Ethylene signal transduction and signaling roles-A Review

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ABSTRACT

The ethylene is a gaseous hormone which plays multiple roles in regulating plant growth and development and also serves as a key modulator of the plant’s response to biotic or abiotic stresses. Its production is tightly regulated by internal signals during development and in response to environmental stimuli from biotic and abiotic stresses. Arabidopsis is a model plant to understand the ethylene signal transduction. In Arabidopsis, ethylene is perceived by a family of five receptors such as ETR1, ETR2, ERS1, ERS2 and EIN4 which are predominantly localized to the ER membrane. Ethylene receptor can be divided into two subfamilies i.e. type I and type II subfamilies, depending on the basis of structural similarities. CTR1 functions as a key mediator of ethylene signal transduction. Ethylene was originally regarded as a stress hormone because its synthesis is induced by a variety of environmental stress signals. Among the environmental stresses, such as ozone, wounding, and UV irradiation are the stimulations for ethylene synthesis. Enhanced ethylene production is an early, active response of plants to perception of pathogen attack and is associated with the induction of defence reactions. The elucidation of the mechanisms of ethylene signal transduction in response to biotic and abiotic stress is providing a framework for understanding how all plants sense and respond to ethylene.

Key words: CTR1, Ethylene, Response, Receptor, Signal transduction, Stress.

Despite its simple two-carbon structure, the ethylene is a potent modulator of plant growth and development (Ecker, 1995). In terms of growth, ethylene is most commonly associated with the regulation of cell size, particularly as an inhibitor of cell elongation. However, ethylene may also serve as a signal to promote cell expansion, an important response to submergence stress in some species (Jackson, 2008). In addition to regulating cell expansion, ethylene has also been found to regulate growth through control of cell division in some instances. A well-known effect of ethylene on plant growth is the so-called ‘triple response’ of etiolated dicotyledonous seedlings. This response has characterized by the inhibition of hypocotyl and root cell elongation, radial swelling of the hypocotyl, and exaggerated curvature of the apical hook. This highly specific ethylene response have been occurred at an early developmental stage (3 days post germination), permitting large mutant populations of seedlings to be screened rapidly for ethylene response defects. Genetic screens based on the triple-response phenotype have been extensively conducted on Arabidopsis. In terms of development, ethylene is most commonly associated with ‘ageing’, particularly for its ability to accelerate such processes as senescence, ripening and abscission (Stepanova and Alonso, 2009; Schaller, 2012). In addition, ethylene serves as a key modulator of the plant’s response to biotic or abiotic stresses and its production is tightly regulated by internal signals during development and in response to environmental stimuli from biotic (e.g., pathogen attack) and abiotic stresses, such as wounding, hypoxia, ozone, chilling, or freezing.

To understand the roles of ethylene in plant functions, it is important to know how its production is regulated and how the signal has transduced. The intent of this review is not to cover all aspects of ethylene biology but to focus on recent findings related to ethylene signal transduction.

Ethylene receptor: Receptor is specialized proteins which are utilized for the reception of signal and to control the transduction pathway. To understand the signal transduction in ethylene Arabidopsis has been used as model plant. In Arabidopsis, ethylene is perceived by a family of five receptors such as Ethylene response 1 (ETR1), Ethylene

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levels of CTR1. The receptors also physically interact with each other to activate. Although the receptors have overlapping roles in the regulation of CTR1, the subfamily I receptors of Arabidopsis play a more predominant role than the subfamily II receptors in CTR1 regulation, in particularly ETR1 activating CTR1 more effectively than other members of the receptor family. Reversion to Ethylene Sensitivity 1 (RTE1) is a regulatory protein which interacts with ETR1 and plays an important role in ethylene signaling. The role of RTE1 appears to be to stabilize or assist folding of ETR1 into the conformation it adopts in air (absence of ethylene), thereby enhancing the ability of ETR1 to repress ethylene signaling. Recent evidence suggests that RTE1 and ETR1 may function together to mediate ethylene signaling through a CTR1-independent pathway.

**Current model for ethylene signal transduction:** After its synthesis, ethylene is perceived and its signal transduced through transduction machinery to trigger specific biological responses. On the basis of the highly reproducible triple response in dark-grown Arabidopsis seedlings, a number of mutants impaired in their response to ethylene have been identified. Cloning and characterization of the genes disrupted in these mutants are leading to a complete picture of the ethylene signal transduction pathway (Figure 1).

