J., et al. (1999). Oligogalacturonic acid and chitosan reduce stomatal aperture by inducing the evolution of reactive oxygen species from guard cells of tomato and *Commelina communis. Plant Physiol.* 121, 147–152. doi: 10.1104/pp.121.1.147

Lee, S., Rojas, C. M., Ishiga, Y., Pandey, S., and Mysore, K. S. (2013). Arabidopsis heterotrimeric G-proteins play a critical role in host and nonhost resistance against *Pseudomonas* syringae pathogens. *PLoS One* 8:e82445. doi: 10.1371/journal.pone.0082445

Lee, S. C., and Luan, S. (2012). ABA signal transduction at the crossroad of biotic and abiotic stress responses. *Plant Cell Environ.* 35, 53–60. doi: 10.1111/j.1365-3040.2011.02426.x

León, J., Castillo, M. C., Coego, A., Lozano-Juste, J., and Mir, R. (2014). Diverse functional interactions between nitric oxide and abscisic acid in plant development and responses to stress. *J. Exp. Bot.* 65, 907–921. doi: 10.1093/jxb/ert454

Lewandowska, M., Keyl, A., and Feussner, I. (2020). Wax biosynthesis in response to danger: its regulation upon abiotic and biotic stress. *New Phytol.* 227, 698–713. doi: 10.1111/nph.16571

Li, J., and Wang, X. (2019). Phospholipase D and phosphatidic acid in plant immunity. *Plant Sci.* 279, 45–50. doi: 10.1016/j.plantsci.2018.05.021

Lim, C. W., Baek, W., Jung, J., Kim, J. H., and Lee, S. C. (2015). Function of ABA in stomatal defense against biotic and drought stresses. *Int. J. Mol. Sci.* 16, 15251–15270. doi: 10.3390/ijms160715251

Liu, J., Elmore, J. M., Fuglsang, A. T., Palmgren, M. G., Staskawicz, B. J., and Coaker, G. (2009). RIN4 functions with plasma membrane H+-ATPases to regulate stomatal apertures during pathogen attack. *PLoS Biol.* 7:e1000139. doi: 10.1371/journal.pbio.1000139

Liu, X., Afrin, T., and Pajerowska-Mukhtar, K. M. (2019). Arabidopsis GCN2 kinase contributes to ABA homeostasis and stomatal immunity. *Commun. Biol.* 2:302. doi: 10.1038/s42003-019-0544-x

Lu, Y., Chen, Q., Bu, Y., Luo, R., Hao, S., Zhang, J., et al. (2017). Flavonoid accumulation plays an important role in the rust resistance of Malus plant leaves. *Front. Plant Sci.* 8:1286. doi: 10.3389/fpls.2017.01286

Luna, E., Pastor, V., Robert, J., Flors, V., Mauch-Mani, B., and Ton, J. (2011). Callose deposition: a multifaceted plant defense response. *Mol. Plant Microbe Interact.* 24, 183–193. doi: 10.1094/MPMI-07-10-0149

Lv, S., Zhang, Y., Li, C., Liu, Z., Yang, N., Pan, L., et al. (2018). Strigolactone-triggered stomatal closure requires hydrogen peroxide synthesis and nitric oxide production in an abscisic acid-independent manner. *New Phytol.* 217, 290–304. doi: 10.1111/nph.14813

Ma, Y., and Berkowitz, G. A. (2016). NO and Ca2+: critical components of cytosolic signaling systems involved in stomatal immune responses. *Adv. Bot. Res.* 77, 285–323. doi: 10.1016/bs.abr.2015.11.001

Ma, Y., Cao, J., He, J., Chen, Q., Li, X., and Yang, Y. (2018). Molecular mechanism for the regulation of ABA homeostasis during plant development and stress responses. *Int. J. Mol. Sci.* 19:3643. doi: 10.3390/ijms19113643

Maksimov, I. V. (2009). Abscisic acid in the plants-pathogen interaction. *Russ. J. Plant Physiol.* 56:742. doi: 10.1134/S102144370906003X

Malcheska, F., Ahmad, A., Batool, S., Müller, H. M., Ludwig-Müller, J., Kreuzwieser, J., et al. (2017). Drought-enhanced xylem sap sulfate closes stomata by affecting ALMT12 and guard cell ABA synthesis. *Plant Physiol.* 174, 798–814. doi: 10.1104/pp.16.01784

Manthe, B., Schulz, M., and Schnabl, H. (1992). Effects of salicylic acid on growth and stomatal movements of *Vicia faba* L.: evidence for salicylic acid metabolization. *J. Chem. Ecol.* 18, 1525–1539. doi: 10.1007/BF00993226

Mazid, M., Khan, T. A., and Mohammad, F. (2011). Role of secondary metabolites in defense mechanisms of plants. *Biol. Med.* 3, 232–249.

