Nitric Oxide and Hydrogen Peroxide in Plant Response to Biotic Stress

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Abstract NO and H_2O_2 act as key regulators in a broad range of physiological processes in algae and higher plants. A large amount of research highlights multiple roles for NO/H_2O_2 in plant defence. They function as protectants but also as signaling molecules that mediate various metabolic processes and activate further systematic plant defence reactions through the regulation of genes involved in pathogen defence. This chapter summarises the current knowledge on NO and H_2O_2 necessity in plant cell resistance response to biotic stressors.

Keywords Reactive oxygen species · Reactive nitrogen species · Signal molecule · Biotic stress · Gene expression · Crosstalk

1 Introduction

Plants and algae possess different signaling molecules (e.g. growth regulators, proteins, amino acids, nucleotides, hormones) which are essential for their growth, development as well as for their response and adaptation to a variety of abiotic and

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biotic stresses (Agostoni and Montgomery 2014; Bickerton et al. 2016; Dobrikova 2017; Górka and Wieczorek 2017). In view of the increasing pollution and more pronounced climate changes that affect plant organisms at the level of molecular function, developmental processes, morphological traits, and physiology (Gray and Brady 2016), influence the severity of plant disease and further coevolution of plants and their pathogens, the investigation of signaling molecules in algae and plants is becoming increasingly important.

Nitric oxide (NO) has been recognised as one of the central players in the cell signaling and attracted great attention of researchers (Mallick et al. 2002; Chung et al. 2008; Neill et al. 2002; Jeandroz et al. 2016). NO is a small gaseous molecule with low density and lipophilic quality (Cevahir et al. 2007). Its production arises from different enzymatic and nonenzymatic pathways (Rőszer 2014; Astier et al. 2018a). The well documented reductive NO production routes in plants are nitrate reductase (NR) and the plasma membrane-bound nitrite: NO reductase (NiNOR) systems. Also, NO can be produced in an arginine-dependent pathway, similar to the nitric oxide synthase (NOS) activity present in animals. Recent investigations showed that terrestrial plants do not possess animal NOS-like enzymes, while these enzymes were found in few algal species (Santolini et al. 2017; Weisslocker-Schaetzel et al. 2017; Astier et al. 2018b). Foresi et al. (2010) isolated protein from the alga *Ostreococcus tauri* (OtNOS) that is about 45% similar to human NOS enzyme and has in vitro NOS activity. Kumar et al. (2015) found NOS-like sequences from the marine green algae *Bathycoccus prasinos* and *Ostreococcus lucimarinus* that exhibited 62% similarity with OtNOS and several conserved residues in cofactor-binding sites. Each monomer of OtNOS homodimer enzyme possesses two domains: a C-terminal reductase domain (NOSred) and an N-oxygenase domain (NOSoxy) which harbours the catalytic site. Furthermore, Weisslocker-Schaetzel et al. (2017) made in-depth structural and functional analysis of OtNOS NOSoxy domain and found weak homology with NOS enzymes from other clades. Still, residues that form the catalytic core of the domain were conserved.

Nonenzymatic pathways include NO synthesis from nitrite NO_2^- under acidic conditions or from hydroxylamine and salicylhydroxamate (Gupta et al. 2011a; Procházková et al. 2014). NO generation has been clearly demonstrated in a several different cell organelles including protoplasts, chloroplasts, mitochondria and peroxisomes (Gupta et al. 2011b; Tewari et al. 2013; Corpas and Barroso 2014), but it also could be synthesised in the cytoplasm, cell membrane, endoplasmic reticulum as well as apoplast (Frohlich and Durner 2011; Sahay and Gupta 2017). Due to the simple structure and small dimensions, NO freely diffuses through biological membranes provoking both beneficial and harmful effects in algae and plant cells (Arasimowicz and Floryszak-Wieczorek 2007). This dual role depends on the NO local concentration, as well as its ability to directly interact with other molecules and signals. Generally, at low concentrations, NO is a signaling molecule with a variety of physiological roles (Galatro and Puntarulo 2014). It plays an important role in many developmental processes of plants (Mur et al. 2013) including seed and pollen germination (Beligni and Lamattina 2000; Pasqualini et al. 2015), pollen tube growth (Prado et al. 2004), root growth (Corpas and Barroso 2015; Moni et al.

2018; Singh and Bhatla 2018; Sun et al. 2018), flowering (Senthil Kumar et al. 2016; Salachna and Zawadzińska 2018), photomorphogenesis (Lozano-Juste and León 2011; Melo et al. 2016), stomatal closure (García-Mata and Lamattina 2001), leaf senescence (Yang et al. 2018), gravitropism (Hu et al. 2005; París et al. 2018) and fertilisation (Domingos et al. 2015). Furthermore, it acts as a signal molecule for the activation of plant and algal defence response. The antioxidant role of NO is mainly based on its ability to maintain the cellular redox homeostasis and regulate the toxicity of reactive oxidative species (ROS) (Sheokand and Kumari 2015). For example, peroxynitrite ($OONO^-$) results from the reaction between NO and superoxide radical ($O_2^{\cdot -}$). It is a relatively short-lived reactive nitrogen species (RNS) which may readily migrate through biological membranes and interact with proteins, lipids and DNA via direct oxidation reactions or indirectly through the formation of highly reactive radicals (Radi 2013; Procházková et al. 2015). However, in systems where the toxicity is predominantly from peroxides, these compounds are much more toxic than NO and $OONO^-$, making NO protective against them (Misra et al. 2011).

