

Plant hormone
and
growth and development

Definition

Plant hormones are small organic compounds that influence physiological responses to environmental stimuli at very low concentrations (generally less than 10^{-7} M). Hormones are not directly involved in metabolic or developmental processes but they act at low concentrations to modify those processes.

What can they do?

Hormones regulate or influence a range of cellular and physiological processes, including

- Cell Division
- Cell Enlargement
- Cell Differentiation
- Flowering
- Fruit Ripening
- Movement (tropisms)

Not all researchers agree that the term "hormone" should be applied to plants.

Plants do not have a circulatory system and therefore hormone action in plants is fundamentally different from hormone action in animals. Many plant biologists use the term "plant growth regulator" instead of "hormone" to indicate this fact. The table below summarizes some of the differences between plant and animal hormones.

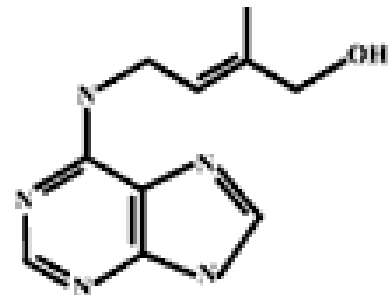
Plant Hormones	Animal Hormones
<ul style="list-style-type: none">1. Small molecules only2. Produced throughout the plant3. Mainly local targets (nearby cells and tissues)4. Effects vary depending on interaction with other hormones5. "Decentralized" regulation	<ul style="list-style-type: none">1. Peptides/proteins and/or small molecules2. Produced in specialized "glands"3. Distant targets ("action at a distance")4. Specific effects5. Regulation by central nervous system



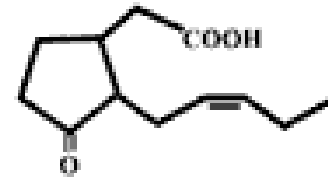
Ethylene



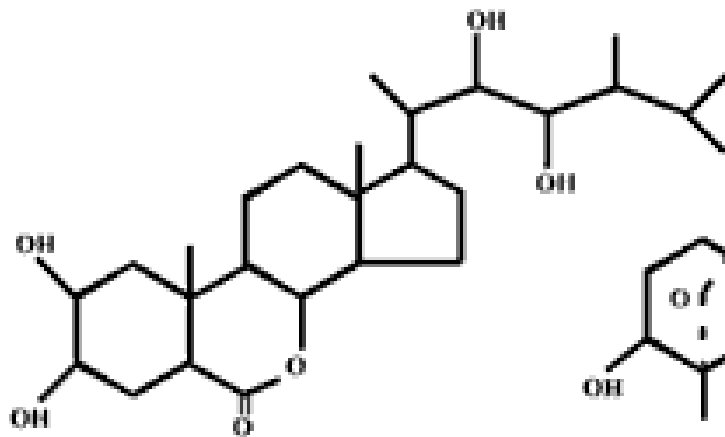
Auxin



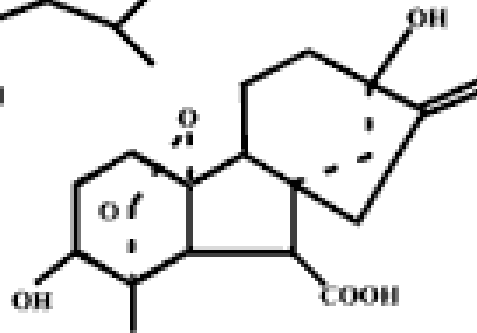
Cytokinins



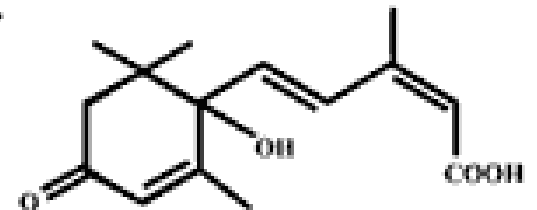
Jasmonic Acid



Brassinosteroids



Gibberellins



Abscisic Acid

Apical dominance

Vascular tissue induction

Tropisms

Stem elongation

Leaf expansion

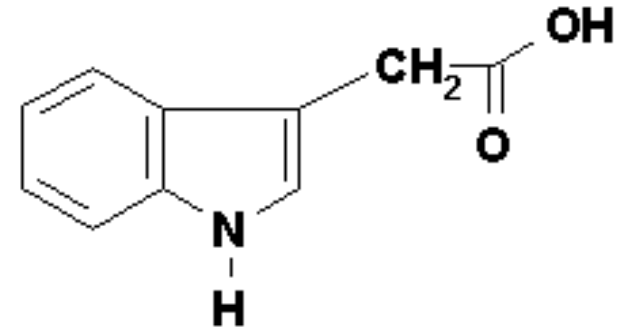
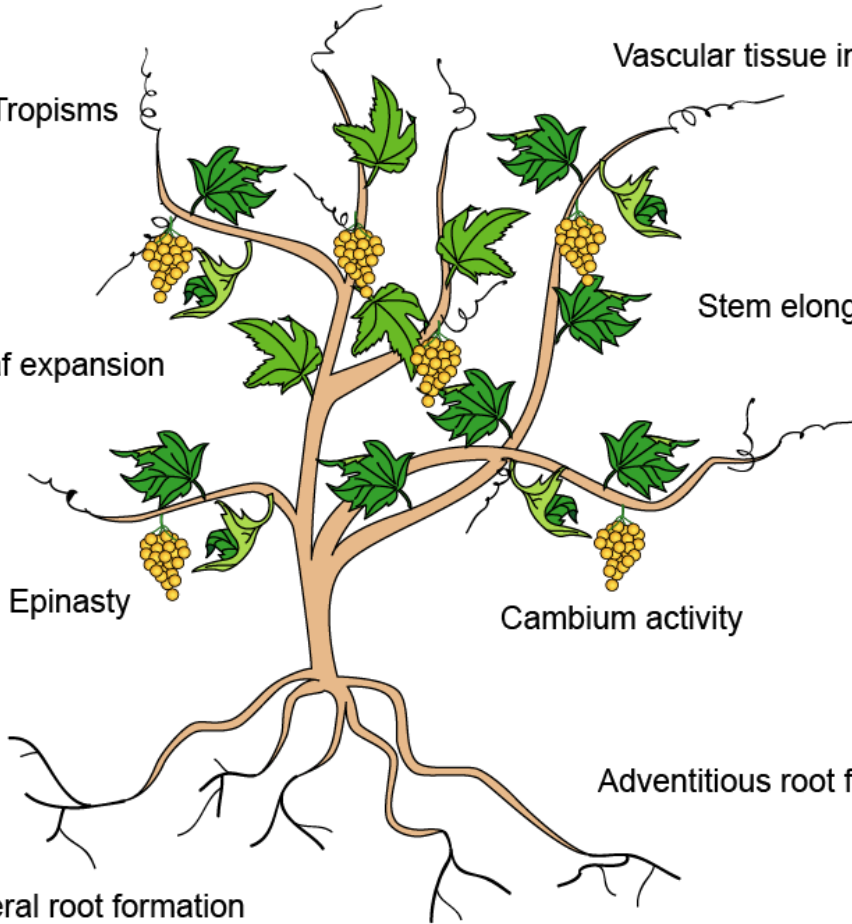
Epinasty