McAdam, S., and Sussmilch, F. C. (2020). The evolving role of abscisic acid in cell function and plant development over geological time. *Semin. Cell Dev. Biol.* 109, 39–45. doi: 10.1016/j.semcdb.2020.06.006

McLachlan, D. H., Kopischke, M., and Robatzek, S. (2014). Gate control: guard cell regulation by microbial stress. *New Phytol.* 203, 1049–1063. doi: 10.1111/nph.12916

Mekonnen, D. W., Flügge, U. I., and Ludewig, F. (2016). Gamma-aminobutyric acid depletion affects stomata closure and drought tolerance of *Arabidopsis thaliana. Plant Sci.* 245, 25–34. doi: 10.1016/j.plantsci.2016.01.005

Melotto, M., Underwood, W., and He, S. Y. (2008). Role of stomata in plant innate immunity and foliar bacterial diseases. *Annu. Rev. Phytopathol.* 46, 101–122. doi: 10.1146/annurev.phyto.121107.104959

Melotto, M., Underwood, W., Koczan, J., Nomura, K., and He, S. Y. (2006). Plant stomata function in innate immunity against bacterial invasion. *Cell* 126, 969–980. doi: 10.1016/j.cell.2006.06.054

Melotto, M., Zhang, L., Oblessuc, P. R., and He, S. Y. (2017). Stomatal defense a decade later. *Plant Physiol.* 174, 561–571. doi: 10.1104/pp.16.01853

Mendgen, K., Hahn, M., and Deising, H. (1996). Morphogenesis and mechanisms of penetration by plant pathogenic fungi. *Ann. Rev. Phytopathol.* 34, 367–386.

Mishra, G., Zhang, W., Deng, F., Zhao, J., and Wang, X. A. (2006). Bifurcating pathway directs abscisic acid effects on stomatal closure and opening in *Arabidopsis. Science* 312, 264–266. doi: 10.1126/science

Moeder, W., Phan, V., and Yoshioka, K. (2019). Ca2+ to the rescue – Ca2+ channels and signaling in plant immunity. *Plant Sci.* 279, 19–26. doi: 10.1016/j.plantsci.2018.04.012

Mona, S. A., Hashem, A., Abd_Allah, E. F., Alqarawi, A. A., Soliman, D. W. K., Wirth, S., et al. (2017). Increased resistance of drought by *Trichoderma harzianum* fungal treatment correlates with increased secondary metabolites and proline content. *J. Integr. Agric.* 16, 1751–1757. doi: 10.1016/S2095-3119(17)61695-2

Montillet, J. L., Leonhardt, N., Mondy, S., Tranchimand, S., Rumeau, D., Boudsocq, M., et al. (2013). An abscisic acid-independent oxylipin pathway controls stomatal closure and immune defense in *Arabidopsis. PLoS Biol.* 11:e1001513. doi: 10.1371/journal.pbio.1001513

Munemasa, S., Hauser, F., Park, J., Waadt, R., Brandt, B., and Schroeder, J. I. (2015). Mechanisms of abscisic acid-mediated control of stomatal aperture. *Curr. Opin. Plant Biol.* 28, 154–162. doi: 10.1016/j.pbi.2015.10.010

Munemasa, S., Oda, K., Watanabe-Sugimoto, M., Nakamura, Y., Shimoishi, Y., and Murata, Y. (2007). The coronatine-insensitive 1 mutation reveals the hormonal signaling interaction between abscisic acid and methyl jasmonate in *Arabidopsis* guard cells. Specific impairment of ion channel activation and second messenger production. *Plant Physiol.* 143, 1398–1407. doi: 10.1104/pp. 106.091298

Murcia, G., Fontana, A., Pontin, M., Baraldi, R., Bertazza, G., and Piccoli, P. N. (2017). ABA and GA3 regulate the synthesis of primary and secondary metabolites related to alleviation from biotic and abiotic stresses in grapevine. *Phytochemistry* 135, 34–52. doi: 10.1016/j.phytochem.2016.12.007

Nakashima, K., Yamaguchi-Shinozaki, K., and Shinozaki, K. (2014). The transcriptional regulatory network in the drought response and its crosstalk in abiotic stress responses including drought, cold, and heat. *Front. Plant Sci.* 5:170. doi: 10.3389/fpls.2014.00170

