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REVIEW

The role of gasotransmitters in movement of stomata: mechanisms of action and importance for plant immunity

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Abstract

Stomatal guard cells are specialized epidermal cells regulating gas exchange. The ability to open or close in response to external and internal cues makes stomata a dynamic and fascinating system. Stomatal closure upon infection ensures restriction of pathogen entry into the plant and forms an essential component of innate immunity. The opening or closure of stomata is dependent on the turgidity or flaccidity of guard cells, respectively, facilitated by several signaling components, including reactive oxygen species, nitric oxide (NO) and Ca^{2+}. Among these, NO is the most extensively studied gasotransmitter. Its pivotal role in stomatal closure by modulating various downstream components as well as regulation of crucial proteins by post-translational modifications makes NO an essential factor. Two more gasotransmitters, carbon monoxide and hydrogen sulfide, also trigger stomatal closure. Other gaseous molecules, like ethylene, methane, sulfur dioxide, ozone, and CO_2, can modulate stomatal closure, but they are not considered strictly as gasotransmitters due to specific criteria. We review the signaling events in guard cells triggered by these gasotransmitters leading to stomatal closure. We point out the dual role of NO to promote stomatal closure and stomatal opening. Both NO and H_2S help in reinforcing the innate immunity against pathogen attack. Although there is extensive information on the mechanism of NO action on stomata, the enzymatic source of NO or CO is still ambiguous. Similarly, research is warranted to establish the relative importance of and interactions among the three main gasotransmitters. Further studies on gasotransmitters would answer the ambiguity about their functions and confirm if they can act independently.

Additional key words: carbon monoxide, guard cells, hydrogen sulfide, nitric oxide, signaling compounds.

Introduction

Given their immobile nature, plants have to adapt against a broad spectrum of stresses. Stomata play a crucial role in such adaptations (Hetherington and Woodward 2003). Stomata, the microscopic pores on the leaf surface, regulate not only CO_2 exchange and transpiration, but also restrict the entry of microbes into leaves. As a result, stomata are considered as essential components of plant innate immunity response, as their closure physically restricts further entry of pathogens (Melotto *et al.* 2017). The closing or opening of stomata is dependent on the pressure potential within guard cells (Underwood *et al.* 2007). Stomatal guard cells can sense and respond to environmental factors, plant hormones, and microbial elicitors (Alcázar *et al.* 2006, Acharya *et al.* 2009).

The process of stomatal closure involves an array of signalling components: phosphatases, kinases, and other secondary messengers, all of which lead to modulation of ion channels, and loss of cations/anions, leading to decrease in pressure potential in guard cells and stomatal closure (Munemasa *et al.* 2015, Agurla and Raghavendra 2016, Saito and Uozumi 2019). These events converge and diverge at specific points while keeping up a dynamic cross-talk among them. The major signalling components in guard cells are reactive oxygen species (ROS), nitric

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Abbreviations: ABA - abscisic acid, cADPR - cyclic ADP ribose, cGMP - cyclic guanosine monophosphate, ET - ethylene, HO - heme oxygenase, IP_3 - inositol 1,4,5-triphosphate, MeJA - methyl jasmonate, OST1 - open stomata1, PA - phosphatidic acid, PLC - phospholipase C, PLD - phospholipase D, PTM - post-translational modification(s), ROS - reactive oxygen species, SA - salicylic acid, SLAC - slow anion channel.

