1 ETHYLENE

Ethylene is another class of hormones with a single representative. It is a simple gaseous hydrocarbon with the chemical structure $H_2C=CH_2$. Ethylene is apparently not required for normal vegetative growth, although it can have a significant impact on the development of roots and shoots. Ethylene appears to be synthesized primarily in response to stress and may be produced in large amounts by tissues undergoing senescence or ripening. It is commonly used to enhance ripening in bananas and other fruits that are picked green for shipment as well.

1.1 Ethylene production

Ethylene occurs in all plant organs – roots, stems, leaves, bulbs, tubers, fruits, seeds, and so on – although the rate of production may vary depending on the stage of development. Ethylene production will also vary from tissue to tissue within the organ, but is frequently located in peripheral tissues. In peach and avocado seeds, for example, ethylene production appears to be localized primarily in the seed coats, while in tomato fruit and mung bean hypocotyls it originates from the epidermal regions.

Ethylene production increases during leaf abscission and flower senescence, **as well as during fruit ripening.**

Any type of wounding can induce ethylene biosynthesis, as can physiological stresses such as flooding, disease, and temperature or drought stress. In additon, infection by various pathogens can also elevate ethylene biosynthesis.

The primary steps in ethylene action are likely similar: binding to a receptor, followed by activation of signal transduction pathways

Unbound ethylene receptors are negative regulators of the response pathway. The observation that ethylene responses, such as the triple response, become constitutive when the receptors are disrupted indicates that the receptors are normally “on” (i.e., in the active state) in the absence of ethylene, and that the function of the receptor minus its ligand (ethylene), is to shut off the signaling pathway that leads to the response. Binding of ethylene “turns off” (inactivates) the receptors, thus allowing the response pathway to proceed.

1.2 Effects of ethylene on plant growth and development

1.2.1 Ethylene affects the transcription of numerous genes via specific transcription factors

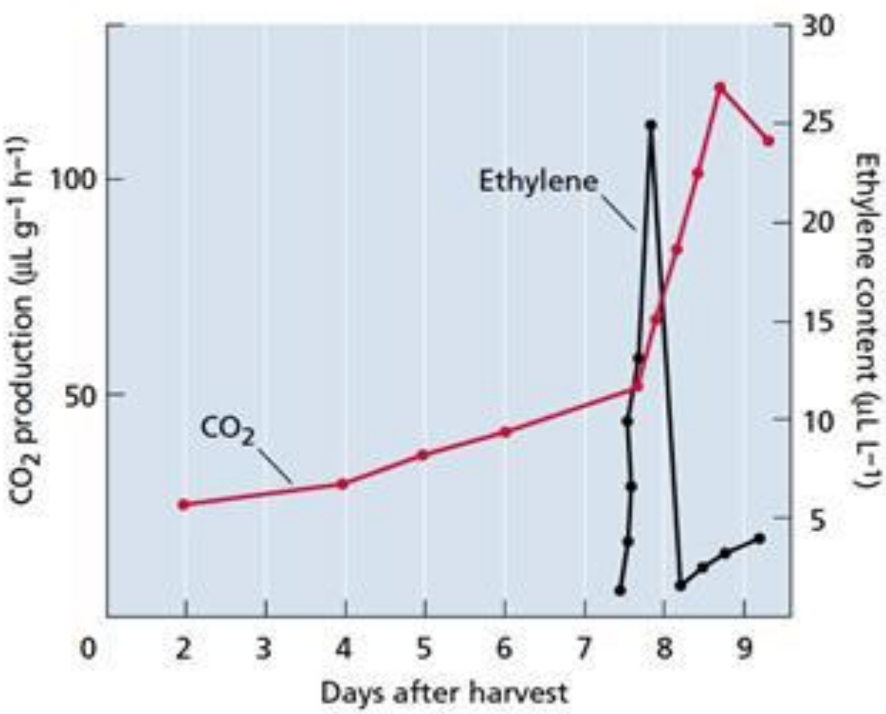
One of the primary effects of ethylene signaling is an alteration in the expression of various target genes. Ethylene affects the mRNA transcript levels of numerous genes, including those that encode cellulase and genes related to ripening and ethylene biosynthesis. Regulatory sequences called ethylene response elements, or EREs, have been identified among the ethylene-regulated genes.

1.2.2 The hormone promotes the ripening of some fruits

In everyday usage, the term fruit ripening refers to the changes in fruit that make it ready to eat. Such changes typically include softening due to the enzymatic breakdown of the cell walls, starch hydrolysis, sugar accumulation, and the disappearance of organic acids and phenolic compounds, including tannins.

Because of their importance in agriculture, the vast majority of studies on fruit ripening have focused on edible fruits. Ethylene has long been recognized as the hormone that accelerates the ripening of edible fruits. Exposure of such fruits to ethylene hastens the processes associated with ripening, and a dramatic increase in ethylene production accompanies the initiation of ripening. However, surveys of a wide range of fruits have shown that not all of them respond to ethylene.