Narula, K., Elagamey, E., Abdellatef, M., Sinha, A., Ghosh, S., Chakraborty, N., et al. (2020). Chitosan-triggered immunity to Fusarium in chickpea is associated with changes in the plant extracellular matrix architecture, stomatal closure and remodeling of the plant metabolome and proteome. *Plant J.* 103, 561–583. doi: 10.1111/tpj.1475

Nejat, N., and Mantri, N. (2017). Plant immune system: crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. *Curr. Issues Mol. Biol.* 23, 1–16. doi: 10.21775/cimb. 023.001

Ng, C. K., Carr, K., McAinsh, M. R., Powell, B., and Hetherington, A. M. (2001). Drought-induced guard cell signal transduction involves sphingosine-1-phosphate. *Nature* 410, 596–599. doi: 10.1038/35069092

Nguyen, D., D'Agostino, N., Tytgat, T. O., Sun, P., Lortzing, T., Visser, E. J., et al. (2016). Drought and flooding have distinct effects on herbivore-induced responses and resistance in *Solanum dulcamara*. *Plant Cell Environ.* 39, 1485–1499. doi: 10.1111/pce.12708

Niu, M., Xie, J., Chen, C., Cao, H., Sun, J., Kong, Q., et al. (2018). An early ABA-induced stomatal closure, Na+ sequestration in leaf vein and K+ retention in mesophyll confer salt tissue tolerance in *Cucurbita* species. *J. Exp. Bot.* 69, 4945–4960. doi: 10.1093/jxb/ery251

Novák, J., Pavlů, J., Novák, O., Nožková-Hlaváčková, V., Špundová, M., Hlavinka, J., et al. (2013). High cytokinin levels induce a hypersensitive-like response in tobacco. *Ann. Bot.* 112, 41–55. doi: 10.1093/aob/mct092

Oide, S., Bejai, S., Staal, J., Guan, N., Kaliff, M., and Dixelius, C. (2013). A novel role of PR2 in abscisic acid (ABA) mediated, pathogen-induced callose deposition in *Arabidopsis thaliana*. *New Phytol.* 200, 1187–1199. doi: 10.1111/nph. 12436

Pál, M., Tajti, J., Szalai, G., Peeva, V., Végh, B., and Janda, T. (2018). Interaction of polyamines, abscisic acid and proline under osmotic stress in the leaves of wheat plants. *Sci. Rep.* 8:12839. doi: 10.1038/s41598-018-31297-6

Pantin, F., and Blatt, M. R. (2018). Stomatal response to humidity: blurring the boundary between active and passive movement. *Plant Physiol.* 176, 485–488. doi: 10.1104/pp.17.01699

Petrov, V., Hille, J., Mueller-Roeber, B., and Gechev, T. S. (2015). ROS-mediated abiotic stress-induced programmed cell death in plants. *Front. Plant Sci.* 6:69. doi: 10.3389/fpls.2015.00069

Planchet, E., Verdu, I., Delahaie, J., Cukier, C., Girard, C., Morère-Le Paven, M. C., et al. (2014). Abscisic acid-induced nitric oxide and proline accumulation in independent pathways under water-deficit stress during seedling establishment in *Medicago truncatula*. *J. Exp. Bot.* 65, 2161–2170. doi: 10.1093/jxb/eru088

Prats, E., Gay, A. P., Mur, L. A., Thomas, B. J., and Carver, T. L. (2006). Stomatal lock-open, a consequence of epidermal cell death, follows transient suppression of stomatal opening in barley attacked by *Blumeria graminis*. *J. Exp. Bot.* 57, 2211–2226. doi: 10.1093/jxb/erj186

Prodhan, M. Y., Munemasa, S., Nahar, M. N., Nakamura, Y., and Murata, Y. (2018). Guard cell salicylic acid signaling is integrated into abscisic acid signaling via the Ca2+/CPK-dependent pathway. *Plant Physiol.* 178, 441–450. doi: 10.1104/pp.18.00321

Prodhan, Y., Issak, M., Munemasa, S., Nakamura, Y., and Murata, Y. (2020). Salicylic acid receptor NPR1 is involved in guard cell chitosan signaling. *Biosci. Biotechnol. Biochem.* 84, 963–969. doi: 10.1080/09168451.2020.1718485

Puli, M. R., and Raghavendra, A. S. (2012). Pyrabactin, an ABA agonist, induced stomatal closure and changes in signalling components of guard cells in abaxial epidermis of *Pisum sativum*. *J. Exp. Bot.* 63, 1349–1356. doi: 10.1093/jxb/err364

Qamar, A., Mysore, K. S., and Senthil-Kumar, M. (2015). Role of proline and pyrroline-5-carboxylate metabolism in plant defense against invading pathogens. *Front. Plant Sci.* 6:503. doi: 10.3389/fpls.2015.00503