ROS have also been shown to play an important role as signaling molecules in response to environmental conditions (Mallick and Mohn 2000; del Río 2015; Mullineaux et al. 2018). Among the ROS compounds, H_2O_2 is generally recognised as one of the most important signaling molecules which has relatively long half-life and small size and thus may migrate in different cell compartments through aquaporin channels (Hooijmaijers et al. 2012; Srivastava et al. 2014; Rodrigues et al. 2017). H_2O_2 is a product of aerobic metabolism in plants and could be generated by several pathways such as photorespiration, electron transport chains and redox reaction (Møller 2001; Voss et al. 2013). It can be synthesised by different enzymes including cell wall peroxidases (Mittler 2002), oxalate oxidases (Hu et al. 2003), amine oxidases (An et al. 2008) and flavin-containing enzymes (Cona et al. 2006), as well as by nicotinamide adenine dinucleotide phosphate (NADPH) oxidases coupled with superoxide dismutases (SOD; Vianello and Macri 1991). At lower concentrations, it acts as a long-distance signaling molecule (Matilla-Vázquez and Matilla 2014) which has a role in various physiological processes, including photosynthesis, respiration, translocation and transpiration (Vranová et al. 2002; Ślesak et al. 2007; Ismail et al. 2015). It is involved in the formation and development of adventitious roots (Li et al. 2007), stomatal closure (Zhang et al. 2001), senescence process (Bieker et al. 2012), protection against pathogen attack (Shetty et al. 2008) as well as in the regulation of various abiotic stresses (Mittler and Berkowitz 2001; Cuypers et al. 2016).

Abiotic and biotic factors induce rapid accumulation of variety of reactive nitrogen species (e.g. nitrosonium cation (NO^+), nitroxyl anion (NO^-), free radical ($NO^\cdot$), dinitrogen trioxide (N_2O_3), nitrogen dioxide (NO_2) and *S*-nitrosothiols (SNOs)) causing nitrosative stress (Corpas et al. 2007; Procházková et al. 2015). In response to different stress factors including infections by pathogenic fungi, bacteria, and viruses, rapid accumulation of a variety of ROS also occurs (Mittler 2017). One of the earliest events following elicitation characterised by high ROS and NO concentrations is generally known as oxidative burst (Wojtaszek 1997). H_2O_2

generated during oxidative bursts under biotic stress may reduce pathogen growth or may cause the expression of genes encoding proteins involved in antioxidant and defensive processes but also may induce programmed cell death (PCD) that occurs during hypersensitive response (HR) in plants (Bhattacharjee 2005).

At higher concentration, all reactive species including NO and H_2O_2 interact with different macromolecules affecting their functionalities (Gadjev et al. 2008; Habibi 2014; Corpas and Palma 2018). The differential reactivity of RNS defines the diversity of the NO potential target molecules and its chemical reactions including nitrosylation, nitration and oxidation (Arasimowicz and Floryszak-Wieczorek 2007; Krasylenko et al. 2017).

Plants have developed an antioxidative system that encompasses both the enzymatic and nonenzymatic components to minimise nitro-oxidative stress caused by RNS and ROS (Corpas and Barroso 2013). The enzymatic components include very efficient various enzymes such as SOD, catalase (CAT), glutathione peroxidase (GPX), glutathione *S*-transferase (GST), guaiacol peroxidase (GPOX) and the ascorbate-glutathione cycle enzymes: ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDAR) and glutathione reductase (GR). Nonenzymatic antioxidants such as ascorbic acid (ASH), glutathione (GSH), phenolic compounds, alkaloids, nonprotein amino acids and α-tocopherols can quench all kinds of ROS directly but also may assist the enzymes to efficiently detoxify ROS (Perl-Treves and Perl 2002; Gill and Tuteja 2010; Štolfa et al. 2016, 2018).

In response to development and different abiotic and biotic factors, both NO and H_2O_2 may interact with a variety of other signaling molecules and phytohormones (Ferreira and Cataneo 2010; Mostofa et al. 2015; Saxena et al. 2016) (Fig. 1). Also, crosstalk between the NO and H_2O_2 has been demonstrated in plants and algae (González et al. 2012; Niu and Liao 2016). These molecules may interact in their different developmental and physiological processes. Thus, it has been found that NO and H_2O_2 are essential signal molecules that mediate abscisic acid (ABA)-induced stomatal closure (Li et al. 2017) and that H_2O_2 and NO signaling pathways are involved in adventitious rooting in mung bean seedlings (Li and Xue 2010) as well as in cell cycle of green alga *Chlamydomonas reinhardtii* (Pokora et al. 2017). During the last decades, the roles of NO and H_2O_2, as well as their crosstalk in mediating plant defence mechanisms, have been largely studied. For example, it has been found that H_2O_2 and NO-signaling pathway overlap during the citrus plant acclimation on salinity (Tanou et al. 2009).

