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Review

Regulation function of nitric oxide (NO) in leaves of plant under environmental stress

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Nitric oxide is an important signaling molecule involved in many physiological processes. This paper expounds the source and biological features of nitric oxide as well as the cognizance of the role of nitric oxide in biotic and abiotic stresses. Finally, the prospect of development in this field is presented.

Key words: Abiotic stress, biotic stress, nitric oxide, oxidative damage.

INTRODUCTION

Nitric oxide (NO), a fat- and water-soluble small molecule of gas is considered to be a key signaling molecule commonly existing in plant leaves in recent years. In plant, NO is mainly formed by four ways: NO synthase pathway which is similar to that of animal (Delledonne et al., 1998; Durner et al., 1998; Neill et al., 2003), nitrate reductase pathway (Morot-Gaudry-Talarmain et al., 2002), other enzymatic pathways and non-enzymatic pathways (Cooney et al., 1994).

PHYSICO-CHEMICAL PROPERTIES OF NO

NO is more extensive on the growth and development of plant. Early studies have shown that NO may regulate the growth of plant leaves (Leshem et al., 1998), affect the growth of plant roots, be involved in plant photomorphogenesis, stimulate seed germination and play the role of de-etiolation (Beligni and Lamattin, 2000). Treatment with exogenous nitric oxide in horticultural plants can increase NO content in tissues and inhibit ethylene formation, thus, delaying the fruit maturation and senescence (Leshem and Haramaty, 1996). The influence of NO depends on the level of concentration, a low concentration level of NO directly act on cell wall components to make cell wall relax and promote cell expansion, thus promoting the growth of plants and help plants resist stress and delay aging. A high concentration level of NO and superoxide iron reaction forming a toxic peroxynitrite compound which causes membrane lipid over oxidation, lead to membrane leakage and may even spreads into the cytoplasm to attack key enzymes, thereby causing destructive impact (Pyor, 1994).

Iron is a necessary element for synthesis and development of chloroplast. Iron need to go through several layers to reach the chloroplast, and the operating mechanism is unclear at present. NO plays an important role in the distribution of iron in the chloroplast in plant leaves (Sun et al., 2007). Thylakoids and starch grains decreased obviously and exist in iron-deficient corn without NO treatment. Vascular bundle of *Zea mays* chloroplast, had no obvious difference between iron-deficient with NO treatment and without NO treatment with regards to morphological characteristics of chloroplasts, thylakoids and starch grains. There was a complex interaction existing between NO and hormone. NO and peroxynitrite can inhibit the biosynthesis of ethylene by regulating the 1-aminocyclopropane-1-carboxylic acid synthase activity regulators and 1-aminocyclopropane-1-carboxylic acid synthase cofactor, so that they can regulate the maturation and senescence of plant tissues. There are more reports about the function of NO and ABA in regulating stoma. Some

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studies reported that there is a positive cooperativity in the regulation of stomatal movement. In *Arabidopsis thaliana* and *Pisum sativum*, NO may participate in the ABA-induced stomatal closure, which may be the transduction signal of stomatal movement under the ABA regulation. NO and NOS are involved in the synthesis of ABA when the *Triticum aestivum* root tip is under drought stress. In corn's response to drought stress, NADPH was increased because of ABA-induction, which make the level of oxygen radical elevated, and the oxygen radical promotes the production of NO, proving that the relationship of ABA and superoxide radical and NO are close (Jiang and Zhang, 2002). Cytokinin can induce NO production (Scherer and Holk, 2002), and NO may mediate the occurrence of adventitious roots of ABA-induced cucumber (Samuel et al., 2000). NO can also induce acid synthesis, and salicylic acid can activate NO synthesis pathway of plants (Guo et al., 2003). NO can not only participate in joint action of plant hormones regulating plant growth, but can also be used as the signal substance to induce hormones synthesis. NO is also induced by hormones.

NO INVOLVED IN ENVIRONMENTAL STRESS

NO involved in abiotic stress

Abiotic stress and biotic stress can induce the production of NO, exogenous and endogenous NO could increase plant stress, but high concentration of NO is toxic to the cells (Durzan and Pedroso, 2002). Abiotic stresses such as drought, salt, heavy metals, extreme temperatures, UV radiation and so on could induce a large number of active oxygen (Uchida et al., 2002; An et al., 2005; Laspina et al., 2005; Song et al., 2006; Chen et al., 2006; Shi et al., 2007; Vital et al., 2008; Zhang et al., 2009; Xu et al., 2010), which can cause oxidative damage and trigger different signaling pathways. NO and active oxygen interaction by different ways, may play an important role as an antioxidant in different stresses. NO can regulate the formation of superoxide and inhibit lipid peroxidation to protect the plant from environmental stress damage, which can explain the potential antioxidation (Neill et al., 2003). In addition, excessive NO may cause nitrosation stress to harm plant, therefore, the balance between NO and active oxygen is very important.

