



REVIEW PAPER

Nitric oxide molecular targets: reprogramming plant development upon stress

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Abstract

Plants are sessile organisms that need to complete their life cycle by the integration of different abiotic and biotic environmental signals, tailoring developmental cues and defense concomitantly. Commonly, stress responses are detrimental to plant growth and, despite the fact that intensive efforts have been made to understand both plant development and defense separately, most of the molecular basis of this trade-off remains elusive. To cope with such a diverse range of processes, plants have developed several strategies including the precise balance of key plant growth and stress regulators [i.e. phytohormones, reactive nitrogen species (RNS), and reactive oxygen species (ROS)]. Among RNS, nitric oxide (NO) is a ubiquitous gasotransmitter involved in redox homeostasis that regulates specific checkpoints to control the switch between development and stress, mainly by post-translational protein modifications comprising S-nitrosation of cysteine residues and metals, and nitration of tyrosine residues. In this review, we have sought to compile those known NO molecular targets able to balance the crossroads between plant development and stress, with special emphasis on the metabolism, perception, and signaling of the phytohormones abscisic acid and salicylic acid during abiotic and biotic stress responses.

Keywords: Abiotic, biotic, developmental cues, nitration, nitric oxide, post-translational modifications, reactive nitrogen species, S-nitrosation.

Introduction

Nitric oxide (NO) is a simple molecule whose production is regulated by complex mechanisms, given the large number of synthesis and scavenging pathways that influence NO homeostasis. Apart from being the most abundant reactive nitrogen species (RNS) in plants, NO is considered a gasotransmitter with a pivotal role in a plethora of physiological processes throughout the plant life cycle, from the regulation of growth and development to biotic and abiotic stress tolerance.

The distribution, concentration, and regulation of NO levels at the specific sites of action are important to exert different

physiological functions. These features make NO a versatile and broad-spectrum signaling molecule, able to regulate numerous processes in a very precise way (Sanz *et al.*, 2015). Considering the impact of NO levels in plants, either deficiency or overaccumulation greatly impair growth and development. Thus, reported mutants with altered NO levels show stunted growth immediately after germination which become visible in adult plants (Fig. 1), although the pleiotropic defects in these mutants may have wider impacts than just NO generation.

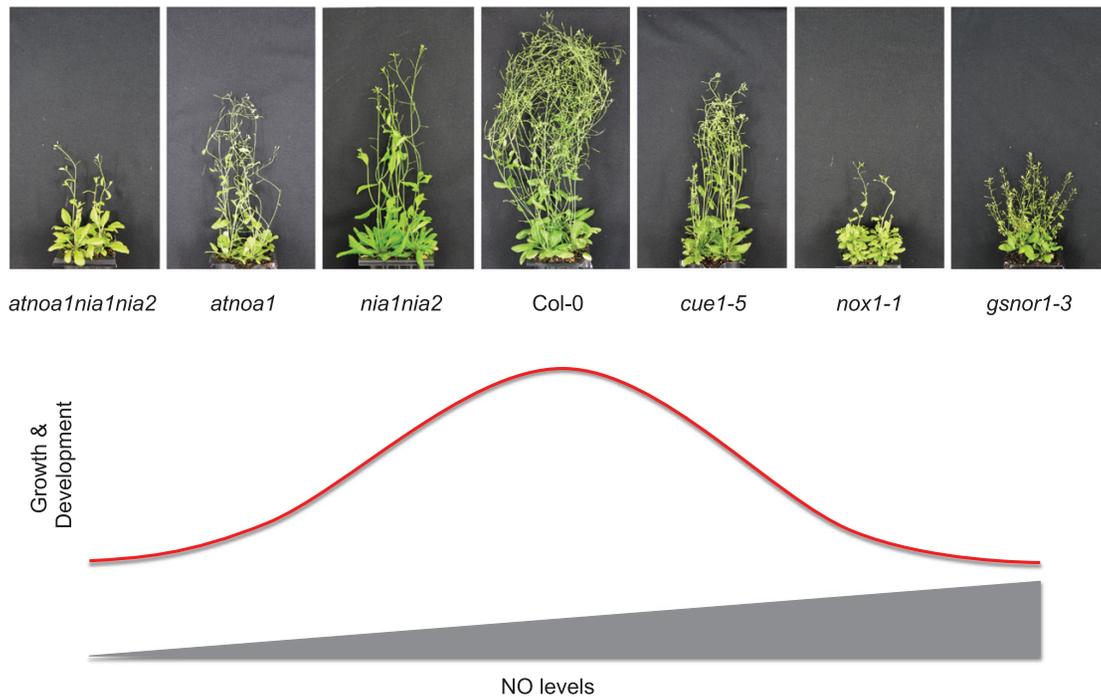


Fig. 1. Phenotype of nitric oxide (NO) homeostasis mutants. Growth and developmental defects of 7-week-old NO-deficient mutants (*nia1nia2*, *atnoa1*, and *atnoa1nia1nia2*) and NO-overproducer mutants (*cue1-5*, *nox1-1*, and *gsnor1-3*), compared with the wild-type Col-0, in terms of endogenous NO levels.

The mode of action of NO as a signaling effector includes the modification of molecules of biological relevance (e.g. proteins, fatty acids, cGMP, DNA, and RNA). Essentially, RNS derived from NO interact with biomolecules to modify both their structure and function. With special emphasis on protein structure, these modifications lead to conformational changes whose result may be an increased or decreased stability, activation or inhibition of activity, disruption of the interactome, translocation, and, in the case of transcription factors, an influence on DNA binding to alter gene expression. To perform these effects in such a diverse range of processes, NO modifies certain proteins through two post-translational mechanisms, the nitration of Tyr residues and the S-nitrosation of Cys residues and metals.

NO post-translational modifications of key regulators by Tyr nitration

The nitration of Tyr residues is carried out mainly by peroxynitrite (ONOO^-) and by the nitrogen dioxide radical ($\cdot\text{NO}_2$). ONOO^- results from the reaction of NO with the superoxide radical ($\text{O}_2^{\cdot-}$), which modifies position 3 of the phenolic ring, adding a nitro group ($-\text{NO}_2$). $\cdot\text{NO}_2$ comes from the reactions of NO in the presence of oxidants, such as H_2O_2 and $\text{O}_2^{\cdot-}$, and transition metals (Radi *et al.*, 2004). Within a protein, not all Tyr residues are susceptible to nitration and depend on the conformational state in order to be more exposed to the redox environment (Abello *et al.*, 2009; Corpas *et al.*, 2013a) and the properties of surrounding amino acids (Souza *et al.*, 1999; Ischiropoulos, 2003; Chaki *et al.*, 2009; Lozano-Juste *et al.*, 2011).

Similar to other RNS, ONOO^- has been considered one of the most potent molecules to produce oxidative damage

to nucleic acids and lipid peroxidation. However, emerging evidence also highlights the great relevance of this molecule for signaling (Arasimowicz-Jelonek and Floryszak-Wieczorek, 2011; Vandelle and Delledonne, 2011). Considering global protein regulation, nitration is an important point of interaction with other signals, since Tyr residues are also susceptible to phosphorylation (Galetskiy *et al.*, 2011). Likewise, NO is able to regulate the amount of ONOO^- through the inhibition of PrxIIIE by S-nitrosation, which detoxifies this compound, promoting its accumulation (Romero-Puertas *et al.*, 2007). Numerous nitrated proteins, the so-called nitroproteome, have been identified under both normal growth (Lozano-Juste *et al.*, 2011; Chaki *et al.*, 2009, 2012; Begara-Morales *et al.*, 2013) and stress conditions (Ceconi *et al.*, 2009; Begara-Morales *et al.*, 2013). Some studies have focused on the analysis of the effect of ONOO^- on specific proteins, with a predominantly inhibitory action (Table 1). Although nitration was classified initially as an irreversible protein modification, the existence of enzymes with denitrase activity in animals has been reported (Irie *et al.*, 2003; Smallwood *et al.*, 2007; Deeb *et al.*, 2013).

