Ethylene Biosynthesis

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ABSTRACT: The suggestion that ethylene is involved in the responses of plants to stress is of no recent date and there are a multiplicity of publications over the last thirty years which tend to support this view. It must be said however that, almost in their entirety, the conclusions in such publications rest on correlations and inferences, which, no matter how logical, do not of themselves constitute proof of causal relationships. In the same context, while it may be a relatively easy task to show that imposition of a stress leads to, say, increased ethylene biosynthesis, it is much more difficult to demonstrate that these effects are specific. Equally, it is difficult to prove that the effect of stress-induced ethylene has an “adaptive” or “survival” value for the plant in relation to the stress. The purpose of this article is to provide a brief overview of the field and to attempt to assess whether, and to what extent, ethylene is involved in the responses of plants to stress.

Key words: ethylene, biosynthesis, stress, adaptive.

INTRODUCTION

The phytohormone ethylene plays roles in physiological processes throughout the life cycle of the plant-(Mattoo and Suttle, 1991; Abeles et al., 1992). Its involvement in such agronomically important processes as senescence, abscission and fruit ripening has made ethylene a target for manipulation by chemical and biotechnological methodologies(Mattoo and Suttle, 1991; Abeles et al., 1992; Schaller, 2003). Ethylene has also been implicated in developmental processes such as the formation of the apical hook in dark-grown seedlings(this hook protects the apical meristem as the young seedling forces its way through soil toward the light), the regulation of cell expansion and flower development. Ethylene also regulates plant responses to biotic stresses such as those induced by pathogens, and to abiotic stresses such as those induced by flooding or drought(Mattoo and Suttle, 1991; Abeles et al., 1992; Roman et al., 1995; O’Donnell et al., 1996, 2003; Penninckx et al., 1998). There is cross-talk between the ethylene signalling pathway and other hormone signalling pathways, particularly with auxin, whose effects are often mediated by ethylene, but also with ABA, cytokinins, gibberellins and brassinosteroids. The wide-ranging effects of ethylene have made it a topic of intense research for decades, and although many components of the biosynthesis and signalling pathways are now known, much remains to be learned about the pathways and the complex regulation of proteins involved. In this review, we focus on recent advances in our knowledge on ethylene signal transduction, in particular on recently proposed components of the pathway, on the interaction between the pathway components, and on the roles of transcriptional and posttranscriptional regulation in ethylene signalling.

Mechanistic View of Ethylene Synthesis

SadoMet is the precursor for ethylene biosynthesis(Yang and Hoffman, 1984; Kende, 1993). In addition to being an essential building block of protein synthesis, nearly 80% of cellular methionine is converted to SAdoMet by SAdoMet synthetase(SAM synthetase, EC 2.5.1.6) at the expense of ATP utilization(Ravanel et al., 1998).

SAdoMet is the major methyl donor in plants and is used as a substrate for many biochemical pathways, including polyamines and ethylene biosynthesis(Ravanel et al., 1998). In addition, SAdoMet is involved in methylation reactions that modify lipids, proteins, and nucleic acids. On the basis of the Yang cycle, the first committed step of ethylene biosynthesis is the conversion of SAdoMet to ACC by ACC synthase(Sadenosyl-L-methionine methylthioadenosine-lyase, EC4.4.14) (Yang and Hoffman, 1984; Kende, 1993). In addition to ACC, ACC synthase(ACS) also produces 5-methylthioadenosine(MTA) in this reaction, which is then converted to methionine by using a modified methionine
This salvage pathway preserves the methyl group for another round of ethylene production. Therefore, ethylene can be synthesized continuously without demanding an increasing pool of methionine. At the same time, the sulfur group of the methionine is also conserved. Finally, ACC is oxidized by ACC oxidase to form ethylene, CO2, and cyanide, which is detoxified to β-cyanoalanine by β-cyanoalanine synthase (β-CAS, EC 4.4.1.9) to prevent toxicity of accumulated cyanide during high rates of ethylene synthesis (Figure 1).

The rate-limiting step of ethylene synthesis is the conversion of S-AdoMet to ACC by ACC synthase (Kende, 1993). The observations that expression of the ACS genes is highly regulated by a variety of signals and that active ACC synthase is labile and present at low levels suggest that ethylene biosynthesis is tightly controlled. Both positive and negative feedback regulation of ethylene biosynthesis have been reported in different plant species (Kende, 1993; Nakatsuka et al., 1998; Barry et al., 2000). Different isoforms of ACS appear to be the principle targets. For example, in tomato, Le-ACS2 and Le-ACS4 are positively regulated, and Le-ACS6 is negatively regulated by ethylene synthesized during fruit ripening (Nakatsuka et al., 1998). Most studies addressing ACS regulation have focused on ACS gene expression in response to various endogenous cues and environmental stimuli. The only feature found in common is that the ACS enzymes are spatially and temporally regulated and are controlled by various internal and external signals.