Cambium activity

Adventitious root formation

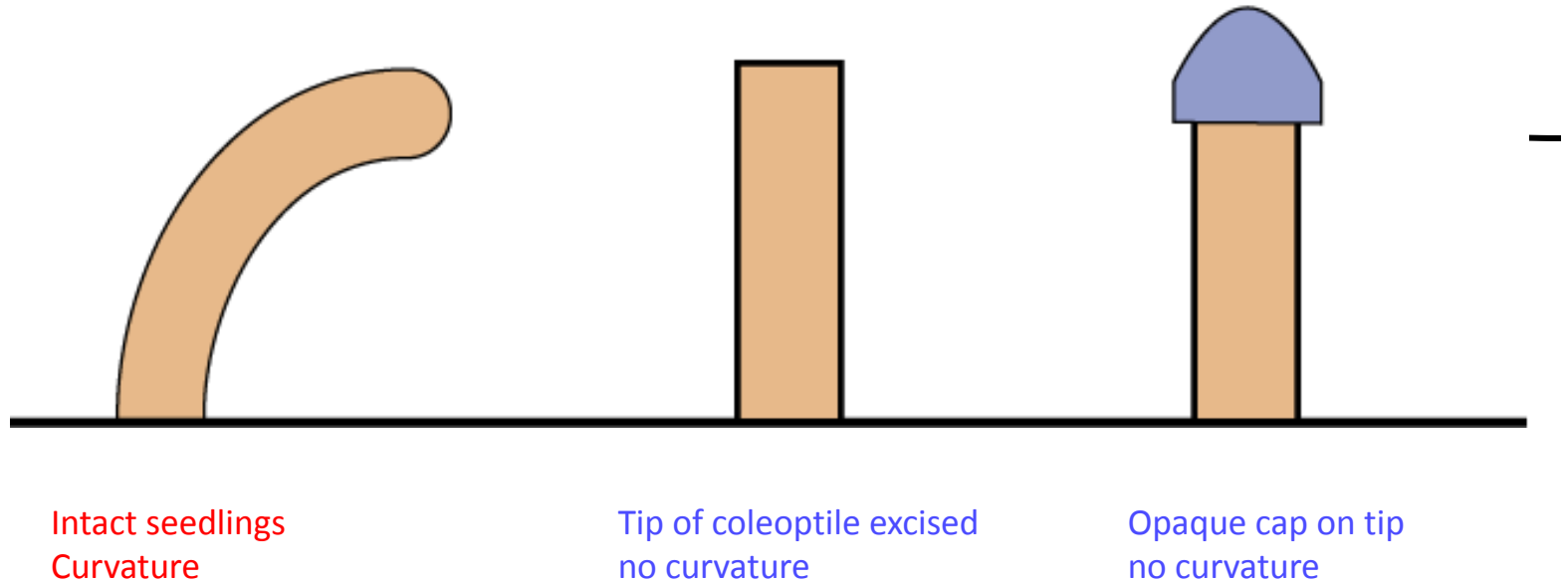
Lateral root formation

Cell division

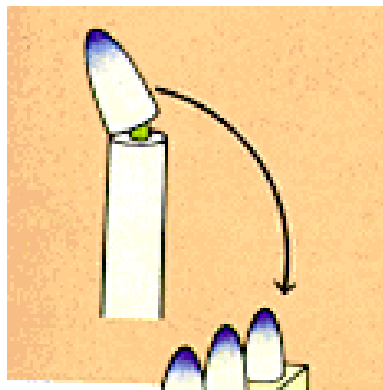


Indole-3-acetic acid (IAA)

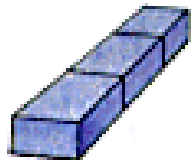
Discovery of auxin



From experiments on coleoptile phototropism, Darwin concluded in 1880 that some sort of signal is produced in the tip, travels to the growth zone and causes the shaded side to grow faster than the illuminated side.



(a)



(b)

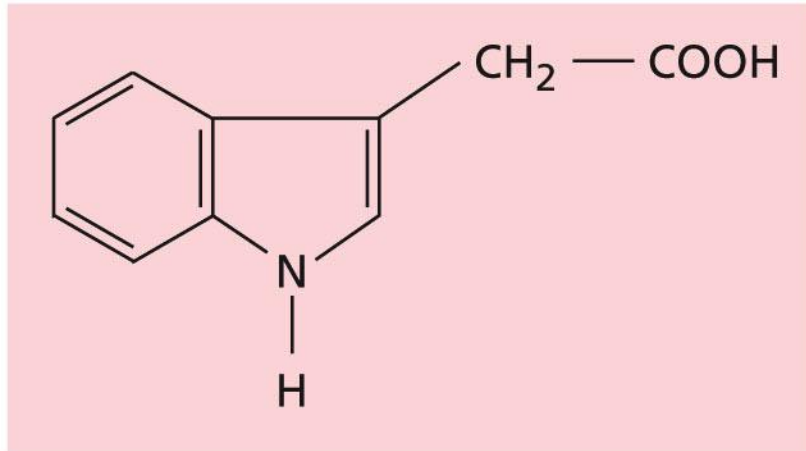


(c)