S-Nitrosation of Cys and metals in key molecular players

Protein S-nitrosation is a post-translational modification that consists of the covalent attachment of an NO molecule to a thiol group of a Cys, forming an S-nitrosothiol (SNO). This modification appears to be the main mechanism by which NO, in its protonated form (NO^+) or in a greater state of oxidation (N_2O_3) (Hill *et al.*, 2010), exerts its effect. S-Nitrosation is highly specific, since it depends not only on the proximity between NO and the target protein, but also on the conformation and amino acid sequence (Lindermayr and Durner,

Table 1. Targets and effects of protein nitration described in plants

Protein	Process	Reference
Catalase	Inhibition of activity against pathogens	Clark <i>et al.</i> (2000)
S-Adenosyl homocysteine hydrolase (SAHH)	Inhibition of activity	Chaki <i>et al.</i> (2009)
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	Inhibition of activity	Lozano-Juste <i>et al.</i> (2011)
Complexes of PSI and PSII	Inactivation and disassembly of complexes dependent on light conditions	Galetskiy <i>et al.</i> (2011)
Ferredoxin-NADP oxidoreductase	Inhibition of activity, causing changes in photosynthetic activity	Chaki <i>et al.</i> (2011)
O-Acetylserine (thiol) lyase 1	Inhibition of activity under stress conditions to regulate cysteine and glutathione metabolism	Alvarez <i>et al.</i> (2011)
Glutamine synthetase (GS1a)	Inhibition of activity to regulate N metabolism in nodules	Melo <i>et al.</i> (2011)
NADP-isocitrate dehydrogenase (ICDH)	Inhibition of activity for the reprogramming of metabolism and redox homeostasis during senescence	Begara-Morales <i>et al.</i> (2013)
NADH-hydroxypyruvate reductase (HPR1)	Inhibition of activity, changes in peroxisomal metabolism	Corpas <i>et al.</i> (2013b)
Ascorbate peroxidase (APX)	Inhibition of activity	Clark <i>et al.</i> (2000); Begara-Morales <i>et al.</i> (2014)
Monodehydro-ascorbate reductase	Inhibition of activity	Begara-Morales <i>et al.</i> (2015)
Superoxide dismutases (MSD1, FSD3, CSD3)	Inhibition of activity	Holzmeister <i>et al.</i> (2015)
Pyrabactin resistance1/ PYR1-like/regulatory component of ABA receptor (PYR/PYL/ RCAR)	Inhibition of activity	Castillo <i>et al.</i> (2015)
Leghemoglobin (Lb)	Putative protective role, scavenging ONOO ⁻	Sainz <i>et al.</i> (2015)

2009; Lamotte *et al.*, 2014). It remains elusive to what extent this modification is mediated by non-enzymatic mechanisms (through the action of free NO/N₂O₃), or by transfer reactions (through the interaction between two components) known as transnitrosation [i.e. from S-nitrosoglutathione (GSNO) to other molecules], since mutants that accumulate either NO (*cue1/nox1*) or GSNO (*gsnor1*) do not behave in a similar way (Fig. 1) (Kneeshaw *et al.*, 2014). A landmark in NO biology is the ability to maintain an optimal concentration at the specific site of action. Thus, the control of nitrosated proteins represents an important point of regulation. Reports on certain enzyme systems able to denitrosate proteins comprise the glutathione/GSNO reductase (GR/GSNOR) and thioredoxin/thioredoxin reductase (Trx/TrxR) systems (Tada *et al.*, 2008; Malik *et al.*, 2011; Paris *et al.*, 2013). Remarkably, NPR1 denitrosation has been described by the system composed of thioredoxin TRXH5 and thioredoxin reductase NTRA (Kneeshaw *et al.*, 2014). Given the high specificity shown by S-nitrosation, the regulation of denitrosation may also display such a specific pattern, as described for glyceraldehyde phosphate dehydrogenase (GAPDH; Zaffagnini *et al.*, 2013). Non-enzymatic mechanisms able to eliminate the SNO moiety have also been reported, including exposure to reducing agents, nucleophilic compounds, or transition metals, together with heat or light (Kovacs and Lindermayr, 2013). Extensive literature refers to the multitude of processes in which this modification is involved (Mengel *et al.*, 2013; Paris *et al.*, 2013; Romero-Puertas *et al.*, 2013) and to the numerous proteins susceptible to S-nitrosation described so far (Lindermayr *et al.*, 2005) by using the biotin switch technique (Jaffrey and Snyder, 2001) (Table 2).

The third and less known NO-driven post-translational modification is the nitrosation of transition metals present in metalloproteins (namely iron, zinc, and copper) causing

conformational changes that affect protein activity (Astier and Lindermayr, 2012) (Table 3). A clear example is the binding to the heme group of phytohemoglobins, affecting the transport/scavenging of NO (Gupta *et al.*, 2011). Interestingly, a self-nitrosation mechanism has been described in animals by intramolecular transfer from the heme group to a Cys in the globin domain (Jia *et al.*, 1996; Gow and Stamler, 1998).

Having outlined the NO-dependent post-translational modifications for NO action and provided a compilation of those NO protein targets described so far, here we emphasized the balanced role of NO in different developmental cues through its interaction with phytohormones during abiotic and biotic stresses.

NO impact on plant development and abiotic stress trade-off

Changing environmental conditions compromise successful plant growth, thus being a critical step that reflects the need for a development and stress trade-off for plant establishment. In this context, abiotic stresses such as drought, hypoxia, salinity, or extreme temperatures are detrimental for plant survival. The phytohormone abscisic acid (ABA) plays a major role in abiotic stress responses such as stomatal closure (Desikan *et al.*, 2002; García-Mata and Lamattina, 2002; Neill *et al.*, 2002; Eisenach *et al.*, 2017), water deficit (Christmann *et al.*, 2007), or high light conditions (Galvez-Valdivieso *et al.*, 2009), but also controlling pathogen responses (Adie *et al.*, 2007). From a developmental point of view, ABA is involved in dormancy maintenance, biosynthesis of embryo storage compounds, seed size and seed germination inhibition (Lopez-Molina *et al.*, 2002; Kanno *et al.*, 2010; Cheng *et al.*, 2014; Albertos *et al.*, 2015), and sophisticated regulation of root development (Dietrich *et al.*, 2017; Belda-Palazon *et al.*, 2018), among others.

Table 2. Targets and effects of protein S-nitrosation described in plants

Protein	Process	Reference
Phytoglobin1 (Phytogb1)	Modulation of NO/O ₂ levels	Perazzolli <i>et al.</i> (2004)
Glyceraldehyde-3-phosphate dehydrogenase (GAPDH)	Inhibition of activity	Lindermayr <i>et al.</i> (2005) ; Zaffagnini <i>et al.</i> (2013) ; Zhang <i>et al.</i> (2017)
Methionine adenosyltransferase (MAT1)	Inhibition of activity	Lindermayr <i>et al.</i> (2006)
Peroxiredoxin II E (PrxII E)	Inhibition of activity resulting in an increase of ONOO ⁻ , which triggers Tyr residues nitration	Romero-Puertas <i>et al.</i> (2007)
Metacaspase MC9 (unprocessed form)	Inhibition of autoprocessing and proteolytic activity	Belenghi <i>et al.</i> (2007)
MYB domain protein (MYB2)	Inhibition of DNA binding	Serpa <i>et al.</i> (2007)
Nonexpresser of PR genes 1 (NPR1)	Conformational changes (oligomerization) in cytoplasm	Tada <i>et al.</i> (2008)
Salicylic acid-binding protein 3 (SABP3)	Prevents salicylic acid (SA) binding and inhibits the activity	Wang <i>et al.</i> (2009)
Glycine decarboxylase complex (GDC)	Inhibition of activity	Palmieri <i>et al.</i> (2010)
TGACG sequence-specific binding protein 1 (TGA1)	Promotes DNA binding in the presence of NPR1	Lindermayr <i>et al.</i> (2010)
Aldolase	Conformational change resulting in the inhibition of activity	van der Linde <i>et al.</i> (2011)
NADPH oxidase (RBOHD)	Inhibition of activity, minimizing the synthesis of ROIs (ROS intermediaries)	Yun <i>et al.</i> (2011)
Transport inhibitor response 1 (TIR1)	Facilitates interaction with Aux/IAA, promoting its degradation and triggering auxin response	Terrile <i>et al.</i> (2012)
Cell division cycle 48 (CDC48)	Inhibition of ATPase activity	Astier <i>et al.</i> (2012)
Histidine phosphotransfer protein 1 (AHP1)	Inhibition of phosphorylase activity, negatively regulating the cytokinin (CK) signaling pathway	Feng <i>et al.</i> (2013)
Ascorbate peroxidase (APX)	Promotes the activity	Begara-Morales <i>et al.</i> (2014) ; Yang <i>et al.</i> (2015)
GSNO reductase (GSNOR)	Inhibition of activity	Frunghillo <i>et al.</i> (2014)
MYB domain protein (MYB30)	Inhibition of DNA binding	Tavares <i>et al.</i> (2014)
Open stomata 1/Sucrose nonfermenting 1-related protein kinase 2.6 (OST1/SnRK2.6)	Inhibition of activity, negative regulation of ABA responses	Wang <i>et al.</i> (2015)
ABA Insensitive 5 (ABI5)	Protein destabilization, promoting proteasome degradation	Albertos <i>et al.</i> (2015)
Peroxiredoxin II F (PrxII F)	Inhibition of peroxidase activity and acquisition of transnitrosylase activity, preventing the aggregation of citrate synthase	Camejo <i>et al.</i> (2015)
Other glycolysis enzymes [fructose 1,6-biphosphate aldolase, triosephosphate isomerase, 2-phosphoglycerate hydrolase (enolase) and phosphoglycerate kinase]	Inhibition of activity	Zhang <i>et al.</i> (2017)
ATP synthase CF1 α-chain and β-chain	Inhibition of activity	Zhang <i>et al.</i> (2017)
Vascular-Related NAC-Domain7 (VND7)	Inhibition of transactivation activity	Kawabe <i>et al.</i> (2018)

The crosstalk between ABA and NO governs the main molecular mechanisms able to integrate external signals to reprogram internal networks leading to plant adaptation (reviewed in [Arc *et al.*, 2013](#); [León *et al.*, 2014](#); [Albertos *et al.*, 2015](#); [Wang *et al.*, 2015a, b](#); [Lombardo and Lamattina, 2018](#)). NO is able to interact with a wide range of ABA metabolism, perception, and signaling targets, modulating protein function and impacting gene expression.