The gaseous hormone ethylene is perceived in plants by a family of five membrane-localized ethylene receptors involved in sensing environmental changes. Genetic and biochemical studies have revealed that the ethylene receptors function as negative regulators of ethylene responses and that ethylene binding inactivates them (Chang and Stadler, 2001; Bleecker and Kende, 2000). Dominant mutations in each of the five receptors confer ethylene-insensitivity, suggesting that all five receptors participate in ethylene perception. In the absence of ethylene, the receptors stimulate the kinase activity of CTR1 (in the cytosol) by regulating the CTR1-dependent pathway.
the subfamily 2 receptors in CTR1 regulation. Activation of CTR1 results in phosphorylation and inhibition of EIN2 activity & ultimately suppresses the ethylene response. Ethylene binding (to the receptor) induces a conformational change in the receptors, resulting in the inactivation of CTR1 and the dephosphorylation of EIN2. As a result, the C-terminal portion of EIN2 is proteolytically cleaved, migrates to the nucleus. In nucleus through an unknown mechanism activates the EIN3 family of transcription factors to initiate the transcriptional response to ethylene.

There are two alternative pathways for ethylene signaling are also depicted which is denoted by ‘?’. A two-component signaling pathway, initiated by the subfamily 1 receptors and involving phosphotransfer proteins (AHPs) and response regulators (ARRs). RTE1 may also facilitate ETR1 kinase kinase kinases signal output through a CTR1-independent pathway.

**Ethylene and abiotic stresses:** Besides its physiological roles in different developmental stages, ethylene was originally regarded as a stress hormone because its synthesis is induced by a variety of stress signals, such as mechanical wounding, chemicals and metals, drought, extreme temperatures, and pathogen infection (Kende, 1993; Johnson and Ecker, 1998). Among the environmental stresses, ozone, wounding, and UV irradiation are the stimulation for ethylene synthesis. It has been reported that this stimulation involve the generation of reactive oxygen species (Surplus et al., 1998; Orozco-Cardenas and Ryan, 1999; Pellinen et al., 1999). Reactive oxygen species (ROS) includes superoxide anions, hydroxyl radicals, and hydrogen peroxide etc has been shown to function as signaling molecules (Levine et al., 1994).

Ozone \((O_3)\) is recognized as an abiotic elicitor that induces plant defense responses like those brought on by pathogen infection (Sandermann et al., 1998). It may represent programmed cell death activated by signals derived from ROS, as suggested for the hypersensitive response (Lamb and Dixon, 1997). ROS generated by ozone results from its reactions with water and other cellular components when it enters from the stomata. Generation of ROS has been shown to be the casual effector for hypersensitive response and regulates the accumulation of SA, which is required for both the hypersensitive response and systemic acquired resistance (SAR) (Sticher et al., 1997).

Invasion stress involving actual penetration of the plant tissue, such as those resulting from wounding or pathogen attack, will be considered together since the response of the plant to these types of stimuli is similar. Wounding caused by herbivore feeding or other mechanical damage can provide possible entry points for pathogens, which is why the plant responds by inducing a defense response involving substantial alteration in gene expression. The main aims of the defense response are wound healing and prevention of pathogen invasion. Ethylene has been shown to potentiate JA action in the wound response (O‘Donnell et al., 1996). The biosynthesis of ethylene has been well known to be stimulated by wounding, most likely by the induction of ACS gene activity (Watanabe et al., 2001). The expression of proteinase inhibitor II \((PIN II)\), a specific marker for the JA wounding pathway, is linked to the induction of ethylene production by either elicitors or ethylene inhibitor treatment. Using inhibitors of ethylene biosynthesis and perception, as well as ACO antisense transgenic lines, it has been demonstrated that ethylene signaling is required for PIN II induction upon wounding in tomato plants. Considering the local and systemic responses to wounding, ethylene may only block the JA-dependent pathway in the local damaged tissues because of its low mobility, although it does not affect JA-dependent functions in the systemic tissues.

Stoma plays a major role in controlling gaseous exchange, especially of photosynthetic carbon dioxide \((CO_2)\) uptake, and in water release by transpiration in response to changes in the surrounding environment. The regulation of stomatal aperture is thus extremely important for the survival of plants. Ozone depletion in the stratosphere has resulted in increased ultraviolet B \((UV-B; 280-315 \text{ nm})\) radiation at the earth’s surface since the 1980s (UNEP, 2002). Studies have shown that, in plants, hydrogen peroxide \((H_2O_2)\) generation from multiple sources can be induced by UV-B radiation (Mackerness et al., 2001). \(H_2O_2\) can function as a signalling molecule mediating a range of responses to environmental stresses, including UV-B radiation. UV-B-induced stomatal closure is also mediated by \(H_2O_2\) \((He et al., 2005)\). The plant hormone ethylene influences many aspects of plant growth and development, as well as mediating a diverse array of abiotic stresses (Wang et al., 2002; Guo and Ecker, 2004). In plants, ethylene is synthesized from Met via S-adenosyl-L-Met and 1-aminocyclopropane-1-carboxylic acid \((ACC)\) [Adams and Yang, 1979]. The conversion from S-adenosyl-L-Met to ACC catalysed by ACC synthase \((ACS)\). Expression of ACS and consequent ethylene production are induced under UV-B radiation (Garty et al., 2002; An et al., 2006). Such UV-B induced production of ethylene is important for some UV-B-induced damage (Nara and Takeuchi, 2002) and gene expression (Wang et al., 2002; Guo and Ecker, 2004). Stomatal movement is also regulated by ethylene, but its effect in this process seems rather contradictory (Acharya and Assmann, 2009; Wilkinson and Davies, 2010). Recent data
indicated that H$_2$O$_2$-induced stomatal closure requires the ethylene receptor ETR1 (Desikan et al., 2005) and ethylene-induced stomatal closure via NADPH oxidase AtrbohF-mediated H$_2$O$_2$ synthesis (Desikan et al., 2006), implying a link between H$_2$O$_2$ and ethylene signal transduction during stomatal movement.