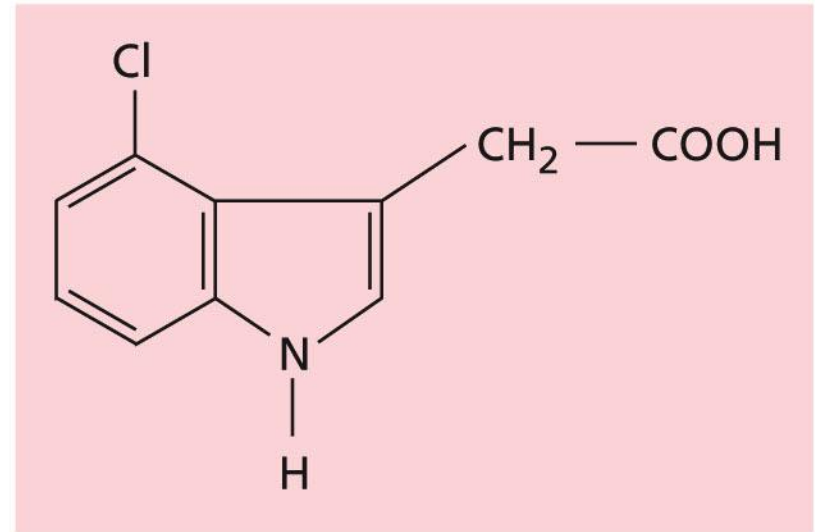
In 1926, Went showed that the active growth substance can diffuse into gelatin block and can cause the bending of coleoptile in absence of a unilateral light source

Because the substance promoted the elongation of the coleoptile sections it was eventually named **auxin** from the Greek *auxein*, meaning “to increase” or “to grow”

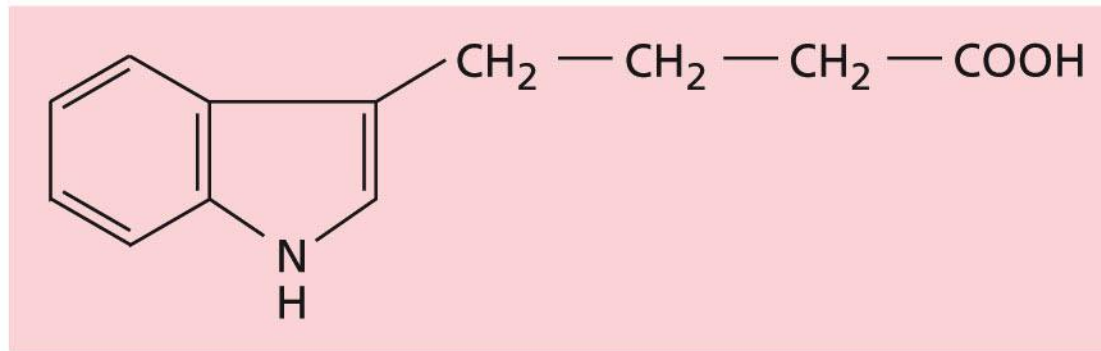
In mid 1930's Kogl and Haagen-Smit isolated several active substances from human urine and the most potent one Indole-3-acetic acid turned out to be the one synthesized and used by the plants