NO effect on ABA synthesis and catabolism

ABA levels are determined by the ratio between synthesis and catabolism. Key steps during ABA synthesis are controlled by zeaxanthin epoxidase (ZEP), 9-*cis*-epoxycarotenoid dioxygenase (NCED), short-chain alcohol dehydrogenase (ABA2), and a final step catalyzed by an abscisic aldehyde

oxidase (AOO3) which is activated by the molybdenum cofactor (MoCo) sulfurase ABA3 (reviewed in [Nambara and Marion-Poll, 2005](#); [Finkelstein, 2013](#)). ABA catabolism takes place mainly through the ABA 8'-hydroxylation pathway catalyzed by the cytochrome P450 enzyme ABA 8'-hydroxylase. In Arabidopsis, these enzymes are encoded by the CYP707A family. Among them, CYP707A1 and CYP707A3 are the most important enzymes required in mid-seed development, and CYP707A2 during the end of seed development and germination ([Kushiro *et al.*, 2004](#); [Okamoto *et al.*, 2006](#)).

A decrease in ABA is mandatory for seed dormancy breakdown and germination in Arabidopsis. An NO-induced ABA sensitivity reduction correlates with the transcription induction of CYP707A2 and protein accumulation ([Liu *et al.*, 2009](#)) (Fig. 2). This NO effect was also evidenced by using genetic approaches with NO-deficient mutants, *nia1nia2* and

Table 3. Targets and effects of metal nitrosation described in plants

Protein	Process	Reference
Lipoxygenase-1	Redox regulation	Nelson (1987)
Catalase	Inhibition of activity to modulate pathogen response	Clark <i>et al.</i> (2000)
Ascorbate peroxidase	Inhibition of activity to modulate pathogen response	Clark <i>et al.</i> (2000)
Nitric oxide-dependent guanylate cyclase (NOGC1)	GTP hydrolysis, NO-dependent generation of cGMP	Mulaudzi <i>et al.</i> (2011)
Phytogloblin1 (Phytogb1)	Modulation of NO/O ₂ levels	Perazzolli <i>et al.</i> (2004)
Aconitase	Inhibition of activity for metabolism modification, favoring amino acid biosynthesis and activation of alternative oxidase	Gupta <i>et al.</i> (2012)

nia1nia2noa1-2, which show increased dormancy and ABA-mediated germination inhibition (Lozano-Juste and León, 2010), and by using NO donors (Bethke *et al.*, 2004, 2006, 2007; Sarath *et al.*, 2007). Additionally, the MoCo sulfurase ABA3 has been identified as a target of protein nitration (Lozano-Juste *et al.*, 2011), which could alter its activity (Fig. 2).

NO alterations of ABA perception and signaling

ABA perception and signal transduction depend on the core PYRABACTIN RESISTANCE (PYR)/PYR1-LIKE (PYL)/REGULATORY COMPONENT OF ABA RECEPTOR (RCAR) (Ma *et al.*, 2009; Park *et al.*, 2009), PROTEIN PHOSPHATASE 2C (PP2C) (Umezawa *et al.*, 2009; Vlad *et al.*, 2009), and SNF1-RELATED PROTEIN KINASE2 (SnRK2) kinases (Mustilli *et al.*, 2002; Yoshida *et al.*, 2006; Nakashima *et al.*, 2009; Umezawa *et al.*, 2009). In the presence of ABA, the formation of PYR/PYL/RCAR-PP2C complexes inhibits the activity of the PP2Cs, thereby activating SnRK2s, which in turns control AREB/ABF-type basic/region leucine zipper (bZIP) transcription factors (Fujii *et al.*, 2009). These bZIP transcription factors bind to *cis*-regulatory elements known as ABA-responsive elements (ABREs) and regulate downstream gene expression (Choi *et al.*, 2000; Uno *et al.*, 2000; Kang *et al.*, 2002; Finkelstein *et al.*, 2005; Reeves *et al.*, 2011; Gao *et al.*, 2016; reviewed in Banerjee and Roychoudhury, 2017).

The control by NO of ABA perception and signaling pathways occurs at different levels (Fig. 2). First, PYR/PYL/RCAR receptors are inhibited by Tyr nitration (Castillo *et al.*, 2015), enabling activation of PP2C which in turn inactivates SnRKs. An additional control point falls in the inhibition of the activity of SnRKs 2.2, 2.3, and 2.6 by *S*-nitrosation and *SnRK2.6* down-regulation by NO treatment impairing seed germination and stomatal closure (Wang *et al.*, 2015a, b; Zhao *et al.*, 2016). Interestingly, the *nia1nia2* NO-deficient mutant is affected in genes involved in the ABA perception core, where *RCAR1*, *RCAR11*, *RCAR12*, and *RCAR14* are up-regulated,

and also presents a higher PP2C activity (Zhao *et al.*, 2016), in accordance with up-regulation of *PP2C* transcription by exogenous NO treatment (Castillo *et al.*, 2018). Finally, NO regulates the ABI5 bZIP transcription factor through *S*-nitrosation of Cys153. This modification targets ABI5 to the proteasome by promoting the interaction with CULLIN4-based and KEEP ON GOING E3 ligases (Albertos *et al.*, 2015). In addition, ABI5 is sumoylated by the SUMO E3 ligase SIZ1 (Miura *et al.*, 2009), which is considered to be a Tyr nitration target (Lozano-Juste *et al.*, 2011).

ABI5 is a key player in ABA-triggered processes (Finkelstein and Lynch, 2000; Lopez-Molina *et al.*, 2001) and also emerges as a molecular hub in the NO-mediated balance between early development and stress (Albertos *et al.*, 2015). *ABI5* expression and protein levels increase during the last steps of seed maturation (Brocard *et al.*, 2002; Bensmihen *et al.*, 2005) and overexpression of *ABI5* confers hypersensitivity to ABA, which promotes its transcription and stabilization (Brocard *et al.*, 2002). ABI5 functions in the ABA signaling pathway by blocking seed germination (Lopez-Molina *et al.*, 2001; Albertos *et al.*, 2015; reviewed in Skubacz *et al.*, 2016) and seedling establishment upon exposure to stress conditions such as drought or salinity (Lopez-Molina *et al.*, 2001; Tezuka *et al.*, 2013). ABI5 also promotes *CATALASE1* transcription during seed germination (Bi *et al.*, 2017), whose protein activity is inhibited by Tyr nitration and metal nitrosation in tobacco (Clark *et al.*, 2000).

Similarly to ABI5, other group A bZIP transcription factors are involved in different developmental cues, including embryo development and seed maturation (Jakoby *et al.*, 2002), and stress responses. Thus, bZIP67 regulates fatty acid composition (Mendes *et al.*, 2013), bZIP14 is necessary for flowering and meristem identity (Gorham *et al.*, 2018), bZIP12/EEL counteracts ABI5's action on the transcription of *Late Embryogenesis Abundant (LEA)* genes (Finkelstein and Lynch, 2000; Lopez-Molina *et al.*, 2002; Bensmihen *et al.*, 2002), and the subfamily of ABFs (ABRE-binding factors) constitute key signaling transcription factors mediating ABA responses during seed germination, drought, and osmotic stresses (Choi *et al.*, 2000; Finkelstein *et al.*, 2005; Fujita *et al.*, 2005; Yoshida *et al.*, 2010, 2015; Fernando *et al.*, 2018). Since ABI5 is an NO target, other members from group A of bZIPs are found to be susceptible to modification by *S*-nitrosation when analyzed using GPS-SNO software (Fig. 3).

The ABA signaling pathway is linked to chromatin remodeling (Saez *et al.*, 2008; Han *et al.*, 2012, 2015), histone deacetylation (Luo *et al.*, 2012; Ryu *et al.*, 2014), and histone demethylation (Zhao *et al.*, 2015), and epigenetic changes appear as mechanisms involved in the response to stress conditions (reviewed in Nonogaki, 2014). In this context, accumulation of histone acetylation marks in Arabidopsis is promoted by the NO donor GSNO while it is decreased by the NO scavenger 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO). This fact correlates with inhibition of the activity of histone deacetylases (HDACs) (Mengel *et al.*, 2017) probably associated with of *S*-nitrosation, as previously described in mammals for HDAC2 and HDAC6 (Nott *et al.*, 2008; Okuda *et al.*, 2015). This post-translational modification