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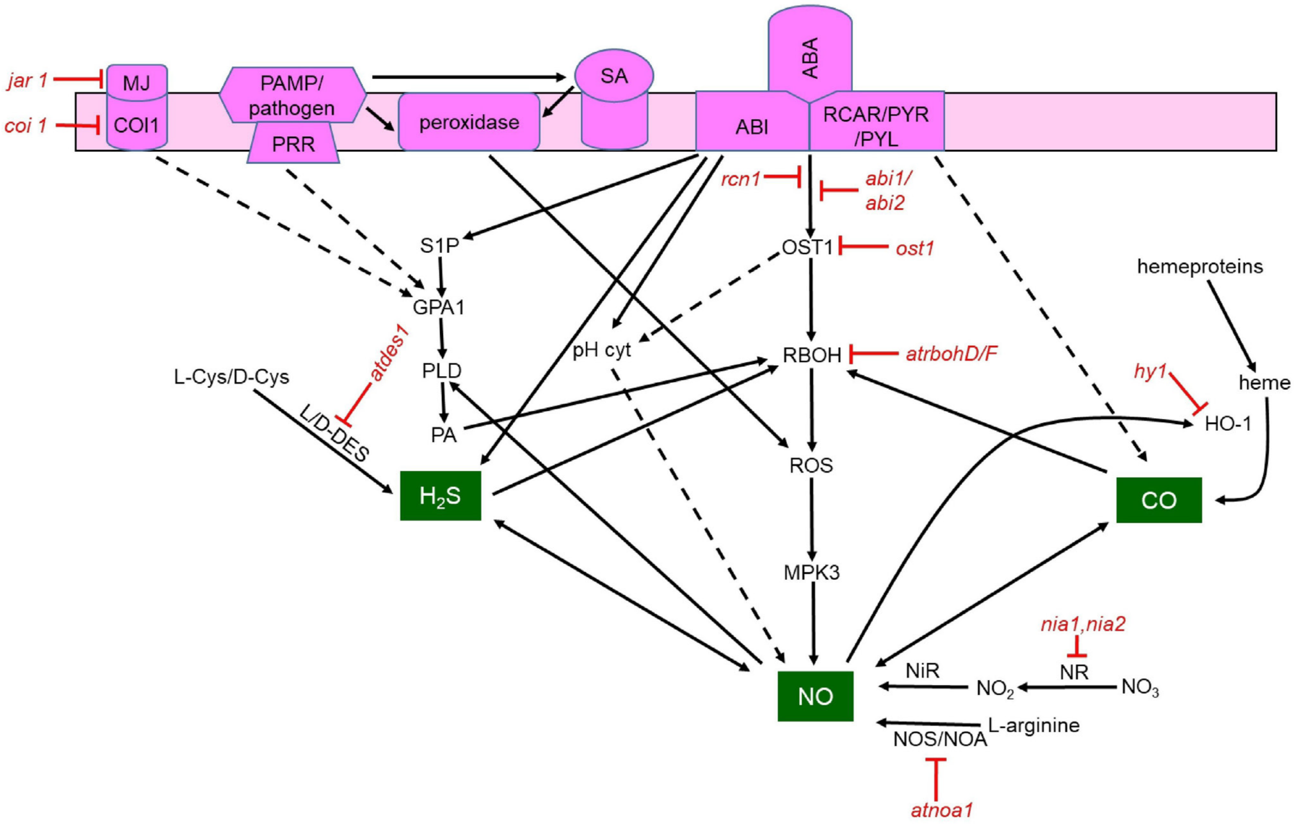

Fig. 1. A schematic representation of the events in guard cells leading to the production of the three typical gasotransmitters: nitric oxide (NO), carbon monoxide (CO), and hydrogen sulfide (H_2S). The guard cells sense hormones/elicitors by receptors and respond by activation of NADPH oxidase (RBOH) or peroxidase. As a result, the levels of reactive oxygen species (ROS) rise. A significant source of ROS in the guard cell is NADPH oxidase, modulated by open stomata 1 (OST1) kinase and phosphatidic acid (PA) produced from either phospholipase C or D (PLC/PLD). The ROS production can be facilitated also by peroxidase. The rise in ROS invariably increases the content of NO, a vital gasotransmitter, in guard cells. The source of NO in plant cells is debatable if produced from nitrate or L-arginine through nitrate/nitrite reductase (NR/NiR) or a nitric oxide synthase-like enzyme (NOS/NOA). A rise in cytosolic pH can also stimulate the content of ROS as well as NO, but the exact mechanism is not clear. The second gasotransmitter, CO, often considered as a co-modulator with NO, can stimulate NADPH oxidase, increase in ROS as well as NO. When present, NO up-regulates the enzyme heme oxygenase (HO) to enhance CO production in the guard cell. The third gasotransmitter, H_2S, is produced from L/D-cysteine by the action of enzyme L/D-cysteine desulfhydrase (L/D-DES). The production of three gasotransmitters appears to be quite interactive and mutually stimulative. Similarly, the rise in ROS content stimulates NO-production and *vice versa*. *Red arrows/letters* indicate the conclusions validated by *Arabidopsis* mutants (details listed in Table 1 Suppl). Other abbreviations: ABI - abscisic acid insensitive; COI - coronatine insensitive; GPA - G-protein alpha subunit; HO - heme oxygenase; L/D-DES - L/D-cysteine desulfhydrase; MJ - methyl jasmonate; MPK - mitogen activated protein kinase; NiR - nitrite reductase; NO - nitric oxide; NO2 - nitrite; NO3 - nitrate; NOA - nitric oxide associated ; NOS - nitric oxide synthase; OST - open stomata; PA - phosphatidic acid; PAMP - pathogen associated molecular pattern(s); PLC - phospholipase C; PLD - phospholipase D; PRR - pattern recognition receptor(s); RBOH - respiratory burst oxidase homolog; SA - salicylic acid; S1P - sphingosine-1-phosphate.

