Ethylene: The Gaseous Hormone(氣體荷爾蒙)

History:

1. 19th century: 路燈使用煤油會造成燈旁行道樹落葉.
2. In 1901, Dimitry Neljubov , 蘇俄研究生在實驗室發現碗豆暗處理會產生黃化苗呈現 三相反應(triple response).
3. In 1910, H. H. Cousins 首次提出植物組織會產生乙稀.
4. In 1934, R. Gane and others 證明乙烯為植物天然產物，少量便可顯著影響植物生長，因此分類為植物何爾蒙。

Structure, Biosynthesis, and Measurement of Ethylene

Structure: the simplest olefin (石蠟), Mr=28; C_2H_4

Biosynthesis: almost all tissues
leaf abscission 葉片離層, flower senescence花老化, fruit ripening, stress, disease

Measurement: gas chromatography (GC) 氣相層析儀

Ethylene biosynthetic pathway

(楊祥發院士)

FIGURE 22.2 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 CH_3—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.)

N-Mnlonyl ACC, a conjuated form of ACC), may play an important role in the control of ethylene biosynthesis.
ACC deaminase:

Ethylene biosynthesis is promoted by several factors

1. **Fruit ripening**: ACC synthase (ACS), ACC oxidase (ACO)↑ → ACC and ethylene↑
   ACC treats with unripe fruits only slightly enhances ethylene production. ACO is the rate-limiting step in ripening.

金冠蘋果

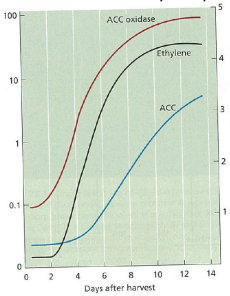

FIGURE 22.3 Changes in the ACC concentrations, ACC oxidase activity, and ethylene during ripening of Golden Delicious apples. The data are plotted as a function of days after harvest. Increases in ethylene and ACC concentrations and in ACC oxidase activity are closely correlated with ripening. (After Yang 1987.)

2. **Stress:** 乾旱、浸水、寒害、臭氧、和機械傷害等。

Ethylene biosynthesis is promoted by several factors

3. **Circadian:** ethylene high at midday and low at midnight.
   (生物時鐘) Circadian regulates a subset of ACSs, which is mediated by the TOC1/CCA1 clock in Arabidopsis.

4. **Auxin-induced:** Auxin promotes ethylene biosynthesis by enhancing ACS activity, **(細胞生長素的誘導)**

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Inhibitors of ethylene biosynthesis or signaling

Epinasty (上偏性,即葉柄上半部細胞生長較快.，使葉片下垂) caused by ethylene and high auxin conc.

Inhibitors of ethylene biosynthesis:
AVG: aminoethoxy-vinylglycine (for ACS)
AOA: aminooxyacetic acid (for ACS)

AIBA: α-aminoisobytyric acid (for ACO)
Co^{2+}: cobalt ions (for ACO)

Inhibitors of ethylene action (signaling):
Silver ions (Ag^+): silver nitrate ($AgNO_3$), silver thiosulfate [$Ag(S^2O^3)_2^{3-}$]
CO_2: at high conc (5 to 10%)
trans-cyclooctene: a strong competitive inhibitor
MCP: 1-Methylcyclopropene, a irreversible binding

Ethylene absorbent: Potassium permanganate ($KMnO_4$)

Epinasty phenotype

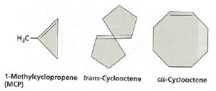

FIGURE 22.4 Two inhibitors that block ethylene binding to its receptor. The cis form of cyclooctene is not an effective inhibitor.

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Ethylene Signal Transduction Pathways

Triple response(乙烯三相反應): Etiolated seedlings show short hypocotyls (短而粗的下胚軸), short roots (短根)and exaggerated apical hoods (過度彎曲頂端罩)at the presence of ethylene.