The mechanisms of stresses response triggered by NO and H_2O_2 include the enhancement of antioxidant systems and specific stress mechanisms, depending on the stress type (e.g. drought, temperature, heavy metals, etc.), and demand the interaction with other signaling molecules, such as mitogen-activated protein kinase (MAPK), plant hormones and calcium (Molassiotis and Fotopoulos 2011; Farnese et al. 2016). MAPK cascades are present in plants and algae (Mohanta et al. 2015) and consist of a few protein kinase modules including MAP kinase kinase (MAP2Ks, also called MKKs, MEKs or MAPKK), MAP kinase kinase kinases (MAP3Ks, also called MAPKKKs or MEKKs) and MAP kinase kinase kinase kinases (MAP4K; Rodriguez et al. 2010; Çakır and Kılıçkaya 2015). Generally,

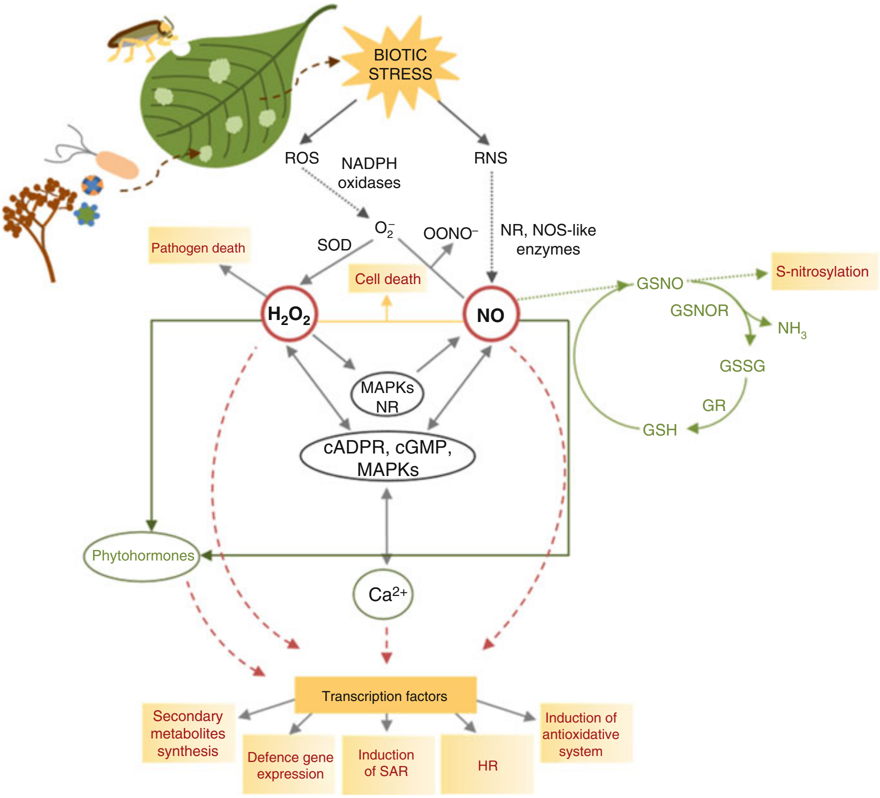

Fig. 1 The signal cascade mediated by NO and H_2O_2 in plant pathogen defence

MAPK is activated via phosphorylation of threonine and tyrosine residues in the catalytic subdomain (Ichimura et al. 2002) and then translocated into the cytoplasm or nucleus to trigger the cellular responses (Nadarajah and Sidek 2010). They are involved in cellular responses to hormones, plant growth and development, regulation of the cell cycle and responses to biotic and abiotic stresses (Sinha et al. 2011; Zhao et al. 2013; Hettenhausen et al. 2015; Chardin et al. 2017). MAPKs can phosphorylate many target molecules including other kinases, enzymes and transcription factors (TFs). The responses mediated by MAPKs involve the induction of a variety of enzymes and may attenuate or amplify the original signal triggered by ROS and NO (Asai et al. 2008; Opdenakker et al. 2012). NO and H_2O_2 may also increase the concentration of some other signaling molecules such as cyclic guanosine 3′,5′-monophosphate (cGMP). This cyclic nucleotide is generated from guanosine 5′-triphosphate (GTP) by enzymes with guanylate cyclase (GCs) activity (Mulaudzi et al. 2011). These molecules have long been known to be present in plants and algae, playing important roles in many biological processes including growth and differentiation, photosynthesis as well as biotic and abiotic defence (Dubovskaya et al. 2011; Nan et al. 2014; Gehring and Turek 2017; Demidchik et al. 2018). Responses associated with cGMP depend on the time between the perception of the stimulus and the peak in nucleotide concentration and consequently involve fast responses, which include the ion channels modulation (e.g. Ca^{2+} channels) or long-term adaptive responses, which result in changes in the transcriptome and in the proteome (Pasqualini et al. 2009).

Thus, considering the very important role of NO and H_2O_2 molecules in a variety of biological process in plant and algae as well as in their response and adaptation to the environmental changes, the present review aims to summarise the recent data concerning the role of NO and H_2O_2 in plant defence mechanisms.