Ethylene also plays an important role in response to deep water environmental condition. Scientists have identified genes SNORKEL 1 and SNORKEL 2, which trigger deepwater response by encoding ethylene response factors involved in ethylene signaling (Hattori et al., 2009). Under deepwater conditions, ethylene accumulates in the plant and induces expression of these two genes. The products of SNORKEL 1 and SNORKEL 2 then trigger remarkable internode elongation via gibberellin (Figure 2).

**FIG 2: Expression of SNORKEL 1 & 2 in response to flood**

**Ethylene in plant disease resistance:** Plants have evolved sophisticated detection and defense systems to protect themselves from pathogen invasion. Enhanced ethylene production is an early, active response of plants to perception of pathogen attack and is associated with the induction of defense reactions (Boller, 1991). Yet, similar to the defense-regulating compounds salicylic acid (SA) and jasmonic acid (JA), plant-derived ethylene is generally considered being involved in resistance (Dong, 1998). Depending on the conditions and the plant–pathogen combination, seemingly contradictory results have been obtained (Abeles et al., 1992; Arshad and Frankenberger, 1992). For example, the causal agent of gray mould, the fungus Botrytis cinerea, is able to infect a wide range of vegetables, ornamentals and fruits, where ethylene treatments typically promote disease development (Elad, 1993) but, on carrot, ethylene appears to be involved in resistance (Hoffman et al., 1988). Often, ethylene treatment must increase disease development simply through its acceleration of ripening or senescence. In addition, the conditions under which experiments have been carried out are not always clearly specified. Furthermore, various abiotic stresses can inadvertently affect plant susceptibility to disease. However, several observations indicate that when ethylene is applied before inoculation with a pathogen, it reduces or has no effect on disease development, whereas disease development is accelerated when plants are treated with ethylene after infection (Abeles et al., 1992). Thus, it seems that the timing of the exposure of plants to ethylene can determine whether resistance is stimulated or reduced.

The capacity of a plant to develop a broad-spectrum, SAR after primary infections with a necrotizing pathogen is well known and its signal transduction pathway extensively studied (Durrant and Dong, 2004). Plants, of which the roots have been colonized by specific strains of non-pathogenic fluorescent Pseudomonas spp., develop a phenotypically similar form a protection that is induced systemic resistance (ISR) [Van Loon et al., 1998]. In contrast to pathogen-induced SAR, which is regulated by SA, rhizobacteria-mediated ISR is controlled by a signalling pathway in which ET and JA play key roles (Pieterse et al., 1998).

In incompatible plant–pathogen interactions, the hypersensitive reaction (HR) is associated with a large burst of ethylene production around the time of necrotic lesion formation. In wild-type tomato, infection by Xanthomonas campestris pv. vesicatoria increased expression of the ethylene receptor genes NR and LeETR4, leading to reduced ethylene sensitivity and reduced necrosis (Ciardi et al., 2000). Conversely, LeETR4 antisense plants displayed a more rapid and extensive cell death during infection, associated with an enhanced defense response (Ciardi, 2001). Because X. campestris pv. vesicatoria is a pathogen with a mixed biotrophic-necrotrophic lifestyle, it is difficult to relate resistance to necrosis in this plant-pathogen interaction.

**CONCLUSION**

The mechanism of ethylene signal transduction helps to understand how all plants sense and respond to ethylene. The interaction of ethylene with SA and JA signaling pathways in biotic and abiotic stresses demonstrates the complex nature of the plant’s decisions and the different outcomes. The most well-characterized components of ethylene signaling network are receptors, secondary messenger and transcription factors and the presence of ethylene is necessary for uniform growth and development of a plant cell. Each stage of development is associated is regulated by a specific signal transduction pathway.
REFERENCES