A study showed that the moisture holding capacity of excised wheat leaves with 150 μM sodium nitroprusside (a NO donor) pretreatment is 15% higher than with water or NO^{2-}/NO^{3-} pretreatment after 3 h (Mata and Lamattina, 2001). It can be observed from wheat seedlings after 7 days drought stress that SNP treatment can help it increase water-retention capacity. The result was consistent with that leaf transpiration rate of detached wheat decreased by 20% which is by SNP treatment. The studies of Song et al. (2008) have shown that NO may act as signal molecules to induce the antioxidative enzyme activity of *Phragmites communis*, thus inducing the accumulation of active oxygen and the level of membrane lipid peroxidation under the high temperature stress. Leshem, (2001) found that short-term heat stress can increase nitric oxide level in alfalfa. Neill et al. (2003) reported that the role of NO can reflect the antioxidant activity that can reduce the accumulation of cold and the levels of reactive oxygen in heat stress.

Zhao et al. (2001) found that the semiochemical of NO is also involved in plant material salt reaction. NO increased obviously and induced the H^+-ATPase gene expression of plasmalemma and increase its vitality, finally, ions within the cell achieve re-balanced, thus maintain a relatively high K^+/Na^+ ratio and induce the salt tolerance of plant cells. In subsequent experiments, Zhao et al. (2004) used the method of T-DNA insertion in the Arabidopsis AtNOSI genes and found that the NOS activity decreased in a vast scale in mutant, the release of NO reduced, and at the meantime, mutant to salt stress is more sensitive than the wild type, this shows the effect of NO in the regulation of plant response to salt stress.

Under low temperature stress, NO can enhance resistance of plants to stress (Lamattina and Beligni, 2001). The experiments show that low concentrations of NO can reduce chlorophyll breakdown, ion leakage, leaf necrosis and loss and other symptoms in *Solanum tuberosum* leaf induced by herbicide, lipid peroxidation, ribulose 1,5-bisphosphate carboxylase/oxygenase and DI protein degradation, and the rupture of mRNA caused by herbicide can be reduced obviously by NO. NO can also make ETR of isolated chloroplast which are raised by herbicide to returned to normal (Lamattina and Beligni, 2001). All of these suggested that the protective effect of NO on plants might be able to reduce the levels of reactive oxygen in plant tissues.

Using an ozone-sensitive *Arabidopsis* ecotype as materials, research suggests that ozone may promote NOS activity, this effect occurred before the salicylic acid accumulation and cell death (Zhang et al., 2009). Accordingly, they believed that the production of NO increased the sensitivity of *Arabidopsis* ecotype, and may act as a signal molecule induced hypersensitive cell death. In *Nicotiana tabacum*, NO can induce the synthesis of salicylic acid (Durner et al., 1998; Shi et al., 2007; Zheng et al., 2009), it is possible that NO can increase the accumulation of salicylic acid under ozone stress.

In recent years, some studies reported that NO was involved in plant response by heavy metals stress (Kopyra and Gwozdz, 2003; Jin et al., 2010). They used lupine bean as the test material to see if exogenous NO can increase superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) and other active oxygen metabolism enzyme activity, thus reduce the heavy metals on lupine seed germination and seedling growth inhibition. Exogenous NO can reduce oxidative stress obviously induced by cadmium, reduce Cd stress on sunflower growth inhibition and chlorophyll degradation, enhance CAT activity and increase glutathione and ascorbic acid content in cell (Laspina et al., 2005). This showed that exogenous NO can increase antioxidant level in plants, thereby improving the resistance to cadmium stress.

NO in biotic stress

The NO level increases more rapidly in the process of plants and pathogens reaction. NO is closely related to plant disease resistance of allergic reactions (hypersensitive response, HR) programmed cell death (PCD) and systemic acquired resistance (SAR). With a laser scanning confocal microscope, Foissner et al. (2000) proved that the combination of tobacco epidermal cells and pathogens will make NO product, scavenger of NO and NO synthase inhibitors prevent this outbreak. It was found that nitric oxide synthase activity increases rapidly in soybean suspension cells induced by directional cell bacteria, *Pseudomonas elicitor*. In the action between tobacco and pseudomonas, the nitric oxide donor can cause allergic reaction (Huang and Knopp, 1997).