2 Enrolment of NO and H_2O_2 in Plant Stress Response

2.1 Sources, Signaling and Interaction

Elicitation by abiotic or biotic stress factors induces oxidative burst as one of the earliest events following plant challenge with pathogenic micro-organisms, including fungi, bacteria and viruses, as well as in cultured cells treated with elicitor preparations, pathogens or plant cell-wall fragments or in response to mechanical wounding (Wojtaszek 1997). To protect themselves against pathogens and herbivores, plants have evolved a complex network of immune responses – HR. It is defined as a programmed execution of infected cells and sometimes additional surrounding cells with a function to restrict pathogen infection (Lamb and Dixon 1997; Greenberg and Yao 2004). Beside local HR, plants react to pathogen attack by establishing systemic-acquired resistance (SAR), a long-lasting systemic immunity that protects the entire plant from the subsequent invasion of a broad range of pathogens associated with the systemic expression of defence gene families encoding pathogenesis-related proteins (Yu et al. 2014). One of the earliest events in the HR is the rapid accumulation of ROS (Zurbriggen et al. 2010) and NO (Delledonne et al. 1998; Durner et al. 1998). Plant species differentiate according to the major ROS building the oxidative burst. New and highly sensitive methods enabled the real-time detection of ROS generation in response to stress. Recently, the use of catalytic amperometric biosensors tested on in vivo spinach (*Spinacia oleracea*) leaf sample showed the continuous generation of $O_2^{\cdot -}$ for minutes after wounding, followed by a decline, while the production increased considerably with the dose of mechanical injury. The total $O_2^{\cdot -}$ concentration was found to be equivalent to 40 nM and 200 nM for a minimal dose of injury and injury at multiple sites, respectively (Prasad et al. 2017). Seaweed species released strong oxidants within 1 min of wounding and/or showed cellular accumulation of strong oxidants over an hour post-wounding (McDowell et al. 2014). However, the inherent interrelationship between H_2O_2 and $O_2^{\cdot -}$ makes it sometimes difficult to clearly identify the ROS behind the oxidative burst (Wojtaszek 1997). Stress treatment induces an oxidative burst in barley (*Hordeum vulgare*) anthers, as revealed by the formation of $O_2^{\cdot -}$ that gives rise to H_2O_2. Among ROS, H_2O_2 may have a central role in anthers as a diffusible signal molecule allowing selective induction of defence-related genes (Varnova et al. 2002).

The bulk of active oxygen species, mainly $O_2^{\cdot -}$, H_2O_2, singlet oxygen ($^1O_2$) as well as NO, are produced to serve not only as protectants but also as signals activating further plant defence reactions (Bolwell 1999). H_2O_2 production is indispensable during plant growth, development and resistance responses. Its great capacity to buffer other ROS molecules and balance the capacity of oxygen scavenging enzymes changes oxygen's relative impact on cells altering its resistance to stress (Quan et al. 2008). However, its beneficial role in integrating signaling network in response to biotic and abiotic stress and during developmental processes is well established (Wojtyla et al. 2016). Due to the large plethora of different signal messages triggered by H_2O_2, plants can sense, transport and induce cellular responses (Quan et al. 2008). The network of signals includes other reactive species such as NO and H_2S, plant phytohormones jasmonic acid (JA), salicylic acid (SA), ABA, ethylene, auxin and gibberellins, as well as ions regulating diverse cellular processes like Ca^{2+} and K^+ (Quan et al. 2008; Kaurilind et al. 2015).

One of the most important roles of H_2O_2 is in the reaction with the invading organisms. After the detection of an invader at the cell wall, the NADPH oxidase at the plasma membrane adjacent to the invasion site produces $O_2^{\cdot -}$ and ultimately H_2O_2 outside the plasma membrane.

Aquaporins in the plasma membrane are crucial for the efficiency of H_2O_2 signaling between cells. Their capacity to facilitate the H_2O_2 diffusion may have physiological significance in many organisms and be important in communication between different species (Bienert et al. 2006).

A number of possible functions for H_2O_2 have been proposed in plant-pathogen reactions: direct killing of pathogens, involvement in cell-wall reinforcing processes, promotion of PCD at the site of infection, phytoalexin synthesis, induction of defence gene expression and signaling in the induction of SAR (Bolwell 1999; Kuźniak and Urbanek 2000). During the pathogen attack on the tea plant (*Camellia sinensis*) leaves, H_2O_2 can accumulate in mesophyll and epidermal cells (Wang et al. 2018). Cellular and subcellular localisation analyses revealed that H_2O_2 was mainly localised in wound zones and spread throughout the veins and tissues. Preferentially, H_2O_2 was found in cell walls of spongy and mesophyll cells facing intercellular spaces in the herbivore-wounded lima bean (*Phaseolus lunatus*) leaves, even though confocal laser scanning microscopy analyses also revealed the presence of H_2O_2 in mitochondria/peroxisomes (Maffei et al. 2006). Like in the case of wounding, H_2O_2 also accumulates in the *Capsicum* leaf abscission zone throughout plant growth, it increases with age and during the execution phase, and its role in leaf abscission is associated with ethylene both in vitro and in planta (Sakamoto et al. 2008).

