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c0024 Cross-talk of NO and phytohormones in the regulation of plant development

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Chapter outline

s0010 1. Introduction

p0015 Plant development is a series of events that lead to changes of plant structure, while during plant growth the dimensions of plants, or an organ of plants are extend. Plant life cycle can be

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considered a strict pattern of distinct developmental phases, in which the plant or its organs have well-specified characteristics. Main phases of this process are germination, vegetative, and reproductive phases, and finally senescence, which usually leads to plant death. Phase-transition among them is regulated by environmental and endogenous signals, integrated into a complex molecular network (Huijser and Schmid, 2011; Dambreville et al., 2015). Plant growth regulators, including hormones, are important in developmental processes (Wang and Irving, 2011). They may cross-talk each other and their interplay regulate distribution and/or expression of genes involved in the regulation of homeostasis and signaling in plant cells (Santner et al., 2009; Santner and Estelle, 2009). Hormones may interact not only with other growth regulators but also with different endogenous molecules. Among them, nitric oxide (NO) is a key signaling molecule. The role of NO was recognized in stress responses, and many studies proved its important role in developmental processes. In plants, NO biosynthesis and elimination can occur in different ways, based on which the importance of endogenous NO regulation can be suggested (Wilson et al., 2008; Neill et al., 2008; Gupta et al., 2011; Mur, 2013). In NO-hormone interaction, NO may be upstream or downstream regulator of developmental processes (Manoly et al., 2016; Pagnussat et al., 2003). Furthermore, their interaction can be antagonistic or synergistic (Melo et al., 2016; Liu et al., 2017). NO can affect them indirectly, through posttranslational modifications (PTM) or directly binding to hormones, regulating their endogenous levels, distributions, or signaling (Freschi, 2013). Several studies indicate that NO level can be also stimulated by hormones (Liu et al., 2017; Zhang et al., 2011). However, in many experiments, the alterations in endogenous NO level was induced by exogenous hormone treatment and this way is not necessarily mean a straightforward relationship-between them (Freschi, 2013). Although the interaction between NO and phytohormones is well studied, molecular and structural background of this mechanisms are not completely revealed. This book chapter will focus on the current state-of-the-art regarding the cross-talk between NO and phytohormones during developmental processes.

s0015 2. NO and abscisic acid interactions

p0020 Abscisic acid (ABA) plays key role in the regulation of several processes of plant growth and development, such as embryo maturation, cell division and elongation, root development, floral induction, seed dormancy, and seed germination (Finkelstein, 2013; Sanz et al., 2015).

p0025 NO usually appears as a downstream regulator of ABA signaling in plant responses (Freschi et al., 2013; Zhang et al., 2009). ABA also can be a positive regulator of NO. Transgenic tobacco lines, overexpressing *S. guianensis* 9 cis-epoxycarotenoid dioxygenase exhibited an enhanced level of ABA, hydrogen peroxide (H_2O_2) and NO, both in guard and mesophyll cells (Zhang et al., 2009). Furthermore, NO reduces seed dormancy (Bethke et al., 2004b) and induces seed germination (Beligni and Lamattina, 2000). In *Arabidopsis thaliana,* rapid accumulation of NO at the early stage of imbibition was required for breaking seed dormancy. Indeed, during imbibition, NO enhanced the transcript level of *CYP707A2* gene, which encodes ABA 8′-hydroxylase, which is a regulator of ABA catabolism. In accordance with this, application of NO donor also induced the accumulation of *CYP707A2* transcripts (Liu et al., 2009). Based on these results, during imbibition, regulatory role of NO in ABA catabolism can be concluded. Furthermore, coapplication of ABA and NO donor, sodium nitroprusside (SNP) treatment enhanced the final germination percentage of Arabidopsis compared to the ABA treated seeds, based on which it can be hypothesized the moderating role of SNP to the sensitivity of Arabidopsis seeds to exogenous ABA (Bethke et al., 2006). Role of NO in the induction of ABA production was further proved genetically using *nia1nia2noa1-2* Arabidopsis mutant seeds. These mutants were hypersensitive to ABA and showed more tendency for dormancy and lower germination rate compared to wild type (WT). Interestingly, exogenous application of NO in this mutant abolished NO deficiency confirming the role of exogenous NO in ABA sensitivity. Nevertheless, as potential targets of NO, PYRABACTIN RESISTANCE/PYRABACTIN RESISTANCE-LIKE/REGULATORY COMPONENTS OF ABA RECEPTORS (PYR/PYL/RCAR) family of ABA receptors and kinases of sucrose nonfermenting 1-related protein kinases2 (SnRK2) family were hypothesized in this process (Lozano-Juste and León, 2010a,b) which was confirmed recently by Castillo et al. (2018). Indeed, exogenous NO (SNP) blocked the activation of SnRK2.2 and SnRK2.3 through S-nitrosylation by which diminished the inhibitory effect of ABA and lead to the breaking of dormancy and allows seed germination (Wang et al., 2015). Number of other NO- regulated genes have been identified encoding proteins involved in the most diverse developmental and stress-related processes. Several studies suggest the involvement of protein modification, such as cysteine S-nitrosylation and tyrosine nitration, in the cross-talk among NO, ABA and ethylene (Arc et al., 2013).

p0030 Interaction between NO and ABA signaling during germination was also investigated (Gibbs et al., 2014 and references therein). The basis of this process is a targeted proteolysis of plant-specific transcriptional regulators. In seed endosperm, group VII Ethylene Response Factors (ERFVIIs) transcription factors (TFs) induce the expression of *ABSCISIC ACID-INSENSITIVE 5* (ABI5) gene, which is one of the main germination repressors. Furthermore, *ABI5* has major role in ABA signaling and represents an integration point of NO and ABA signaling pathways. Altogether, effect of ERFVIIs on *ABI5* gene in the regulation of NO-triggered ABA signaling was observed not only in seed germination and stomata closure, but also in the control of photomorphogenesis-related processes, such as hypocotyl elongation (Gibbs et al., 2014b).

p0035 ABA also can inhibit root elongation and lateral root (LR) formation and emergence, in which processes in the regulatory role of NO depends on its concentration and the experimental conditions (Hong et al., 2013; Sun et al., 2017). Nevertheless, interaction between NO and ABA was observed during the development of root architecture, however the mechanism by which it is regulated has not been cleared yet (Lozano-Juste and León, 2010a).

p0040 For root-hair development a strictly defined range of ABA and NO concentration was required in Arabidopsis by which cytoskeleton organization is regulated. The deviation from this “steady state” concentration causes aberrant root-hair formation or inhibits this process (Lombardo and Lamattina, 2018).

p0045 In addition, leaf senescence and fruit ripening can also be regulated by the interaction between NO and ABA. However their effect in these processes is antagonistic: ABA usually promotes while NO delays them. Both ABA and NO act via the modulation of redox homeostasis: ABA usually induces reactive oxygen species (ROS) formation, while NO activates antioxidant machinery (León et al., 2014; Prakash et al., 2019). Although the cross-talk between NO and ABA in many developmental processes was identified definitely (421.1, Table 24.1), in some cases the regulatory role of NO and its potential targets in ABA signaling has not been cleared yet.

s0020 3. NO and auxin interactions

p0050 Regulatory effects of auxin on plant growth and development are influenced by its distribution within plant tissues and also its cross-talk with other phytohormones and signaling molecules (Brumos et al., 2018; Vanneste and Friml, 2009; Vanstraelen and t0010

Table 24.1 Interaction between NO and phytohormones during plant growth and development.

