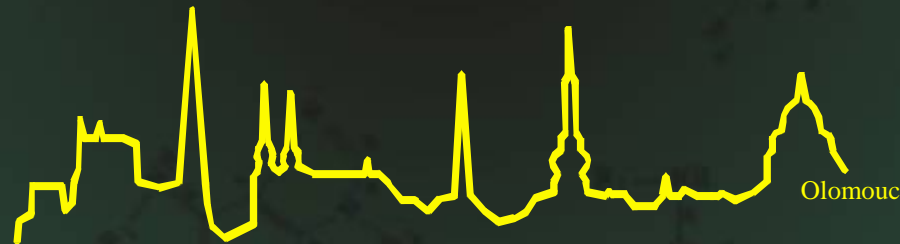


Laboratoř růstových regulátorů

Miroslav Strnad

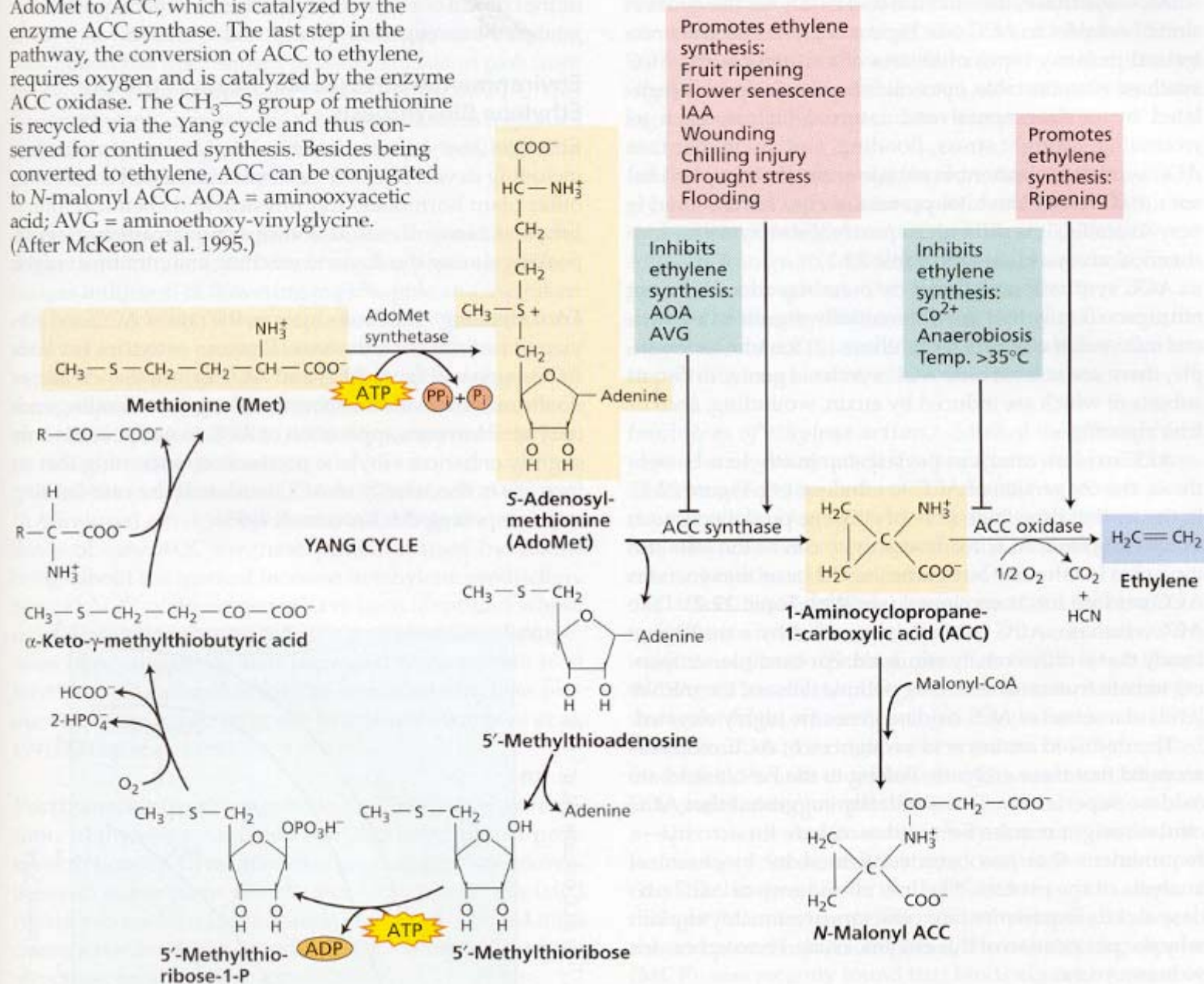
Ethylen
[kap. 22]



- Univerzita Palackého & Ústav experimentální botaniky AV ČR



FIGURE 22.1 Ethylene biosynthetic pathway and the Yang cycle. The amino acid methionine is the precursor of ethylene. The rate-limiting step in the pathway is the conversion of AdoMet to ACC, which is catalyzed by the enzyme ACC synthase. The last step in the pathway, the conversion of ACC to ethylene, requires oxygen and is catalyzed by the enzyme ACC oxidase. The $\text{CH}_3\text{-S}$ group of methionine is recycled via the Yang cycle and thus conserved for continued synthesis. Besides being converted to ethylene, ACC can be conjugated to *N*-malonyl ACC. AOA = aminooxyacetic acid; AVG = aminoethoxy-vinylglycine. (After McKeon et al. 1995.)