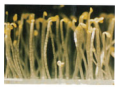
How to isolate ethylene signaling mutants? (如何篩選乙稀突變株)
Mutagenized Arabidopsis seeds were grown on agar plates with or without ethylene in the dark. (誘變劑，如EMS，讓種子突變)

FIGURE 22.5 The triple response in Arabidopsis. Three-day-old etiolated seedlings grown in the presence (right) or absence (left) of 10 ppm ethylene. Note the short-

1. Ethylene-resistant or ethylene-insensitive mutants.

FIGURE 22.6 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 exhibit 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. Steppitz of the MSU/DOE Plant Research Laboratory.)

2. Constitutive mutants



ctr1: constitutive triple response

Biosynthesis:
Met → → ACC → ethylene

Signal transduction:
Receptor → → → → Transcription factor (TF) (轉錄因子)

promoter

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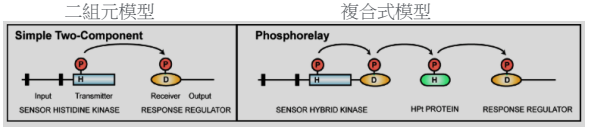
細菌的信息傳遞

Bacterial two-component system

二組元模型 複合式模型



P: PO_4^{3-}
H: Histidine組氨酸
D: aspartate residue天冬氨酸

HPt: histidine phosphotransfer

Biosynthesis:
Met → → ACC → ethylene

Signal transduction:
Receptor → → → → Transcription factor (TF)

promoter

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Ethylene Signal Transduction Pathways

Ethylene receptors (乙烯接受體)are related to bacterial two-component system histidine kinase(雙組分系統組氨酸激酶 (HK）

The first ethylene-insensitive mutant isolated was *etr1* (*ethylene-response1*). The C-terminal half of *etr1* is similar to bacterial two-component histidine kinase.

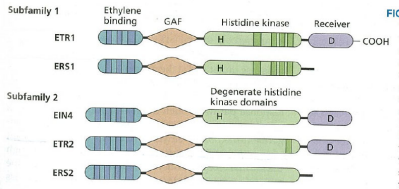

FIGURE 22.7 Schematic diagram of five ethylene receptor proteins and their functional domains. The GAF domain is a conserved cGMP-binding domain, found in a diverse group of proteins, that generally acts as small molecule–binding regulatory domains. H and D are histidine and aspartate residues that participate in phosphorylation. Note that EIN4, ETR2, and ERS2 have degenerate histidine kinase domains, meaning that they are missing critical, highly conserved amino acids that are required for histidine kinase catalytic activity.

ERS: ETHYLENE RESPONSE SENSOR 1
EIN: ETHYLENE INSENSITIVE

All of these five receptors share at least two domains:
1. Membrane-spanning domain at N-terminus.
2. Histidine kinase catalytic domains.

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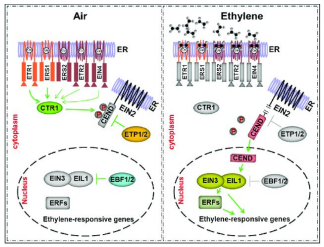
Ethylene Signal Transduction Pathways

Receptors (ETR1—etc) → CTR1 ⊣ EIN2 → EIN3 –etc → ethylene response

CTR1: constitutive triple response 1

EIN2 encodes a transmembrane protein **EIN2: ethylene insensitive**

EIN3: a transcription factor



January 2015Molecular Plant 8(4)
DOI: 10.1016/j.molp.2015.01.003

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Developmental and Physiological Effects of Ethylene

Ethylene promotes the ripening of some fruits

乙烯促進一些果實的成熟

Fruits that respond to ethylene exhibit a climacteric （更年性果實）

更年性果實在成熟前會產生大量的呼吸作用並拌隨著大量乙烯產生, such as apples, bananas, avocados, and tomatoes

Nonclimacteric fruits(非更年性果實): grapes

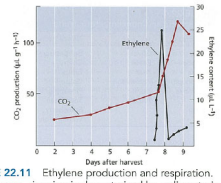


FIGURE 22.11 Ethylene production and respiration. In banana, ripening is characterized by a climacteric rise in respiration rate, as evidenced by the increased CO_2 production. A climacteric rise in ethylene production precedes the increase in CO_2 production, suggesting that ethylene is the hormone that triggers the ripening process. (After Burg and Burg 1965.)