NO effect	Interacting hormone	Nature of interaction	References
Seed			
Breaking of seed dormancy	ABA	Inhibition	Liu et al. (2009); Wang et al. (2015); Lozano-Juste and León (2010a,b)
	ET	Positive interaction	Gniazdowska et al. (2010); Kolbert et al. (2019)
	GB	Positive interaction	Bethke et al. (2007)
Germination			
Promotes	ABA	Inhibition	Bethke et al. (2006); Lozano-Juste and León (2010a,b); Castillo et al. (2018)
	GB	Positive interaction	Bethke et al. (2008)
	JA	Positive interaction	Jacobsen et al. (2013)
Light-induced cotyledon greening			
Promotes	AUXIN	Mutually positive feedback	Melo et al. (2016)
	ET	Mutual antagonism	Melo et al. (2016)
Hypocotyl development			
Induce shortening	ET	Positive interaction	Kolbert et al. (2019)
Primary root			
Inhibition (concentration dependent effect)	ABA	Inhibition/ positive interaction	Lozano-Juste and León (2010a)
	AUXIN	Inhibition/ positive interaction	Sanz et al. (2015); Fernández-Marcos et al. (2011); Liu et al. (2018)
	BR	Positive interaction	Tossi et al. (2013)
Promote embryonic root emergence	GB	Negative interaction	Lozano-Juste and León, (2011)

Continued

Table 24.1 Interaction between NO and phytohormones during plant growth and development.—*continued*

NO effect	Interacting hormone	Nature of interaction	References
Lateral root			
Promotes	AUXIN	Positive interaction	Correa-Aragunde et al. (2006); Cao et al. (2017)
	BR	Positive interaction	Tossi et al. (2013)
	ET	Antagonism	Singh and Bhatla (2018); Feigl et al. (2019)
	JA	Positive interaction	Hsu and Kao (2012)
	SL	Negative interaction	Bharti and Bhatla (2015)
Adventitious root development			
Promotes	AUXIN	Positive interaction	Pagnussat et al. (2003); Liao et al. (2011); Yadav et al. (2010, 2013)
	BR	Positive interaction	Li et al. (2020)
	ET	Positive interaction	Jin et al. (2017)
Root hair formation			
Promotes	ABA	Positive interaction	Lombardo and Lamattina (2018)
	ET	Mutually positive feedback	Lombardo et al. (2006); Masucci and Schiefelbein (1996); Takahashi et al. (2003); Liu et al. (2017)
	JA	Positive interaction	Wang et al. (2013)
Aerenchima development			
Promote	ET	Positive interaction	Igamberdiev et al. (2005)
Coleorhiza emergence			
Promotes	JA	Positive interaction	Jacobsen et al. (2014)
Leaf development			
Promotes	CK	Induction	Wilhelmová et al. (2006)

Table 24.1 Interaction between NO and phytohormones during plant growth and development.—*continued*

NO effect	Interacting hormone	Nature of interaction	References
Flowering			
Promotes	SA	Positive interaction	Khurana et al. (2014)
Ripening			
Delays	ABA	Antagonism	Prakash et al. (2019)
	ET	Inhibition	Zhu et al. (2006); Manjunatha et al. (2012)
Leaf senescence			
Delays	ABA	Antagonism	León et al. (2014)
	CK	Positive interaction	Mishina et al. (2007), Misra et al. (2012)
	ET	Inhibition/ antagonism	Zhu et al. (2006); Manjunatha et al. (2012); Liao et al. (2013); Hassan et al. (2020)
PCD			
Delays	CK	Negative interaction	Carimi et al. (2005)
	GB	Negative interaction	Beligni et al. (2002)

Benková, 2012). Implication of NO in auxin responses was identified in several processes such as root organogenesis, gravitropic responses, root nodule formation, root responses to iron deficiency, activation of cell division, and embryogenic cell formation (Correa-Aragunde et al., 2004; Freschi, 2013 and references therein; Sanz et al., 2015). However, the regulatory role of this linkage in shoots and reproductive tissues was reported only in a few studies, most of them were focused on root development (421.2, Table 24.1) and its response to environmental stimuli (Freschi, 2013).

s0025 3.1 NO-auxin cross-talk in primary root formation

p0055 Exogenous NO has similar effect to auxin on the expansion of plant tissues. NO, in dose-dependent manner, induced root tip expansion was observed in maize root segments (Gouvêa et al., 1997). Further experimental reports confirmed the regulatory role of NO in primary root (PR) growth and elongation (Sanz et al., 2015). Furthermore, organization of PR is sensitive to changes in NO level. Treatment with NO donors decreased the PR growth by the reduction of dividing cells within root apical meristem, affecting the distribution of mitotic cells and meristem size by promoting cell elongation and early differentiation in the PR meristem. Furthermore, NO negatively affected rootward auxin transport, through the posttranslational modification of PIN-FORMED1 (PIN1) protein, which lead to proteosome-independent degradation and which is restricted exclusively to the PR (Fernández-Marcos et al., 2011). Elevated levels of NO in the meristem promoted elongation, however through PIN1 degradation NO, could partially increase the activity of DELLA (aspartic acid—glutamic acid—leucine—leucine—alanine) protein, which inhibited cell elongation in the elongation-differentiation zone (EDZ) (Fernández-Marcos et al., 2011). However, NO affects not only auxin distribution, but also biosynthesis. NO donor inhibited, while NO scavenger induced TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1/WEI8) and TRYPTOPHAN AMINOTRANSFERASE RELATED 2 (TAR2) enzymes. Furthermore, the root growth factor WD40-REPEAT 5a (WDR5a) affected TAA1-mediated auxin biosynthesis through the regulation of NO homeostasis and consequently root growth was suppressed (Liu et al., 2018). Interestingly, NO depletion also can reduce PR growth. Treatment of WT Arabidopsis seedlings with NG-monomethyl-L-arginine (L-NMMA), a mammalian NO synthase inhibitor, showed a phenotype with reduced root growth which phenotype was similar to *nia1nia2-noa1* mutants. Based on this result, the involvement of NO biosynthesis in root growth reduction can be concluded. Taken together, these data indicates that NO is required for the maintenance of PR meristem organization and auxin sensitivity. Suppression in the inhibitory effect of auxin and reduction of auxin response in NO deficient plants indicates the role of NO in the regulation of auxin responses (Sanz et al., 2015).

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3.2 NO-auxin cross-talk in lateral root development

p0060

NO and auxin has a positive role in LR formation. Treatment with a polar auxin transport inhibitor, N-1-naphthylphthalamic acid (NPA) inhibited LR initiation which was restored by 1-naphthaleneacetic acid or SNP. Hypothetically, in this process, NO affects auxin in two ways: either protects auxins from oxidation or influences auxin signaling through the regulation of cell-cycle genes or enzymes (Correa-Aragunde et al., 2006). Indeed, NO participates in the regulation of the cell cycle at G1-to-S transition phase influencing LR formation (Correa-Aragunde et al., 2006). Furthermore, hydrogen can also be implicated in auxin-induced LR formation through the modulation of NO synthesis by the nitrate reductases (NRs) (Cao et al., 2017).