Qi, J., Song, C. P., Wang, B., Zhou, J., Kangasjärvi, J., Zhu, J. K., et al. (2018). Reactive oxygen species signaling and stomatal movement in plant responses to drought stress and pathogen attack. *J. Integr. Plant Biol.* 60, 805–826. doi: 10.1111/jipb.12654

Raghavendra, A. S., Gonugunta, V. K., Christmann, A., and Grill, E. (2010). ABA perception and signalling. *Trends Plant Sci.* 15, 395–401. doi: 10.1016/j.tplants. 2010.04.006

Raghavendra, A. S., and Reddy, K. B. (1987). Action of proline on stomata differs from that of abscisic acid, G-substances, or methyl jasmonate. *Plant Physiol.* 83, 732–734. doi: 10.1104/pp.83.4.732

Robert-Seilaniantz, A., Grant, M., and Jones, J. D. (2011). Hormone crosstalk in plant disease and defense: more than just jasmonate-salicylate antagonism. *Ann. Rev. Phytopathol.* 49, 317–343. doi: 10.1146/annurev-phyto-073009-114447

Rodrigues, O., Reshetnyak, G., Grondin, A., Saijo, Y., Leonhardt, N., Maurel, C., et al. (2017). Aquaporins facilitate hydrogen peroxide entry into guard cells to mediate ABA- and pathogen-triggered stomatal closure. *Proc. Natl. Acad. Sci. U.S.A.* 114, 9200–9205. doi: 10.1073/pnas.1704754114

Romero-Puertas, M. C., Perazzolli, M., Zago, E. D., and Delledonne, M. (2004). Nitric oxide signalling functions in plant-pathogen interactions. *Cell Microbiol.* 6, 795–803. doi: 10.1111/j.1462-5822.2004.00428.x

Sadhu, A., Moriyasu, Y., Acharya, K., and Bandyopadhyay, M. (2019). Nitric oxide and ROS mediate autophagy and regulate *Alternaria alternata* toxin-induced cell death in tobacco BY-2 cells. *Sci. Rep.* 9:8973. doi: 10.1038/s41598-019-45470-y

Saijo, Y., and Loo, E. P. (2020). Plant immunity in signal integration between biotic and abiotic stress responses. *New Phytol.* 225, 87–104. doi: 10.1111/nph.15989

Saito, S., and Uozumi, N. (2019). Guard cell membrane anion transport systems and their regulatory components: An elaborate mechanism controlling stress-induced stomatal closure. *Plants* 8:9. doi: 10.3390/plants8010009

Salam, M. A., Jammes, F., Hossain, M. A., Ye, W., Nakamura, Y., Mori, I., et al. (2013). Two guard cell-preferential MAPKs, MPK9 and MPK12, regulate YEL signalling in *Arabidopsis* guard cells. *Plant Biol.* 15, 436–442.

Salam, M. A., Jammes, F., Hossain, M. A., Ye, W., Nakamura, Y., Mori, I. C., et al. (2012). MAP kinases, MPK9 and MPK12, regulate chitosan-induced stomatal closure. *Biosci. Biotechnol. Biochem.* 76, 1785–1787. doi: 10.1271/bbb.1 20228

Sato, H., Takasaki, H., Takahashi, F., Suzuki, T., Iuchi, S., Mitsuda, N., et al. (2018). *Arabidopsis thaliana* NGATHA1 transcription factor induces ABA biosynthesis by activating NCED3 gene during dehydration stress. *Proc. Natl. Acad. Sci. U.S.A.* 115, E11178–E11187. doi: 10.1073/pnas.1811491115

Savchenko, T., Kolla, V. A., Wang, C. Q., Nasafi, Z., Hicks, D. R., Phadungchob, B., et al. (2014). Functional convergence of oxylipin and abscisic acid pathways controls stomatal closure in response to drought. *Plant Physiol.* 164, 1151–1160. doi: 10.1104/pp.113.234310

Savouré, A., Hua, X. J., Bertauche, N., Van Montagu, M., and Verbruggen, N. (1997). Abscisic acid-independent and abscisic acid-dependent regulation of proline biosynthesis following cold and osmotic stresses in *Arabidopsis thaliana*. *Mol. Gen. Genet.* 254, 104–109. doi: 10.1007/s004380050397

Schmidt, K., Pflugmacher, M., Klages, S., Mäser, A., Mock, A., and Stahl, D. J. (2008). Accumulation of the hormone abscisic acid (ABA) at the infection site of the fungus *Cercospora beticola* supports the role of ABA as a repressor of plant defence in sugar beet. *Mol. Plant Pathol.* 9, 661–673. doi: 10.1111/j.1364-3703.2008.00491.x

