Ethylene: Inhibitor and Stimulator of Plant Growth

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Abstract Ethylene is a gaseous hormone which plays an essential role in a myriad of plant developmental processes. It promotes root hair formation, flowering in a number of species, fruit ripening and abscission and leaf and petal abscission. Ethylene can stimulate growth in hypocotyls of light-grown plants, and shoot growth in shaded conditions. On the other hand, it inhibits root growth, and hypocotyl elongation in the dark. In recent years, compelling molecular evidence has been gathered to support intricate connections between ethylene and other hormonal pathways that yield its well-known effects on plant growth. In this chapter, we will discuss the role of ethylene in both growth-stimulating and growth-inhibiting processes.

1 Ethylene Synthesis

Plant hormones, just like animal hormones, function in a dose-dependent manner (Taiz and Zeiger 2006). The most direct way to regulate endogenous ethylene concentrations is to change the rate at which it is synthesized. In this paragraph we will briefly summarize the ethylene biosynthesis pathway and discuss the different mechanisms that influence the rate of ethylene synthesis.

1.1 Biosynthesis Pathway

The precursor for ethylene synthesis is methionine. This amino acid is converted to S-adenosyl methionine (SAM) from ATP and methionine. The reaction is catalyzed by SAM synthetase (Ravanel et al. 1998). Arabidopsis has two genes encoding this enzyme (Peleman et al. 1989). Analysis for subcellular localization signals using Target P (Emanuelsson et al. 2000) did not reveal potential subcellular targeting, suggesting cytosolic localization of the enzyme.

The next step is the conversion of SAM to 1-aminocyclopropane-1-carboxylic acid (ACC). This step is catalyzed by ACC synthase (ACS). This is a cytosolic enzyme that requires PLP (pyridoxal-5'-phosphate) as a cofactor (Adams and Yang 1979; Yang and Hoffman 1984). ACS isoforms function as homodimers (Capitani et al. 1999; Yamagami et al. 2003). In Arabidopsis,
ACS is encoded by a gene family containing 12 members (ACS1 and ACS2 of Van Der Straeten et al. 1992 are named ACS2 and ACS4 respectively by Yamagami et al. 2003). Ten of the 12 family members encode ACS isozymes; of these ACS1 and ACS3 are not biologically active, and ACS10 and ACS12 function as aminotransferases. It has been proven that ACS is encoded by a multigene family in other plants too (for a review, see Vandenbussche et al. 2006). The catalytic activity of ACS results in not only ACC but also 5′-methylthioadenosine (MTA). MTA is recycled to methionine in the Yang cycle (Miyazaki and Yang 1987). ACS is the main enzyme that controls the synthesis of ethylene and is, in turn, controlled by multiple signals. We will discuss these signal interactions in the next paragraphs.

ACO (ACC oxidase) catalyzes the conversion of ACC to ethylene. During this reaction ACC is oxidized and forms ethylene, CO$_2$ and HCN (Yang and Hoffman 1984). In Arabidopsis ACO is part of a multigene family, as is ACS (Gomez-Lim et al. 1993). It was proposed that under particular conditions, such as upon wounding or during ripening and senescence, ACO also plays a role in regulating ethylene levels in plants (Kende 1993).

1.2 Regulation of Synthesis

ACS is the major factor regulating the rate of ethylene synthesis. This regulation is in part dependent on the level of ACS. One of the mechanisms used by plants to control the concentration of ACS is the transcriptional regulation of ACS genes.

Using promoter-GUS fusions, Rodrigues-Pousada et al. (1993, 1999) and Tsuchisaka and Theologis (2004b) showed that the different functional ACS genes in Arabidopsis each have a unique pattern of expression. Although the patterns are specific to each gene, they show overlapping regions of expression. The GUS expression also differs according to changes in environmental conditions. For instance, the expression of ACS1/2, 2/4 (see remark concerning ACS gene numbering above), 6, 7, 8 and 11 in five-day-old etiolated seedlings is confined to the elongation zone of the hypocotyl, the embryonic root region, the cotyledons and the root vascular tissue. In the light, however, these genes are expressed in the cotyledons, the embryonic root, the roots, and in primary leaves, while ACS1/2, 5, 8 and 11 are active in the shoot apex.

In addition, different stress-promoting factors (cold, wounding, heat) have been shown to alter the transcriptions of ACS genes, with each factor altering the transcription of each individual ACS gene in a specific manner (Tsuchisaka and Theologis 2004b). Wounding (by cutting) the hypocotyls of five-day-old light-grown seedlings inhibits the expression of the genes that are constitutively expressed in the intact tissue, like ACS1 and ACS5, and induces the expression of ACS1/2, 2/4, 6, 7 and 8, which were not expressed before wounding. Cold treatment inhibits the expression of ACS5