**Indole-3-acetic acid
(IAA)**

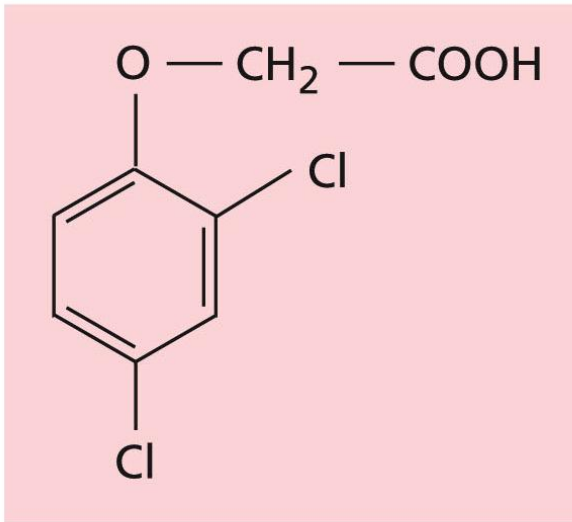


**4-Chloroindole-3-acetic acid
(4-Cl-IAA)**

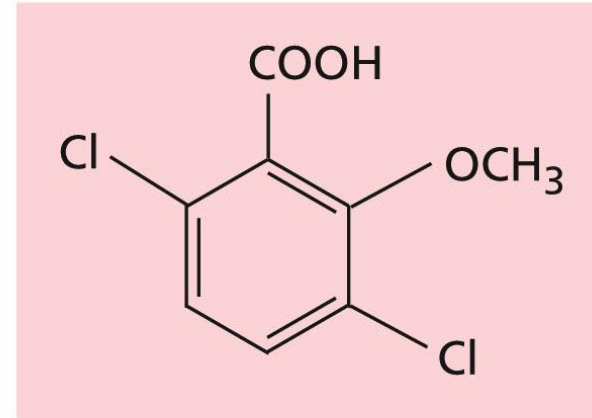


**Indole-3-butyric acid
(IBA)**

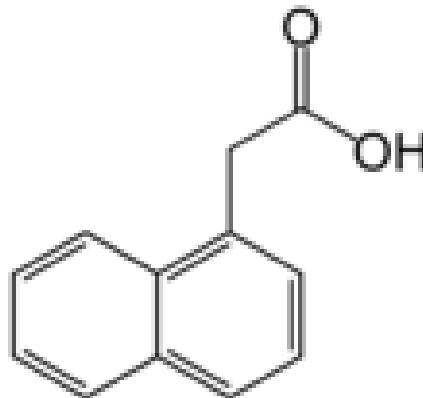
Synthetic auxin



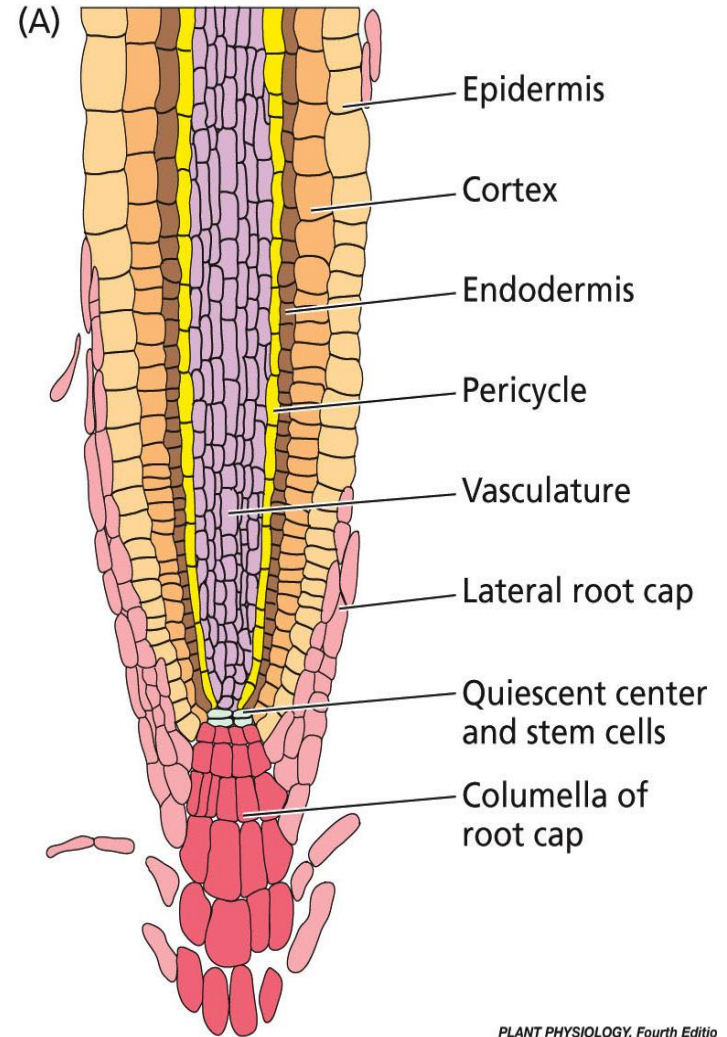
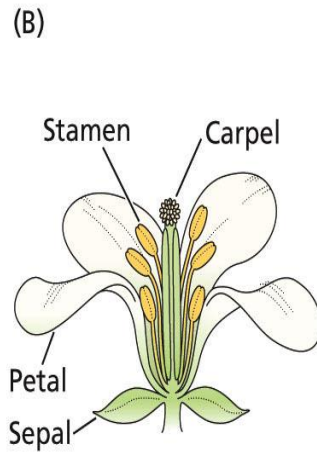
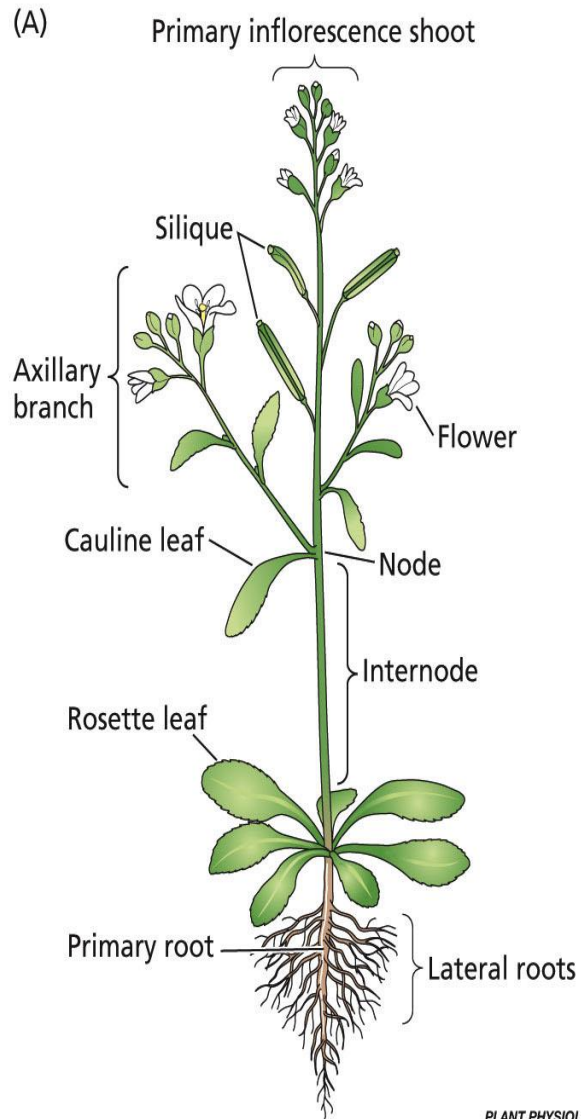
2,4-Dichlorophenoxyacetic acid (2,4-D)