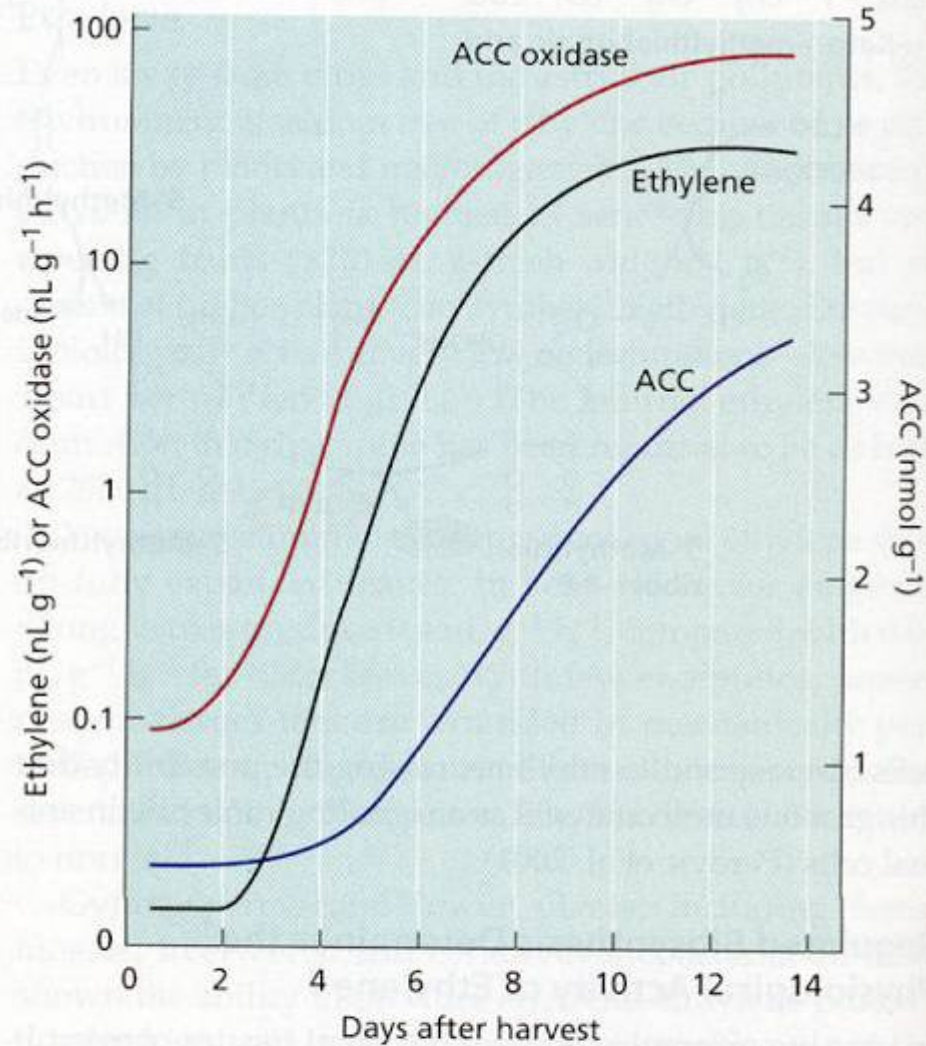
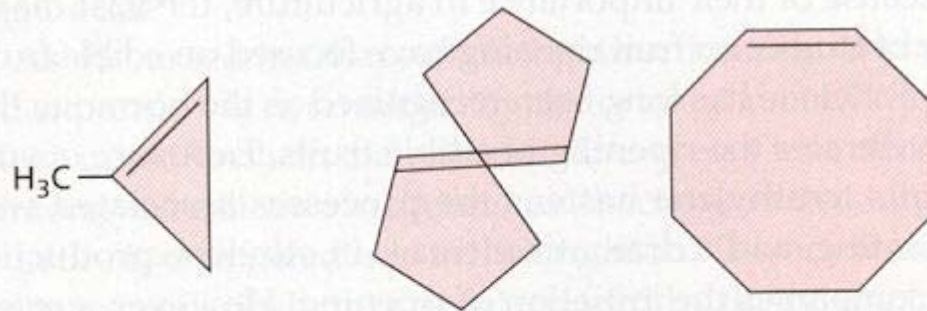


FIGURE 22.2 Changes in ethylene and ACC content and ACC oxidase activity during fruit ripening. Changes in the ACC oxidase activity and ethylene and ACC concentrations of Golden Delicious apples. The data are plotted as a function of days after harvest. Increases in ethylene and ACC concentrations and in ACC oxidase activity are closely correlated with ripening. (A from Hoffman and Yang 1980; B from Yang 1987.)



1-Methylcyclopropene (MCP) *trans*-Cyclooctene *cis*-Cyclooctene

FIGURE 22.3 Inhibitors that block ethylene binding to its receptor. Only the *trans* form of cyclooctene is active.

