

# Interaction of Nitric Oxide with Phytohormones under Drought Stress

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## Abstract

Plants are often exposed to a plethora of stress conditions such as salinity, extreme temperatures, drought, and heavy metals that can greatly impact farmer's income. Nitric oxide (NO) has been implicated in resistance to various plant stresses and hence gaining increasing attention from plant researchers. NO mediate various abiotic and biotic stresses in plants including drought stress. However, it is still unclear about the actual involvement of NO in drought stress responses at a whole plant level. Whether NO act alone or in coherence with other phytohormones and signaling molecules is an open question till now. Here we summarized the interaction of NO with the well-known phytohormones in coping with the drought stress.

**Keywords:** nitric oxide (NO), drought stress, phytohormones, auxin, abscisic acid, abiotic stress

Being highly reactive, nitric oxide involves interactions with various signaling pathways to execute cell-, tissue- or organelle-specific roles in plants (Simontacchi et al., 2013; Freschi, 2013). After a series of experimental reports in the recent decade, the participation of NO in plant hormone mediated responses was highlighted by various research groups (Freschi, 2013). Nitric oxide interaction with phytohormones in drought stress can be broadly in three ways:

- 1) NO and phytohormones mutually get induced under drought stress.
- 2) NO gets recruited by plant hormones under stress condition.
- 3) NO acts as a cross talk node for interacting hormones.

A majority of the research publications highlighted the interaction between ABA and NO during drought stress conditions. An intensive synergistic and antagonistic cross talks has been described between NO and ABA depending on the physiological response and tissue during drought stress (Freschi, 2013; Santisree et al., 2015). Garcia-Mata and Lamattina (2001) suggested that NO was a part of ABA signaling pathways during drought induced stomatal closure in *Vicia faba* epidermal trips. The synergistic relation between NO and ABA was also reported during some responses like stomatal closure as in *Arabidopsis thaliana* and *Pisum sativum* (Neill et al., 2008). NO and ABA share many signaling components like cGMP, Ca<sup>2+</sup>, cADPR, and G proteins during drought stress (Xing et al., 2004). For instance, in *V. faba* guard cells, NO is involved in the ABA induced stomatal closure by selectively activating intracellular Ca<sup>2+</sup> channels through a cGMP/cADPR-dependent signaling pathway (Mioto, & Mercier, 2013). Furthermore, NO and ABA are mutually regulated under drought stress. For example, NO via NOS like activity induce ABA accumulation in wheat root tips under drought stress. In corn, elevation of NADPH by ABA led to the production of NO, proving the functional relationship between ABA and NO during drought stress. Another well-known response of ABA and NO interaction is the induction of antioxidant defenses under drought-induced oxidative stress in plants (Zhang et al., 2007; Lu et al., 2009). ROS and NO are implicated as co-signaling molecules acts by stimulating ABA synthesis during maintenance of plant water status under drought stress (Bright et al., 2006; Hancock et al., 2011; Desikan et al., 2004). Despite these reports, NO and ABA also known to act antagonistically by counteracting each other's effects in some cases such as seed dormancy breaking during drought stress (Bethke et al., 2006; Liu et al., 2011; Liu et al., 2010).

The interaction between cytokinins and NO during the regulation of plant drought responses has also been studied recently. Shao et al. (2010) reported increased NO levels during the cytokinin-induced photosynthetic

adaptability to drought stress suggesting an antisenesescence role of NO. This study described the possible synergistic relation between cytokinin-induced photosynthetic adaptability and NR-generated NO production in response to drought stress. Synergistic interaction between cytokinins and NO was also reported previously during the control of leaf senescence, programmed cell death, cell division, and differentiation (Shen et al., 2012; Simontacchi et al., 2013).

Auxin is known to regulate a number of plant growth processes in association with NO. For instance, root growth and iron uptake stimulation are the two well-studied auxin regulated responses that operate by mediation of endogenous NO (Simontacchi et al., 2013; Yadav et al., 2011; Liao et al., 2011). Recent pharmacological and mutant analysis studies infer that NO acts downstream of auxin through a direct signaling pathway during root growth and development with close cooperation with molecules like cGMP (Negi et al., 2010; Liao et al., 2011; Fernandez-Marcos et al., 2011; Li et al., 2013). Increased NO production has been observed by auxin over producing mutants and after exogenous application (Negi et al., 2010; Simontacchi et al., 2013; Kolbert et al., 2008). Kolbert et al. (2008) reported nitrate reductase derived NO accumulation in *Arabidopsis* root primordia when treated with auxin exogenously. Noteworthy, NO was proven to influence auxin content in plants by modulating auxin synthesis, transport and degradation (Fernandez-Marcos et al., 2011; Xu et al., 2010). Recently some of the transporters were shown to play a major role during drought stress (Remy et al., 2013). However a direct link showing NO mediated modulation of auxin transport or synthesis under drought stress needs further study.

In most of the cases, an antagonistic interaction was reported between ethylene and NO (Freschi, 2013). Both exogenous and endogenous NO levels can influence ethylene biosynthesis during senescence in plants (Freschi, 2013; Manjunatha et al., 2012). A report in *Arabidopsis* showed that NO down regulates ethylene precursor S-adenosylmethionine (SAM) levels through S-nitrosylation of methionine adenosyltransferase (MAT1) (Lindermayr et al., 2005). This kind of negative relation is also observed during stomatal closure, where ethylene inhibited stomatal closure when combined with either ABA or NO (Desikan et al., 2006). Similarly, a negative correlation between both of these gases was also reported during fruit ripening (Freschi, 2013; Manjunatha et al., 2012). By contrast, NO is shown to stimulate ethylene production by up regulating the ethylene biosynthesis genes in *Arabidopsis* and cucumber, while ethylene precursor promoted NO production in senescing leaves (Manjunatha et al., 2012). Similar to ethylene, a general antagonism was documented between Gibberellic acid (GA) and NO during root growth and photomorphogenesis in *Arabidopsis* (Freschi, 2013; Leon et al., 2011). DELLA proteins known to operate as key molecules in the crossroads of NO and GA signaling pathways (Hui et al., 2009). GA negatively regulated NO production, by promoting DELLA protein accumulation. Indeed, it is clear that cross talk between auxin, GA and ethylene with NO was not studied much under drought stress. Besides its regulation of plant hormone biosynthesis and sensitivity, NO also appears to be involved in modulation of various enzymes of nitrogen metabolism under drought stress (Hui et al., 2009). In addition to major plant hormones, NO has been known to interact with other signaling molecules like salicylic acid (SA), jasmonic acid, polyamines, calcium, ROS and other kinases corroborating its versatile role during various stress conditions (Misra et al., 2011; Freschi, 2013; Simontacchi et al., 2013). Although, now we can evidently show the potential involvement of NO in hormone mediated pathways, the cross talk study is fragmental under individual stress conditions like drought stress. Moreover, the integration of these rudimentary signaling events with respect to individual stress responses is very important to understand how this single molecule modulates other signaling molecules/hormones to elicit specific and common stress responses.

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