Schulze-Lefert, P., and Robatzek, S. (2006). Plant pathogens trick guard cells into opening the gates. *Cell* 126, 831–834. doi: 10.1016/j.cell.2006.08.020

Scuffi, D., Lamattina, L., and García-Mata, C. (2016). Gasotransmitters and stomatal closure: is there redundancy, concerted action, or both? *Front. Plant Sci.* 7:277. doi: 10.3389/fpls.2016.00277

Sewelam, N., Kazan, K., and Schenk, P. M. (2016). Global plant stress signaling: reactive oxygen species at the cross-road. *Front. Plant Sci.* 7:187. doi: 10.3389/fpls.2016.00187

Shafiei, R., Hang, C., Kang, J. G., and Loake, G. J. (2007). Identification of loci controlling non-host disease resistance in *Arabidopsis* against the leaf rust pathogen *Puccinia triticina. Mol. Plant Pathol.* 8, 773–784. doi: 10.1111/j.1364-3703.2007.00431.x

Shen, J., Diao, W., Zhang, L., Acharya, B. R., Wang, M., Zhao, X., et al. (2020). Secreted peptide PIP1 induces stomatal closure by activation of guard cell anion channels in *Arabidopsis. Front. Plant Sci.* 11:1029. doi: 10.3389/fpls.2020.01029

Shi, H., Ye, T., Han, N., Bian, H., Liu, X., and Chan, Z. (2015). Hydrogen sulfide regulates abiotic stress tolerance and biotic stress resistance in *Arabidopsis. J. Integr. Plant Biol.* 57, 628–640. doi: 10.1111/jipb.12302

Sierla, M., Waszczak, C., Vahisalu, T., and Kangasjärvi, J. (2016). Reactive oxygen species in the regulation of stomatal movements. *Plant Physiol.* 171, 1569–1580. doi: 10.1104/pp.16.00328

Solanki, S., Ameen, G., Borowicz, P., and Brueggeman, R. S. (2019). Shedding light on penetration of cereal host stomata by wheat stem rust using improved methodology. *Sci. Rep.* 9:7939. doi: 10.1038/s41598-019-44280-6

Song, S., Huang, H., Gao, H., Wang, J., Wu, D., Liu, X., et al. (2014). 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, X. G., She, X. P., and Zhang, B. (2008). Carbon monoxide-induced stomatal closure in Vicia faba is dependent on nitric oxide synthesis. *Physiol. Plant.* 132, 514–525.

Srivastava, N., Gonugunta, V. K., Puli, M. R., and Raghavendra, A. S. (2009). Nitric oxide production occurs downstream of reactive oxygen species in guard cells during stomatal closure induced by chitosan in abaxial epidermis of *Pisum sativum. Planta* 229, 757–765. doi: 10.1007/s00425-008-0855-5

Staiger, D., Korneli, C., Lummer, M., and Navarro, L. (2013). Emerging role for RNA-based regulation in plant immunity. *New Phytol.* 197, 394–404. doi: 10.1111/nph.12022

Stewart, C. R. (1980). The mechanism of abscisic acid-induced proline accumulation in barley leaves. *Plant Physiol.* 66, 230–233. doi: 10.1104/pp.66.2.230

Su, J., Zhang, M., Zhang, L., Sun, T., Liu, Y., Lukowitz, W., et al. (2017). Regulation of stomatal immunity by interdependent functions of a pathogen-responsive MPK3/MPK6 cascade and abscisic acid. *Plant Cell* 29, 526–542. doi: 10.1105/tpc.16.00577

Suhita, D., Raghavendra, A. S., Kwak, J. M., and Vavasseur, A. (2004). Cytoplasmic alkalization precedes reactive oxygen species production during methyl jasmonate- and abscisic acid-induced stomatal closure. *Plant Physiol.* 134, 1536–1545. doi: 10.1104/pp.103.032250

Sun, L. R., Yue, C. M., and Hao, F. S. (2019). Update on roles of nitric oxide in regulating stomatal closure. *Plant Signal Behav.* 14:e1649569. doi: 10.1080/15592324.2019.1649569

Sussmilch, F. C., and McAdam, S. (2017). Surviving a dry future: abscisic acid (ABA)-mediated plant mechanisms for conserving water under low humidity. *Plants* 6:54. doi: 10.3390/plants6040054

Suzuki, N., and Katano, K. (2018). Coordination between ROS regulatory systems and other pathways under heat stress and pathogen attack. *Front. Plant Sci.* 9:490. doi: 10.3389/fpls.2018.00490