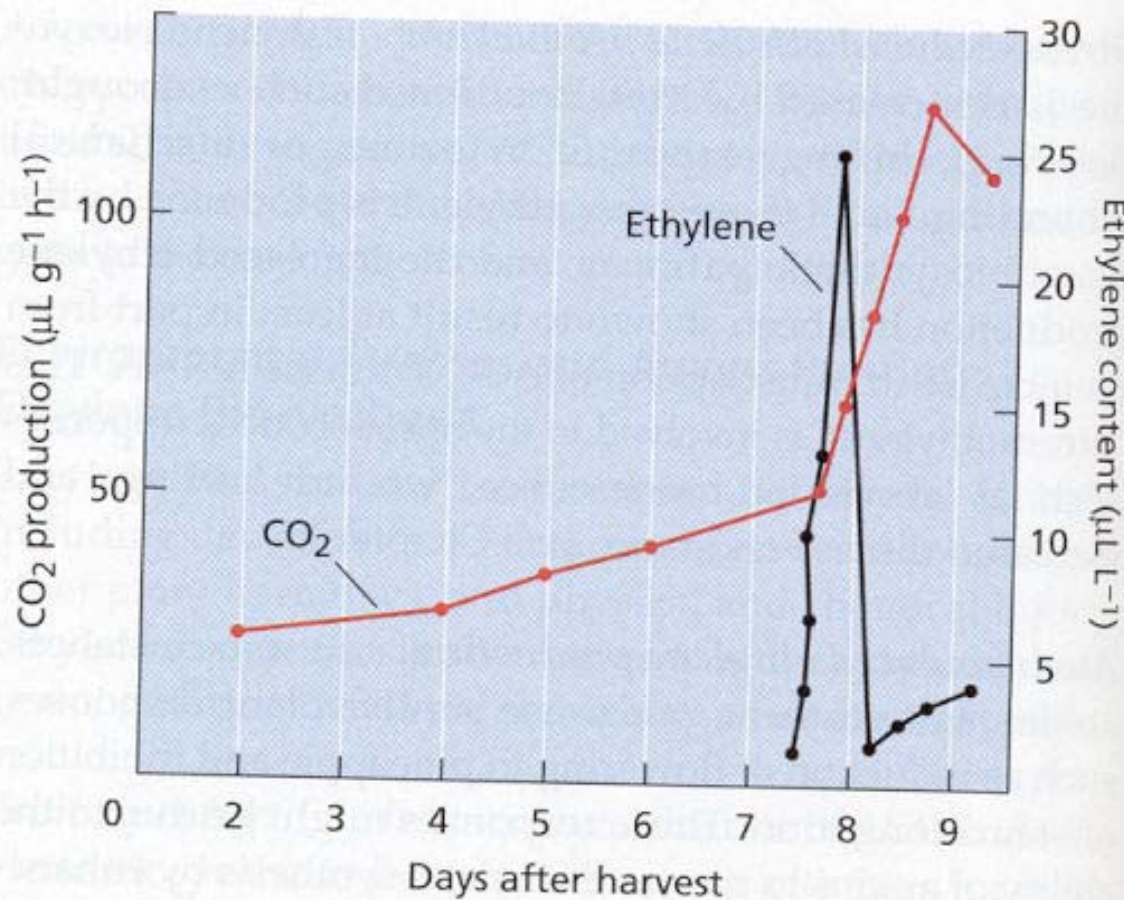


FIGURE 22.4 Ethylene production and respiration. In banana, ripening is characterized by a climacteric rise in respiration rate, as evidenced by the increased CO₂ production. A climacteric rise in ethylene production precedes the increase in CO₂ production, suggesting that ethylene is the hormone that triggers the ripening process. (From Burg and Burg 1965.)

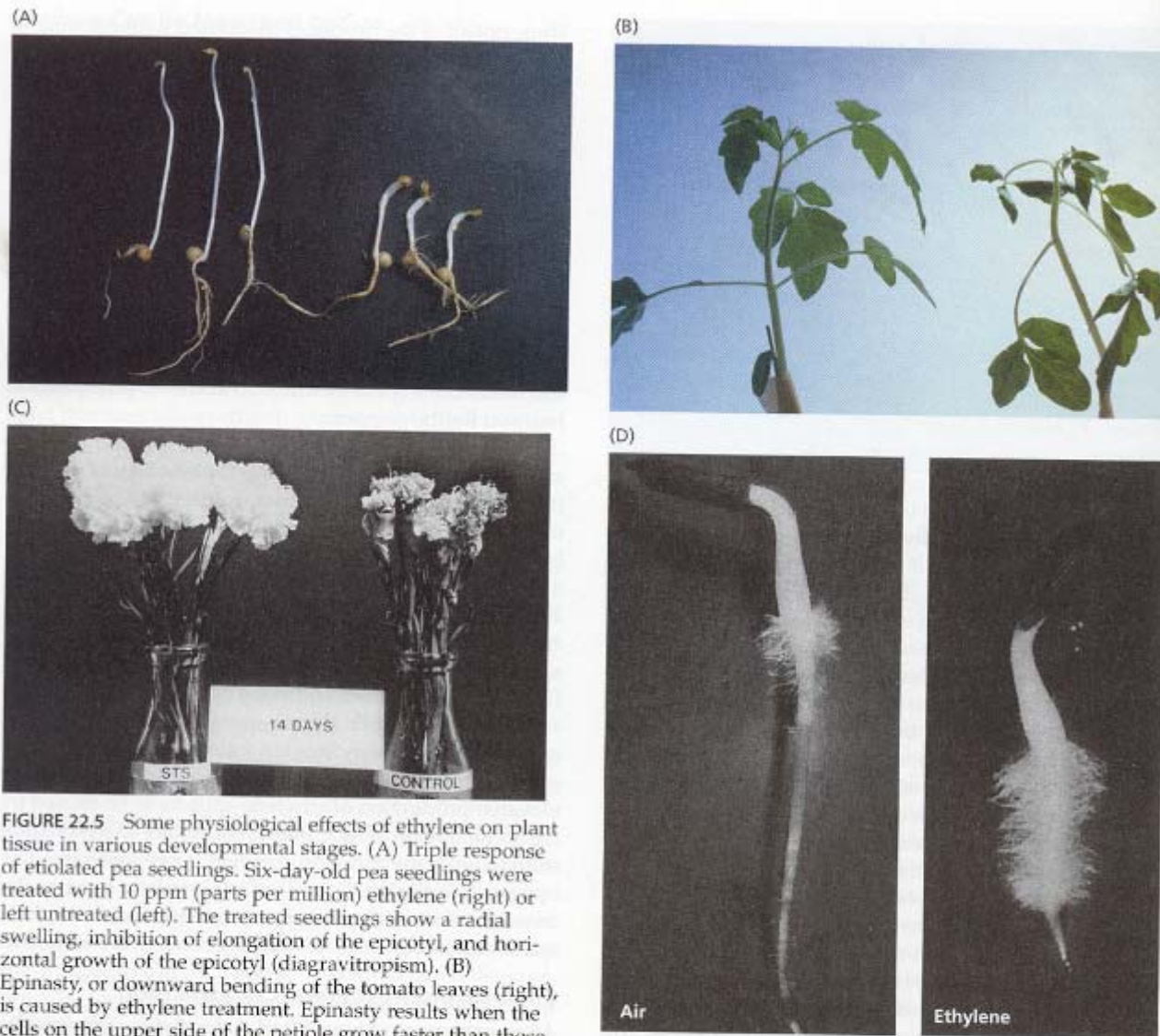


FIGURE 22.5 Some physiological effects of ethylene on plant tissue in various developmental stages. (A) Triple response of etiolated pea seedlings. Six-day-old pea seedlings were treated with 10 ppm (parts per million) ethylene (right) or left untreated (left). The treated seedlings show a radial swelling, inhibition of elongation of the epicotyl, and horizontal growth of the epicotyl (diagravitropism). (B) Epinasty, or downward bending of the tomato leaves (right), is caused by ethylene treatment. Epinasty results when the cells on the upper side of the petiole grow faster than those on the bottom. (C) Inhibition of flower senescence by inhibition of ethylene action. Carnation flowers were held in deionized water for 14 days with (left) or without (right) silver thiosulfate (STS), a potent inhibitor of ethylene action. Blocking of ethylene results in a marked inhibition of floral senescence. (D) Promotion of root hair formation by ethylene in lettuce seedlings. Two-day-old seedlings were treated with air (left) or 10 ppm ethylene (right) for 24 hours before the photo was taken. Note the profusion of root hairs on the ethylene-treated seedling. (A and B courtesy of S. Gepstein; C from Reid 1995, courtesy of M. Reid; D from Abeles et al. 1992, courtesy of F. Abeles.)