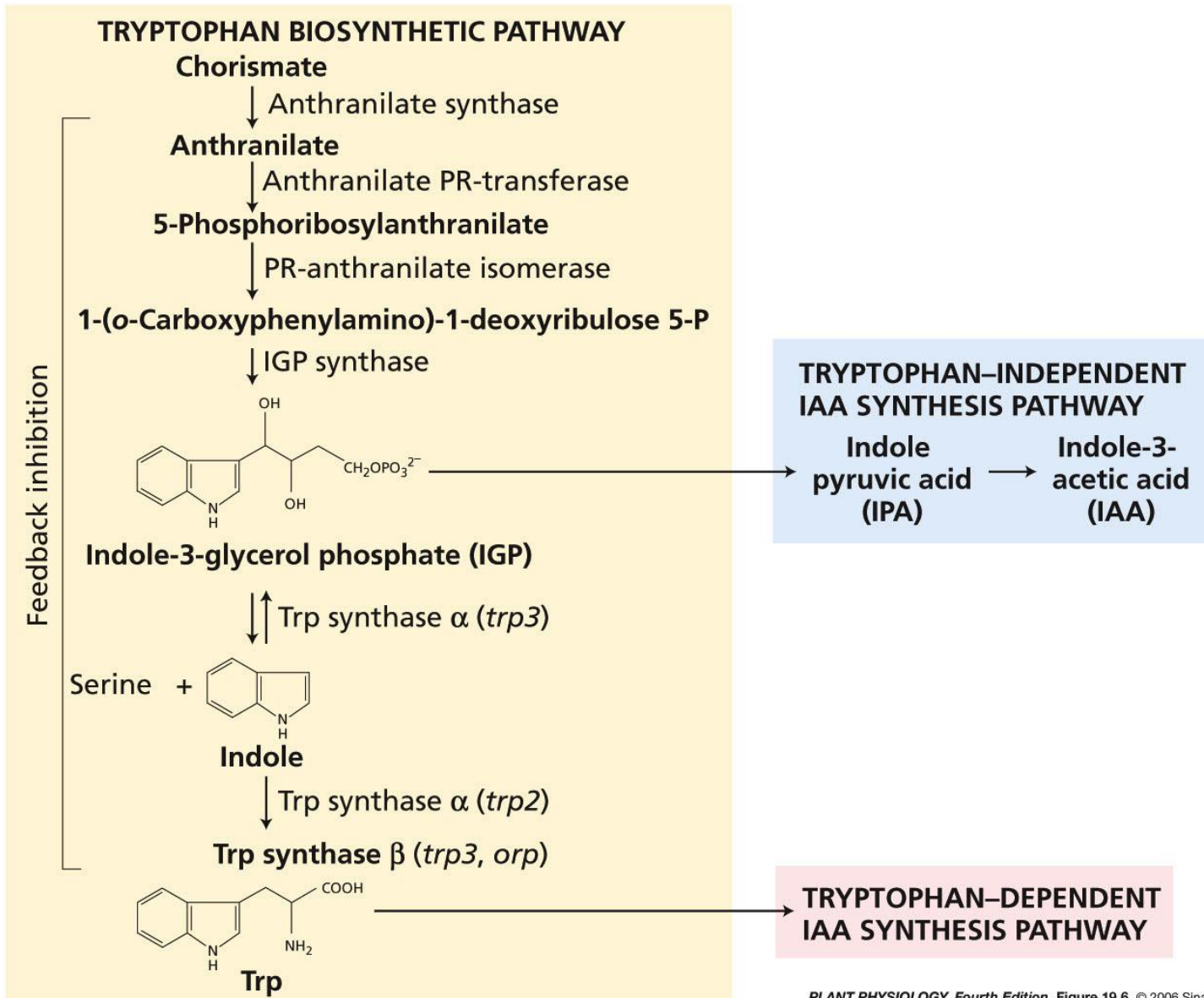
2-Methoxy-3,6-dichlorobenzoic acid (dicamba)

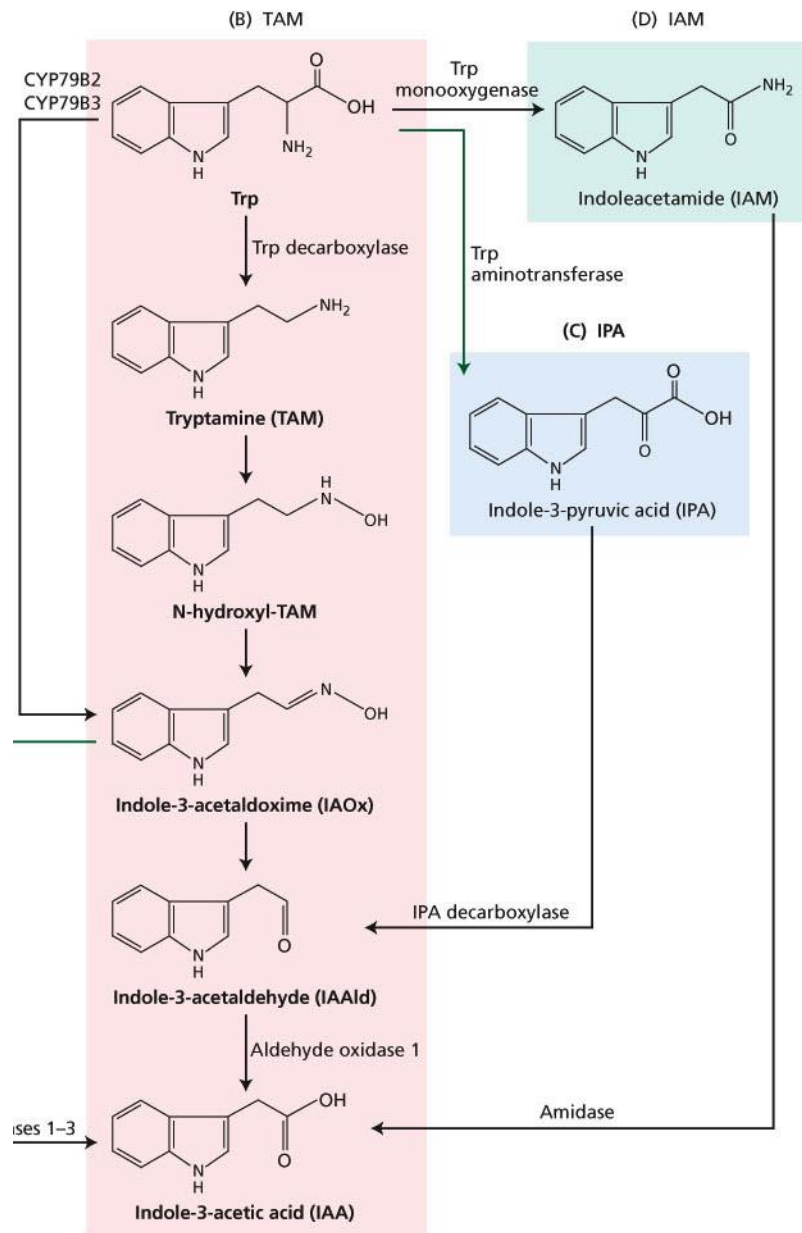


1-naphthaleneacetic acid (NAA)