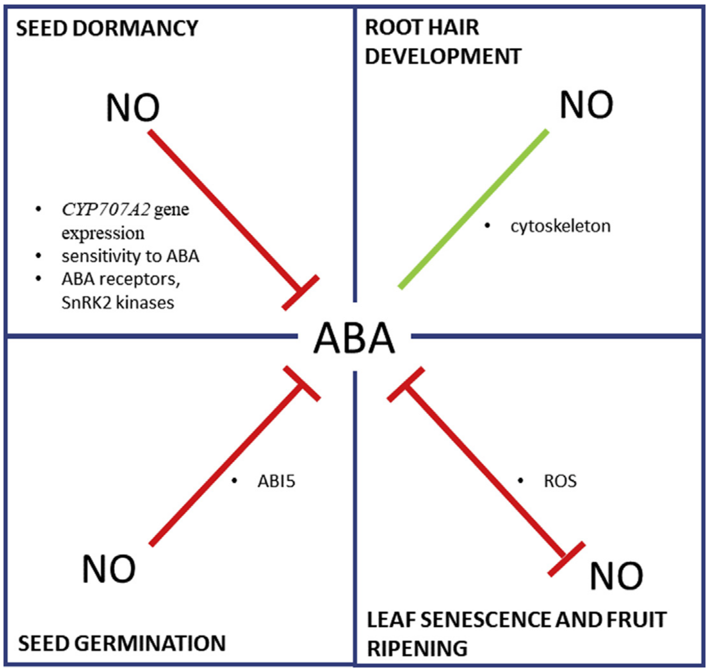
s0035 3.3 Involvement of NO-induced auxin in adventitious root formation

p0065 Role of NO in auxin-induced adventitious root (AR) development was demonstrated in several studies. As a downstream regulator, NO is involved in auxin induced AR formation in cucumber and marigold (Pagnussat et al., 2003; Liao et al., 2011). Three phases of auxin-induced AR can be distinguished: the induction phase does not depend on NO synthesis while the initiation and elongation phases are NO dependent (Yadav et al., 2010). NPA treatment inhibited NO accumulation in hypocotyl explants derived protoplasts, which further supported the negative role of NO in auxin-induced AR (Yadav et al., 2013). Furthermore, NO affected cytoskeleton organization through the modification of auxin synthesis in sunflower (Yadav et al., 2011). Nevertheless, the distribution and amount of tyrosine nitrated proteins during AR was dependent from the phase of development (Yadav et al., 2013) (Fig. 24.1).

p0070 Interaction between NO and auxin was also observed during light-induced cotyledon greening in tomato. Experiments with mutant lines confirmed the existence of a mutually positive feedback regulatory loop between them. Until recently three hypothesis were established for the interaction between auxin and NO: (1) TRANSPORT INHIBITOR RESPONSE1 receptor may be modified posttranslationally by NO, (2) NO may affect auxin biosynthesis and/or transport, and (3) NR may be regulated both transcriptionally and posttranscriptionally by auxin (Fig. 24.2). However, until recently none of these hypotheses has been proved (Melo et al., 2016).

s0040 4. NO and brassinosteroid interactions

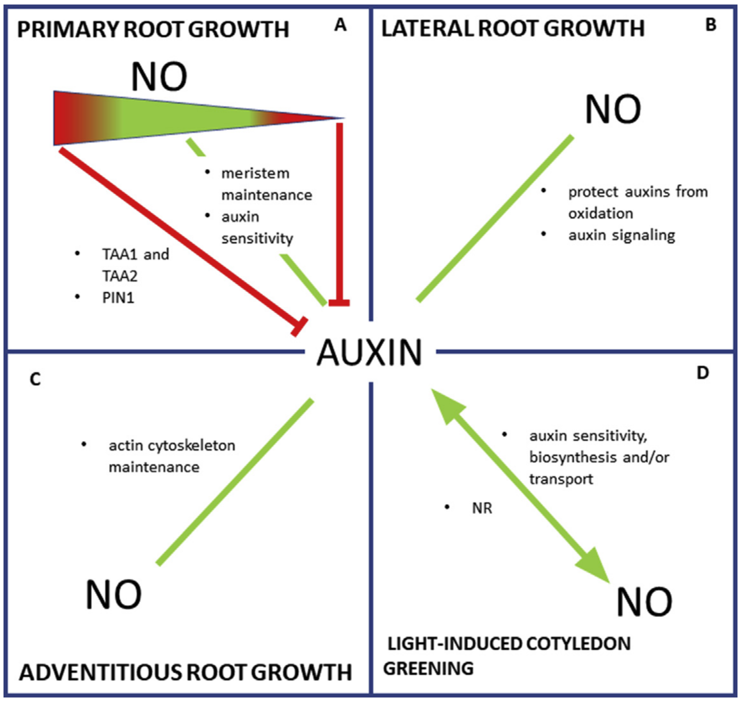
p0075 Brassinosteroids (BRs) are essential regulators of many plant cellular processes, such as membrane polarization, cell expansion and division, proton pumping, senescence, vascular, reproductive development, and stress responses. Although the interaction



f0010 **Figure 24.1** Summary of NO and abscisic acid cross-talk. NO has a negative effect on ABA-dependent regulation of seed dormancy, through the modulation of ABA catabolism, signaling, and perception (⊣). NO acts antagonistically during fruit ripening and leaf senescence via modulation of redox homeostasis (⊣) and has a positive interaction (—) with ABA for the maintenance of their appropriate endogenous level and the cytoskeleton organization during root-hair development.

between NO and BRs in a few stress-related processes was investigated, their involvement in developmental processes has not been deeply studied (Clouse and Sasse, 1998; Freschi, 2013).

p0080 It was shown that BR enhanced the generation of NO in mesophyll cells of maize leaves. However, pretreatment with NO scavenger reduced the BR-induced accumulation of ABA. Overall, BR-induced ABA accumulation was dependent on NO production under water stress (Zhang et al., 2011). Exogenously applied BR, similarly to the treatment with NO donor, caused NO burns through the activation of NR. Therefore, BR increased endogenous NO, which is required for changes in root morphology. Presumably NO acted downstream of BR (Tossi et al., 2013). Nevertheless, BR induced formation of adventitious roots through the upregulation of NR was showed recently by Li et al. (2020). The interplay between NO and BR was also investigated in some studies during the production of secondary metabolites. Among them, in tea plants the importance of the optimal level of endogenous NO in BR-induced flavonoid biosynthesis was