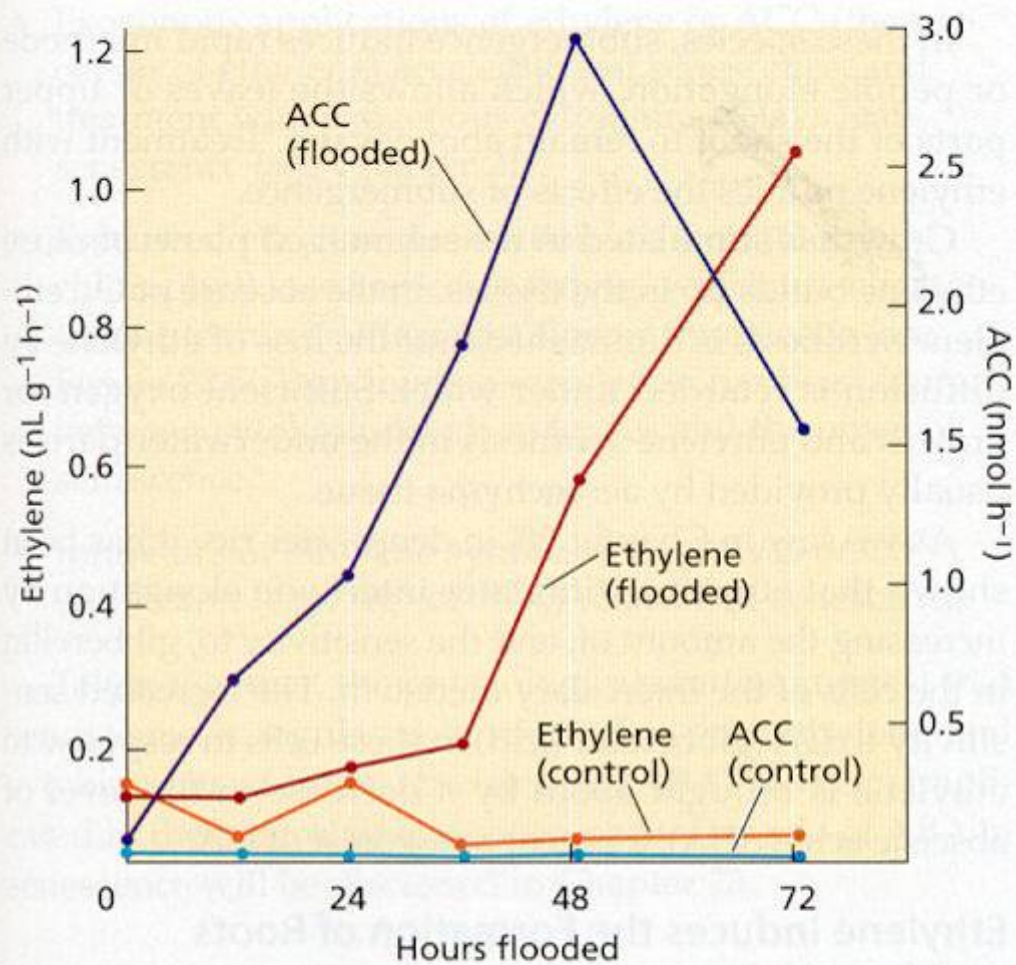


FIGURE 22.6 Changes in the amounts of ACC in the xylem sap and ethylene production in the petiole following flooding of tomato plants. ACC is synthesized in roots, but it is converted to ethylene very slowly under anaerobic conditions of flooding. ACC is transported via the xylem to the shoot, where it is converted to ethylene. The gaseous ethylene cannot be transported, so it usually affects the tissue near the site of its production. The ethylene precursor ACC is transportable and can produce ethylene far from the site of ACC synthesis. (From Bradford and Yang 1980.)

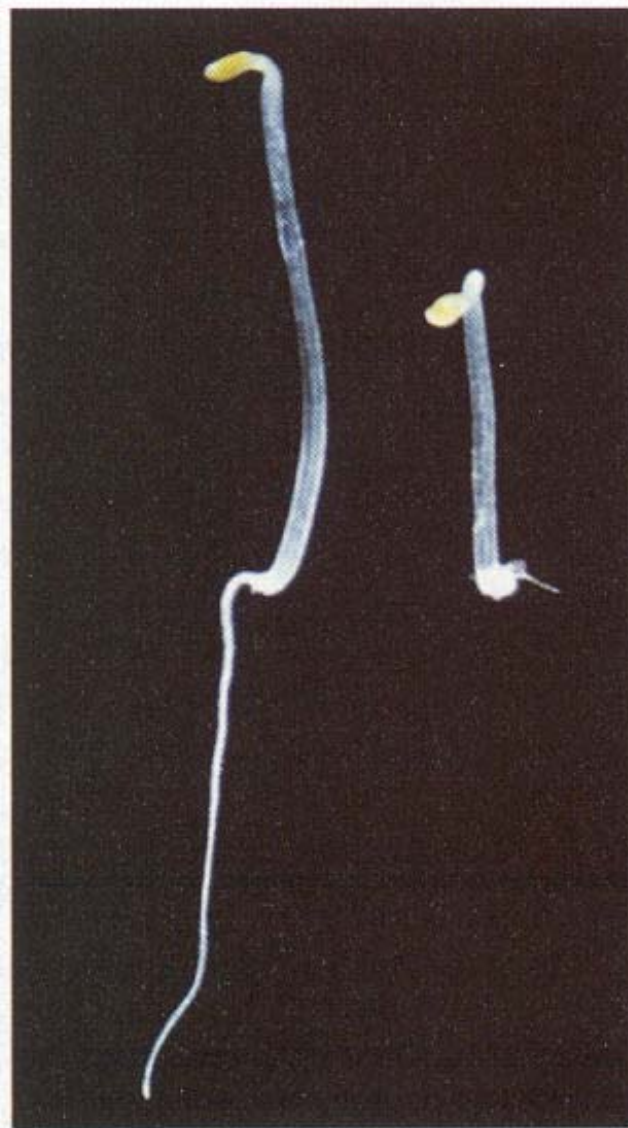
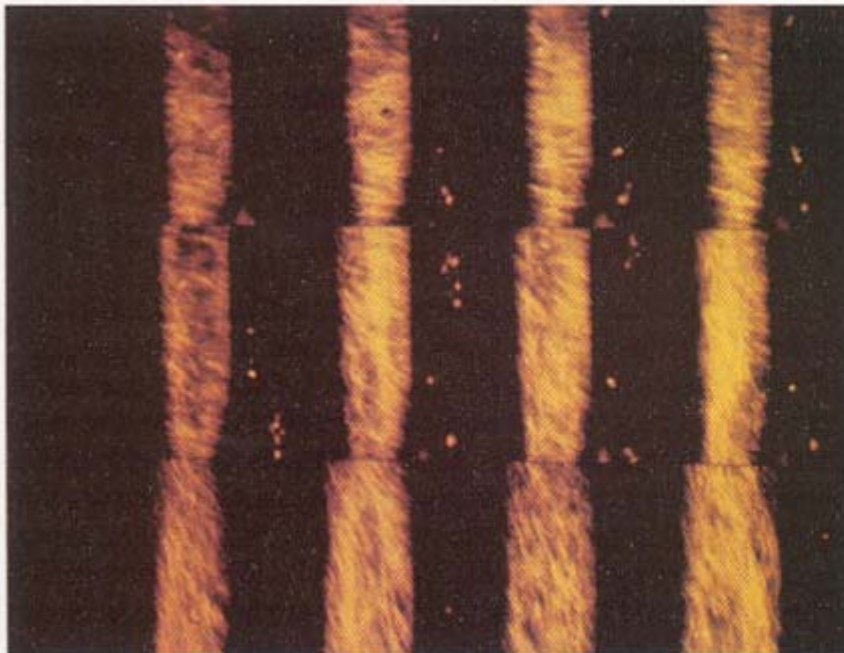