Takahashi, F., Suzuki, T., Osakabe, Y., Betsuyaku, S., Kondo, Y., Dohmae, N., et al. (2018). A small peptide modulates stomatal control via abscisic acid in long-distance signalling. *Nature* 556, 235–238. doi: 10.1038/s41586-018-0009-2

Tanaka, Y., Sano, T., Tamaoki, M., Nakajima, N., Kondo, N., and Hasezawa, S. (2005). Ethylene inhibits abscisic acid-induced stomatal closure in Arabidopsis. *Plant Physiol.* 138, 2337–2343. doi: 10.1104/pp.105.063503

Tao, Z. Q., Chen, Y. Q., Chao, L. I., Zou, J. X., Peng, Y. A. N., Yuan, S. F., et al. (2016). The causes and impacts for heat stress in spring maize during grain filling in the North China Plain-A review. *J. Integr. Agric.* 15, 2677–2687. doi: 10.1016/S2095-3119(16)61409-0

Tõldsepp, K., Zhang, J., Takahashi, Y., Sindarovska, Y., Hõrak, H., Ceciliato, P. H. O., et al. (2018). Mitogen-activated protein kinases MPK4 and MPK12 are key components mediating CO2 -induced stomatal movements. *Plant J.* 96, 1018–1035. doi: 10.1111/tpj.14087

Ulferts, S., Delventhal, R., Splivallo, R., Karlovsky, P., and Schaffrath, U. (2015). Abscisic acid negatively interferes with basal defence of barley against *Magnaporthe oryzae. BMC Plant Biol.* 15:7. doi: 10.1186/s12870-014-0409-x

Ullah, C., Tsai, C. J., Unsicker, S. B., Xue, L., Reichelt, M., Gershenson, J., et al. (2019). Salicylic acid activates poplar defense against the biotrophic rust fungus *Melampsora larici*-populina via increased biosynthesis of catechin and proanthocyanidins. *New Phytol.* 221, 960–975. doi: 10.1111/nph.15396

Uraji, M., Katagiri, T., Okuma, E., Ye, W., Hossain, M. A., Masuda, C., et al. (2012). Cooperative function of PLDδ and PLDα1 in abscisic acid-induced stomatal closure in *Arabidopsis. Plant Physiol.* 159, 450–460. doi: 10.1104/pp.112.195578

Vaidya, A. S., Helander, J., Peterson, F. C., Elzinga, D., Dejonghe, W., Kaundal, A., et al. (2019). Dynamic control of plant water use using designed ABA receptor agonists. *Science* 366:eaaw8848. doi: 10.1126/science.aaw8848

Verma, V., Ravindran, P., and Kumar, P. P. (2016). Plant hormone-mediated regulation of stress responses. *BMC Plant Biol.* 16:86. doi: 10.1186/s12870-016-0771-y

Vishwakarma, K., Upadhyay, N., Kumar, N., Yadav, G., Singh, J., Mishra, R. K., et al. (2017). Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. *Front. Plant Sci.* 8:161. doi: 10.3389/fpls.2017.00161

Wang, H. Q., Sun, L. P., Wang, L. X., Fang, X. W., Li, Z. Q., Zhang, F. F., et al. (2020). Ethylene mediates salicylic-acid-induced stomatal closure by controlling reactive oxygen species and nitric oxide production in *Arabidopsis. Plant Sci.* 294:110464. doi: 10.1016/j.plantsci.2020.110464

Wang, J., Song, L., Gong, X., Xu, J., and Li, M. (2020). Functions of jasmonic acid in plant regulation and response to abiotic stress. *Int. J. Mol. Sci.* 21:1446. doi: 10.3390/ijms21041446

Wang, M., and Liao, W. (2016). Carbon monoxide as a signaling molecule in plants. *Front. Plant Sci.* 7:572. doi: 10.3389/fpls.2016.00572

Wang, W., Wang, X., Huang, M., Cai, J., Zhou, Q., Dai, T., et al. (2018). Hydrogen peroxide and abscisic acid mediate salicylic acid-induced freezing tolerance in wheat. *Front. Plant Sci.* 9:1137. doi: 10.3389/fpls.2018.01137

Wang, W. H., Yi, X. Q., Han, A. D., Liu, T. W., Chen, J., and Wu, F. H. (2012). Calcium-sensing receptor regulates stomatal closure through hydrogen peroxide and nitric oxide in response to extracellular calcium in *Arabidopsis. J. Exp. Bot.* 63, 177–190. doi: 10.1093/jxb/err259

Wang, X., Kong, L., Zhi, P., and Chang, C. (2020). Update on cuticular wax biosynthesis and its roles in plant disease resistance. *Int. J. Mol. Sci.* 21:5514. doi: 10.3390/ijms21155514

