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

S. GAHIR, P. BHARATH, and A.S. RAGHAVENDRA*

Department of Plant Sciences, School of Life Sciences, University of Hyderabad, Hyderabad 500046, India

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\(_2\)S 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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* Corresponding author; e-mail: as_raghavendra@yahoo.com
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\(_2\)S). 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 H₂S. The ability of other gaseous molecules, like sulfur dioxide (SO₂), ozone (O₃), 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). Parallely, NO can elevate cytosolic free Ca²⁺, 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                       | Czekus 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⁺ increase in ROS, followed by NO | Wu et al. 2017 |
| Polyamines (putrescine, spermine, Arabidopsis thaliana, spermidine) | Vicia faba | peroxidase dependent ROS production, and rise in NO | Agurla et al. 2018b |
| Allyl isothiocyanate (AITC)  | Pisum sativum          | cytosolic alkalinization promotes the rise in NO     | Gonugunta et al. 2008    |
| Alkalizer (methylamine)      | Pisum sativum          | marked rise in pH as well as NO                       | Puli et al. 2016         |
| Sphingolipids (phyto-S1P, S1P) | Pisum sativum         | stimulation of NO synthesis                          | Bright et al. 2006       |
| Hydrogen peroxide            | Arabidopsis thaliana   | NO production mediated by NOS-like enzyme            | Kolla and Raghavendra 2007 |
| Bicarbonate                  | Pisum sativum          |                                                      |                         |
| **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        |

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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\textsuperscript{2+} in guard cells. Elevated NO-mediated guanylyl cyclase dependent increase in cyclic guanosine monophosphate (cGMP) production, raising the content of cyclic ADP ribose (cADPR) and release of Ca\textsuperscript{2+} from internal sources (García-Mata et al. 2003). Parallely, 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\textsuperscript{2+}. Together, the rise in cytosolic Ca\textsuperscript{2+} inhibits K\textsuperscript{+} 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\textsuperscript{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* | Garcia-Mata et al. 2003 |
| 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 Ca²⁺                                      | *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* | Garcia-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. 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-sulfhydrylation, 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-sulfhydration 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 H₂S is not clear. A cross-talk can occur between NO-induced nitrosylation and ROS-induced carbonylation (Lounifi et al. 2013).

**CO and H₂S: two gasotransmitters other than NO**

Besides NO, two more gasotransmitters, CO and H₂S, promote stomatal closure (Garcia-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 H₂O₂ signalling pathway in *V. faba* (She and Song 2008). Thus, CO and NO exhibited similar regulation in the stomatal movement.
Hydrogen sulfide (H$_2$S) 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$_2$S was an essential component of stomatal closure induced by ABA and ethylene (ET) during drought adaptation (Wang et al. 2015). H$_2$S 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$_2$S 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$_2$S was enzymatically produced from cysteine by L/D-cysteine desulphydrase (L/D-DES). Even exogenous H$_2$S 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$_2$S, may be operating in guard cells. H$_2$S 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$_2$S on stomatal closure, implying that NO acted downstream of H$_2$S (Pandey 2014). Both H$_2$S 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 ethephon (an ET releasing compound) or 1-aminocyclopropane-1-carboxylic acid (ACC) helped stomatal closure in Arabidopsis leaves (Desikan et al. 2006). Cytosolic alcalization 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 (AtbthoD/F)-dependent H$_2$O$_2$ 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$_2$S 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$_2$O$_2$ 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$_2$O$_2$ 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$_2$S 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, Héloïr 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$_2$S 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$_2$S 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$_2$S 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$_2$S 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$_2$S 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$_2$S as a signal to modulate stomatal function appears to be physiologically relevant. Strong interactions occurred between ROS, NO, H$_2$S, and CO (Hancock and Whitman 2016, Wang and Liao 2016). Reports were indicating that NO could promote the activity of HO and H$_2$S 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$_2$S or if all the three are capable of acting independently.

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