FIGURE 22.7 The triple response in *Arabidopsis*. Three-day-old etiolated seedlings grown in the presence (right) or absence (left) of 10 ppm ethylene. Note the shortened hypocotyl, reduced root elongation and exaggeration of the curvature of the apical hook that results from the presence of ethylene.



Transverse microtubules

FIGURE 22.8 Reorientation of microtubules from transverse to vertical in pea stem epidermis cells in response to wounding. A living epidermal cell was microinjected with rhodamine-conjugated tubulin, which incorporates into the plant microtubules. A time series of approximately 6-minute intervals shows the cortical microtubules undergoing reorientation from net transverse to oblique/longitudinal. The reorientation seems to involve the appearance of patches of new “discordant” microtubules in the new direction, concomitant with the disappearance of microtubules from the previous alignment. (From Yuan et al. 1994, photo courtesy of C. Lloyd.)

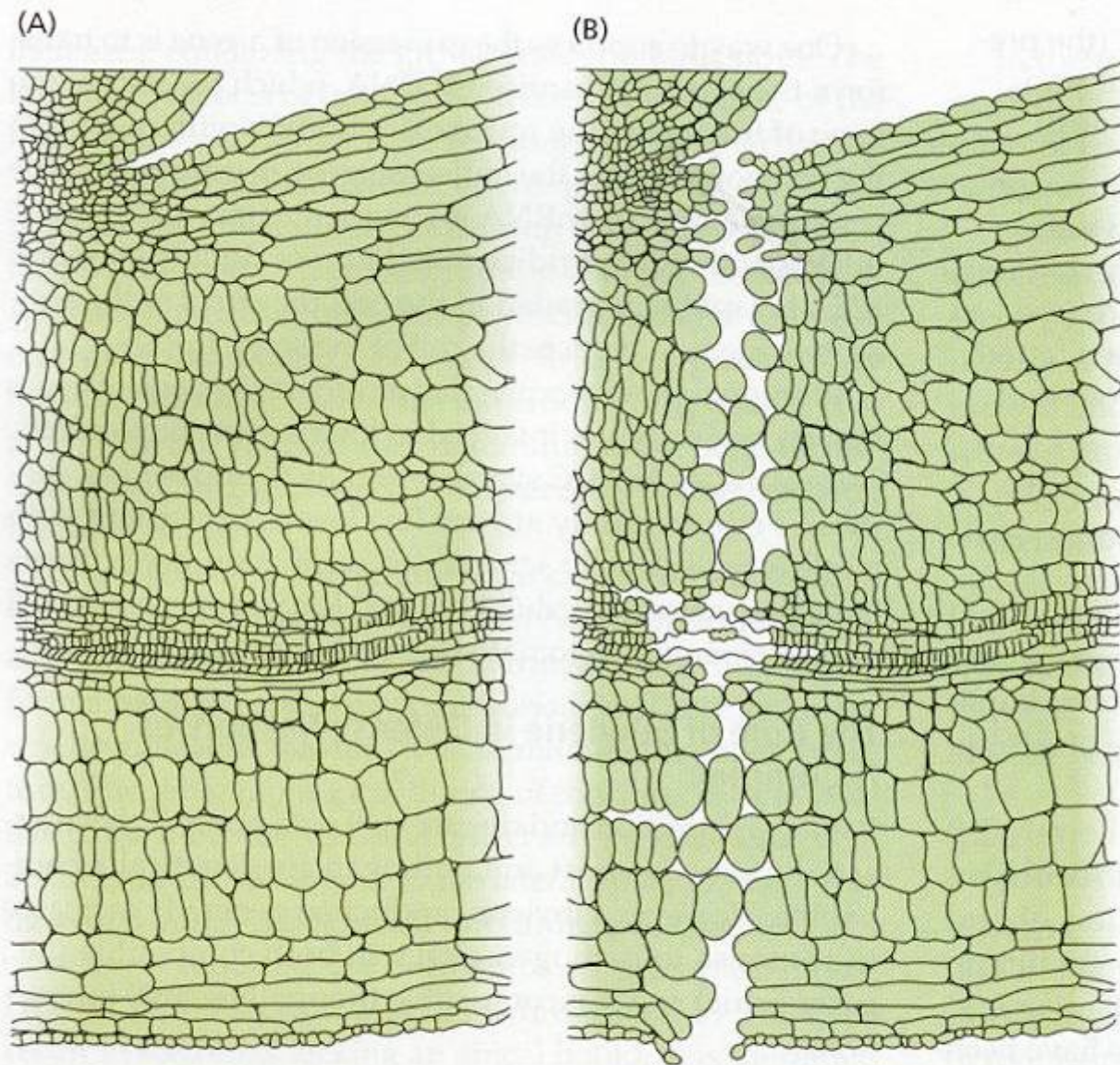
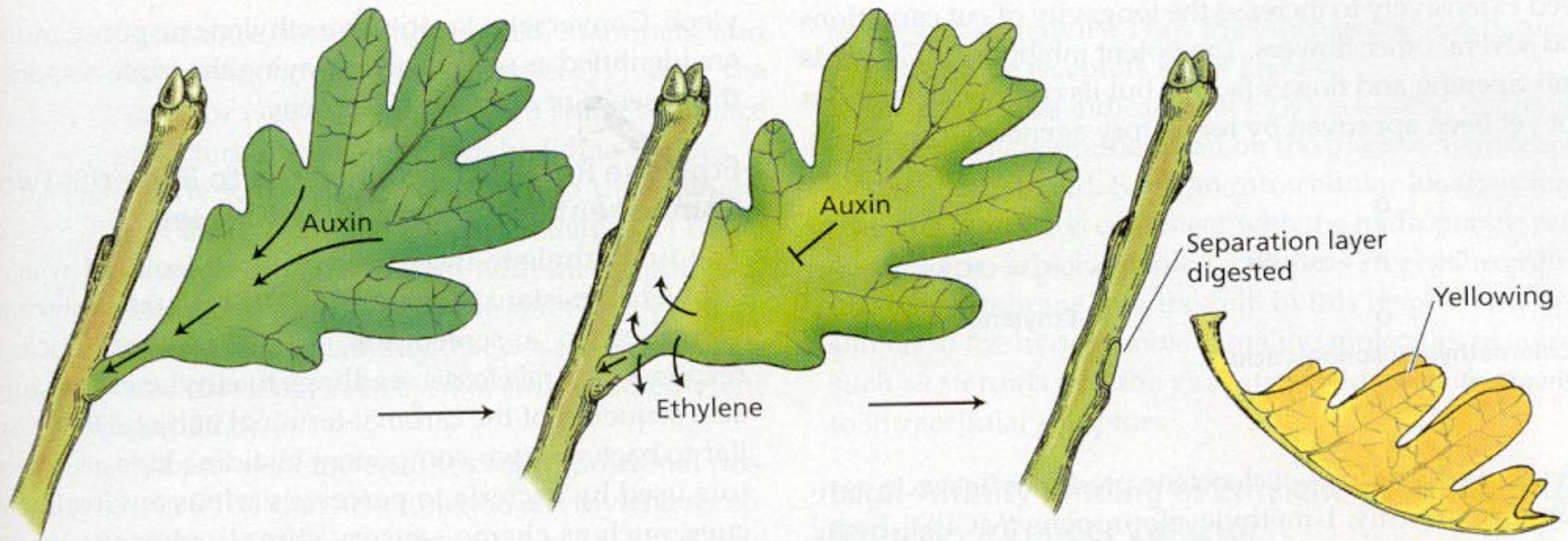