In the unicellular green alga *Micrasterias denticulata*, chloroplasts and mitochondria are generally the main production sites of H_2O_2 independent of the treatment (salt and osmotic stress), followed by cytoplasm, while levels remained unchanged or even slightly decreased in cell walls of treated cells and elevated concentration at the plasma membrane of KCl-treated cells (Darehshouri and Lütz-Meindl 2010). Increased H_2O_2 production can also be a defensive mechanism against epiphytism in algae. Green macroalga *Caulerpa taxifolia* enhanced the production of H_2O_2 and toxin caulerpenyne as well as the antioxidant enzymes activities to compete against epiphytic rhodophyte *Lophocladia lallemandii* (Box et al. 2008). H_2O_2 is also engaged in signal transduction and defence reactions in the nonhost-pathogen interactions, like the formation of callose-containing papilla for cell wall reinforcement and HR. HR and papilla deposition was highly associated with H_2O_2 accumulation in pepper epidermal cells, which has a key role in nonhost resistance against *Blumeria graminis* f. sp. *tritici* preventing its colonisation and disease development (Hao et al. 2011). Although being the most prominent oxidant in the algal oxidative burst cocktail (Potin 2008), some seaweeds show the smaller role of H_2O_2 upon wounding and oxidant release. For example, in several species of Antarctic brown and red macroalgae, other oxidant(s) besides H_2O_2 are released upon wounding (McDowell et al. 2014). H_2O_2 was a component of immediate oxidant release in one of five species, while in some it was not detected at all. Even the two close sister algal taxa may produce different amounts of ROS and have a different composition of chemical species in the oxidative burst. While after sonic injury endosymbiotic dinoflagellate *Symbiodinium* sp. produced a small oxidative burst of 0.042 ± 0.0045 pmol H_2O_2 min^{-1} cell^{-1} composed of nearly 100% H_2O_2, the oxidative burst in *Heterocapsa pygmaea*, the species similar in size and genetically related, was nearly 80 times greater (3.37 ± 0.26 pmol H_2O_2 min^{-1} cell^{-1}) and also produced a fraction of other free radicals (Mydlarz and Jacobs 2004). The amount of produced H_2O_2 can vary with the different type of wounding, e.g. herbivore-wounded lima bean (*Phaseolus lunatus*) leaves produced higher H_2O_2 concentrations compared to mechanically damaged leaves (Maffei et al. 2006). As a response to oxidative burst, many species of marine algae produce volatile organic compounds, such as halogenated, sulphur containing, aldehydes, non-methane hydrocarbons and oxygenated species as one of the ways to lower the content of produced H_2O_2 (Potin 2008). An oxidative burst of H_2O_2 and the consequent production of volatile organic compounds in brown alga *Laminaria digitata* after elicitation induce defence response which can even be transmitted as a warning message to neighbouring conspecifics (Thomas et al. 2011).

Exogenously applied H_2O_2 is known as a good microbicidal agent which can benefit seed health and performance. Soaking the zinnia (*Zinnia elegans*) seeds regardless of time (10, 20, 30 and 60 min) and H_2O_2 concentration (3, 6, 9 and 12%, respectively) significantly reduced seed infestation with *Alternaria* spp. and *Fusarium* spp. fungi, while 3% solution positively influenced seed germination and vigour at 20 min and 10 min application, respectively (Szopińska 2014).

Foliar application of H_2O_2 (18 mM) in chili pepper plants (*Capsicum chinense*) significantly increased the amount of phenolics, flavonoids and capsaicinoids contents in fruits, thus concomitantly increasing antimicrobial activity of its extracts against bacteria and yeast (Vargas-Hernández et al. 2017). H_2O_2 is also utilised as an efficient algicide for the management of waste waters. The dose of 3.0×10^{-3} g H_2O_2 μg^{-1} phytoplankton chlorophyll-a was the most effective in the removal of nuisance phytoplankton, including toxic cyanobacteria (Barrington and Ghadouani 2008). Sensing the increased H_2O_2 concentrations can also be one of the phytoplankton survival strategies under unfavourable environmental conditions. The encystment of some dinoflagellate species, an effective strategy that enables them to survive, is redox-mediated, presumably by H_2O_2 (Ganini et al. 2013).

NO burst can be detected very early after inoculation with pathogens and directly precedes H_2O_2 generation. NO production in affected cells can be monitored with the application of fluorescent dyes (Foissner et al. 2000; Prats et al. 2005).