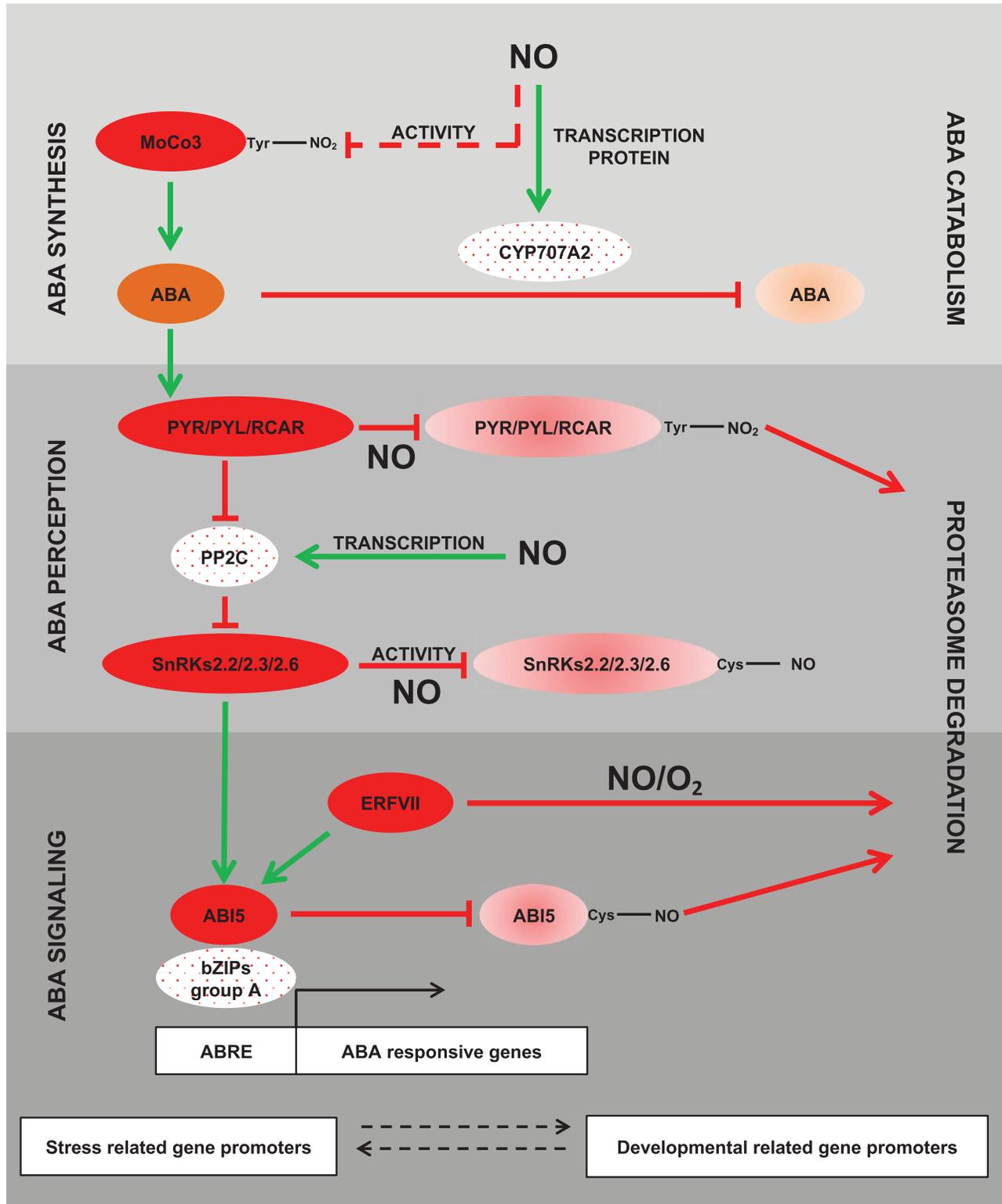


Fig. 2. Network of NO and ABA interactions in a stress- and developmental stage-based context. Impact of NO on specific molecular targets related to ABA synthesis (MoCo3, molybdenum cofactor sulfurase ABA3), catabolism (CYP707A2, cytochrome P450 ABA 8'-hydroxylase), perception (PYR/PYL/RCAR, pyrabactin resistance/PYR-like/regulatory component of ABA receptor), and signaling (SnRKs, SNF1-related protein kinases; ERFVII, ethylene response factor group VII; ABI5, abscisic acid insensitive5 bZIP). The putative role of Cys S-nitrosation (Cys-NO) and Tyr nitration (Tyr-NO₂) is included. Arrows and bars indicate positive and inhibitory effects, respectively. Dotted arrows and bars indicate putative regulations.

linked to the chromatin state can also be responsible of the reprogramming of expression triggered by NO (Huang *et al.*, 2002; Polverari *et al.*, 2003; Palmieri *et al.*, 2008; Hussain *et al.*,

2016; Imran *et al.*, 2018). SWI/SNF chromatin-remodeling ATPase BRAHMA (BRM), whose switch activity is modulated by phosphorylation/dephosphorylation mediated by

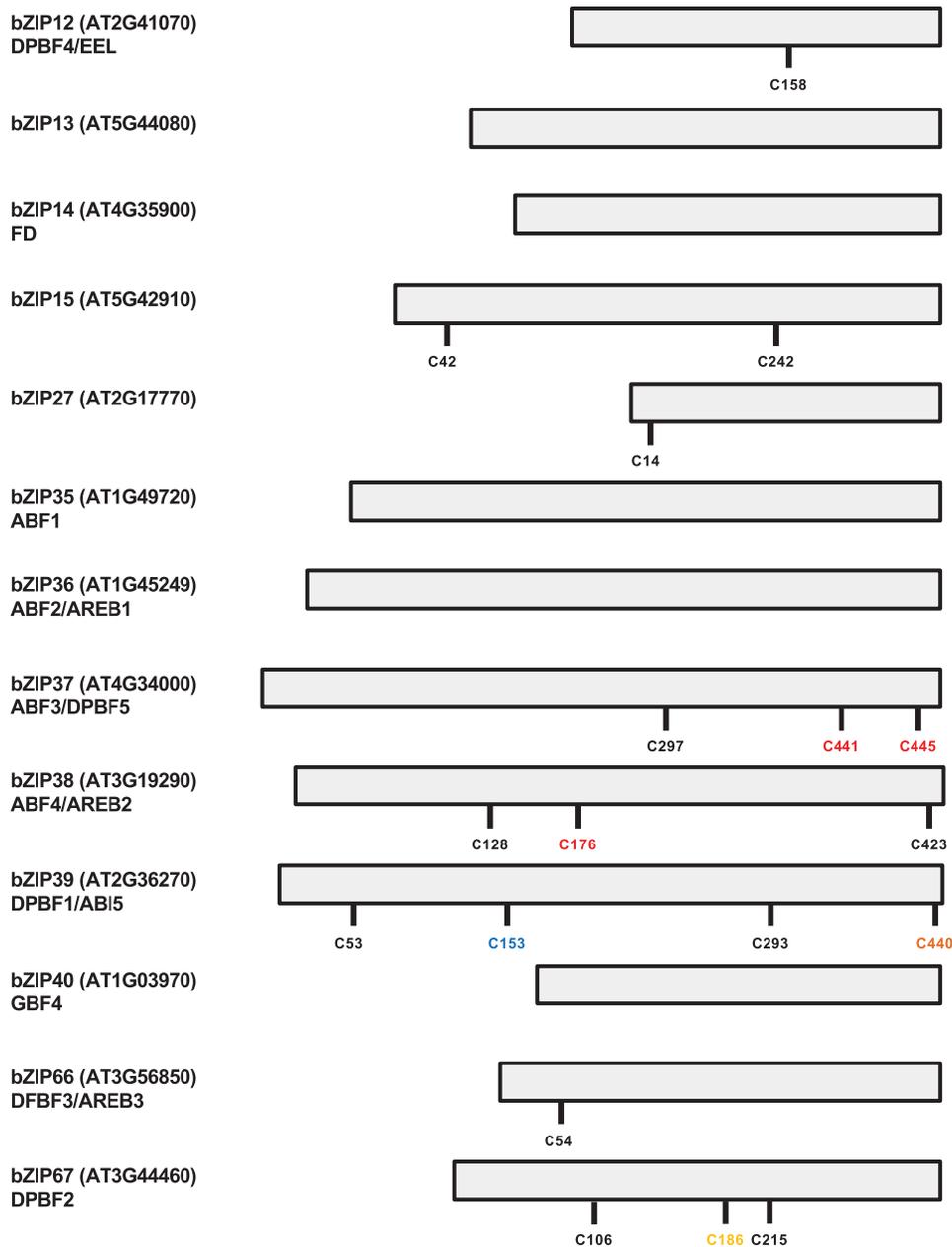


Fig. 3. S-Nitrosation analysis in group A of the bZIP transcription factor family. All the Cys (C) residues are indicated in the protein sequence. *In silico* prediction of S-nitrosation Cys targets by using the GPS-SNO 1.0 software (Xue *et al.*, 2010). The analysis shows target Cys in red, orange, and yellow depending on the S-nitrosation score (high, medium, and low, respectively). The Cys residue highlighted in blue corresponds to *in vivo* and/or *in vitro* S-nitrosation.

SnRK2/PP2CA (Peirats-Llobet *et al.*, 2016), is also susceptible to S-nitrosation, as revealed by GPS-SNO analysis. In addition, BRAHMA represses *ABI5* transcription in the absence of ABA (Han *et al.*, 2012).

Hormonal networks regulate developmental and stress processes in response to internal and external cues. Thus, ABA and gibberellins (GAs) play antagonistic roles in many physiological events (reviewed in Liu and Hou, 2018) where NO represents a key modulator between both pathways. The NO donor sodium nitroprusside (SNP) promotes DELLA protein accumulation by repressing E3 ubiquitin ligase *SLEEPY1* (*SLY1*), inhibiting GA signaling (Lozano-Juste and León, 2011). This result was also demonstrated by genetic evidence using *nia1,2noa1-2*

NO-deficient mutant seedlings (Lozano-Juste and León, 2011). In addition, *GA20ox3*, involved in GA biosynthesis, is up-regulated in *nia1,2noa1-2* and down-regulated upon NO treatment (Lozano-Juste and León, 2011). Nevertheless, NO plays a synergistic role with GAs during seed dormancy break (Bethke *et al.*, 2007), in accordance with the NO burst detected during early seed germination (Simontacchi *et al.*, 2004, Albertos *et al.*, 2015). In wheat roots, an increase in GA content after the addition of SNP under aluminum stress has also been described (He *et al.*, 2012). In this framework, NO controls the specific hormonal balance, leading to a continuous reprogramming of the signaling pathways that govern stress and developmental networks.