oxide (NO), cytosolic pH, and calcium (Ca^{2+}), which modulate ion channels (Raghavendra and Murata 2017, Agurla *et al.* 2018a). The rise in NO in guard cells is an essential event during stomatal closure (Fig. 1). Several compounds induce NO production: plant hormones [abscisic acid (ABA), ethylene (ET), and methyl jasmonate (MeJA)], elicitors [salicylic acid (SA), cryptogein, harpin, flagellin22, and chitosan], environmental factors (darkness, CO_2, ultraviolet-B radiation) and even polyamines (Table 1). There have been several reviews on the role of NO in plants, emphasizing the importance of NO in plants, particularly in stomatal closure (Agurla and Raghavendra 2016, Agurla *et al.* 2018a, Hancock and Neill 2019, Kolbert *et al.* 2019a, b).

Since the past two decades, the role of gasotransmitters in modulating stomatal closure, as a part of plant innate immunity response to protect against biotic/abiotic stress conditions has drawn considerable attention (García-Mata and Lamattina 2013, Scuffi *et al.* 2016, Yao *et al.* 2019). Examples of such gasotransmitters that induce stomatal closure are NO, carbon monoxide (CO) and hydrogen sulfide (H_2S). Gasotransmitters have to fulfill specific criteria, such as small size, ability to pass freely across the biological membranes, no involvement of receptors, specific effects at physiological concentration, enzymatic and regulated production, specific molecular targets, and finally the application of their donors can mimic their functions (Wang *et al.* 2002). There are other gaseous molecules known to mediate stomatal closure, but are not considered as typical gasotransmitters (see the section on "Stomatal regulation by ethylene and other gaseous molecules").

This article presents an account of gasotransmitters operating in plants, with particular emphasis on stomatal closure. Our primary focus has been on NO, CO, and H_2S. The ability of other gaseous molecules, like sulfur dioxide (SO_2), ozone (O_3), or ethylene (ET), is pointed out, though these gases are not considered strictly as "gasotransmitters". The interactions among the gasotransmitters, as well as with other signalling components, are highlighted. Finally, concluding remarks are made to emphasize the need for further research on this fascinating topic.

Nitric oxide: dual effects

Nitric oxide is a vital secondary messenger in various signalling pathways during plant responses to stress (Fancy *et al.* 2017). On exposure to stress conditions, the elevated ROS amount in guard cells can stimulate NO production and promote stomatal closure. Accumulation of NO in guard cells appears to be essential for abscisic acid (ABA)-induced stomatal closure (Gayatri *et al.* 2013). Elevated NO releases phosphatidic acid (PA), which can activate NADPH oxidase, to promote ROS production and stomatal closure (Distefano *et al.* 2008). Parallelly, NO can elevate cytosolic free Ca^{2+}, which modulates ion channels, loss of cations/anions from guard cells, and stomatal closure.

Table 1. Nitric oxide (NO) production and associated events triggered by different compounds/factors in guard cells leading to stomatal closure. MPK - mitogen activated protein kinase, NIA1 - nitrate reductase 1, OST - open stomata, ROS - reactive oxygen species, S1P - sphingosine-1-phosphate.