One of the most important NO signaling mechanism during plant defence is based on its chemical reaction with proteins (Leitner et al. 2009). The fine balance between *S*-nitrosylation and denitrosylation is critical for NO signaling. *S*-Nitrosylation regulates numerous defence-related proteins such as enzymes, transcriptional activators, or co-activators involved in plant immune response in the way of protein relocalisation or activity modulation (Bellin et al. 2013). *S*-nitrosylation is a chemical reaction in which a NO moiety is covalently added to the sulfhydryl group of reactive cysteine residues in target proteins to form an *S*-nitrosothiol (SNO) (Stamler et al. 2001). The SNO turnover represents an alternative mechanism to control the process of protein *S*-nitrosylation. Namely, the main enzymatic systems which mediate denitrosylation in plants are described: the glutathione/*S*-nitrosoglutathione reductase (GSH/GSNOR) and the thioredoxin-*h*5 (Trx-*h*5) (Kneeshaw et al. 2014). An *S*-nitrosylated form of glutathione, *S*-nitrosoglutathione (GSNO) is a global reservoir of NO bioactivity (Liu 2001). Experiments with *Arabidopsis* knockout mutants of this enzyme, known as GSNO Reductase 1 (GSNOR1), accumulate high levels of protein-SNO and consequently have impaired SA-dependent immune signaling and are highly disease susceptible (Feechan et al. 2005). In contrast, plants expressing antisense GSNOR1 show enhanced SAR, likely due to a partial reduction in GSNOR1 activity, which increases NO levels to the extent that is ideal for stimulating SAR (Rustérucci et al. 2007; Espunya et al. 2012). In plants, GSNOR has been found to be important in resistance to bacterial and fungal pathogens like *Blumeria graminis*, *Hyaloperonospora parasitica*, and *Pseudomonas syringae* (Feechan et al. 2005) and possibly also involved in plant-herbivore interactions (Wünsche et al. 2011). The enzyme GSNOR does not directly reverse the *S*-nitrosylation of Cys residue but rather turns over GSNO thereby reducing the cells store of NO bioactivity and controls intracellular levels of both GSNO and SNO affecting the global level of *S*-nitrosylation (Feechan et al. 2005; Malik et al. 2011). On the other hand, the mechanism of Trx denitrosylation directly interacts with SNO-proteins by the formation of an intermolecular disulphide intermediate in which Trx is covalently linked to the substrate protein through a disulphide bridge or transnitrosylation in which Trx is transiently *S*-nitrosylated. This mechanism is described in detail in animal cells (Benhar et al. 2008), while Kneeshaw et al. (2014) proved the similar mechanism of Trx-h5 in plant cells.

A number of experiments using NO donors, scavengers and NOS inhibitors proved that NO plays a central role in plant defence against biotic stress, in combination with ROS (Delledonne et al. 1998, 2001; Yun et al. 2011). Keshavarz-Tohid et al. (2016) found the positive interaction of NO and H_2O_2 in bean plant defence against *Pseudomonas fluorescens* and *Rhizoctonia solani*. Namely, NO donor *S*-nitroso-N-acetyl D-penicillamine increased the production of

H_2O_2, thereby increasing the activity of antioxidant enzymes as well as the activity of phenylalanine ammonia lyase (PAL). NO action upstream of H_2O_2 was also shown in plants responses to herbivore attacks and *Tobacco Mosaic Virus* infection (Orozco-Cárdenas and Ryan 2002; Liao et al. 2013). Reversely, Qiao et al. (2015) found that Ca^{2+} and H_2O_2 are involved in upstream of NO production to induce the HR cell death in the wheat cells during *Puccinia triticina* infection.

H_2O_2 and NO display both prooxidant and antioxidant properties. For example, they serve as prooxidant agents and putative redox signals for in vitro encystment of the dinoflagellate *Lingulodinium polyedrum*. Oxidative stress induced by high H_2O_2 dose (500 mM) forced *L. polyedrum* cells to rapidly encyst (<30 min), while slower cyst formation was observed in lower H_2O_2 concentrations (Ganini et al. 2013). NO may induce scavenging of excess H_2O_2 and inhibit peroxide signaling pathways but also may collaborate with H_2O_2 to switch on SAR or stress tolerance. Two faced NO molecule can act as an antioxidant and an antiapoptotic modulator that prevents cell death and in the same time can have a cytotoxic effect. These cytotoxic and protective effects of NO are often concentration dependent (Wink and Mitchell 1998).

The mechanism of NO/H_2O_2 interaction in the induction of cell death is largely unknown. The in vitro chemical reaction between NO and H_2O_2 produces either $^1O_2$ or hydroxyl radicals ($^{\cdot}OH$) which can mediate cell killing (Noronha-Dutra et al. 1993). Although $^1O_2$ formation in plant system is merely dependent on light, especially pronounced in the highlight, temperature, heavy metal stress or wounding, its light-independent generation in plant cells under multiple stresses has also been proposed (Mor et al. 2014; Chen and Fluhr 2018; Prasad et al. 2018). NO can also interact with $O_2^{\cdot -}$ to produce another highly reactive species, $OONO^-$. Alamillo and Garcia-Olmedo (2001) found that direct application of $OONO^-$ induced plant cell death, which was not observed in the case when urea ($OONO^-$ scavenger) was added. $OONO^-$ may have a toxic effect on microorganisms, although so far it has not been clarified whether NO and its derivatives are directly toxic to pathogens in plants (Garcia-Olmedo et al. 2001). In tobacco cell suspensions, only a simultaneous increase in NO and H_2O_2 activated cell death, whereas an independent increase of only one of the factors mentioned above induced cell death only slightly (de Pinto et al. 2002). Moreover, only the synergistic effect of H_2O_2 and NO was effective in control of tomato bacterial wilt (Hong et al. 2013).