NO and ABA network during drought, salinity, and extreme temperatures

ABA acts to save water and energy during stress conditions. This phytohormone prevents turgor loss under low water availability mainly through stomatal closure (Eisenach *et al.*, 2017) and contribution to the synthesis of osmoprotectants (Verslues and Bray, 2006), thus improving plant cell adaptation to drought. NO is also a key player inside the network required for stomatal closure since nitrate reductase (NR) and NOS-like activities linked to NO production are mandatory for the ABA signal transduction cascade in guard cells (García-Mata and Lamattina, 2001, 2002; Desikan *et al.*, 2002; Neill *et al.*, 2002). In *Arabidopsis* guard cells, ABA correlates with H₂O₂ and NO in the regulation of stomatal closure. ABA increases the generation of endogenous H₂O₂, which promotes NO production in order to regulate stomatal movement (Bright *et al.*, 2006). In addition, pea and *Arabidopsis* guard cells are able to generate NO in response to ABA, while removal of NO with scavengers inhibits ABA-induced stomatal closure (García-Mata and Lamattina, 2002). However, genetic evidence showed that stomata from the *nia1nia2noa1-2* NO-deficient mutant were hypersensitive to ABA during stomatal closure (Lozano-Juste and León, 2010). The involvement of NO in ABA perception and signaling has been described above. Specifically, *SnRK2.6*, which is preferentially expressed in guard cells, is inhibited through S-nitrosation (Fujii and Zhu, 2009; Wang *et al.*, 2015b). *SnRK2.6* phosphorylates the slow (S-type) anion channel associated1 (SLAC1) and inward potassium channel in *Arabidopsis thaliana* 1 (KAT1) promoting stomatal closure (Vahisalu *et al.*, 2008; Geiger *et al.*, 2009; Sato *et al.*, 2009). Nevertheless, pharmacological assays showed that NO application triggered stomatal closure, whereas this was inhibited by the NO scavenger cPTIO (Neill *et al.*, 2002), suggesting a positive role for NO in stomatal closure. Other studies reported that NO may affect KAT1 (García-Mata *et al.*, 2003; Sokolovski and Blatt, 2004), SLAC1 (Vahisalu *et al.*, 2008), and nitrated cGMP generation (Joudoi *et al.*, 2013). Consequently, NO-dependent modulation of ion channels at the plasma membrane of guard cells facilitates osmotic solute loss, reducing guard cell turgor and promoting stomatal closure. Fu *et al.* (2016) showed promotion of stomatal development by NO up-regulation of the basic helix-loop-helix (bHLH) genes *SPEECHLESS* (*SPCH*), *MUTE*, and *SCRM2*, and down-regulation of *MITOGEN-ACTIVATED PROTEIN KINASE 6* (*MPK6*) expression. Further research will be necessary to decipher these NO dual effects, where the level of channel modulation promotes stomatal development and stomatal closure while *SnRK2.6* S-nitrosation inhibits this closure.

Soil salinity becomes one of the main threats for crop production. A reduction in the protein S-nitrosation pattern under salt treatment was previously reported (Camejo *et al.*, 2013). NO promotes salt tolerance by different mechanisms, including the increase in transcription of H⁺-ATPase and the Na⁺/H⁺ antiporter in *Avicennia marina* in order to maintain ion homeostasis (Chen *et al.*, 2010), synthesis of protective metabolites, and induction of the oxidative defense system (Fan and Du, 2012; Manai *et al.*, 2014; Ahmad *et al.*, 2016).

Additionally, NO ameliorates salinity stress through stomatal closure by reducing water loss as mentioned above. Oxidative stress constitutes a common effect linked to drought, salinity, or osmotic stress. In rice, exogenous treatment with the NO donor SNP increases enzyme activity related to redox control, such as guaiacol peroxidase (POX), superoxide dismutase (SOD), and ascorbate peroxidase (APX) (Uchida *et al.*, 2002). APX is modulated by NO at the post-translational level by S-nitrosation of Cys residues, which in turn promotes its activity (Begara-Morales *et al.*, 2014), and by metal nitrosation and Tyr nitration, which both inhibit its activity (Clark *et al.*, 2000; Begara-Morales *et al.*, 2014). Furthermore, other NO targets are SOD, since Tyr nitration decreases its activity (Holzmeister *et al.*, 2015), and pea Prx IIF, where S-nitrosation inhibits its activity (Camejo *et al.*, 2013). Phosphoenolpyruvate carboxylase-kinase (PEPCK) regulates photosynthetic C₄ phosphoenolpyruvate carboxylase in sorghum, is enhanced by salinity, and presents a high activity under short NO treatments (Monreal *et al.*, 2013), highlighting a novel role for NO in linking carbon fixation with salt stress mitigation. ABA exogenous application, drought, and salt stress induce *ABI5* at early post-germinative stages (Lopez-Molina *et al.*, 2001). *ABI5* together with *ABI3* modulate the expression of *Em1* and *Em6* (class I LEA proteins) genes which are involved in desiccation tolerance (Lopez-Molina *et al.*, 2002; Carles *et al.*, 2002). The *ABI5* mutant allele *abi5-9* shows ABA and salinity insensitivity (Tezuka *et al.*, 2013), highlighting another point of ABA-NO crosstalk during abiotic stresses. Other ABFs are involved in salt, osmotic, and drought stresses. *ABF3* transcription is up-regulated during salt treatment while *ABF1* and *ABF4* are repressed (Fujita *et al.*, 2005; Fernando *et al.*, 2018). In addition, *ABF3* and *ABF4* display putative Cys residues susceptible to be modulated by NO through S-nitrosation (Fig. 3). All together, these findings demonstrate a key role for NO during salinity stress alleviation.

Low and high temperatures promote changes in the S-nitrosoproteome and nitration level as described in *Brassica juncea* and pea plants (Corpas *et al.*, 2008; Abat and Deswal, 2009), showing that NO is involved in plant tolerance to chilling and freezing (reviewed in Puyaubert and Baudouin, 2014). Recently, NO has been proposed to scavenge ROS and regulate the levels of polyamines, osmoprotective metabolites, and hormonal balance, since NO-deficient mutants are more tolerant to cold stress (Zhao *et al.*, 2009; Fan *et al.*, 2015; Costa-Broseta *et al.*, 2018). Other NO mechanisms involve the negative regulation of the synthesis of phosphorylated sphingolipids during cold transduction (Cantrel *et al.*, 2011). GSNOR controls the S-nitrosothiol concentration, which is modulated by cold conditions at the level of gene expression and activity but, depending on the species analyzed, can be promoted or repressed (Ziogas *et al.*, 2013; Kubiánová *et al.*, 2014; Lv *et al.*, 2017). NO is also involved in heat responses since previous exogenous treatment led to a better thermotolerance acquisition while this effect is blocked by the NO scavenger cPTIO (Song *et al.*, 2013). This molecule is able to modulate heat stress alleviation at different levels, including the induction of genes belonging to subunits of the PSII core reaction center (Psb) complex (*psbA*, *psbB*, and *psbC*) (Chen *et al.*, 2013), the

increase in DNA binding of heat shock transcription factors, and heat shock protein18.2 (HSP18.2) accumulation through calmodulin 3 (CaM3) (Xuan *et al.*, 2010) and the promotion of *HSP26* transcription (Uchida *et al.*, 2002).

NO and hypoxic stress crosstalk

As aerobic organisms, plants have evolved to maintain specific requirements for oxygen (O₂) that lead to a correct respiratory energy supply. A close relationship between both O₂ and NO sensing is mediated by the N-degron pathway, which operates through N-terminal recognition that targets proteins for degradation, and by phytooglobins, which are able to modulate the level of diatomic gases such as carbon monoxide, NO, and O₂. Hypoxic conditions lead to an increase in NO levels, suggesting a key role for the NO/O₂ balance during this stress (Dordas *et al.*, 2003; Borisjuk *et al.*, 2007; Ma *et al.*, 2016).

Phytooglobins are ubiquitous proteins found in all organisms that bind diatomic gases such as NO and O₂ through the presence of a heme group (reviewed in Hoy and Hargrove, 2008; Gupta *et al.*, 2011), controlling its transport, scavenging, and detoxification (Arredondo-Peter *et al.*, 1998). There are three types of phytooglobins, symbiotic (SymPhytogb), non-symbiotic (Phytogb1 and 2), and truncated (Phytogb3). Phytogb1 and 2 have a significant function in regulating NO and O₂ levels mainly during cellular hypoxic conditions (Dordas *et al.*, 2003, 2004). *Phytogb1* overexpression regulates NO levels and improves growth and development under hypoxic stress (Hunt *et al.*, 2002; Perazzolli *et al.*, 2004; Thiel *et al.*, 2011). A complex self-regulatory mechanism closes this cycle since Phytogb1 is S-nitrosated both in the Cys and in the metal (Perazzolli *et al.*, 2004), and leghemoglobin is modulated by Tyr nitration (Sainz *et al.*, 2015), leading to a specific and fine-controlled NO/O₂ balance, closely related to inhibition or promotion of plant development.

