B4. Biosynthesis and Metabolism of Ethylene

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INTRODUCTION

Ethylene is a plant hormone that is involved in the regulation of many physiological responses (2). In addition to its recognition as a "ripening hormone", ethylene is involved in other developmental processes from germination of seeds to senescence of various organs and in many responses to environmental stresses.

In many ways, ethylene is the ideal plant hormone to investigate. As a simple gaseous hydrocarbon, it is readily isolated from plant material and it can be easily quantified down to 0.01 µl/l using a gas chromatograph equipped with a flame ionization detector. Moreover, the levels of ethylene to which a plant is exposed can be controlled with a flow system. Thus, ethylene is far easier to work with than other plant hormones.

Ethylene was recognized as a plant-produced hormone over 50 years ago, yet the biosynthetic pathway of ethylene in plants remained elusive until the key intermediate, ACC, was shown to be the immediate precursor of ethylene. Although in the past decade much progress has been made in understanding ethylene biosynthesis and action, there are many challenges remaining. The purpose of this chapter is to describe both the progress in ethylene biochemistry and avenues for future research.

Abbreviations: ABA = abscisic acid; ACC = 1-aminocyclopropane-1-carboxylic acid; AEC = 1-amino-2-ethylycyclopropane-1-carboxylic acid; AOA = aminooxyacetic acid; AVG = aminooxyhexylglycine [L-2-amino-4-(2-aminooxy)-trans-3-butenolic acid]; IAA = indole-3-acetic acid; KMB = 2-keto-4-methylthiobutyrate; MACC = 1-malonylamincyclopropane-1-carboxylic acid; MTA = 5'-methylthio-adenosine; MTR = 5-methylthioribose; MTR-1-P = 5-methylthioribose-1-phosphate; SAM = S-adenosylmethionine.
ELUCIDATION OF THE ETHYLENE BIOSYNTHETIC PATHWAY

The pathway for ethylene biosynthesis is shown below. Although a number of ethylene precursors were proposed after testing in plant tissue or in model systems, it was eventually shown that methionine was rapidly converted to ethylene in a chemical model system consisting of Cu$^{2+}$ and ascorbic acid (29). Following up this work on the model system, Lieberman and coworkers showed that L-methionine labelled at the C-3,4 positions was readily converted by apple fruit tissue to labelled ethylene (29). Later, SAM was inferred as an ethylene precursor because the conversion of methionine to ethylene was inhibited by oxidative phosphorylation inhibitors, thus implying an energy(ATP)-dependent step in the biosynthesis of ethylene from methionine. Adams and Yang (5) confirmed this proposal by demonstrating that the labelled [35S] methionine and [3H-methyl] methionine released labelled MTA and its hydrolysis product MTR upon its conversion to ethylene in apple tissue. Thus, methionine must be converted into SAM before ethylene is released.

The next step in the pathway is the conversion of SAM to ACC. Adams and Yang (6) identified ACC, MTA and MTR as the labelled products which accumulated when L-[U-14C]methionine was incubated with apple tissue under anaerobic conditions which block ethylene production. Subsequent incubation of the tissue in air resulted in the production of labelled ethylene from the accumulated labelled ACC. Coinciding with these findings, Lürssen et al., (36), while screening a number of compounds as possible plant growth regulators, demonstrated that ACC dramatically stimulated ethylene production in plant tissues. Based on analogy to the chemical synthesis of ACC, they deduced that ACC would be derived from SAM and were thus able to propose the correct biosynthetic pathway for ethylene.

ACC had been isolated in 1957 from ripe cider apples and perry pears (16) and was postulated to be involved in ripening. However, interest in