Inducer	Plant	Observation	Reference
Hormones and elicitors			
Abscisic acid (ABA)	*Pisum sativum*	rise in pH precedes the NO increase	Gonugunta *et al.* 2008
Salicylic acid (SA)	*Arabidopsis thaliana*	promotion of nitric oxide synthesis	Sun *et al.* 2010
Methyl jasmonate (MeJA)	*Arabidopsis thaliana*	rise in ROS and NO	Munemasa *et al.* 2007
Strigolactone (SL)	*Arabidopsis thaliana*	marked increase in ROS as well as NO	Lv *et al.* 2018
Ethylene	*Arabidopsis thaliana*	rise in the cytosolic pH precedes NO production	Liu *et al.* 2010
Cryptogein, harpin (Microbial elicitors)	*Arabidopsis thaliana*	rise in ROS and NO	Gayatri *et al.* 2017
Flagellin22 (flg22)	*Arabidopsis thaliana*	activation of OST1	Melotto *et al.* 2006
Chitosan	*Solanum lycopersicum*	production of ROS as well as NO	Czékus *et al.* 2020
Lipopolysaccharides (LPS)	*Arabidopsis thaliana*	induces NO production	Melotto *et al.* 2006
Yeast elicitor (YEL)	*Arabidopsis thaliana*	peroxidase dependent ROS production and subsequent NO rise	Khokon *et al.* 2010
Other compounds			
Cyclodipeptides (made of two residues of proline)	*Nicotiana benthamiana*	ROS and NO production and enhancement of cytosolic Ca2+	Wu *et al.* 2017
Polyamines (putrescine, spermine, spermidine)	*Arabidopsis thaliana*	increase in ROS, followed by NO	Agurla *et al.* 2018b
Allyl isothiocyanate (AITC)	*Vicia faba*	peroxidase dependent ROS production, and rise in NO	Sobahan *et al.* 2015
Alkalinizer (methylamine)	*Pisum sativum*	cytosolic alkalinization promotes the rise in NO	Gonugunta *et al.* 2008
Sphingolipids (phyto-S1P, S1P)	*Pisum sativum*	marked rise in pH as well as NO	Puli *et al.* 2016
Hydrogen peroxide	*Arabidopsis thaliana*	stimulation of NO synthesis	Bright *et al.* 2006
Bicarbonate	*Pisum sativum*	NO production mediated by NOS-like enzyme	Kolla and Raghavendra 2007
Environmental factors			
Ambient CO2	*Solanum lycopersicum*	rise in ROS and NO	Shi *et al.* 2015c
Ultraviolet-B (UV-B)	*Arabidopsis thaliana*	MPK6 activation and rise in ROS and NO	Li *et al.* 2017
Darkness	*Arabidopsis thaliana*	NIA1 dependent NO rise	Zhang *et al.* 2017