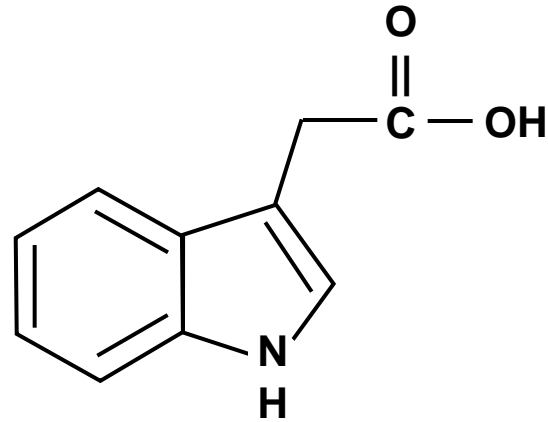
Auxin Biosynthesis





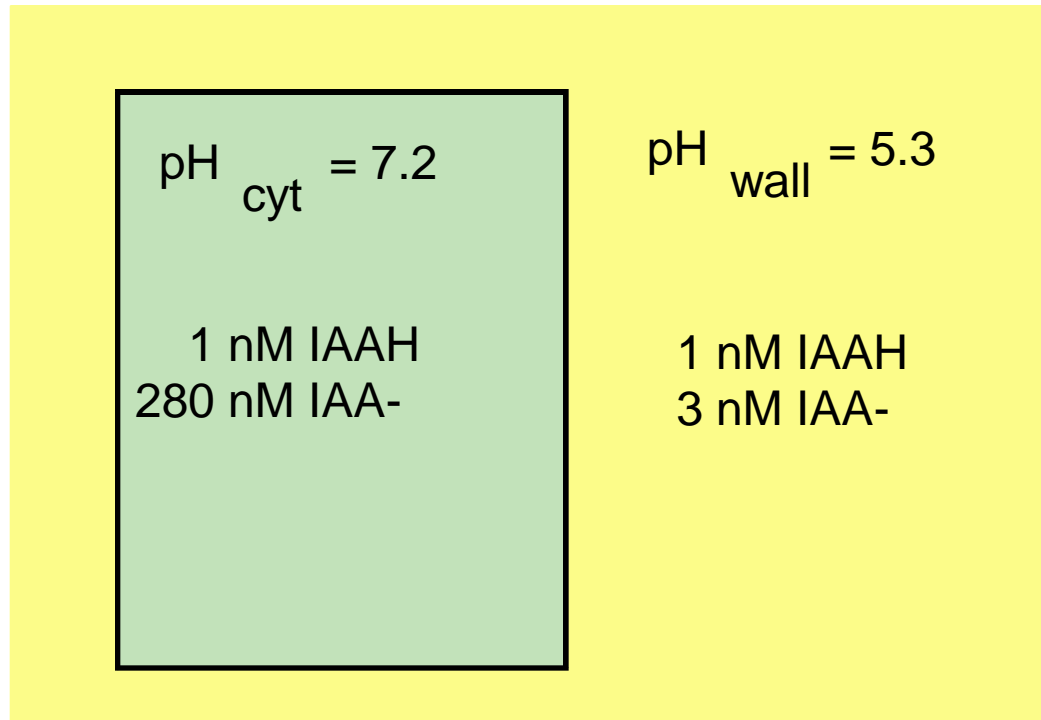
PLANT PHYSIOLOGY, Fourth Edition, Figure 15

Indole-3-acetic acid (IAA)



- Mol wt 175
- A weak acid ($pK_a = 4.8$)
- IAAH is “membrane permeable”, IAA⁻ impermeable.
- Transported through shoots and roots towards root tips through parenchyma (also phloem?).

“Acid trapping”



If the IAAH concentration is in equilibrium, the cytoplasmic auxin concentration is 70x higher than the cell wall.