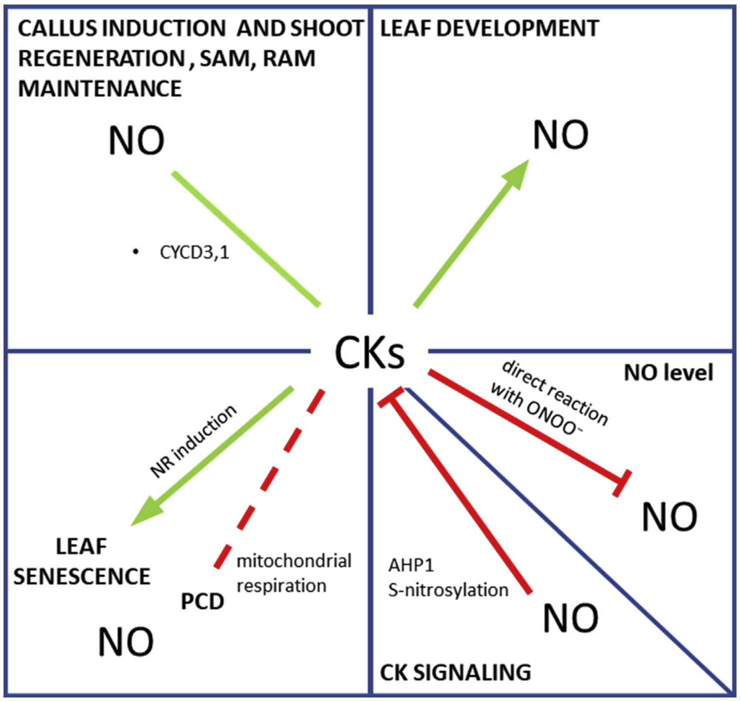


f0015 **Figure 24.2** Schematic model of NO-auxin interplay. In developmental processes NO and auxin mostly exhibit a positive relationship. (A) NO inhibit primary root growth in a concentration dependent way. (B—C): NO and auxin regulate lateral root (LR) and adventitious root (AR) growth interdependently (—). (D) Under light-induced cotyledon greening, NO and IAA have mutually positive effect (↔). Auxin regulates NO level through the modulation of nitrate reductase (NR) and NO modifies auxin perception, homeostasis, and transport.

demonstrated (Li et al., 2017). Another interesting observation regarding the interaction between NO and BR is their antagonistic effect on chlorophyll content and other photosynthesis traits: while NO decreased, BRs induced these processes (Hayat et al., 2010). Based on this result, it can be hypothesized that the regulatory role of NO and BRs work on developmental processes through the modification of photosynthetic machinery (Table 24.1).

s0045 5. Interaction between NO and cytokinin

p0085 Scherer and Holk's (2000) experiment on betalain accumulation in *Amaranthus candidatus* seedlings provided the first evidence of the possible involvement of NO in cytokinin signaling. Since, the role of cytokinin in NO induction was studied in several species, such as in tobacco, parsley and Arabidopsis (Tun et al., 2008; Shen et al., 2013). Their interplay (Fig. 24.3, Table 24.1) could be both



f0020 **Figure 24.3** Interaction between NO and cytokinin. NO has positive effect on cell cycle regulation by the activation of *CYCLIN D3;1 (CYCD3;1)* in cytokinin (CK) induced callus formation (—). Under leaf senescence CK increases endogenous NO level through the regulation of NR (→). During leaf development CK at low concentration induces NO production (→). NO negatively regulates (-----) CK and PCD, which may be occur by the inhibition of mitochondrial respiration. CK affects reduction of NO level (⊣) which can occur by binding of CK to peroxynitrite NO can reduce (⊣) CK signaling through S-nitrolysation of histidine phosphotransfer protein 1 (AHP1).

synergistic, such as in the regulation of cell division and differentiation, leaf senescence and programmed cell death (PCD), and antagonistic, e.g., in root growth (Freschi, 2013; Shen et al., 2013).

p0090 During the regulation of cell division, NO participated in callus formation and shoot regeneration from somatic tissues through the activation of *CYCLIN D3;1 (CYCD3;1)* at G1-S cell-cycle phase transition. NO deficiency in *nos/noa1* mutants resulted a phenotype with reduced root apical meristem (RAM) and shoot apical meristem size which was complemented by the overexpression of *CYCD3;1* indicating that this process is positively affected by NO. Antagonistic effect was observed in *chorophyll a/b binding protein unexpressed 1/NO overproducer 1* (*cue1/nox1)* mutant, in which overproduction of NO caused RAM defects and inhibited root growth (Shen et al., 2013). However, during regeneration, NO overproduction in *nox1-1* induced callus formation and greening. Based on these findings it can be concluded that shoot regeneration is less sensitive to NO overaccumulation than root growing (Shen et al., 2013).

p0095 Leaf senescence is also regulated by cytokinin. Cytokinin induced the expression or activity of NR which caused a delayed leaf senescence. The involvement of receptor CYTOKININ-INDEPENDENT 1 (CKI-1) and ARABIDOPSIS RESPONSE REGULATOR (ARR) 2 were shown in this process (Mishina et al., 2007; Misra et al., 2012). It was also reported that overexpression of Hmp, an *Escherichia coli* NO dioxygenases (NOD) enzyme causing NO deficiency, in Arabidopsis after its activation, induced a senescence-like process which had many similarities with natural senescence (Mishina et al., 2007). Interestingly, treatment of Hmp plants with cytokinin [6-Benzylaminopurine (BAP)] diminished leaf yellowing. Furthermore, in higher concentration cytokinins may induce PCD (Carimi et al., 2003, 2005). In accordance, BAP treatment promoted the development of necrotic lesions in leaves during NOD-induced senescence (Mishina et al., 2007). The mechanism by which cytokinin may regulate PCD was investigated in some studies. In Arabidopsis cell culture cytokinin induced ROS formation and accumulation, however the reduction of cell death was not observed in the presence of superoxide scavengers (Carimi et al., 2005). Furthermore, cryptogenin-induced PCD requires NO but is independent of H_2O_2 (Lamotte et al., 2004). Moreover, cytokinin BAP reduced total cell respiratory but the reduction was lower in the presence of NO scavenger. Taken together, these results suggested the involvement of NO in cytokinin signaling, most precisely in BA-induced PCD, probably via inhibition of mitochondrial respiration (Carimi et al., 2005).

p0100 During leaf development, in low concentration, cytokinin may induce NO production. Furthermore, cytokinins may have protective effect against damages in cells caused by reactive nitrogen species (Wilhelmová et al., 2006). Cytokinin can react directly with peroxynitrite ($ONOO^-$), leading the production of a cytokinin derivates with almost no biological activity, thereby it can down-regulates endogenous NO level (Liu et al., 2013). However, NO also can regulate cytokinin signaling. During different developmental processes, including root and hypocotyl elongation, regulation of root meristem size, induction of shoot regeneration, NO overproducing Arabidopsis lines *gsnor1-3* (deficient in S-nitrosoglutathione reductase 1; GSNOR) and *nox1* mutant plants showed decreased sensitivity to cytokinin. Furthermore, in *gsnor1-3* lines, the expression level of the primary response genes of cytokinin signaling (type-A ARRs) and the expression domain of a TCS-GFP cytokinin reporter gene were significantly reduced, similarly to the NO donor treated plants. Indeed, cytokinin signaling was negatively regulated by NO through the S-nitrosylation of Cys 115 of phosphotransfer protein 1 (AHP1) in Arabidopsis with phosphorylation activity being repressed during cytokinin-mediated phosphorelay (Feng et al., 2013).

s0050 6. NO and ethylene interactions

p0105 Ethylene (ET) is a small gaseous hydrocarbon molecule, and as a multifunctional phytohormone participates in the regulation of most of plant life processes, mainly in growth and senescence. Its effect depends on plant species, the application period, and also its concentration (Iqbal et al., 2017).