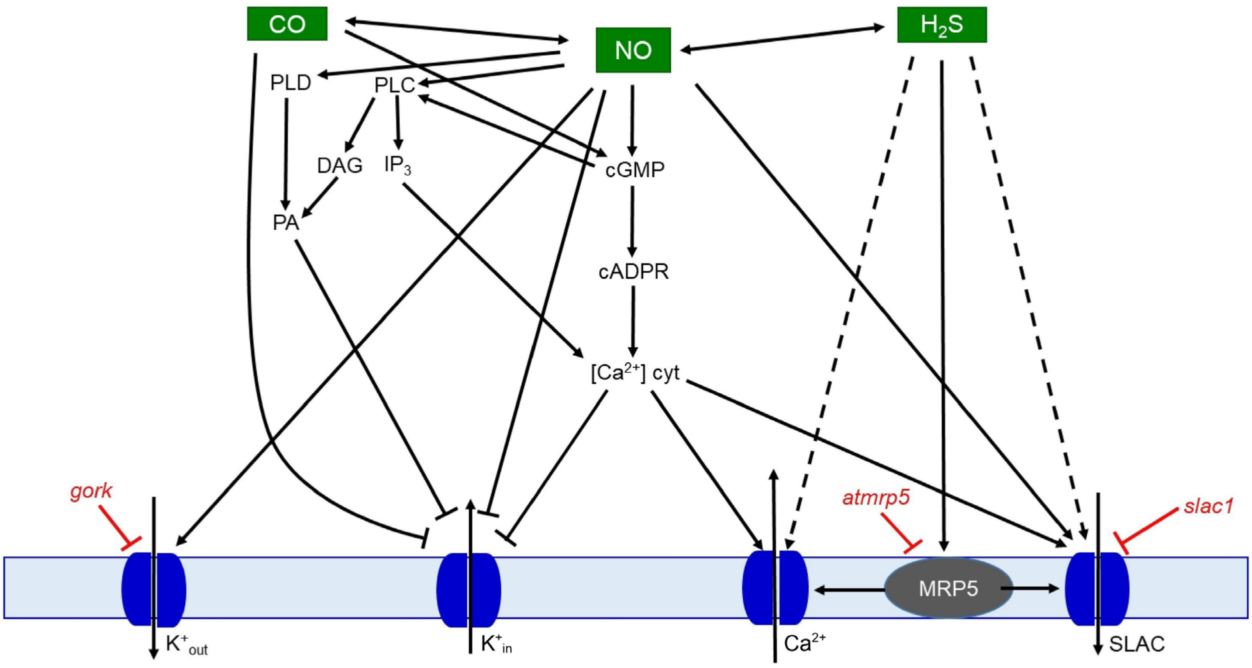

Fig. 2. Events downstream of gasotransmitters leading to the modulation of ion flux and stomatal closure due to the decreased pressure potential in the turgid guard cells. Readers may note the altered position of CO and H_2S from Fig. 1. Any rise in NO elevates cytosolic free calcium (Ca^{2+}-cyt) content in the guard cells by upregulating the chain of cyclic guanosine monophosphate (cGMP)-cyclic ADP ribose (cADPR) and phospholipase C (PLC)-inositol-1,4,5-triphosphate (IP3). In turn, Ca^{2+} inhibits potassium ion (K^+) influx channels. Additionally, NO can activate K^+ out channels as well as slow anion channel 1 (SLAC1), to trigger ion efflux from guard cells. Both CO and H_2S can stimulate NADPH oxidase (RBOH), thus ROS production. The H_2S regulates both SLAC and Ca^{2+} channels, but the direct action of H_2S is still obscure. The effect of H_2S on SLAC can be mediated by a plasma membrane ABC transporter protein (multidrug resistant protein 5, MRP5). Besides inducing stomatal closure, H_2S can also reduce the content of NO and promote the stomatal opening. *Red arrows* illustrate the use of *Arabidopsis* mutants (details listed in Table 1 Suppl). Other abbreviations: DAG - diacylglycerol; NO - nitric oxide; PA - phosphatidic acid; PLD - phospholipase D.

The regulation of various components by NO leading to stomatal closure is described in the following section.

In contrast, NO can also interfere with ABA signalling by restricting ROS production due to post-translational modifications (PTMs) of some pivotal proteins and down-regulation of their activity (Laxalt *et al.* 2016). S-nitrosylation of open stomata 1 (OST1) and NADPH oxidase rbohD/F disrupts the enzymatic activity and lowers ROS, required for stomatal closure. Even the S-nitrosylation of ABA receptor can lead to inhibition of protein phosphatase 2C, showing the opposite effect to stomatal closure. Such a dual role of NO to promote and inhibit stomatal closure and their mechanisms involved need to be studied in future.

Mechanism of stomatal closure by NO

The mechanism of action of NO can be through multiple ways (Fig. 2). An important consequence of the rise in NO is the increase in Ca^{2+} in guard cells. Elevated NO-mediated guanyl cyclase dependent increase in cyclic guanosine monophosphate (cGMP) production, raising the content of cyclic ADP ribose (cADPR) and release of Ca^{2+} from internal sources (García-Mata *et al.* 2003). Parallelly, NO promoted the activities of phospholipase C (PLC) or phospholipase D (PLD). Inositol 1,4,5-trisphosphate (IP3) produced from PLC induces the release of Ca^{2+}. Together, the rise in cytosolic Ca^{2+} inhibits K^+ influx channel and activates slow anion channel (SLAC), leading to stomatal closure (Gayatri *et al.* 2013, Arnaud and Hwang 2015, Agurla *et al.* 2018a). Selected downstream components regulated by NO in the guard cell are listed in Table 2. Besides, causing an increase in Ca^{2+} content, the rise in NO promotes PTMs, as described in the following section.

Arabidopsis mutants had been excellent tools to dissect and understand the mechanisms of NO production and action on stomatal closure. A detailed list of such *Arabidopsis* mutants studied for unraveling the role of NO in guard cells is given in Appendix (Table 1 Suppl).