The formation of S-AdoMet is catalyzed by SAM synthetase from the methionine at the expense of one molecule of ATP per molecule of S-AdoMet synthesized. S-AdoMet is the methyl group donor for many cellular molecules (Methylated Acceptors), including nucleic acids, proteins, and lipids. In addition, S-AdoMet is the precursor of the polyamine synthesis pathway (Spermidine/Spermine biosynthesis pathway). ACC is the immediate precursor of ethylene. The rate-limiting step of ethylene synthesis is the conversion of S-AdoMet to ACC by ACC synthase under most conditions. ACC oxidase catalyses the final step of ethylene synthesis using ACC as substrate and generates carbon dioxide and cyanide. Transcriptional regulation
of both ACC synthase and ACC oxidase is indicated by dashed arrows. Reversible phosphorylation of ACC synthase is hypothesized and may be induced by unknown phosphatases (Ptase) and kinases, the latter presumably activated by stresses. Both native and phosphorylated form (ACC synthase-Pi) of ACC synthase are functional, although the native ACC synthase may be less stable or active in vivo. A hypothetical inhibitor is associated with ACC synthase at the carboxyl end and may be dissociated from the enzyme if it is modified by phosphorylation at the vicinity.

**Ethylene biosynthesis underwater**

Demonstrations of enhanced accumulation of ethylene within submerged plants raises the question of whether this is entirely attributable to entrapment of basal ethylene production by the covering water or whether enhanced biosynthesis also makes a contribution. The answer depends on the species and duration of submergence. In deep-water rice, the partial O2 shortage and CO2 enrichment that stems experience at the base of the shoot system while it is partially submerged stimulate increased stem ethylene production about 4-fold. This faster synthesis is association with increases in the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) (Raskin and Kende, 1984) commencing within 2 h (Cohen and Kende, 1987) and with a delayed increase in mRNA coding for one member of a family of ACC synthase enzymes that generate ACC from its precursor S-adenosylmethionine (Zarembinski and Theologis, 1997).

Expression of a gene coding for the enzyme ACC oxidase that catalyses the conversion of ACC to ethylene also increases within 4 h (Mekhedov and Kende, 1996). However, stimulation of ethylene formation by shoots suffering partial O2 shortage is an uncommon phenomenon generally, although several examples in roots are known (Jackson et al., 1984). More usual is a slowing of biosynthesis by low O2 (Jackson et al., 1984) probably because the last step in ethylene production (ACC oxidase) that converts ACC to ethylene is O2-dependant, and also subject to inhibition by ethylene itself (Bleecker et al., 1987). Thus, submergence of Rumex palustris and Rumex acetosa slows rather than accelerates their ethylene production (Bang et al., 1996). This suppression takes place despite a rise in activity of ACC synthase, ACC production and an enhanced accumulation of mRNA coding for ACC oxidase genes detectable within 1–2 h of submergence (Vriezen et al., 1999). Even in rice, the coleoptiles and small seedlings do not make more ethylene when partially O2 deficient (Ku et al., 1970; Pearce et al., 1992), even though transcript levels coding for ACC synthase (OS-ACS5) rise within 1 h of imposing submergence (Zhou et al., 2001). The resulting accumulations of ACC may have an adaptive value by lowering the Km for O2 of the ACC oxidase enzyme to below 5% (v/v) (Yip et al., 1988) thereby limiting the extent to which biosynthesis is inhibited by O2 shortage. Claims for hypoxia-stimulated ethylene production in rice, other than by the stem, may be misplaced. Most papers claiming this actually report ethylene production in air as a recovery from a preceding hypoxic or anoxic episode and not ethylene production during the stress itself (Khan et al., 1987; Zhou et al., 2001; Fukao and Bailey-Serres, 2004). This post-stress ethylene, presumably formed from the previously accumulated and unused ACC, cannot be involved in regulating underwater elongation. However, it may well be relevant to regulating growth once contact with air is regained and the O2 supply returns to normal. None of these biosynthetic details apply to the aquatic fern Regnellidium diphyllum and the liverwort Rieila helicophylla.

These plants accumulate ethylene underwater and respond with faster elongation but, unlike angiosperms, they do not derive their ethylene from methionine or ACC and their biosynthetic rates remain remarkably constant under a range of treatments. The mystery pathway does not include an O2-requiring step (Osborne et al., 1996). These findings reinforce the notion that it is trapping rather than modulation of biosynthetic rate that ensures concentrations of ethylene in submerged plants attain growth-active levels.

**CONCLUSIONS**

There is no doubt that ethylene biosynthesis is responsive to environmental stress of whatever kind. There is also increasing evidence of a degree of specificity in such responses in that particular genes may respond to particular stimuli. It is also clear that many of the developmental responses to stress are in fact transduced by the increased rates of ethylene biosynthesis induced by the stress. In one case at least, namely mechanical impedance, it can be demonstrated that the induction of increased ethylene biosynthesis does have adaptive (survival) value. It would be naive however to assume that all stress-related ethylene controlled phenomena have adaptive value and each case must be judged on its merits. In any case, it is doubtful if most responses to stress, adaptive or otherwise are controlled by a single growth regulator, or indeed by growth regulators alone at all. The definitive results with seedling emergence outlined here probably indicate that in this case ethylene is the single
most important factor but do not exclude the possible intervention of others. Similar arguments could be advanced for abscisic acid whose role in the control of stomatal aperture is undisputed but where other factors also intervene. Nevertheless, the evidence is compelling that ethylene does have a role in mediating the responses to stress and as more work is performed at the biochemical and molecular levels it is likely that a clearer understanding will emerge.

REFERENCES