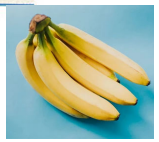
Developmental and Physiological Effects of Ethylene

TABLE 22.1
Climacteric and nonclimacteric fruits

Climacteric 更年性		Nonclimacteric非更年性
Apple	Olive 橄欖	Bell pepper
Avocado	Peach	Cherry
Banana	Pear	Citrus
Cantaloupe 哈密瓜	Persimmon 柿子	Grape
Cherimoya 釋迦	Plum	Pineapple
Fig	Tomato	Snap bean 四季豆
Mango		Strawberry
		Watermelon

更年性和非更年性果實的採收期?

Practical application:實際應用
1. 外加乙烯可以促進一致性果實成熟。
2. 乙烯抑製劑延緩果實成熟。
3. 蕃茄轉殖株表現 ACS or ACO基因的反義股可以抑制果實成熟;外加乙烯則可以恢復果實成熟。(基因靜默, gene silencing)



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Developmental and Physiological Effects of Ethylene

The receptors of *never-ripe* mutants of tomato fail to bind ethylene

60 DPA (days after anthesis, 授粉後)

A

LA2453 LA2455

B

正常組 AC

Gr

Nr-2

Nr

42 DPA

60 DPA

Gr: *green-ripe* mutant
Nr: *never-ripe* mutant

Barry et al., 2005; Plant Physiol 138: 167-75

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Developmental and Physiological Effects of Ethylene

Ethylene breaks seed and bud dormancy in some species

1. 對一些穀類，乙烯可以打破休眠促進種子發芽。
2. 乙烯也可以打破芽休眠; 如乙烯處理可以打破塊根類的芽休眠，如馬鈴薯。

Ethylene induces the formation of roots and root hairs

1. 乙烯可以誘導葉子,莖或根產生根毛

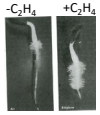

FIGURE 22.16 Promotion of root hair formation by ethylene in lettuce seedlings. Two-day-old seedlings were treated with air (left) or 10 ppm ethylene (right) for 24 hours before the photo was taken. Note the profusion of root hairs on the ethylene-treated seedling. (From Abeles et al. 1992, courtesy of F. Abeles.)

萬苣幼苗

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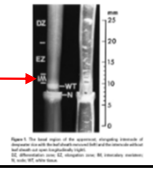
Developmental and Physiological Effects of Ethylene

Ethylene promotes the elongation growth of submerged aquatic species(水生種類)

1. Although usually thought of as an inhibitor of stem elongation, ethylene is able to promote stem and petiole elongation in various submerged or partially submerged aquatic plants.(一般乙烯抑制莖的延長，但對一些水生或部分水生植物，乙烯會促進莖或葉柄的延長。)
2. Deep-water rice:深水水稻(見於低窪區)
   Submergence induces rapid internode elongation, which allow the leaves or upper parts of the shoot to remain above water.
3. Ethylene stimulates internode elongation in deep-water rice by increasing the amount of, and the sensitivity to, GA in the cells of the intercalary meristem.
4. Ethylene-mediated expression of SNORKEL1 and SNORKEL2 was identified to trigger the dramatic internode elongation. (snorkel:水下呼吸管)

Deep-water rice

居間分生組织



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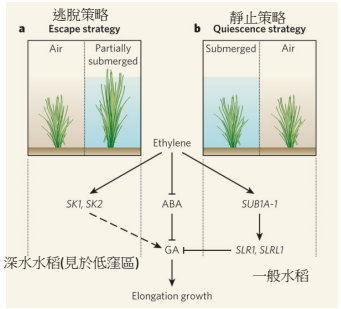

Ethylene and flooding-tolerance strategies in rice

From the following article:
Plant biology: Genetics of high-rise rice
Laurentius A. C. J. Voesenek & Julia Bailey-Serres
Nature **460**, 959-960(20 August 2009)
doi:10.1038/460959a

一般陸生水稻使用靜止策略，減少能量耗盡。

深水水稻使用逃脫策略，讓葉片一直保持在水面上，可以行光合作用。

How rice with the SNORKEL gene survives a flood

https://vimeo.com/6208007

Movies illustrating the deepwater response to rising water levels. Deepwater rice has evolved and adapted to flooding by acquiring the ability to significantly elongate its stem.