p0110 During recent decades, interaction between NO and ethylene was investigated in several scientific reports. Among them, one of the first study examined their antagonistic interplay during fruit ripening and senescence. However, positive effects of NO on ET production and signal transduction was also proved (Freschi, 2013). Furthermore, ET can interact with ABA, gibberellins (GAs) and other hormones, including JAs and auxins, during the regulation of seed dormancy in numerous plant species. It was observed that ET promoted dormancy release and germination (reviewed by Corbineau, 2014 and references therein). NO also reduced seed dormancy (Bethke et al., 2006). Altogether, during seed germination, the interaction between NO and ET is synergetic and they cross-talk with ABA at multiple levels in metabolism and signaling pathways (Arc et al., 2013). Furthermore, ET as a helpful factor interacted with NO and ABA signaling during the regulation of dormancy in apple (Gniazdowska et al., 2007). Nevertheless, NO scavenger and ethylene vapors decreased germination. Altogether, NO-triggered ET production associated with elevated 1-aminocyclopropane-1-carboxylate synthase (ACS) and 1-aminocyclopropane-1-carboxylic acid (ACC) oxidase (ACO) activity. Based on these results it can be suggested the involvement of the interaction between NO and ET in the regulation of dormancy loss and germination (Gniazdowska et al., 2010; Kolbert et al., 2019). These results were confirmed in other species. In dormancy release on secondary dormant *Brassica oleracea* seeds, the plant growth regulator karrikin1 was shown as a new participant of this process (Sami et al., 2019). In *Amaranthus retroflexus* seeds, NO-induced dormancy release depended on ET, while ET-induced germination seemed to be NO-dependent and both compounds are involved in the initiation of cell cycle before to radical emergence (Kolbert et al., 2019).

p0115 Involvement of protein modifications in NO cross-talk with ethylene was also suggested in some studies. Among them, hypoxia caused NO accumulation induced ethylene biosynthesis, supposedly, through the S-nitrosylation of ACS and ACO. In contrast, NO inhibited ethylene biosynthesis through S-nitrosylation of methionine adenosyltransferase (Arc et al., 2013 and references therein).

p0120 During plant vegetative development, the interaction between NO and ET seems to be antagonistic, but it highly depends on the experimental setup (Kolbert et al., 2019).

p0125 During primary root development only a few information is available about the role of the interplay between NO and ET and it needs further studies. In Arabidopsis roots, ET inhibited cell proliferation in the meristem, while NO reduced cell division and elongation. Furthermore, during the development of root architecture, JA-induced PR growth leading to NO accumulation. In this process ETHYLENE INSENSITIVE 2 (EIN2), a member of the canonical ethylene signal transduction pathway, was shown as an important player (Barrera-Ortiz et al., 2017).

p0130 Adventitious root development is regulated both by ET and NO, respectively. However their interplay in this process is hardly known. Exogenous coapplication of ethephon and SNP enhanced adventitious root development. Indeed, NO might be required for ethylene-induced adventitious rooting and acted downstream regulator in ethylene signaling based on which their effect is synergistic in this process (Jin et al., 2017). This observation was further proved with alfalfa in which ethylene biosynthesis was induced by NO during aerenchyma development (Igamberdiev et al., 2005).

p0135 During LR development, antagonistic effect of ET and NO was observed in several species, such as in Arabidopsis and tomato plants (Singh and Bhatla, 2018, references therein; Correa-Aragunde et al., 2004). Indeed, during LR initiation NO could bind to ACO, one of the key enzyme of ET biosynthesis, reducing ET production and enhancing LR formation. Supposedly, inhibitory effect of NO might occur through the modification of ferreous site of ACO, either with blocking ACO gene expression, or via an indirect way by interaction of different transcription factors (Singh and Bhatla, 2018). Nevertheless, NO-ET antagonism was also observed during the emergence of LR in Arabidopsis under Selenium-stress (Feigl et al., 2019).

p0140 Both NO and ET were shown as positive regulators of root-hair development in Arabidopsis and lettuce (Lombardo et al., 2006; Masucci et al., 1996; Takahashi et al., 2003). Under Mg-deficiency, ET and NO acted synergistically in the induction of root-hair formation. Indeed, according to the suggested model, Mg-deficiency increased the production of NO and ET in roots. ET facilitated NO generation by the activation of NR. In turn, NO stimulated ACC and ACS contributing ET synthesis. Overall, in this process NO and ET formed a positive feedback loop (Liu et al., 2017). Based on a recent observation, NO and ET is required for a multiwalled carbon nanotube (MWCNTs)-induced root-hair morphogenesis with, supposedly, ET acting as a downstream regulator of Noin (Zhao et al., 2020).

p0145 During light-induced greening in tomato seedlings mutual NO-ET antagonism was observed at biosynthetic levels through the inhibition of ACO by NO and NR by ET (Melo et al., 2016). Furthermore, hypocotyl length was not affected in *etr1-3* ethylene receptor mutant, and *ein2-5* ET insensitive mutants by exogenous NO indicating the involvement of ET in NO-induced hypocotyl shortening (Kolbert et al., 2019). Novikova et al. (2017) investigated the effect of variable NO concentration to NO-ET interplay in suspension cell cultures of *Arabidopsis thaliana* WT (*Col-0*) and ethylene-insensitive mutant, *ein2-1*. The authors suggested the role of NO in the modulation of cell cycle in a concentration dependent manner which was depended on EIN2.

p0150 Both NO and ET are involves in the regulation of several aspects of reproductive growth of plants (Lin et al., 2009; Domingos et al., 2015; Kolbert et al., 2019 and references therein). Among them, their interaction was mostly investigated during ripening where ET level usually increases. However, a high level of ET induces senescence. It was proved in several studies that NO treatment can improve the self-life of climacteric and a few nonclimacteric fruit through its influence on certain components of ET biosynthesis pathway (Manjunatha et al., 2012). NO could bind ACO resulting ACO-NO and then ACC-ACO-NO complex reducing ET production by the inhibition of its biosynthesis. One of the secondary effects of NO may be the induction of ET to 1-malonyl aminocyclopropane-1-carboxylic acid conversion (Zhu et al., 2006). Moreover, NO could inhibit ACS activity (Zhu et al., 2007). ET production could be influenced by NO also through the alteration of H_2O_2 level, which is a positive regulator of ET biosynthesis. Furthermore, NO regulated ET production was observed via triggering ROS-linked redox changes, suppression of ROS generating enzymes or upregulation of the expression of enzymatic antioxidants, such as catalase (CAT), peroxidases (POD), and superoxide dismutase (SOD) (Manjunatha et al., 2012).