The N-degron pathway is involved not only in hypoxic stress (Gibbs *et al.*, 2011; Licausi *et al.*, 2011) but also in seed storage mobilization (Zhang *et al.*, 2018a, b), germination (Holman *et al.*, 2009; Gibbs *et al.*, 2014), photomorphogenesis (Abbas *et al.*, 2015), shoot and leaf development (Graciet *et al.*, 2009), stomatal closure (Gibbs *et al.*, 2014), flowering (Vicente *et al.*, 2017), vernalization (Gibbs *et al.*, 2018), leaf senescence (Yoshida *et al.*, 2002), and pathogen attack (de Marchi *et al.*, 2016; Vicente *et al.*, 2019). This pathway senses O₂ and NO through the regulation of ethylene response factor (ERF) Group VII transcription factors, which are degraded via PROTEOLYSIS6 (PRT6) in the presence of both gases due to a characteristic conserved motif at the N-terminus initiating with Met-Cys. In *Arabidopsis* and rice, ERFVIIIs are associated with hypoxia responses, and their protein stabilization improves growth under this abiotic stress (Gibbs *et al.*, 2011; Licausi *et al.*, 2011). ABA also participates in the response to hypoxic conditions, such as root flooding (Hsu *et al.*, 2011) or seed environment before germination (Benech-Arnold *et al.*, 2006), and its exogenous application promotes hypoxia tolerance in roots (Ellis *et al.*, 1999). In fact, ABA perception and signaling constitute a key hormonal network affected by the N-degron pathway (Holman *et al.*, 2009; Vicente *et al.*,

2017). Gibbs *et al.* (2014) identified a mechanism for NO/O₂ sensing during ABA signaling through degradation of ERFVIIIs, which are *ABI5* transcriptional activators. ERFVIIIs are degraded in the presence of both NO and O₂, affecting seed germination, although NO-mediated *ABI5* degradation is independent of this pathway (Albertos *et al.*, 2015). In addition, the *ABI5* transcriptional repressor BRAHMA could be modulated by ERFVII (Vicente *et al.*, 2017). This mechanism integrates NR-dependent NO production with the regulation of the chromatin-remodeling ATPase BRAHMA mediated by ERFVII, ending in a genetic reprogramming that controls development and stress responses to enhance plant survival. A deregulation in *PYL2* ABA receptor transcription in the *prt6* knockout mutant is dependent on ERFVII, RAP2.12, RAP2.2, and RAP2.3 (Zhang *et al.*, 2018b). Additionally, the interaction between RAP2.3 and DELLAs contributes to regulate hormonal networks able to control the balance between growth and stress responses (Marín-de la Rosa *et al.*, 2014). Recently, the NO modulation by S-nitrosation of GSNOR has been described, which promotes a conformational change that drives its autophagy-dependent degradation, linking hypoxia and NO to selective autophagy (Zhan *et al.*, 2018). At the physiological level, GSNOR degradation regulates NO cellular homeostasis, which is involved in low-O₂ tolerance and promotion of seed germination by modulating *ABI5* expression. These results confirm the key function of the N-degron pathway in the regulation of genetic and molecular networks through NO/O₂ balance sensing.

NO signaling at the crossroads between plant development and biotic stress

Upon pathogen attack, the plant must resume growth. In this context, whether the plant uses the same arsenal of molecules for both development and defense, or if a genetic reprogramming occurs between these two key processes, constitutes a major question concerning the complex cellular environment. Pieterse *et al.* (2009) asserted that the contribution of plant growth regulators (i.e. hormone signaling pathways) to plant immunity is indicative of an extensive crosstalk between development and defense. Consequently, it is hypothesized that both are regulated by a network of interconnecting signaling pathways in a cost-efficient manner. Several phytohormones have been related to plant defense, among them salicylic acid (SA), jasmonate (JA), ethylene (ET), and ABA within the context of disease suppression. Of particular importance is the NO-SA interaction during biotic stress responses, based on the well-known molecular effectors and the extensive literature that places NO at the center of both SA synthesis and signaling pathways.

Interconnections between NO and SA during plant immunity and developmental cues

SA has been linked to plant response to abiotic stresses such as drought (Munné-Bosch and Peñuelas, 2003; Chini *et al.*, 2004; Horváth *et al.*, 2007), chilling (Janda *et al.*, 1999; Ding *et al.*, 2008), heavy metal tolerance (Pál, 2002; Metwally *et al.*,

2003), heat (Dat *et al.*, 1998; Shi *et al.*, 2006), and osmotic stress (Borsani *et al.*, 2001). Furthermore, SA participates in plant growth and developmental processes such as seed germination, vegetative growth, flower formation, respiration, photosynthesis, stomatal closure, and gene expression associated with senescence, among others (reviewed in Rivas-SanVicente *et al.*, 2011). Nevertheless, the most prominent SA function falls into the local and systemic response against microbial pathogens (Durner and Klessig, 1995; Innes, 2018).

In plant immunity, NO was first described as a molecule with a role in plant disease resistance, being a signal that is activated upon pathogen attack (Delledonne *et al.*, 1998; Durner *et al.*, 1998; Bellin *et al.*, 2013). Knowledge of the involvement of NO in plants has increased greatly and it has been shown to be involved in many cellular processes, not only immune response related, but also growth and development associated (reviewed in Sanz *et al.*, 2015). In this framework, it is difficult to separate NO, and other RNS, from ROS molecules, as both are considered as signaling effectors undergoing reciprocal regulation, which is pivotal in early stages of biotic interactions (Scheler *et al.*, 2013; Del Río, 2015). Nowadays some controversy still surrounds the NO homeostasis in plant immunity, at the level of both production and turnover (reviewed in Vandelle *et al.*, 2016).

Accordingly, GSNO, which is not only a bioactive NO species but also a stable NO reservoir and NO transport form (Kovacs *et al.*, 2015), is becoming increasingly relevant (Feechan *et al.*, 2005; Frungillo *et al.*, 2014). In turn, GSNO is irreversibly degraded by GSNOR (Liu *et al.*, 2001). GSNOR is present in almost all plant tissues and participates in numerous plant processes throughout the plant life cycle. The Arabidopsis GSNOR null mutant *gsnor1-3*, also known as SENSITIVE TO HOT TEMPERATURE5 (HOT5) from a thermotolerance genetic screening (Lee *et al.*, 2008), presents enhanced levels of SNO and proteome-wide increased S-nitrosation (Hu *et al.*, 2015). This translates into pleiotropic deficiencies in multiple plant growth and development pathways and physiological processes (Kwon *et al.*, 2012), and altered responses to biotic and abiotic stresses (Feechan *et al.*, 2005; Lee *et al.*, 2008; Chen *et al.*, 2009; Kwon *et al.*, 2012). It is noteworthy that *gsnor* mutants have altered chlorophyll content and photosynthetic properties (Hu *et al.*, 2015) and, additionally, they show early flowering, a loss of apical dominance due to a higher number of axillary shoots, reduced hypocotyl elongation and primary root growth, impaired germination, and decreased seed production, among other aspects.

It should be noted that the crosstalk between NO and targets of SA synthesis and signaling affects phenylalanine ammonia lyase expression in the former (Klessig *et al.*, 2000), and the expression of pathogenesis-related genes in particular or the systemic acquired response in general in the latter (Song and Goodman, 2001; Rustérucci *et al.*, 2007; Espunya *et al.*, 2012; Mur *et al.*, 2013). Another example is the participation of both molecules, SA and NO, in mitigating the toxicity caused by heavy metals and, thus, enhancing plant development (Zhou *et al.*, 2009; Singh *et al.*, 2009, 2017). It has been described that GSNO influences the function of proteins related to plant defensive responses but, interestingly, these proteins

also affect developmental processes (Table 2). S-Nitrosation of SA-binding protein 3 (SABP3) is prompted by bacterial infection and inhibits SA binding capacity and carbonic anhydrase (CA) activity. Since CA activity is required for the establishment of plant disease resistance, this post-translational modification could participate in a negative feedback loop in the modulation of the SA-dependent plant defense mechanism (Slaymaker *et al.*, 2002; Wang *et al.*, 2009). Loss or overexpression of CA activity causes defective tapetal cell differentiation in early anther development (Huang *et al.*, 2017). Similarly, S-nitrosation of the NADPH oxidase AtRBOHD abolishes its ability to synthesize ROS, giving a role to NO in limiting the hypersensitive response (Torres and Dangl, 2005; Yun *et al.*, 2011). Once more, this enzyme, together with AtRBOHF, negatively regulates lateral root development by changing the accumulation of superoxide in Arabidopsis roots (Li *et al.*, 2015). Interestingly, there is a reduced NADPH oxidase activity in *gsnor* mutants, probably because of inhibition of AtRBOHD by S-nitrosation (Karapetyan and Dong, 2018).

NO also targets several ROS-detoxifying enzymes by nitration or S-nitrosation (Tables 1, 2), including APX, monodehydroascorbate reductase, CAT, SODs, PrxIIE, and PrxIIF, all of which are related to H₂O₂ detoxification (Romero-Puertas *et al.*, 2007; Lin *et al.*, 2012; Ortega-Galisteo *et al.*, 2012; de Pinto *et al.*, 2013; Begara-Morales *et al.*, 2013, 2016; Holzmeister *et al.*, 2015; Yang *et al.*, 2015). Recently, the contribution of many of these enzymes to plant tolerance to chilling temperatures, having an effect in vegetative tissues, has been described in a priming process providing plant memory formation (Baier *et al.*, 2019).