Post-translational modifications mediated by gasotransmitters

Post-translational modification (PTM) of specific amino acid residues causes marked changes in protein structure and function. The rise in NO can initiate PTM of selected proteins. Reversible covalent attachment of NO to the thiol group of cysteine or tyrosine forming an S-nitrosothiol (S-nitrosylation) in stress-related proteins and signalling components are well documented (Neill *et al.* 2008, Agurla

Table 2. Downstream components modulated by nitric oxide (NO) during stomatal closure. cADPR - cyclic ADP ribose, cGMP - cyclic guanosine monophosphate, GORK - guard cell outward-rectifying K^+ channel, OST - open stomata, PLC - phospholipase C, PLD - phospholipase D, PYL - pyrabactin resistance-like, PYR - pyrabactin resistance, RCAR - regulatory component of ABA receptors.

Target	Consequences of NO action	Plant	Reference
Calcium channel	release of Ca2+ from internal stores mediated by IP3 and cADPR	*Vicia faba* review	García-Mata *et al.* 2003 Gayatri *et al.* 2013
Slow anion channel (SLAC)	upregulation of anion efflux	review	Gayatri *et al.* 2013
Non-expressor of PR1 (NPR1)	S-nitrosylation of NPR1	review	Yu *et al.* 2014
Phosphatidic acid (PA)	inhibition of K^+ influx and activation of NADPH oxidase	*Vicia faba*	Distefano *et al.* 2008
Potassium influx channel	inhibition of K^+ channel by elevated cytosolic Ca^{2+}	*Vicia faba*	Zhao *et al.* 2013
Outward-rectifying K^+ channel	inactivation of GORK due to nitrosylation of channel proteins	*Vicia faba*	Sokolovski and Blatt 2004
PYR/PYL/RCAR	inactivation of ABA receptors due to tyrosine nitration	opinion	Laxalt *et al.* 2016
OST1	inactivation due to nitrosylation of ABA receptors and OST1	opinion	Laxalt *et al.* 2016
NADPH oxidase	NADPH oxidase inactivation due to S-nitrosylation	opinion	Laxalt *et al.* 2016
cGMP and cADPR	activation of guanyl cyclase, rise in cADPR, Ca2+ release	*Vicia faba*	García-Mata *et al.* 2003
PLC	production of PA	*Arabidopsis thaliana*	Uraji *et al.* 2012
PLD	production of PA	*Vicia faba*	Distefano *et al.* 2008

et al. 2014, Sehrawat and Deswal 2014, Yu *et al.* 2014, Gross and Durner 2016). PTMs such as phosphorylation and dephosphorylation also play an essential role in stomatal movement (Zhang *et al.* 2014). Phosphorylation of H^+-ATPase in response to blue radiation-induced stomatal opening was reported (Takemiya *et al.* 2013). Phosphatase mediated dephosphorylation prevented stomatal closure by down-regulating the protein kinases (Yang *et al.* 2017). ROS generated during ABA signalling initiate these phosphorylation events (Balmant *et al.* 2016).

In contrast to ROS, NO-mediated PTMs are S-nitrosylation, S-nitration, S-sulfihydration, and S-guanylation. S-nitrosylation of OST1/SnRK2.6 inhibited the kinase activity and prevented stomatal closure (Fancy *et al.* 2017). A bacterial peptide, flg22, induced stomatal closure in *Arabidopsis*, by the rise in ROS and then NO, followed by nitrosylation of several proteins (Lawrence *et al.* 2020). Persulfidation/S-sulfihydration is the second major PTM after nitrosylation, which can protect against oxidative damage. Almost 50 % of the cytosolic proteins were persulfidated in plants, with many of the proteins involved in stress responses (Gotor *et al.* 2019). Glutathionylation and S-guanylation are the other PTMs, promoted by NO. Dehydroascorbate reductase was glutathionylated in *Arabidopsis* (Honda *et al.* 2015, Sami *et al.* 2018). Selected examples of PTMs and their role during stomatal closure are listed in Table 2 Suppl.

Carbonylation, sumoylation, and ubiquitination, are also among the PTMs, but their role regarding NO or CO or H_2S is not clear. A cross-talk can occur between NO-induced nitrosylation and ROS-induced carbonylation (Lounifi *et al.* 2013).