2.2 Regulation of Gene Expression

Both NO and H_2O_2 influence gene expression from transcription to protein synthesis. They regulate genes involved in the induction of pathogen defence, such as genes encoding pathogenesis-related (PR) proteins, genes involved in accumulation of phenylpropanoid compounds, genes encoding H_2O_2 detoxifying enzymes, enzymes involved in JA biosynthesis (Jacquard et al. 2009), upregulate cellulase expression (Sakamoto et al. 2008) and control genes involved in the hypersensitive cell death (Kaurilind et al. 2015). The large-scale gene expression analysis in *Arabidopsis* performed using the paired-end RNA-seq technology showed a different response to GSNO treatment in leaves and roots, suggesting that NO signaling mechanisms are organ specific (Begara-Morales et al. 2014). Another study on *Arabidopsis* transcriptome also showed that NO modulates gene expression in a concentration-dependent manner (Parani et al. 2004).

NO and ROS signaling is important in the establishment of plant disease resistance through modulation of defence-related genes encoding phenylalanine ammonia lyase (PAL) and pathogenesis-related protein 1 (PR1), markers for phenylpropanoid biosynthesis and SA-mediated signaling, respectively.

The key redox control of SAR exerts through nitrosylation of NPR1 (pathogenesis-related (PR)1), the key protein in plant immunity that co-activates defence gene expression and is an important component of SA-mediated signal transduction (Mou et al. 2003; Tada et al. 2008). Moreover, Wu et al. (2012) showed this protein to bind SA, working as an SA receptor directly. In unaffected cells, NPR1 is normally present as a high molecular weight oligomer formed with intermolecular disulphide bridges. After the pathogen attack as well as accumulation of SA, changes in cellular redox potential lead to the reduction of cysteines through the activity of thioredoxins (TRX-h3 and TRX-h5) and translocation of NPR1 monomers to the nucleus. In the nucleus, NPR1 interacts with the TGACG motif-binding factor (TGA) that binds to elements of the PR1 promoter, promoting PR gene expression and defence (Tada et al. 2008; Bellin et al. 2013). On the other hand, Tada et al. (2008) also found that S-nitrosylation in vivo promotes disulphide bond formation and oligomerisation. This reaction may be required to maintain NPR1 oligomer/monomer homeostasis, thereby facilitating the steady supply of monomeric protein to support SA-dependent gene expression. Beside NO, increased levels of H_2O_2 also inhibit NPR1 translocation (Peleg-Grossman et al. 2010). On the other hand, an oxidative burst and accumulation of H_2O_2 induced by the fungus *C. gloeosporioides* in the resistant cowpea genotype TE97 enhanced the levels of PR proteins (GLU and CHI) as a defence strategy against pathogen attack (Oliveira et al. 2014).

However, Lindermayr et al. (2010) found that NO also promotes NPR1-dependent defence responses by facilitating the translocation of NPR1 into the nucleus. Notably, TGA, an interaction partner of NPR1, can also be oxidised and S-nitrosylated. The oxidised form carries disulphide bonds that block interactions with NPR1, while the GSNO-mediated S-nitrosylation of cysteine residues protects TGA proteins from oxidative modification and improves its binding activity to PR1 promoter region (Lindermayr et al. 2010). This additional positive regulatory mechanism also involves the NO-dependent regulation of GSH biosynthesis and accumulation, which increases SA levels and thus activates NPR1-dependent defence responses (Kovacs et al. 2015). However, the nuclear translocation of NPR1 was much slower when driven by GSNO instead of SA. This finding suggests that this process was not the direct consequence of NPR1 S-nitrosylation but, instead, was dependent on a signaling pathway involving GSH biosynthesis. These findings revealed evidence of additional crosstalks among NO, GSH and SA pathways in the establishment of immunity in plants.

Besides NPR, *S*-nitrosylation modulates the activity of another SA-binding protein AtSABP3 (*A. thaliana* SA-binding protein 3). Namely, it suppresses both binding of SA and also its carbonic anhydrase activity that could contribute to negative feedback that modulates plant defence response and cell death (Wang et al. 2009).

Another important defence-related gene PAL is also modulated via NO signaling (Durner et al. 1998; de Pinto et al. 2002). Moreover, inhibition of NOS activity significantly reduces the accumulation of transcripts encoding PAL and chalcone synthase enzymes important for flavonoids and isoflavonoid synthesis (Delledonne et al. 1998). Additionally, an increase in cinnamate-4-hydroxylase transcripts, a key enzyme in the synthesis of phenolic compounds, has been found in *Arabidopsis* treated with a NO donor (Polverari et al. 2003). Likewise, exogenous H_2O_2 treatment induces *PAL1* mRNA expression in *Arabidopsis* where this enzyme mediates biosynthesis of lignin and SA (Desikan et al. 1998).

NO is involved in the regulation of gene expression of NO-responsive TFs such as MYB, WRKY, C2H2, Aux/IAA, bZIP, etc. included in the mediation of abiotic and biotic stress responses (Imran et al. 2018). Novel information about a large number of genes involved in NO signaling is discovered with the use of next-generation sequencing (NGS) technologies. Imran et al. (2018) showed that almost 30% of total NO-responsive TFs were related to stress tolerance, among which 95.5% were related to biotic stress. For example, bZIP-binding elements associated with defence formed by octopine synthase (OCS) are very important for the expression of above-mentioned PR1 gene in *Arabidopsis* where OCS element-binding factor interacts with NPR1 (Lebel et al. 1998; Zhou et al. 2000). Likewise, WRKY transcription factors involved in plant response to wounding and pathogen infection were upregulated in seedlings of *Larix olgensis* Henry treated with NO (Hu et al. 2015). Expression of transcription factor WRKY8 can also be activated through ROS-mediated signaling mechanism (Chen et al. 2010). Also, a large number of genes encoding TFs involved in NO signaling are characterised by RNA-Seq in root nodules formed in the symbiotic relationship of *Medicago truncatula* and its bacterial symbiont *Sinorhizobium meliloti* (Boscari et al. 2013).