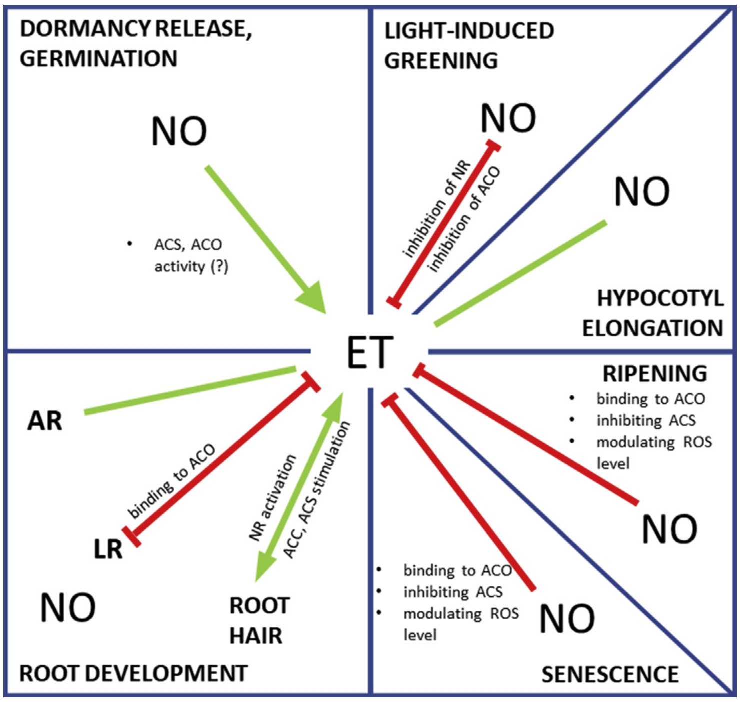
p0155 As it was mentioned earlier, excessive ET accumulation induces senescence which is the final stage of ontogeny and which can be describe as a series of precisely coordinated processes occurring in a specific order and lead to destruction. Furthermore, PCD and senescence are often inseparable, although this two processes are separated to each other (Wojciechowska et al., 2018). ET is considered as a key hormone in the regulation of flower and leaf senescence in plants (Iqbal et al., 2017). In contrast, NO delayed these processes (Bowyer and Wills, 2003). However, the mechanism by which senescence can be regulated by ET-NO cross-talk is hardly known. It can be hypothesized the inhibitory effect of NO on ET biosynthesis in this process in the aforementioned ways. SNP treated cut roses exhibited decreased ACO activity and ET production (Liao et al., 2013) and cut [**AU3**] carnivoles showed increased longevity in parallel with a decrease in ACS activity (Hassan et al., 2020). Furthermore, involvement of EIN2, which is a positive regulator of ET-induced senescence, in NO-induced early leaf senescence was also proved in Arabidopsis (Niu and Guo, 2012).

p0160 NO and ET are involved in the regulation of most of plant growth and developmental processes (Fig. 24.4, Table 24.1). Both compounds could be a promoter or an inhibitor in these processes and their effects depend on their concentration. NO and ET interaction in some cases is antagonistic and in others, synergistic. Overall, cross-talk between NO and ET is multifactorial and very complex, affected by external and internal stimuli. Furthermore, it can be regulated by their concentration, distribution, and interaction with other hormones or growth regulators (Fig. 24.5).

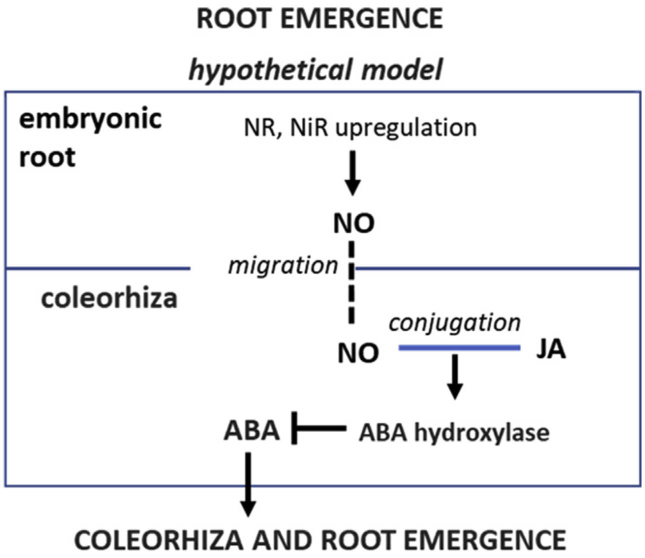
s0055 7. NO and gibberellin interactions

p0165 Role of NO was reported during several developmental processes in which GAs are also involved, such as the growth of pollen tubes (Prado et al., 2004; Singh et al., 2002; Chun et al., 2007), breaking seed dormancy, seed germination, primary root growth, hypocotyl elongation, photomorphogenesis, etc. However, the interplay between NO and GAs is very complex. NO may inhibit and promote, respectively, GA biosynthesis, perception/transduction according to the regulated developmental process. In this section we try to specify their interaction during the aforementioned developmental processes, although only a few physiological points of evidence are available about the mechanism by which it is regulated (Table 24.1).

p0170 Usually, DELLA proteins regulate GA signaling and integrates signaling pathways of other hormones. This pathway is essential for pollen development. In GA signaling, active GA interacts with



f0025 **Figure 24.4** Summary of NO and ethylene cross-talk. NO may induce (→) ethylene (ET) biosynthesis through activation of ACS and ACO during dormancy release and germination and has positive interaction with them (—) during adventitious (AR) root development and hypocotyl elongation. NO and ET show mutually positive interaction in the regulation of root-hair formation, during which ET may activate nitrate reductase, while NO stimulate ACC and ACS enzymes. NO has negative impact (⊣) on ET production through the modulation of ROS homeostasis. There is an antagonistic (⊣) effect between them during the regulation of LR development and light-induced greening.



f0030 **Figure 24.5** Hypothetical model of the interaction between NO and JA during root and coleorhiza development. After seed ripening the embryonic root produce NO by nitrate (NR) and nitrite reductase (NiR). NO migrates to the coleorhiza and conjugate JA, which lead to reduction of ABA hydroxylase level. Thus, ABA level decreased allows the emergence of root and coleorhiza. [**AU1**] its receptor, GA INSENSITIVE DWARF1 (GID1), and the formed complex is able to bind to GRAS family protein DELLA, and can direct GA-GID1- DELLA complex to SCF E3 ubiquitin ligase SLY1 (SLEEPY1). Furthermore, DELLA proteins mainly repress the transcription of GA regulated genes. In rice plants this pathway is negatively regulated by the phosphorylation of DELLA proteins, by the rice early flowering1 (EL1) casein kinase I. Altogether, *eli1* mutants showed low fertility and early flowering. Nevertheless, the AMYB TF which seems to be the key TF in GA signaling pathway, is also essential in pollen development (McGinnis et al., 2003; Ueguchi-Tanaka et al., 2007; Sharma et al., 2016).

p0175 Involvement of NO in pollen tube–pistil communication was also investigated. Indeed, NO had negative chemotropic effect on pollen tube growth. Furthermore, NO mediates pollen tube reorientation through the activation of guanylate cyclase and NO-mediated guanosine-3′,5′-cyclic monophosphate (cGMP) pathway leading to the accumulation of cytoplasmic calcium ([Ca^{2+}]cyt) (Prado et al., 2004; Prado et al., 2008, Bright et al., 2009; Domingos et al., 2015; Gross et al., 2016). In pollen tube elongation Ca^{2+} oscillation, while in pollen reorientation Ca^{2+} distribution plays important role (Holdaway-Clarke and Helper, 2003). Although, the counteraction between NO and GA in the regulation of DELLA protein accumulation (Lozano-Juste and León, 2011; detailed subsequently) and the involvement of GA in the induction of [Ca^{2+}]cyt accumulation was previously demonstrated (Okada et al., 2017), the interaction between NO and GA during pollen tube development is still not known.