CO and H_2S: two gasotransmitters other than NO

Besides NO, two more gasotransmitters, CO and H_2S, promote stomatal closure (García-Mata and Lamattina 2013, Scuffi *et al.* 2016). The ability of CO to close stomata could be due to the binding of gas to heme proteins (Song *et al.* 2008), based on the evidence that the closure induced by CO was relieved by hemoglobin (a CO/NO scavenger). Stomatal closure caused by hematin and CO gas was reversed by 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO) and N(gamma)-nitro-L-arginine methyl ester (L-NAME), reflecting the similarity between the action of CO and NO on stomata (Song *et al.* 2008).

In plants, the degradation of heme by heme oxygenase (HO) can produce CO (Song *et al.* 2008). Among the three HO isoforms, HO1 was the primary enzymatic source of CO production (He and He 2014). In *Vicia faba* leaves, CO production and HO activity increased in response to ABA treatment, resulting in stomatal closure (Wang and Liao 2016, Cao *et al.* 2007). Both NO and cGMP were downstream components of CO signalling in stomatal guard cells (Cao *et al.* 2007). Stomatal closure induced by CO was dependent on the H_2O_2 signalling pathway in *V. faba* (She and Song 2008). Thus, CO and NO exhibited similar regulation in the stomatal movement.

Hydrogen sulfide (H_2S) is the third gasotransmitter after NO and CO, which can mediate stomatal closure in response to different stimuli (Scuffi *et al.* 2016). For example, H_2S was an essential component of stomatal closure induced by ABA and ethylene (ET) during drought adaptation (Wang *et al*. 2015). H_2S acted downstream of NADPH oxidase during stomatal closure induced by ABA, or ET, or NO (Hou *et al.* 2013, Scuffi *et al.* 2014, 2018). Stomatal closure by H_2S was also similar to that by ABA in regulating K^+, Ca^{2+}, and Cl^- transport in guard cells, when plants were exposed to drought stress (Jin *et al.* 2013, Malcheska *et al.* 2017). Scuffi *et al.* (2014) observed that H_2S was enzymatically produced from cysteine by L/D-cysteine desulfhydrase (L/D-DES). Even exogenous H_2S could induce stomatal closure in *Vicia faba* and *Arabidopsis thaliana*, by activating SLAC *via* Ca^{2+} (Wang *et al.* 2016).

A cross-talk between the three gasotransmitters: NO, CO, and H_2S, may be operating in guard cells. H_2S and NO regulate each other source by modulating the enzymatic production of the other (Scuffi *et al.* 2016). Lack of endogenous NO significantly reduced the effect of H_2S on stomatal closure, implying that NO acted downstream of H_2S (Pandey 2014). Both H_2S and NO were involved in the signal transduction pathway of ET-or ABA-induced stomatal closure (Liu *et al.* 2011, Wang *et al.* 2015).

Stomatal regulation by ethylene and other gaseous molecules

Ethylene, a gaseous phytohormone, is actively involved in stomatal function besides plant growth and development (Acharya *et al.* 2009). However, it is not clear if ET promotes or interferes with stomatal closure. Application of ethepon (an ET releasing compound) or 1-aminocyclopropane-1-carboxylic acid (ACC) helped stomatal closure in *Arabidopsis* leaves (Desikan *et al.* 2006). Cytosolic alkalization and NO generation were vital for ET induced reduction of stomatal aperture (Shi *et al.* 2017). ET-induced stomatal closure was associated with NADPH oxidase (AtrbohD/F)-dependent H_2O_2 production targeting S-type anion channels (Ge *et al.* 2015, Munemasa *et al.* 2019).

In contrast, ET was antagonistic to ABA and MeJA and interacted also with 24-epibrassinolide and even UV or H_2S during stomatal closure (Huang *et al.* 2008, Shi *et al.* 2015a, Munemasa *et al.* 2019). We believe that the indirect action of ET by its interaction with other hormones dominates over its likely direct effect on stomata. Further description of ET effects on stomata can be found in the reviews of Acharya *et al.* (2009) and Daszkowska-Golec and Szarejko (2013). Although a potent regulator of stomatal function and a gaseous molecule, ET is not considered as a gasotransmitter as it is perceived by a well-characterized receptor complex (Kolbert *et al.* 2019b).