Credit: M. Ashikari

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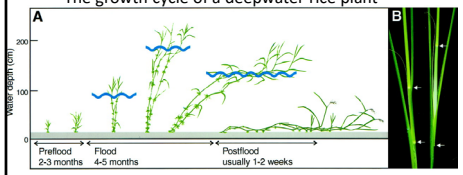
Deepwater Rice: A Model Plant to Study Stem Elongation

Hans Kende, Esther van der Knaap, Hyung-Taeg Cho
Published December 1998. DOI: https://doi.org/10.1104/pp.118.4.1105

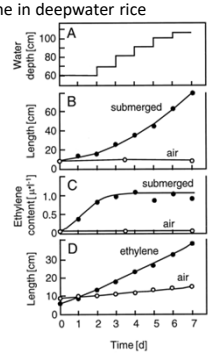
Plant Physiol. (1998) 118: 1105–1110

The growth cycle of a deepwater rice plant



Submergence
↓
Altered internal gas atmosphere
($\downarrow O_2$, $\uparrow CO_2$, $\uparrow C_2H_4$)
↓
C_2H_4
↓
Reduced abscisic acid levels
↓
Increased responsiveness to gibberellin
↓
Internodal elongation

Promotion of growth by submergence and ethylene in deepwater rice



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Developmental and Physiological Effects of Ethylene

Ethylene regulates flowering and sex determination in some species
(乙烯調節一些植物的開花和花的性別)

Promote flowering: pineapple and mango
加電土或電石水於生長點)

Sex determination:花的性別
雌雄同株
On plants that have separate male and female flowers (monoecious species), ethylene may change the sex of developing flowers. e.g., cucumber(黃瓜).

Ethylene mediates some defense responses

乙烯和植物荷爾蒙jasmonic acid (茉莉酸)合作活化植物防疫基因的表現，達到抗病菌的攻擊。

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Developmental and Physiological Effects of Ethylene

Ethylene acts on the abscission layer

Abscission(離層): The shedding of leaves, fruits, flowers, and other plant organs.

Abscission layer: Abscission takes place in specific layers of cells.

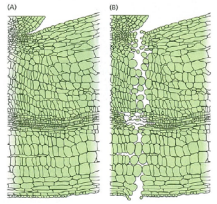

FIGURE 22.18 Formation of the abscission layer of jewelweed (*Impatiens*). (A) During leaf abscission, two or three rows of cells in the abscission zone undergo cell wall breakdown because of an increase in cell wall–hydrolyzing enzymes. (B) The protoplasts, released from the restraint of their cell walls, expand and push apart the xylem tracheary cells, facilitating the separation of the leaf from the stem. (After Sexton et al. 1984.)

birch tree (樺樹)

Transgenic plant expressing Arabidopsis *etr1* mutant gene

FIGURE 22.19 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. 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 for 3 days with 50 ppm ethylene. (From Vahala et al. 2003.)

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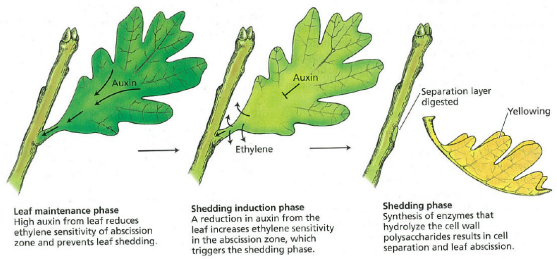
Developmental and Physiological Effects of Ethylene

Schematic view of the roles of auxin and ethylene during leaf abscission

乙烯 (ethylene)和細胞生長素(auxin)對落葉的影響。



Removal of the leaf blade promotes petiole abscission.

移除葉片會促進葉柄離層的產生。

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