Wendehenne, D., Durner, J., and Klessig, D. F. (2004). Nitric oxide: a new player in plant signalling and defence responses. *Curr. Opin. Plant Biol.* 7, 449–455. doi: 10.1016/j.pbi.2004.04.002

Wilkinson, S., and Davies, W. J. (2010). Drought, ozone, ABA and ethylene: new insights from cell to plant to community. *Plant Cell Environ.* 33, 510–525. doi: 10.1111/j.1365-3040.2009.02052.x

Wu, L., Chen, X., Ren, H., Zhang, Z., Zhang, H., Wang, J., et al. (2007). ERF protein JERF1 that transcriptionally modulates the expression of abscisic acid biosynthesis-related gene enhances the tolerance under salinity and cold in tobacco. *Planta* 226, 815–825. doi: 10.1007/s00425-007-0528-9

Wu, L., Wu, H., Chen, L., Zhang, H., and Gao, X. (2017). Induction of systemic disease resistance in *Nicotiana benthamiana* by the cyclodipeptides cyclo (l-Pro-l-Pro) and cyclo (d-Pro-d-Pro). *Mol. Plant Pathol.* 18, 67–74. doi: 10.1111/mpp.12381

Wu, Y., Deng, Z., Lai, J., Zhang, Y., Yang, C., Yin, B., et al. (2009). Dual function of *Arabidopsis* ATAF1 in abiotic and biotic stress responses. *Cell Res.* 19, 1279–1290. doi: 10.1038/cr.2009.108

Xu, X., Fang, P., Zhang, H., Chi, C., Song, L., Xia, X., et al. (2019). Strigolactones positively regulate defense against root-knot nematodes in tomato. *J. Exp. Bot.* 70, 1325–1337. doi: 10.1093/jxb/ery439

Xylogiannis, E., Sofo, A., Dichio, B., Montanaro, G., and Mininni, A. N. (2020). Root-to-shoot signaling and leaf water-use efficiency in peach trees under localized irrigation. *Agronomy* 10:437. doi: 10.3390/agronomy10030437

Yamasaki, H., and Cohen, M. F. (2006). NO signal at the crossroads: polyamine-induced nitric oxide synthesis in plants? *Trends Plant Sci.* 11, 522–524. doi: 10.1016/j.tplants.2006.09.009

Yang, C., Li, W., Cao, J., Meng, F., Yu, Y., Huang, J., et al. (2017). Activation of ethylene signaling pathways enhances disease resistance by regulating ROS and phytoalexin production in rice. *Plant J.* 89, 338–353. doi: 10.1111/tpj.13388

Yao, Y., Yang, Y., Li, C., Huang, D., Zhang, J., Wang, C., et al. (2019). Research progress on the functions of gasotransmitters in plant responses to abiotic stresses. *Plants (Basel)* 8:605. doi: 10.3390/plants8120605

Ye, W., Adachi, Y., Munemasa, S., Nakamura, Y., Mori, I. C., and Murata, Y. (2015). Open stomata 1 kinase is essential for yeast elicitor-induced stomatal closure in *Arabidopsis*. *Plant Cell Physiol.* 56, 1239–1248. doi: 10.1093/pcp/pcv051

Ye, W., Ando, E., Rhaman, M. S., Tahjib-Ul-Arif, M., Okuma, E., Nakamura, Y., et al. (2020a). Inhibition of light-induced stomatal opening by allyl isothiocyanate does not require guard cell cytosolic Ca2+ signaling. *J. Exp. Bot.* 71, 2922–2932. doi: 10.1093/jxb/eraa073

Ye, W., Munemasa, S., Shinya, T., Wu, W., Ma, T., Lu, J., et al. (2020b). Stomatal immunity against fungal invasion comprises not only chitin-induced stomatal closure but also chitosan-induced guard cell death. *Proc. Natl. Acad. Sci. U.S.A.* 117, 20932–20942. doi: 10.1073/pnas.1922319117

Ye, W., and Murata, Y. (2016). Microbe associated molecular pattern signaling in guard cells. *Front. Plant Sci.* 7:583. doi: 10.3389/fpls.2016.00583

Yoshida, T., Christmann, A., Yamaguchi-Shinozaki, K., Grill, E., and Fernie, A. R. (2019). Revisiting the basal role of ABA - roles outside of stress. *Trends Plant Sci.* 24, 625–635. doi: 10.1016/j.tplants.2019.04.008

You, J., and Chan, Z. (2015). ROS Regulation during abiotic stress responses in crop plants. *Front. Plant Sci.* 6:1092. doi: 10.3389/fpls.2015.01092