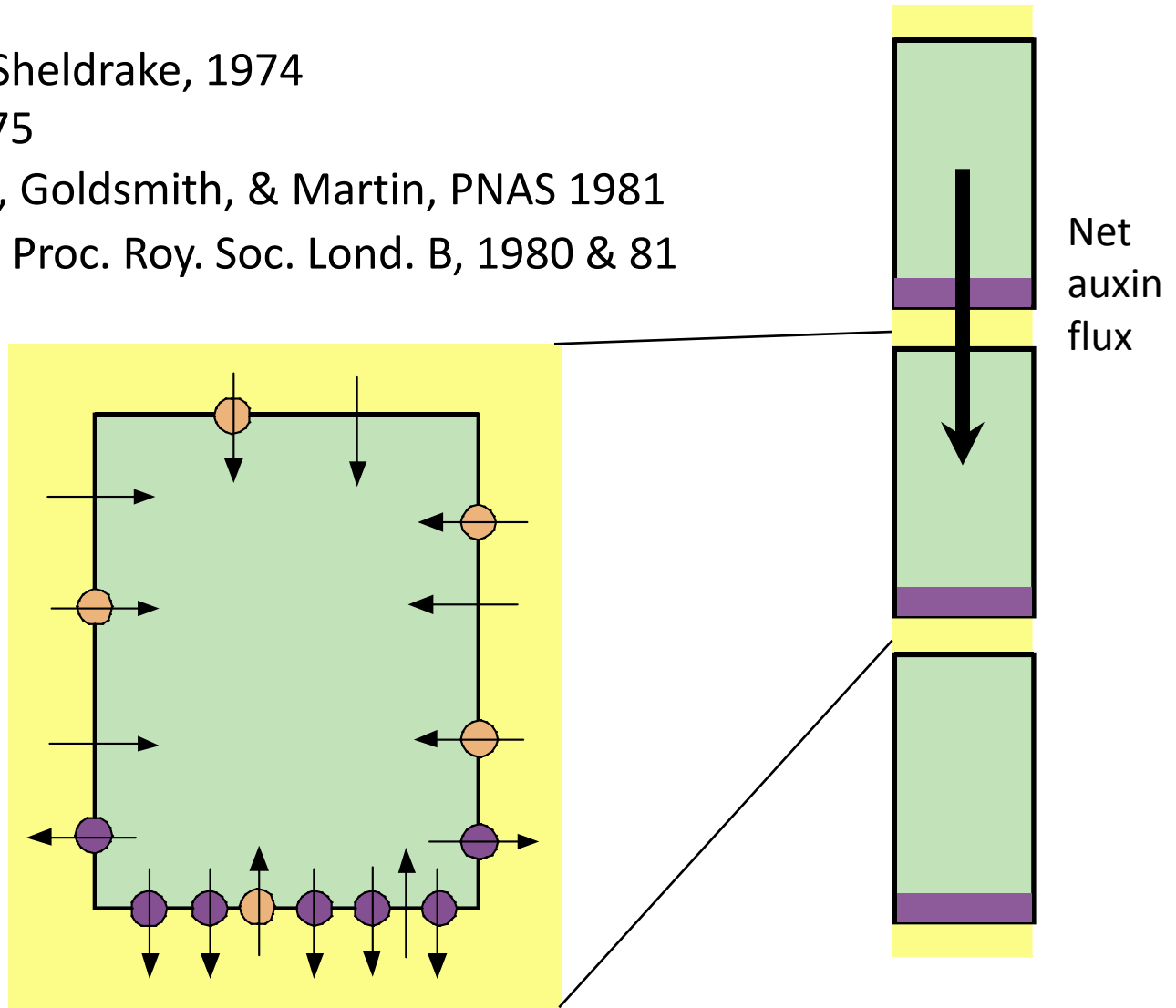
Chemiosmotic theory

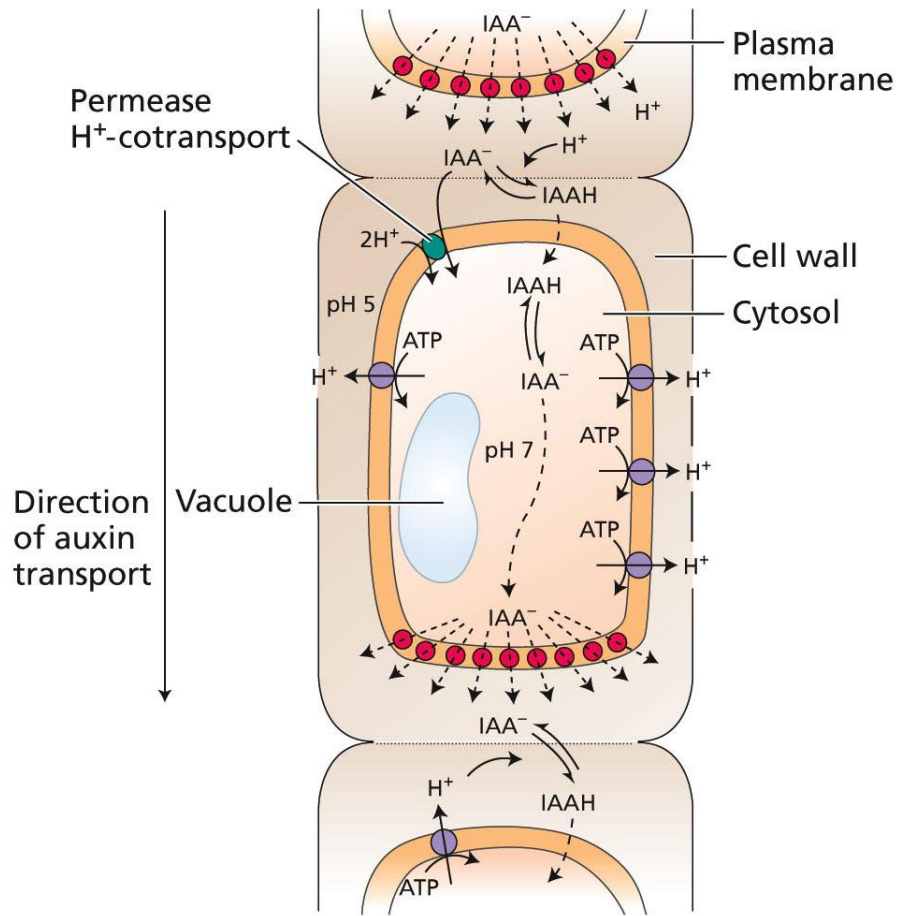
Rubery & Sheldrake, 1974

Raven, 1975

Goldsmith, Goldsmith, & Martin, PNAS 1981

Mitchison, Proc. Roy. Soc. Lond. B, 1980 & 81



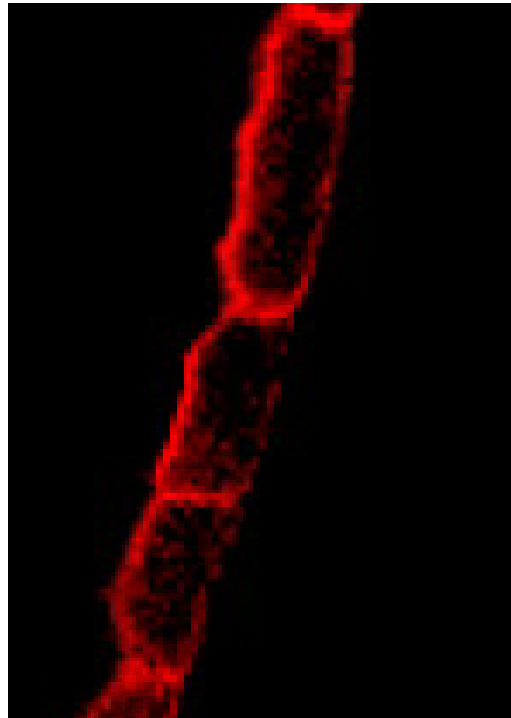
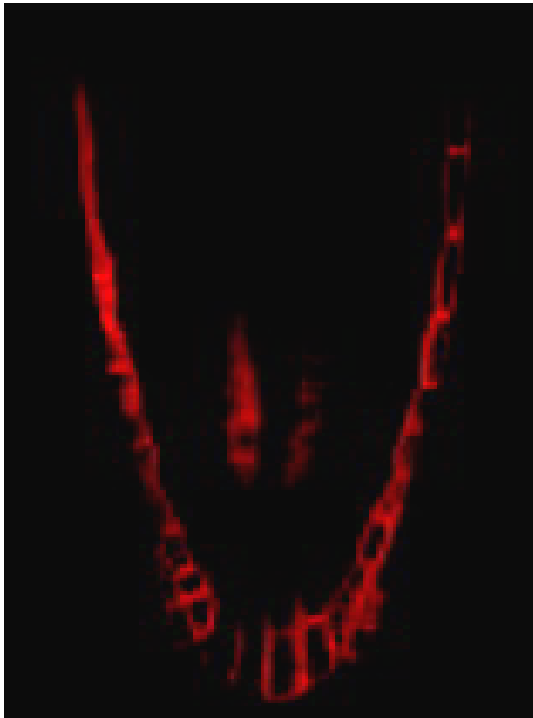