Ozone, an atmospheric pollutant (and an oxidant), promotes the rise in ROS in plant tissues while triggering the synthesis of plant hormones, such as ET, SA, and jasmonic acid (Tamaoki 2008). Ozone induced H_2O_2 can up-regulate NO production in guard cells, stimulate SLAC1, and close stomata (Kangasjärvi *et al.* 2005, Kollist *et al.* 2007, Vahisalu *et al.* 2010). Another pollutant gas, SO_2, also closed stomata, but the mechanism was not understood (Ooi *et al.* 2019). Bicarbonate, a form of CO_2 induced stomatal closure by elevating H_2O_2 as well as NO in guard cells of *Arabidopsis* (Kolla *et al.* 2007, Kolla and Raghavendra 2007). Elevated CO_2 promoted stomatal closure by activating SLAC1 in guard cells (Poschenrieder *et al.* 2018).

Methane (CH_4, a greenhouse gas), promoted stomatal closure. CH_4 induced stomatal closure appeared to be due to the increased sensitivity towards ABA of methyl-coenzyme M reductase, the enzymatic source of CH_4 (Su *et al.* 2019). Since ammonia (NH_3) and CH_4 appear to qualify the criteria, they may be potential candidates as gasotransmitters (Pei *et al.* 2018).

The relevance of NO/CO/H_2S to the plant innate immunity

The role of NO in plant innate immunity had been emphasized (Agurla *et al.* 2014, Rosnoblet *et al.* 2016, Mur *et al.* 2017). The production of ROS, as well as NO, was a common feature in response to pathogen infection or elicitors. Similarly, microbe-associated molecular patterns initiated innate immune defense is activating by downstream components, like NO production (Newman *et al.* 2013, Héloir *et al.* 2019). Upon invasion of pathogens onto the leaf surface, a series of signalling events ensure stomatal closure to restrict the further entry of pathogens. The secondary messenger, NO, is a pivotal component during such defense responses (Ma *et al.* 2016). A strong association exists between H_2S content in plants and their defense responses to pathogen attack (Calderwood *et al.* 2014, Shi *et al.* 2015b, Li *et al.* 2016). The enzyme L/D-DES and its product H_2S helped in defense responses against the bacterial pathogens by activating SA signalling-related genes and confer abiotic stress tolerance (Shi *et al.* 2015b). Since H_2S is known to have a synergistic effect with ROS during oxidative stress responses, such interaction can also provide defense against biotic stresses by stomatal closure (Tao *et al.* 2020).

We could not find any report on the direct ability of CO to impart pathogen resistance. However, the interactions of CO with NO may play a role in the abiotic stress responses of plants. readers interested in further details on the roles of H_2S and CO can refer to some of the recent reviews (Shekhawat and Verma 2010, He and He 2014, Li *et al.* 2016, Tao *et al.* 2020).

Concluding remarks

Of the three signalling molecules considered as gasotransmitters, NO is undoubtedly the most studied and well-accepted player during stomatal closure (Gayatri *et al.* 2013, Hancock and Neill 2019). However, it is necessary to establish the origin of NO in plants. Unlike the case of animal cells, where an inducible nitric oxide synthase (NOS) provides the primary source of NO, the status in plants is far from clear. The relative roles of NR, NOS-like enzyme, and even others like HO need to be re-examined, and their importance be established. The interaction between NO and ROS is intriguing as NO can play a dual role of oxidant and anti-oxidant (Agurla and Raghavendra 2016). The abundance of both ROS and NO could cause a synergistic effect because peroxynitrite (formed by the combination of ROS and NO) can be a more powerful regulator than either ROS or NO alone (Vandelle and Delledonne 2011).

The origin and mechanism of action of the other two gasotransmitters, H_2S and CO, are exciting but intriguing. Despite being a potent metabolic, respiratory poison, the role of CO as a signal to promote stomatal closure and plant innate immunity warrants further studies. On the other hand, being an essential component of sulfur metabolism, the importance of H_2S as a signal to modulate stomatal function appears to be physiologically relevant. Strong interactions occurred between ROS, NO, H_2S, and CO (Hancock and Whiteman 2016, Wang and Liao 2016). Reports were indicating that NO could promote the activity of HO and H_2S content, while CO can up-regulate the release of NO (Song *et al.* 2008, Santa-Cruz *et al.* 2010). Further experiments are needed to establish if there is a master-player among NO, CO, and H_2S or if all the three are capable of acting independently.

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