Yu, W., Zhao, R., Wang, L., Zhang, S., Li, R., Sheng, J., et al. (2019). ABA signaling rather than ABA metabolism is involved in trehalose-induced drought tolerance in tomato plants. *Planta* 250, 643–655. doi: 10.1007/s00425-019-03195-2

Zegada-Lizarazu, W., and Monti, A. (2019). Deep root growth, ABA adjustments and root water uptake response to soil water deficit in giant reed. *Ann. Bot.* 124, 605–616. doi: 10.1093/aob/mcz001

Zeng, W., Melotto, M., and He, S. Y. (2010). Plant stomata: a checkpoint of host immunity and pathogen virulence. *Curr. Opin. Biotechnol.* 21, 599–603. doi: 10.1016/j.copbio.2010.05.006

Zhang, H., Fang, Q., Zhang, Z., Wang, Y., and Zheng, X. (2009). The role of respiratory burst oxidase homologues in elicitor-induced stomatal closure and hypersensitive response in *Nicotiana benthamiana*. *J. Exp. Bot.* 60, 3109–3122. doi: 10.1093/jxb/erp146

Zhang, L., Takahashi, Y., Hsu, P. K., Kollist, H., Merilo, E., Krysan, P. J., et al. (2020). FRET kinase sensor development reveals SnRK2/OST1 activation by ABA but not by MeJA and high CO2 during stomatal closure. *eLife* 9:e56351. doi: 10.7554/eLife.56351

Zhang, L., Zhang, F., Melotto, M., Yao, J., and He, S. Y. (2017). Jasmonate signaling and manipulation by pathogens and insects. *J. Exp. Bot.* 68, 1371–1385. doi: 10.1093/jxb/erw478

Zhang, T. Y., Li, F. C., Fan, C. M., Li, X., Zhang, F. F., and He, J. M. (2017). Role and interrelationship of MEK1-MPK6 cascade, hydrogen peroxide and nitric oxide in darkness-induced stomatal closure. *Plant Sci.* 262, 190–199. doi: 10.1016/j.plantsci.2017.06.010

Zhang, X., Wang, X., Zhuang, L., Gao, Y., and Huang, B. (2019). Abscisic acid mediation of drought priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*) and *Arabidopsis*. *Physiol. Plant.* 167, 488–501. doi: 10.1111/ppl.12975

Zhao, Y., Gao, J., Im Kim, J., Chen, K., Bressan, R. A., and Zhu, J. K. (2017). Control of plant water use by ABA induction of senescence and dormancy: an overlooked lesson from evolution. *Plant Cell Physiol.* 58, 1319–1327. doi: 10.1093/pcp/pcx086

Zheng, X., Kang, S., Jing, Y., Ren, Z., Li, L., Zhou, J. M., et al. (2018). Danger-associated peptides close stomata by OST1-independent activation of anion channels in guard cells. *Plant Cell* 30, 1132–1146. doi: 10.1105/tpc.17.00701

Zhu, J. K. (2016). Abiotic stress signaling and responses in plants. *Cell* 167, 313–324. doi: 10.1016/j.cell.2016.08.029

APPENDIX

TABLE A1 | List of sentences used in the syntactic awareness task.

12-OPDA,	12-oxo-phytodienoic acid;
AAO,	Abscisic aldehyde oxidase;
ABA,	Abscisic acid;
ABI,	ABA insensitive;
AGB1,	Arabidopsis G β-subunit;
AITC,	Allyl isothiocyanate;
BABA,	β-aminobutyric acid;
COI1,	Coronatine insensitive1;
CPK,	Ca^{2+}-dependent protein kinases;
CTOS,	Chitin oligosaccharide;
EDS1,	Enhanced disease susceptibility;
ERA1,	Enhanced response to ABA1;
ET,	Ethylene;
GABA,	γ-aminobutyric acid;
GCN2,	General control non-depressible2;
H_2S,	Hydrogen sulfide;
IP3,	Inositol 1,4,5-triphosphate;
LCBK1,	Long-chain base kinase1;
LOX,	Lipoxygenase;
LPS,	Lipopolysaccharide;
MJ,	Methyl jasmonate;
MPK,	Mitogen-activated protein kinase;
OGA,	Oligogalacturonic acid;
OST,	Open stomata;
PA,	Phosphatidic acid;
PIP2/1,	PAMP-induced peptide 2/1;
PLD,	Phospholipase D;
RBOH-	Respiratory burst oxidase homologue;
RPF,	Regulation of pathogenicity factor;
S1P,	Sphingosine-1-phosphate;
SA,	Salicylic acid;
SL,	Strigolactone;
SLAC,	Slow anion channel;
YEL,	Yeast elicitor.