FIGURE 22.9 During the formation of the abscission layer, in this case that of jewelweed (*Impatiens*), two or three rows of cells in the abscission zone (A) undergo cell wall breakdown because of an increase in cell wall-hydrolyzing enzymes (B). The resulting protoplasts round up and increase in volume, pushing apart the xylem tracheary cells, and facilitating the separation of the leaf from the stem. (From Sexton et al. 1984.)

FIGURE 22.10 Effect of ethylene on abscission in birch (*Betula pendula*). The plant on the left is the wild type; the plant on the right was transformed with a mutated version of the *Arabidopsis* ethylene receptor, ETR1-1. The expression of this gene was under the transcriptional control of its own promoter. One of the characteristics of these mutant trees is that they do not drop their leaves when fumigated 3 days with 50 ppm of ethylene.





Leaf maintenance phase
 High auxin from leaf reduces ethylene sensitivity of abscission zone and prevents leaf shedding.

Shedding induction phase
 A reduction in auxin from the leaf increases ethylene production and ethylene sensitivity in the abscission zone, which triggers the shedding phase.

Shedding phase
 Synthesis of enzymes that hydrolyze the cell wall polysaccharides, resulting in cell separation and leaf abscission.

FIGURE 22.11 Schematic view of the roles of auxin and ethylene during leaf abscission. In the shedding induction phase, the level of auxin decreases, and the level of ethylene increases. These changes in the hormonal balance increase the sensitivity of the target cells to ethylene. (After Morgan 1984.)

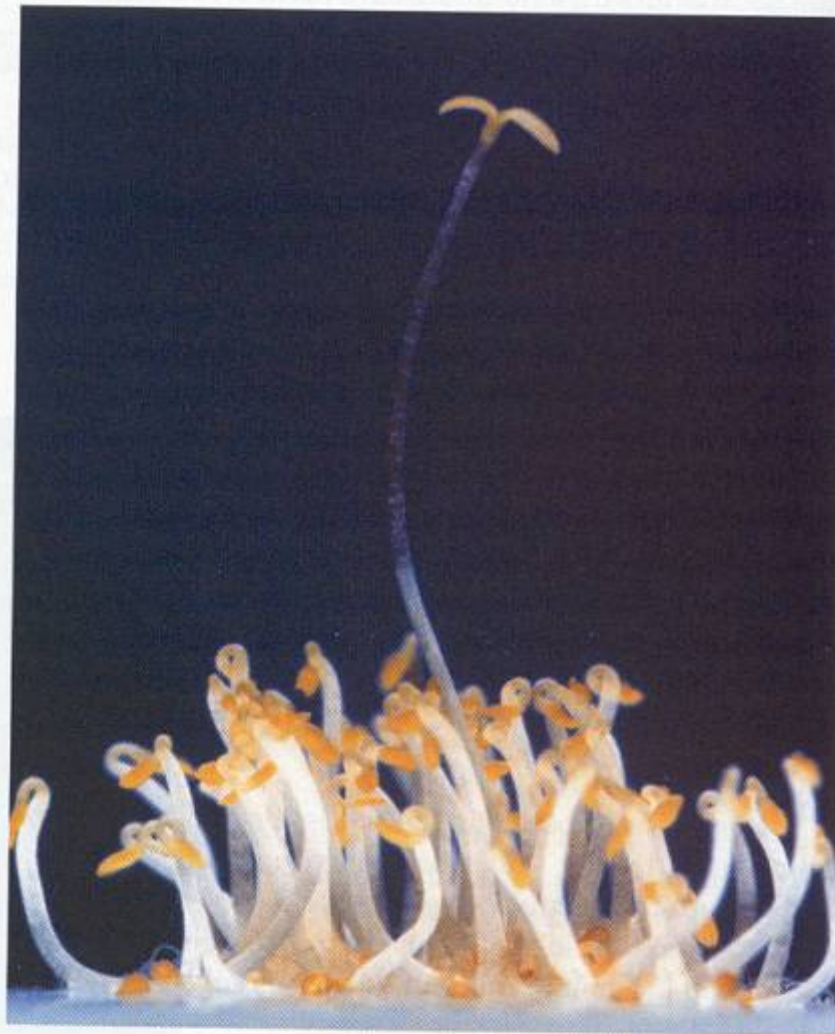


FIGURE 22.12 Screen for the *etr1* mutant of *Arabidopsis*. Seedlings were grown for 3 days in the dark in ethylene. Note that all but one of the seedlings are exhibiting the triple response: exaggeration in curvature of the apical hook, inhibition and radial swelling of the hypocotyl, and horizontal growth. The *etr1* mutant is completely insensitive to the hormone and grows like an untreated seedling. (Photograph by K. Stepnitz of the MSU/DOE Plant Research Laboratory.)