The NO/ROS crosstalk during plant defence was also reflected through modulation of NO reactivity by *S*-nitrosylation of ROS producers and ROS or RNS scavengers. NADPH oxidase AtRBOHD is a major participant in ROS production induced by pathogens in *Arabidopsis* (Torres et al. 2005) and in grass roots infected with fungal phytopathogen *Rhizoctonia solani* (Liu et al. 2018). Yun et al. (2011) found that cysteine 890 S-nitrosylation of AtRBOHD during plant defence decreases NADPH oxidase activity and consequently reduces ROS accumulation, limiting the later stages of HR cell death. Also, different NO-responsive TFs knockout *Arabidopsis* mutants showed significantly higher expression of the *NADPH oxidase 1* (*NOX1*) and consequently more ROS accumulation. However, these mutants also showed higher expression of important antioxidative enzyme genes *CAT1*, *2* and *3* and *APX1* and *2* (Imran et al. 2018). Another way of oxidative burst inhibition triggered by NO is through its reaction with $O_2^{\cdot-}$ to form $ONOO^-$ and thus work directly as an antioxidant. Through this interaction, NO direct competes with SOD activity that could, therefore, inhibit the oxidative burst and decrease the accumulation of H_2O_2. Also, Holzmeister et al. (2015) found that NO modifies and inhibits three of the seven *A. thaliana* SODs by tyrosine nitration. The relevance of this modification in plant defence is still undefined, but it could be important for regulating ROS levels in HR cell death. Also, different antioxidant enzymes involved in H_2O_2 detoxification are exposed to S-nitrosylation or nitration according to in vitro studies, like APX, MDAR, CAT and peroxiredoxins, all of which are involved in H_2O_2 detoxification (Romero-Puertas et al. 2007; de Pinto et al. 2013; Begara-Morales et al. 2015; Camejo et al. 2015). Another antioxidative enzyme, Peroxidase 2 (PA 2) gene, may be a negative regulator of H_2O_2 production and is suppressed by an unknown TF to increase H_2O_2 levels in an anthracnose-resistant tea plant (*Camellia sinensis*) cultivar as a defence to *Colletotrichum fructicola*. H_2O_2 also upregulated a cell signaling receptor (wall-associated kinase 3) connected with cell wall reinforcement in *C. sinensis* at the penetration sites of pathogen hyphae (Wang et al. 2018). Activated resistance genes also regulate the thickening of cell wall tissue to defend against hyphal growth.

H_2O_2 accumulation also regulates the expression of cellulase genes. H_2O_2 is involved in the abscission signaling downstream of ethylene to upregulate cellulase expression. Moreover, salinity induced the production of H_2O_2 before leaf abscission, indicating that H_2O_2 might generally be involved in stress-induced leaf abscission (Sakamoto et al. 2008). Increased H_2O_2 accumulation in herbivore-wounded leaves was also correlated with increased SOD enzyme activity and gene expression (Maffei et al. 2006).

Besides NO, ROS metabolism localised in the peroxisome is usually controlled by the protein peroxin 11a (PEX11a) under stress conditions which was distinctly upregulated in the resistant tea plant during *C. fructicola* infection and may also be associated with H_2O_2 production (Wang et al. 2018).

In the recent years, the physiological relevance of H_2S signaling and its tight connection with H_2O_2 and NO gained considerable interest (Zhang 2016). As a part of ROS/NO antioxidative network, H_2S is involved in plant responses to different abiotic stress factors, although its role in plant response to a pathogen is still largely unknown (Hancock 2018). For example, spermidine-induced H_2O_2 in leaves of white clover could be an upstream signal molecule of NO and H_2S, and derived H_2S might act as the downstream signal of NO. Moreover, accumulation of H_2S can significantly improve antioxidant enzyme (SOD, CAT, GPOX, APX, GR, DAR and MDAR) activities and transcript levels of dehydration-regulated TFs (bZIP37, bZIP107, DREB2, DREB4 and WRKY108715) and genes encoding antioxidant enzymes (Li et al. 2017).

3 Conclusion

The review highlights important roles and tight relationship between NO and H_2O_2 signaling in plants subjected to biotic stress. Stressors (e.g. pathogen attack, wounding) initiate a myriad of reactions resulting in the oxidative burst, i.e. bulk production of reactive species such as NO and H_2O_2. These trigger the defence signaling through different pathways including phytohormones, MAPKs, NR, cGMP, cADPR and Ca^{2+}, and further activate transcriptional factors inducing the expression of genes involved in plant defence (secondary metabolism, SAR, HR, antioxidative system). New studies are awaited to identify further biochemical and functional characteristics of NO and H_2O_2, their interactions and mechanisms which lead to plant defence responses.

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