HR is triggered by rapid and transient ROS large formation. In plants, nitric oxide through two ways: directly or indirectly affect plant disease resistance. On one hand, NO mainly prevent the spread of pathogens from the injection site to participate in allergic mediated disease resistance of plants (Hammond-Kosack and Jones, 1996; Manjunatha et al., 2009). One of the plant cell response to pathogens invasion is oxygen burst, which produce large amount of reactive oxygen, with the occurrence of oxygen burst, and NO is also rapidly generated, which directly kill bacteria. On the other hand, indirect effects of NO can also induce the HR of plant; this is believed to be the main way of signal transduction to induce resistance gene expression. Oxygen burst can release H_2O_2 and O^{2-}, which can react with NO to produce a more active lethal pathogen, O^{2-} and $ONOO^-$ which can react against pathogenic invasion. At the same time, NO can stimulate the infected cell walls lignification (Ferrer and Barcelo, 1999; Palmieri et al., 2010), involved in the regulation of cell death and defense mechanisms induced during pathogen defense (Morot-Gaudry-Talarmain et al., 2002).

NO can obviously reduce cell death caused by ion leakage and potato leaf infected by pathogen. This process is controlled by cPTIO (carboxy-2-pheny 1-4,4,5,5-tetrmethyliidazoline-1-oxy13-oxide, cPTIO). As an antioxidant, NO can offset the bane action mediated by the reactive oxygen (Beligni and Lamattina, 1999; Palmieri et al., 2010).

PROSPECT OF RESEARCH ON NO

Animal cells synthesize NO primarily by the activity of NOS. However, at present, the mechanism of NO production in plant organs is still a controversial problem (Crawford et al., 2006; Moreau et al., 2008). Previous studies have shown that NO source in plants includes enzymatic sources like nitric oxide synthase-like enzymes and nitrate reductase (NR), and non-enzymatic sources (Neill et al., 2003). NR was shown to be involved in NO production in several physiological situations, such as ABA-induced stomatal closure (Bright et al., 2006) and auxin-induced lateral root development (Kolbert et al., 2008). However, most researches still supported that NO generation was mainly mediated by a putative NOS-like enzyme which catalyses the formation of NO from L-arginine, rather than NR (Tian et al., 2007; Corpas et al., 2008). Furthermore, several studies have identified NOS-dependent NO generation during plants exposure to stress conditions (Corpas et al., 2008; Chaki et al., 2009).

The present of NO in plant resistance is mainly through exogenous donor of NO, NO synthase inhibitor, NO removal agent under environmental stress effects on plant physiological indicators, analysis of NO in the application of stress response and gradually to gene transcription, enzyme protein and other molecular mechanism of action. Under almost all environmental stress factors, NO can play its physiological role. However, exogenous nitric oxide through which function intermediary or signal transduction components affect the response of plants to stress factors, by plant hormones, reactive oxygen metabolism, stress proteins or genes associated with stress and functional protein need to be deeply explored further with extensive research in depth. For example, In the high temperature stress, Ca^{2+}, abscisic acid, ethylene, salicylic acid and stress-related genes, antioxidant system and HSPS and so on are all related to heat tolerance of plant, but in the process of stress signal transmitting from outside to inside, the order of exogenous or endogenous NO and these function intermediary and whether there is chain among them are worthy to be clarified. In addition, according to Pastori and Foyer (2002), plants adapt to biotic and abiotic stress by starting a series of physiological events, these physiological events begin with the perception of stress stimuli, and end at the expression of target genes. The signaling components mainly contain signaling molecules and their transformation, transcription regulation elements, target genes, and finally the stress response, including plant morphology and physiological and biochemical changes. From an evolutionary point of view, the function of components close to the end of stress response is single, and components near the beginning of stress response is likely to be all the stress response mutual pathway or factor, this "cross resistance" can make plants adapt to a number of other stresses when experiencing a particular stress. Since NO play a role in so many plant stress responses, it is suggested that NO in the stress signal chain or the signal net should be close to the beginning of transduction. But how exactly, stress stimulation is transferred to NO and how to pass on ulteriorly are not clear. NO itself is likely to be the main component of plant "cross resistance ", which is worthy of further study.

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