Regulation of the nonexpressor of pathogenesis-related genes (NPR) family mediated by NO

The Arabidopsis genome contains six members of the nonexpressor of pathogenesis-related genes (NPR) family including NPR1-4, NPR5/BLADE-ON-PETIOLE2 (BOP2), and NPR6/BLADE-ON-PETIOLE1 (BOP1) (Fig. 4). The corresponding proteins have in common two BTB/POZ (Broad-Complex, Tramtrack, and Bric-a-brac/Pox virus and Zinc finger) domains for protein-protein interaction, involved in degradation by the ubiquitin-proteasome system, and a series of four ankyrin repeats, which allow the interaction with the TGA (TGACG motif-binding protein) family of transcription factors (Aravind and Koonin, 1999; Sedgwick and Smerdon, 1999).

NPR1 is a transcription cofactor (reviewed in Withers and Dong, 2016) key in SA perception and signaling since the *npr1* mutant is SA insensitive (Cao *et al.*, 1997; Canet *et al.*, 2010a, b). However, not all the genes induced by SA depend on NPR1 (Blanco *et al.*, 2009), mostly due to the function of other family members such as NPR3 and NPR4 (Canet *et al.*, 2010a, b). NPR1 is also involved in the induced systemic resistance (ISR) (Pieterse *et al.*, 1998) and in the crosstalk between SA and JA (Spoel *et al.*, 2003). NPR1 function is regulated at the post-translational level by a monomerization/oligomerization mechanism dependent on the cellular redox state and determines protein subcellular localization (Fig. 5). During pathogen

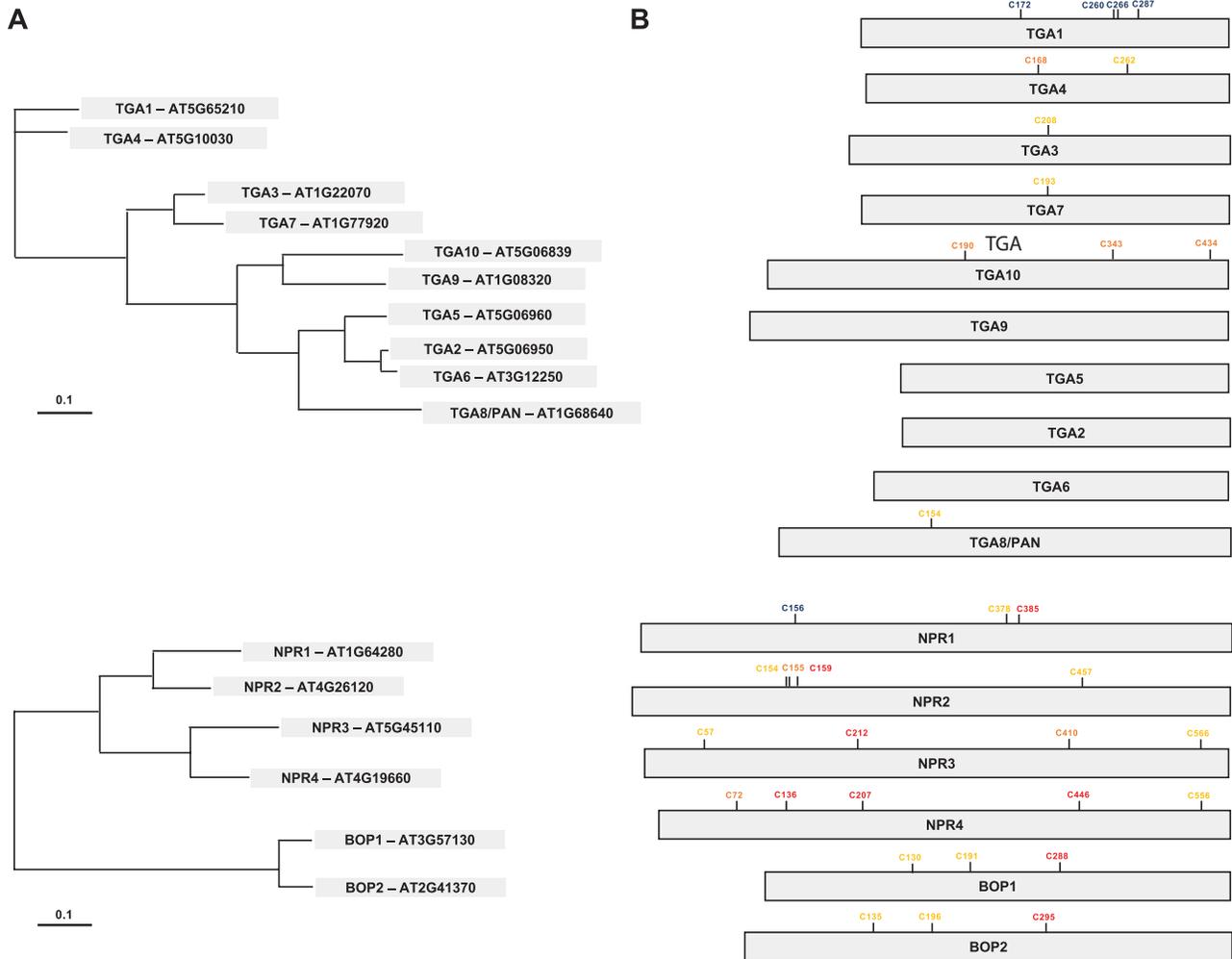


Fig. 4. S-Nitrosation analysis in group D of bZIP transcription factor and NONEXPRESSOR OF PATHOGENESIS-RELATED GENES (NPR) families. (A) Dendrograms of TGA members of the group D bZIP transcription factor family and NPR-like proteins. The branch length is proportional to the number of substitutions per site (<http://phylogeny.lirmm.fr>). (B) *In silico* prediction of S-nitrosation Cys (C) targets by using the GPS-SNO 1.0 software (Xue *et al.*, 2010). The analysis shows target Cys in red, orange, and yellow depending on the S-nitrosation score (high, medium, and low, respectively). The Cys residues highlighted in blue correspond to *in vivo* and/or *in vitro* S-nitrosation.

attack, SA concentration increases, promoting the partial reduction of the oligomer NPR1 (formed by disulfide bridges in the cytoplasm) to a monomer in the nucleus, then targeted by a C-terminal nuclear localization sequence (Mou *et al.*, 2003; Spoel *et al.*, 2009). In addition to other post-translational modifications that regulate NPR1, such as phosphorylation (reviewed in Withers and Dong, 2016), it was later discovered that S-nitrosation of Cys156 facilitates protein oligomerization *in vivo*, providing a negative regulation of defense-related gene expression by NO. Upon pathogen infection or SA accumulation, changes in cellular redox potential lead to the reduction of Cys through the activity of thioredoxins (mainly TRX-h5), and NPR1 monomers are released to the nucleus (Tada *et al.*, 2008; Kneeshaw *et al.*, 2014). In the cell nucleus, the mechanism proposed to modulate NPR1 gene expression is through its interaction with the TGA family of bZIP transcription factors, which bind specifically to SA response elements. However, it has also been observed that NPR1 can be present in the nucleus when SA levels are low (Després *et al.*, 2000). Rivas-San Vicente *et al.* (2011) suggested an additional

function of NPR1 in regulating genes related to germination, plant growth, and development; in fact, NPR1 has been related to the promotion of cell division and/or suppression of endoreduplication during leaf development (Vanacker *et al.*, 2001). Moreover, redox changes related to the circadian clock motivated by SA upon pathogen infection act via NPR1 to trigger a transcriptional reprogramming, thus minimizing fitness costs on plant growth (Zhou *et al.*, 2015). For this reason, NPR1 could be suggested to be a key molecular player in the balance between defense and growth.

Except for a minor role in SA perception (Canet *et al.*, 2010b), the functions of NPR2, the NPR1 paralog with greater homology in the primary sequence, are unknown. Interestingly, NPR3 and NPR4 have been characterized as SA receptors, able to bind the hormone with different affinities and regulate the degradation of NPR1 via the ubiquitin-proteasome by a mechanism dependent on SA concentration (Fu *et al.*, 2012). A role for NPR3 in root growth and storage compound accumulation in seeds has also been proposed, as a result of repression of the basal pathogen immune system (Shi *et al.*, 2013). In