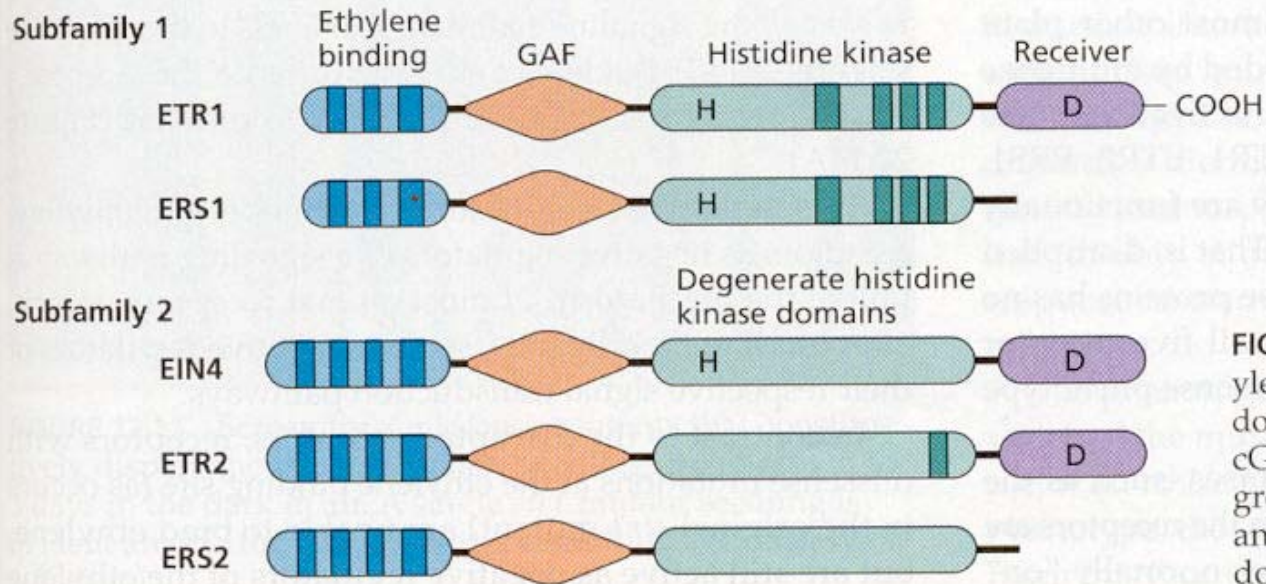


FIGURE 22.13 Schematic diagram of five ethylene receptor proteins and their functional domains. The GAF domain is a conserved cGMP-binding domain found in a diverse group of proteins. Note that EIN4, ETR2, and ERS2 have degenerate histidine kinase domains.

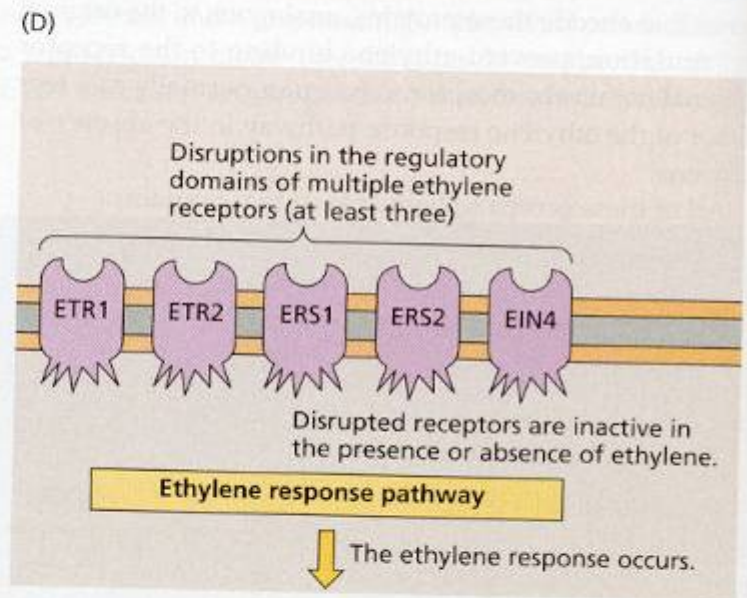
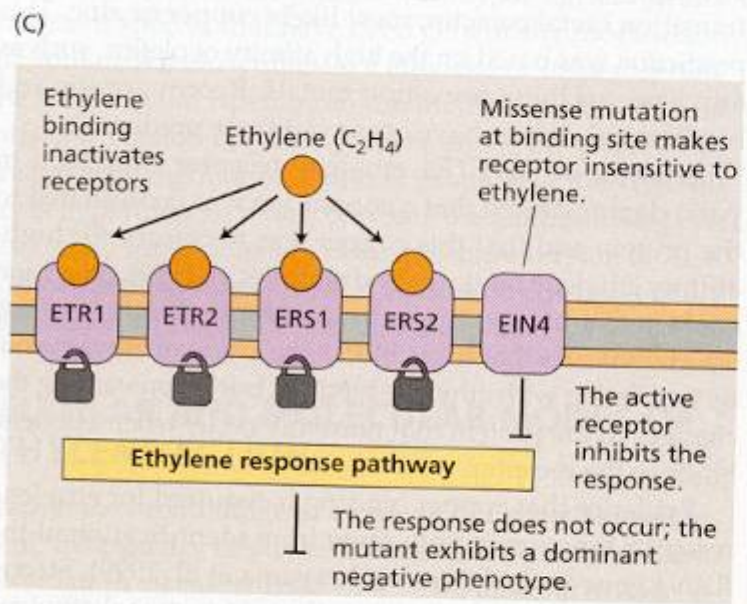
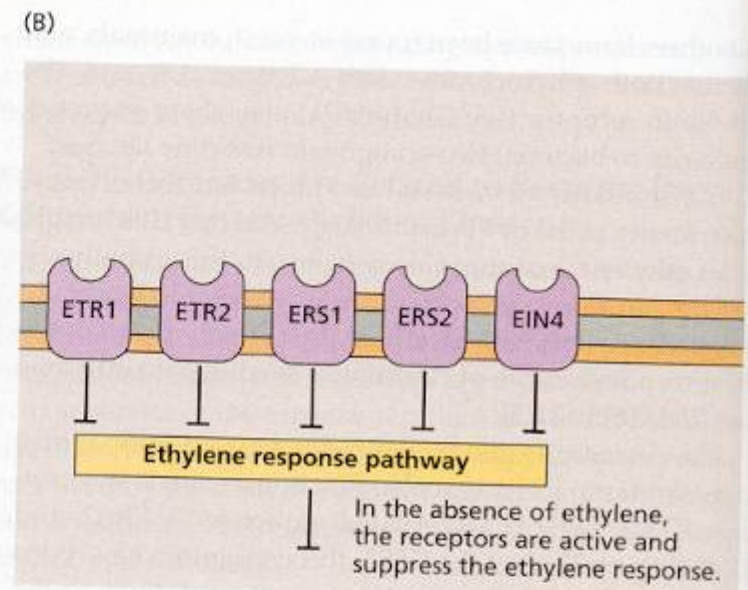
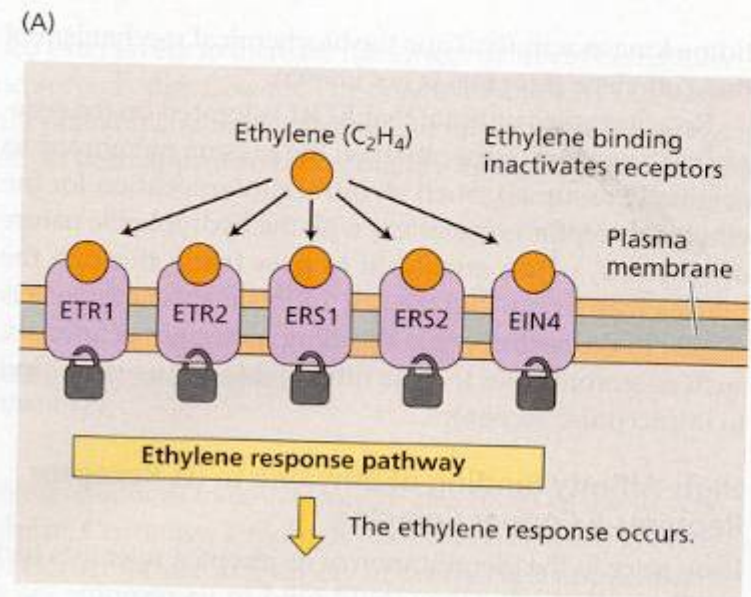