All fruits that ripen in response to ethylene exhibit a characteristic respiratory rise called a climacteric before the ripening phase. Such fruits also show a spike of ethylene production immediately before the respiratory rise. Apples, bananas, avocados, and tomatoes are examples of **climacteric** fruits. In contrast, fruits such as citrus fruits and grapes do not exhibit the respiration and ethylene production rise and are called **nonclimacteric** fruits. In climacteric fruits, treatment with ethylene induces the fruit to produce additional ethylene, a response that can be described as **autocatalytic**.



Ethylene production and respiration during banana ripening (source: Taiz L., Zeiger E., 2010)

1.2.3 Ethylene inhibits hypocotyl elongation

At concentrations above 0.1 µL L-1, ethylene changes the growth pattern of seedlings by reducing the rate of elongation and increasing lateral expansion, leading to swelling of the hypocotyl or the epicotyl. In dicots, this swelling is part of the triple response, which, in Arabidopsis, consists of inhibition of hypocotyl elongation combined with hypocotyl swelling, inhibition of root elongation, and exaggeration of the curvature of the apical hook.

1.2.4 It regulates flowering, sex determination, and defense responses in some species

Although ethylene inhibits flowering in many species, it induces flowering in pineapple and its relatives, and it is used commercially for synchronization of pineapple fruit set. Flowering of other species, such as mango, is also initiated by ethylene. On plants that have separate male and female flowers (monoecious species), ethylene may change the sex of developing flowers. The promotion of female flower formation in cucumber is one example of this effect. Recently, a gene responsible for andromonoecy (plants carrying both male and bisexual flowers) in melons was identified as encoding an ACC synthase. A mutation that reduces the activity of this ACC synthase gene results in the formation of the bisexual flowers in these andromonoecious lines.

Pathogen infection and disease will occur only if the interactions between host and pathogen are genetically compatible. However, ethylene production generally increases in response to pathogen attack in both compatible (i.e., pathogenic) and no compatible (nonpathogenic) interactions. The discovery of ethylene-insensitive mutants has facilitated the assessment of the role of ethylene in the response to various pathogens. The involvement of ethylene in pathogenesis is complex and depends on the particular host-pathogen interaction. For example, blocking ethylene responsiveness does not affect the resistance responses of Arabidopsis to Pseudomonas bacteria or of tobacco to tobacco mosaic virus. In compatible interactions of these pathogens and hosts, however, elimination of ethylene responsiveness prevents the development of disease symptoms, even though the growth of the pathogen appears to be unaffected.

1.2.5 Ethylene is active in leaf and flower senescence and in leaf abscission

Senescence is a genetically programmed developmental process that affects all tissues of the plant. Research has provided several lines of physiological evidence that support roles for ethylene and cytokinins in the control of leaf senescence:

• Exogenous applications of ethylene or the precursor of ethylene accelerate leaf senescence, and treatment with exogenous cytokinins delays leaf senescence;

• Enhanced ethylene production is associated with chlorophyll loss and color fading, which are characteristic features of leaf and flower senescence; an inverse correlation has been found between cytokinin levels in leaves and the onset of senescence;

• Inhibitors of ethylene synthesis (e.g., AVG or Co2+) and action (e.g., Ag+ -STS- or CO2) retard leaf and flower senescence.

Taken together, these physiological studies suggest that senescence is regulated by the balance of ethylene and cytokinin. In addition, abscisic acid has been implicated in the control of leaf senescence.

Inhibition of flower senescence by inhibition of ethylene action (source: Taiz L., Zeiger E., 2010)

The shedding of leaves, fruits, flowers, and other plant organs is termed abscission. Abscission takes place in specific layers of cells called abscission layers, which become morphologically and biochemically differentiated during organ development. Weakening of the cell walls at the abscission layer depends on cell wall-degrading enzymes such as cellulase and polygalacturonase. Ethylene appears to be the primary regulator of the abscission process, with auxin acting as a suppressor of the ethylene effect. However, supra optimal auxin concentrations stimulate ethylene production, which has led to the use of auxin analogs as defoliants. Its action is based on its ability to increase ethylene biosynthesis, thereby stimulating leaf abscission.

1.2.6 Prevent leaf abscission

During the early phase of leaf maintenance, auxin from the leaf prevents abscission by maintaining the cells of the abscission zone in an ethylene-insensitive state. It has long been known that removal of the leaf blade (the site of auxin production) promotes petiole abscission. Application of exogenous auxin to petioles from which the leaf blade has been removed delays the abscission process. However, application of auxin to the proximal side of the abscission zone (i.e., the side closest to the stem) actually accelerates the abscission process.

1.2.7 Reduction in the concentration of free auxin

In the shedding induction phase, the amount of auxin from the leaf decreases and the ethylene level rises. Ethylene appears to decrease the activity of auxin both by reducing its synthesis and transport and by increasing its destruction. The reduction in the concentration of free auxin increases the response of specific target cells to ethylene. The shedding phase is characterized by the induction of genes encoding specific hydrolytic enzymes of cell wall polysaccharides and proteins.

The target cells, located in the abscission zone, synthesize cellulase and other polysaccharide-degrading enzymes, and secrete them into the cell wall. The activities of these enzymes lead to cell wall loosening, cell separation, and abscission.