p0180 During dormancy release and germination both NO, GB, and ABA have a central role. While ABA maintained seed dormancy and inhibited seed germination, GB and NO, had the opposite effect on both in Arabidopsis and barley (*Hordeum vulgare*), respectively (Bethke et al., 2007; Gómez-Cadenas et al., 2001; Beligni and Lamattina, 2000; Beligni et al., 2002). In Arabidopsis, during dormancy release, the aleuron layer is indispensable for the perception and response to NO signal. NO is necessary for the transcription of 2 GA biosynthesis genes [*gibberellin 3β-hydroxylase 1* (*GA3ox1)* and *GA3ox2*], which shows a positive regulatory role of NO in GA signaling during the control of aleurone cell vacuolation (Bethke et al., 2007). Under other processes, NO can interfere with GA-induced pathways. In details, NO donors delayed GA-induced PCD of barely aleurone layer, but the synthesis and secretion of GA-induced α-amylase was not affected (Beligni et al., 2002). Moreover, after germination, during photomorphogenesis, seedlings undergo deetiolation (Wang et al., 2014). Light promotes cotyledon development, chloroplast differentiation and the activation of light-regulated genes and inhibits hypocotyl growth. It seems that photomorphogenesis is a default program and during skotomorphogenesis (growing in darkness) photomorphogenesis is repressed throughout the degradation of photomorphogenesis-promoting TFs, including LAF1 (LONG AFTER FAR-RED LIGHT 1), HFR1 (LONG HYPOCOTYL IN FAR-RED 1), HY5 (LONG HYPOCOTYL 5), and HYH (HY5 homologue) by the COP1 (CONSTITUTIVE PHOTOMORPHOGENIC1) E3 ubiquitin ligase. During skotomorphogenic growth phytochrome-interacting factors PIF1, PIF3, and PIF4 maintain etiolated growth, but during photomorphogenic growth they became phosphorylated and degraded by light-activated phytochromes (Lozano-Juste and León, 2011). NO promoted photomorphogenesis (Lozano-Juste and León, 2011) and participated in partial deetiolation of wheat seedlings. Nevertheless, NO donors promoted deetiolation and inhibited hypocotyl elongation (Beligni and Lamattina, 2000). These results were supported by experiments using nia1 and 2noa1-2 Arabidopsis mutants in which plant hypocotyl elongation and root shortening were enhanced under light, while were similar to WT under darkness (Lozano-Juste and León, 2011). In contrast with NO, GAs repressed photomorphogenesis (Alabadí et al., 2008). According to the suggested model, which explain the role of NO and GAs in photomorphogenesis, dark-to-light transition increased NO and decreased GA level. Reduction in GA level led to DELLA accumulation resulting less GID1-GA-DELLA-SLY1 functional interactions. Enhanced DELLA level is associated with transcription factors, such as PIFs, whose transcription have been otherwise repressed by NO (Lozano-Juste and León, 2011). Nevertheless, cell elongation is positively regulated by GAs. Arabidopsis *gai1* (GA biosynthesis) and *gai* (GA signaling) mutants displayed a reduction in hypocotyl length compared to the WT (Cowling et al., 1999). NO can reduce PR growth and promote LR development (Correa-Aragunde et al., 2004). Based on the results of Fernández-Marcos and Sanz, presumably, NO may inhibit cell elongation in the EDZ of the root by promoting DELLA activity (Fernández-Marcos et al., 2011).

s0060
8. NO and jasmonate interactions

p0185 Jasmonates (JAs) are phospholipid-derived hormones which belong to oxylipins (Wasternack and Song, 2017; Acosta and Farmer, 2010). Several studies are available about the involvement of JAs in stress responses and defense mechanisms, as well as their role in the regulation of different plant developmental processes, such as seed dormancy and germination (Jacobsen et al., 2013) root growth, stamen development, flowering, and leaf senescence (Huang et al., 2017). The role of NO in these processes is also known (Mur et al., 2013) (Table 24.1), however its interaction with JAs has not been completely cleared.

p0190 The effect of NO on JA signaling mainly depends on the type of process (Hu et al., 2009; Hsu et al., 2012). In the regulation of several developmental processes, NO and methyl JA acted interdependently (Jacobsen et al., 2013). A hypothetical model was created to explain the relationship between NO and methyl JA in the regulation of coleorhiza and root emergence. In details, after-ripening, when seeds are in nondormant stage, NR and nitrite reductase (NiR) are upregulated leading NO production by embryonic root. NO migrates to coleorhiza, where it conjugates with JA and causes a reduction of ABA content by enhancing the level of ABA hydroxylase (ABA8′OH-1), which results in coleorhiza and root emergence (Jacobsen et al., 2013).

p0195 The role of NO as downstream component of methyl JA (MeJA)- promoted LR formation was also investigated (Hsu et al., 2012). Furthermore, NO-induced LR formation and emergence might be mediated by endogenous JA under osmotic stress. In this process, lipoxygenase might be served as a target of NO, which contributed to JA production in root pericycle during root-hair emergence (Wang et al., 2012).

p0200 MeJA-induced leaf senescence through the induction of H_2O_2 accumulation, the activities of some antioxidant enzymes, such as ascorbate peroxidase (APX), glutathione reductase (GR), catalase (CAT), and peroxidases (POD) and the reduction of glutathione (GSH) and ascorbic acid (AsA) contents in rice leaves (Hung and Kao, 2004). In contrast with previous studies, which demonstrated the direct inhibitory effect of NO on antioxidant enzymes (Ferrer and Barceló, 1999; Clark et al., 2000), in this study NO donor PBN (N-tert-butyl-alfa-phenylnitrone), alone, did not affect antioxidant enzyme activities. However, coapplication of PBN and MeJA reduced H_2O_2 content and the activity of antioxidant enzymes, based on which indirect effect of NO on H_2O_2 could be discussed (Hung and Kao, 2004). Indeed, NO might act as a free radical scavenger inhibiting or delaying MeJA-promoted senescence (Hung and Kao, 2004). However, MeJA-induced leaf senescence is a complex developmental process which is regulated not only by H_2O_2 through MeJA and NO but also by other plant growth regulators, such as salicylic acid (SA). However, their cross-talk during senescence has not been completely clarified yet.

s0065 9. NO and salicylic acid interactions

p0205 SA is a phenolic compound which can synthesized by plants in response to a broad range of biotic and abiotic stresses (Singh et al., 2004; Loake et al., 2007; Horváth et al., 2007; Hayat et al., 2010; Khan et al., 2015; Koo et al., 2020). Furthermore, in concentration dependent manner, SA is involved in the regulation of plant growth and development, including seed germination, photosynthesis, stimulation of shoot and root growth, induction of flowering, senescence and biomass production (reviewed by Rivas-San Vicente et al., 2011 and Koo et al., 2020). Although, the involvement of NO in these processes is also well known, its interplay with SA has been investigated mainly under stress, but not under normal conditions (Table 24.1).