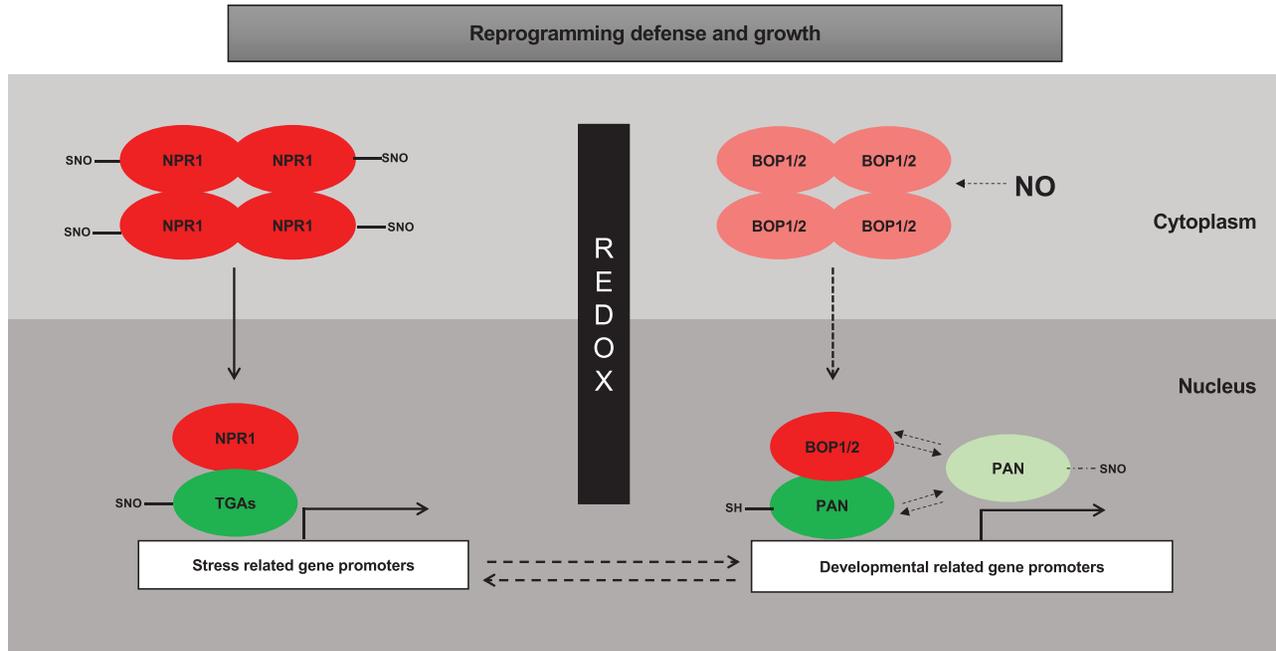


Fig. 5. Crosstalk of NO during developmental cues and biotic stress responses. Upon pathogen attack, a redox change in the cellular context promotes NONEXPRESSOR OF PATHOGENESIS-RELATED GENES1 (NPR1) monomerization and interaction with different TGAs in the nucleus to activate the expression of stress-related genes. Similarly, a hypothetical model shows the interaction of other NPR-like proteins with TGA members to activate developmental gene expression. BLADE-ON-PETIOLE1/2 (BOP1/2) proteins interact with PERIANTHIA (PAN) in the nucleus where PAN binds DNA under reducing conditions. The putative role of Cys S-nitrosation (SNO) is included. Arrows indicate positive effects and dotted arrows putative regulations.

addition, BOP1 and BOP2 are the most divergent proteins of the NPR family, both lacking a recognizable nuclear localization sequence. Although a role for these proteins as mediators of the methyl jasmonate-induced resistance in plant immunity has been described (Canet *et al.*, 2012), the most studied function is as regulators of development; especially in the establishment of axes of asymmetry in the organogenesis of leaf and flower (Hepworth *et al.*, 2005).

Group D of bZIP transcription factors are NO targets

Group D of bZIP transcription factors comprises the so-called TGA factors, according to their conserved TGACG DNA-binding motif. All of them are characterized by a short zipper domain consisting of three repeats, two conserved Q-rich domains in the C-terminus, and a more variable N-terminal part (Dröge-Laser *et al.*, 2018). In the Arabidopsis genome, 10 members of the TGA family are present, falling into five clades (Jakoby *et al.* 2002) (Fig. 4). Clade I comprises TGA1 and TGA4, and Clade II consists of three closely interconnected factors TGA2, TGA5, and TGA6, which contain a shorter N-terminus than the other TGA proteins. TGA3 and TGA7 constitute clade III. PERIANTHIA or TGA8 comprise clade IV, and TGA9 and TGA10 form clade V.

The presence of TGACG motifs in the promoters of different plant glutathione S-transferase genes (Ellis *et al.* 1993; van der Zaal *et al.*, 1996) opened up the hypothesis that TGA proteins trigger plant stress responses. In the case of TGA1 and TGA4, both are related to control of basal resistance against pathogens (reviewed in Gatz, 2013). These proteins present a regulation through Cys residues sensitive to the cellular redox

state. Thus, in the absence of SA, Cys260 and Cys266 of these proteins form an intramolecular disulfide bond that prevents interaction with NPR1; this link is reduced after the accumulation of SA, allowing this interaction and improving their binding to defense-related gene promoter regions (Després *et al.*, 2003). The Cys residues 260 and 266 of TGA1 are regulated by both S-nitrosation and S-glutathionylation, affecting protein conformation and preventing formation of disulfide bonds (Lindermayr *et al.*, 2010). At the same time, NPR1 ameliorates not only the DNA binding activity of the reduced TGA1 (Després *et al.*, 2003), but also the DNA binding activity of TGA1-SNO. Although TGA1 and TGA4 regulate target genes involved in systemic acquired resistance (SAR; Sun *et al.*, 2018), they also modulate nitrate responses in Arabidopsis roots (Alvarez *et al.*, 2014).

TGA2, TGA5, and TGA6 play key roles in pathways linked to SA (Zhang *et al.*, 2003; Kesarwani *et al.*, 2007), JA/ET (Zander *et al.*, 2010, 2012, 2014), xenobiotics, and reactive oxylipin signaling (Fode *et al.*, 2008; Mueller *et al.*, 2008; Findling *et al.*, 2018). Interestingly, *tga2tga5tga6* triple mutant roots are considerably shorter than those of the wild type in control medium (Stotz *et al.*, 2013). The interaction between NPR1 and TGA2 protein to stimulate the DNA binding activity to the SA-responsive element in the *PR-1* gene promoter has also been reported (Wu *et al.*, 2012).

The TGA3 transcription factor mediates NPR1 SA-dependent gene expression *in planta* (Sarkar *et al.*, 2018) and its role in the hormonal crosstalk between SA and cytokinin has also been reported (Choi *et al.*, 2010). Apart from that, TGA3 is also related to metal detoxification (Fang *et al.*, 2017). TGA9 and TGA10 play essential roles in anther development

by the action of two CC-type floral glutaredoxins, ROXY1 and ROXY2 (Murmu *et al.*, 2010), again exemplifying a redox-regulated TGA factor function in plants.

PERIANTHIA (PAN)/TGA8, which is part of an independent clade of the TGA family, has important functions in plant development, as a negative regulator of floral organ initiation and the number of petals and sepals (Running and Meyerowitz, 1996; Chuang *et al.*, 1999). PAN functions in floral development are mediated by the positive regulation of the *AGAMOUS* (*AG*) gene, which antagonizes the meristematic activity by repression of *WUSCHEL* (*WUS*) (Das *et al.*, 2009). *pan* mutants have flowers with five petals, similar to those of the *bop1bop2* double mutant, and *PAN* is co-expressed with *BOP1/2* during floral development. Hepworth *et al.* (2005) demonstrated by yeast two-hybrid assays that, similarly to NPR1, BOP1 and BOP2 interact with transcription factors of the TGA family but with different specificities, showing preference for PAN. This fact was corroborated by a bimolecular fluorescence complementation (BiFC) assay in Arabidopsis mesophyll protoplasts which verified their location in the cell nucleus (Xu *et al.*, 2010). Indeed, BOP1/2–PAN interaction was described in the binding to regulatory sequences of the *AP1* promoter, as a mechanism to promote the identity of the floral meristem. Although initially PAN was described as a regulator of the development of aerial parts of the plant, PAN also has a fundamental role in the stem cell niche of the root apical meristem (de Luis Balaguer *et al.*, 2017).

At the biochemical level, PAN ability to bind DNA (and, specifically, *AG*-regulating elements) is altered according to the cell redox conditions. PAN contains an N-terminal end with five Cys residues able to form intramolecular disulfide bridges, which is in agreement to the regulatory mechanism of other TGAs (Gutsche and Zachgo, 2016). In addition, a sixth Cys residue at the C-terminal end, Cys340, is essential for PAN function because it undergoes S-glutathionylation in a specific manner (Li *et al.*, 2009; Gutsche and Zachgo, 2016). Remarkably, the ROXY1 CC-type glutaredoxin negatively regulates PAN protein (Li *et al.*, 2009).

In summary, NPR-like proteins interact with TGA factors, which in turn are regulated by glutaredoxins. A clear parallelism seems to have evolved between the mechanism regulating the defense responses and that regulating floral development (Gatz, 2013) (Fig. 5).

Concluding remarks

Our understanding of the molecular basis for plant development and stress trade-off is still very limited, although the balanced function of plant growth and stress regulators is known to contribute to plant survival and fitness. The severe growth and developmental defects of NO-deficient and NO-overaccumulator mutants (even though they have complex pleiotropic phenotypes), together with impaired responses to biotic and abiotic stresses, may be indicative of a prominent role for this gasotransmitter in these trade-offs.

Thus, to gain full appreciation of how NO post-translational protein modification controls transcriptional reprogramming

of plant development upon stress, the future challenge is to uncover the reversible post-translational regulation and those molecular targets across different interconnected signaling pathways.

As we move away from Arabidopsis to other model species (i.e. the low redundancy species *Marchantia polymorpha*) and crops, it is important to have a clear vision not only of NO function and target specificity, but also of gene abundance and the evolutionary signaling pathways for translational biology.

Future research should reveal if precise amino acid substitutions in key targets will lead to the design of more accurate molecular tools for biotic and abiotic stress tolerance and improvement in growth and development in crops.

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