FIGURE 22.14 Model for ethylene receptor action based on the phenotype of receptor mutants. (A) In the wild type, ethylene binding inactivates the receptors, allowing the response to occur. (B) In the absence of ethylene the receptors act as negative regulators of the response pathway. (C)

A missense mutation that interferes with ethylene binding to its receptor, but leaves the regulatory site active, results in a dominant negative phenotype. (D) Disruption mutations in the regulatory sites result in a constitutive ethylene response.

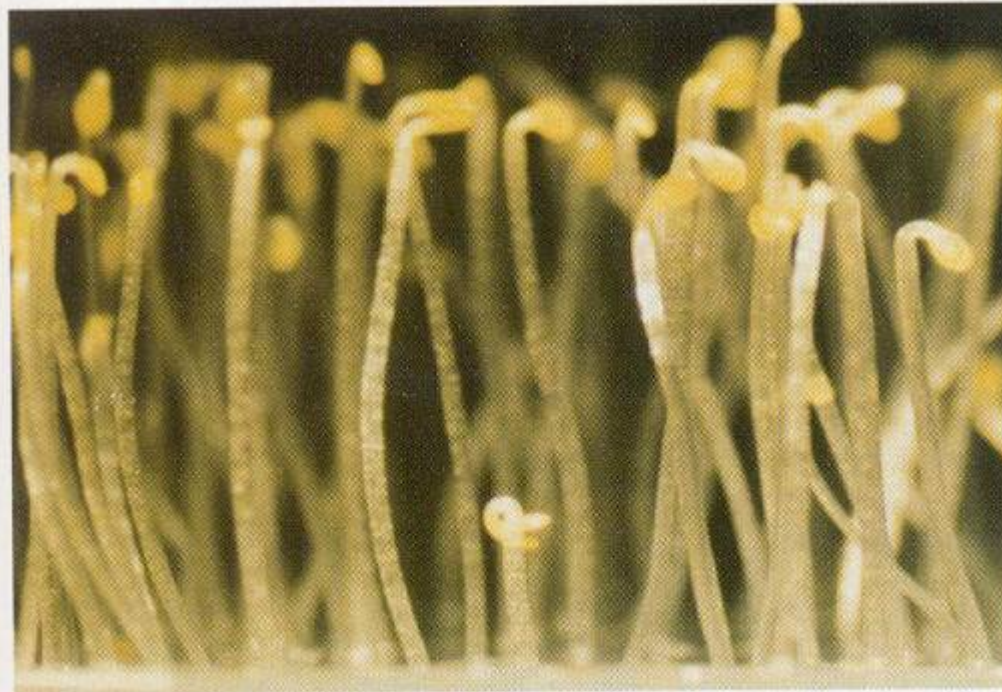


FIGURE 22.15 Screen for *Arabidopsis* mutants that constitutively display the triple response. Seedlings were grown for 3 days in the dark in air. A single *ctr1* mutant seedling is evident among the taller, wild-type seedlings. (Courtesy of J. Kieber.)

The RAN1 protein is required to assemble the copper cofactor into the ethylene receptor.

In the absence of ethylene, ETR1 and the other ethylene receptors activate the kinase activity of CTR1. This leads to a repression of the ethylene response pathway, possibly through a MAP kinase cascade. The binding of ethylene to the ETR1 dimer results in its inactivation, which causes CTR1 to become inactive.

The inactivation of CTR1 allows the transmembrane protein EIN2 to become active.

Activation of EIN2 turns on the EIN3 family of transcription factors, which in turn induce the expression of ERF1. The activation of this transcriptional cascade leads to large-scale changes in gene expression, which ultimately bring about alterations in cell functions.

FIGURE 22.16 Model of ethylene signaling in *Arabidopsis*. Ethylene binds to the ETR1 receptor, which is an integral membrane protein of the ER membrane. Multiple isoforms of ethylene receptors may be present in a cell; only ETR1 is shown for simplicity. The receptor is a dimer, held together by disulfide bonds. Ethylene binds within the trans-membrane domain, through a copper co-factor, which is assembled into the ethylene receptors through the RAN1 protein.