p0210 Exogenous SA induced NO biosynthesis through the activation of *AtNIA1* and *AtNIA2* (coding NRs) during stomatal closure (Hao et al., 2010). Furthermore, during salinity, exogenous NO and SA supply upregulated the antioxidant system reducing ROS level and contributing to the improvement of mineral uptake and osmolyte accumulation and the enhancement of photosynthesis and growth in *Vigna angularis* (Ahanger et al., 2019).

p0215 NO can be involved in the initiation phase of flowering, which could be induced by exogenous SA in *Lemna aequinoctialis.* Application of NO scavenger or NR inhibitors reduced flowering response which provided further evidence for the possible cross-talk between NO and SA in this process (Khurana et al., 2014). Among other developmental processes, the interplay of NO and SA during senescence was mostly studied. During MeJa-induced leaf senescence, which is delayed by NO, SA can be a promoter or an inhibitor and the interaction between SA and NO depends on their relative concentration (Mur et al., 2006). Interestingly, SA alone could not affect MeJA-induced senescence (Ji et al., 2016). Furthermore, at high concentration, SA accelerated senescence, which can be explained by the different conformation and cellular localization of the SA signaling transducer NONEXPRESSOR OF PR GENES1 (NRP1) (Chai et al., 2014). Nevertheless, nuclear accumulation of NRP1 was also promoted by GSNO in SA dependent defense responses (Kovacs et al., 2015), this effect was also observed during lipopolysaccharide induction (Sun and Li., 2013). Furthermore, NO may contribute to the elimination or decreased accumulation of ROS per se by inducing antioxidant machinery, may react directly with ROS or modulate the proteins by S-nitrosylation, which process, interestingly, one of the targets is the NPR1 (Ji et al., 2016).

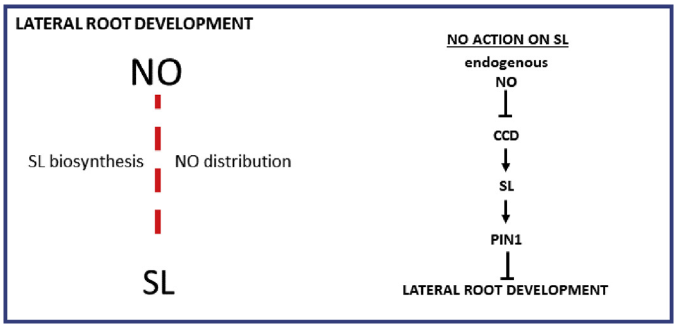
s0070 10. NO and strigolactone interactions [AU4]

p0220 SLs are relatively newly discovered molecules categorized as a new class of plant hormones. Their beneficial role was recognized during mycorrhizal symbiosis, whereas they regulate hyphal branching, and this symbiosis increases abiotic and biotic stress tolerance. The discovery that SLs are branching inhibitors was the first description about their role as a plant hormone. Since then, with the identification and characterization of shoot branching mutants other hormonal functions have emerged. Indeed, SLs act exogenously to the rhizosphere and endogenously as a regulator of plant growth and development affecting plant architecture. They have a negative regulatory role in lateral root initiation, while root-hair elongation, leaf shape, internode elongation, and secondary growth are mostly positively regulated by them. They also affected senescence and had important role in different plant stress responses (Kapulnik et al., 2011; Pandey et al., 2016; Banerjee and Roychoudhury, 2018).

p0225 Interaction between SLs and NO is well described during stomatal closure in Arabidopsis. Their involvement in this process did not depend on ABA, however, similarly to ABA, activation of SLs signaling pathways also lead to elevated H_2O_2 and NO level and activation of SLAC1 (SLOW ANION CHANNEL-ASSOCIATED 1) anion channels. In contrast to ABA, components of this signaling pathway has not been yet known (Lv et al., 2018). However, NO and SLs were considered as common regulators in the induction of stomatal closure (Zhang et al., 2018).

p0230 *Arabidopsis thaliana* SL biosynthesis (max*3-11,* max*4-1*) and SL signaling (max*2-1*) mutants developed more LRs compared to WT plants (Kapulnik et al., 2011). This was the first evidence that SLs may have role in the control of root architecture (Marzec and Melzer, 2018). According to this observation, in tomato the treatment with GR24, a synthetic strigolactone analog had a suppressive effect on root-hair development and elongation and high concentration of SLs caused distortion of linear root growth (Koltai et al., 2010).

p0235 Experiments with sunflower seedlings revealed the possibility of the interplay between NO and SL (Bharti and Bhatla, 2015; [AU5] Fig. 24.6). In this study, application of GR24 inhibited, while SL biosynthesis inhibitor promoted LR and AR formation. During SL-modulated lateral root development, endogenous NO diminished SL biosynthesis through inhibition of carotenoid cleavage dioxygenase (CCD) activity. Taken together, an enhancement in endogenous NO caused a reduction in CCD activity, through its direct binding to the enzyme or other enzymes involves in CCD



f0035 **Figure 24.6** Hypothetical model of the interplay between NO and strigolactone during lateral root development. SL may affect NO distribution, but NO may also affect SL through the modulation of its biosynthesis, suggesting a negative interaction (-----) between them. During LR formation, endogenous NO may inhibit the activity of carotenoid cleavage dioxygenase (CCD). Alternation of SL level may cause changes in PIN1 distribution inducing LR development.

precursor production. This resulted in a decrease in SL level which promoted LR development through the modification of PIN1 distribution (Bharti and Bhatla, 2015). This result was further confirmed by Manoli et al. (2016). They hypothesized that NO appears as an upstream regulator of SL during nitrate-induced root elongation.

p0240 Involvement of SLs in NO induction of root elongation during nitrogen-deficient (LN)- and phosphate-deficient (LP) conditions by the induction of meristem cell activity but not cell elongation was investigated (Sun et al., 2016). LN and LP conditions may induce the elongation of seminal root, being NO considered as a key regulator of this process. Under LN and LP conditions, GR24 and SNP treatment enhanced the expression of D14 and D53 genes, respectively, but reduced D53 protein level, which was caused by D14-SCFD3 -mediated degradation of D53 signaling repressor (Sun et al., 2006). Interestingly, none of the applied [**AU6**] treatments had effect on root length in Arabidopsis mutants compared to the WT. These results suggested that, similarly to SLs, NO triggered the degradation of D53 protein by the proteosome (Sun et al., 2006).

p0245 Moreover, a recent study demonstrated the interaction between SLs and/or Karrikin (KAR) and S-nitrosoglutathione reductase (GSNOR)-regulated levels of NO/S-nitrosothiol (SNO) in Arabidopsis PR elongation under normal conditions (Oláh et al., 2020). It is well known that NO is able to modify its target proteins through posttranslational modifications, like S-nitrosylation and tyrosine nitration, thus making an impact on their structure and/or activity. In *Arabidopsis thaliana* and *O. sativa* some proteins involved in SL biosynthesis (CCD7, CCD8, D27, MAX1) and SL signaling (D14, MAX2, D3) were predicted as potential NO-dependent posttranslational modification targets (Kolbert, 2019).

p0250 As listed earlier, strigolactones and NO are involved in several developmental processes in plants; however, their interaction was proved in only a few cases, such as during the regulation of root architecture and stoma closure (Table 24.1).

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