Auxin influx carrier protein

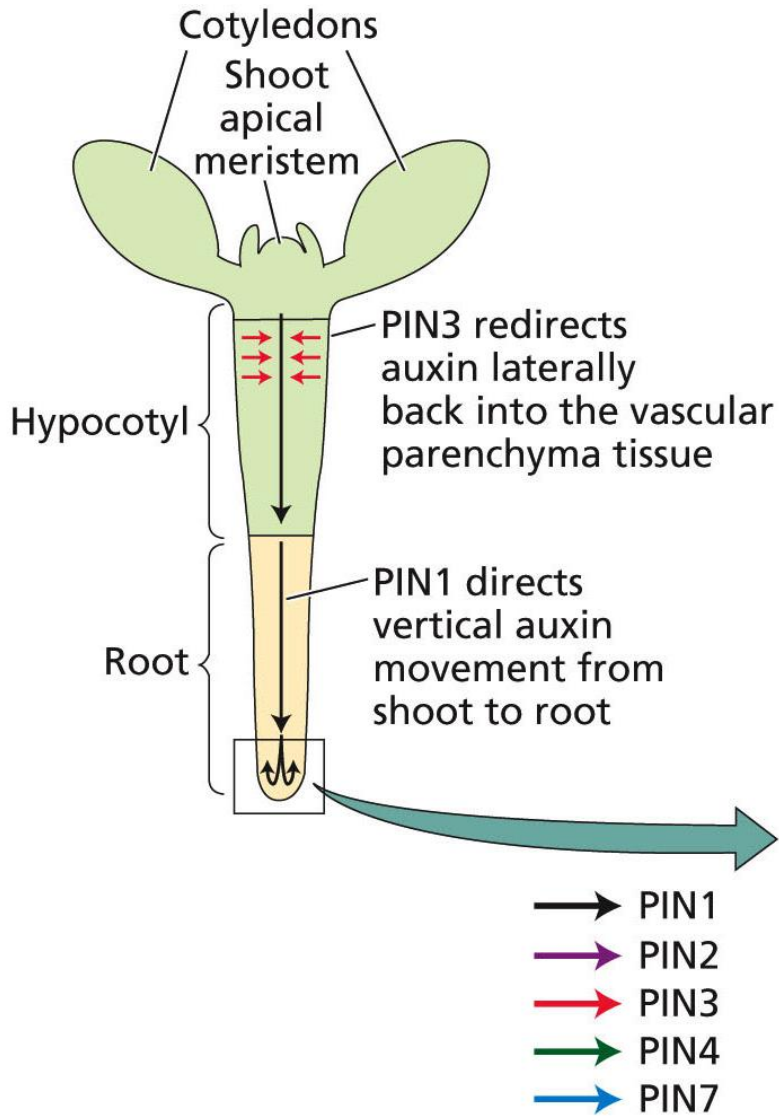
Auxin efflux carrier proteins

Our current understanding of the transport system originated from the analyses of several mutants

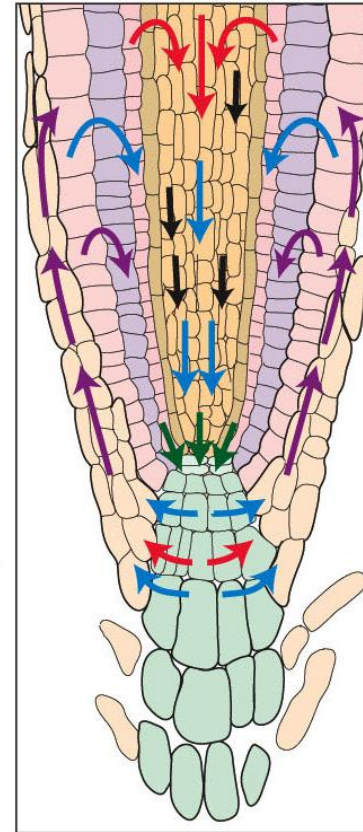
aux1 (1996): The roots are agravitropic and resistant to IAA and 2,4-D but sensitive to NAA. AUX1 encodes a permease-like regulator of root gravitropism. The uptake assay confirmed that this mutant has a reduced uptake capacity compared with wild-type. AUX1 is expressed in the LRC and epidermal cells in the root meristem and in the phloem of root vascular tissue. In the phloem AUX1 is polarly localized whereas in LRC and epidermal cell files it is axially localized.



AUX1 cellular localization
in Arabidopsis root



Auxin efflux carrier proteins
PIN family proteins

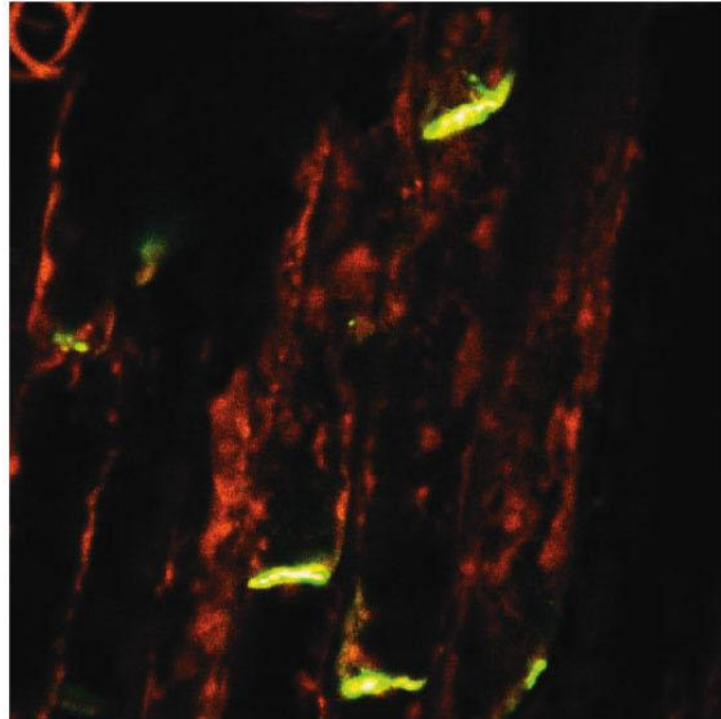


Some ABC transporters also
Play a role in auxin influx and
efflux

(A)

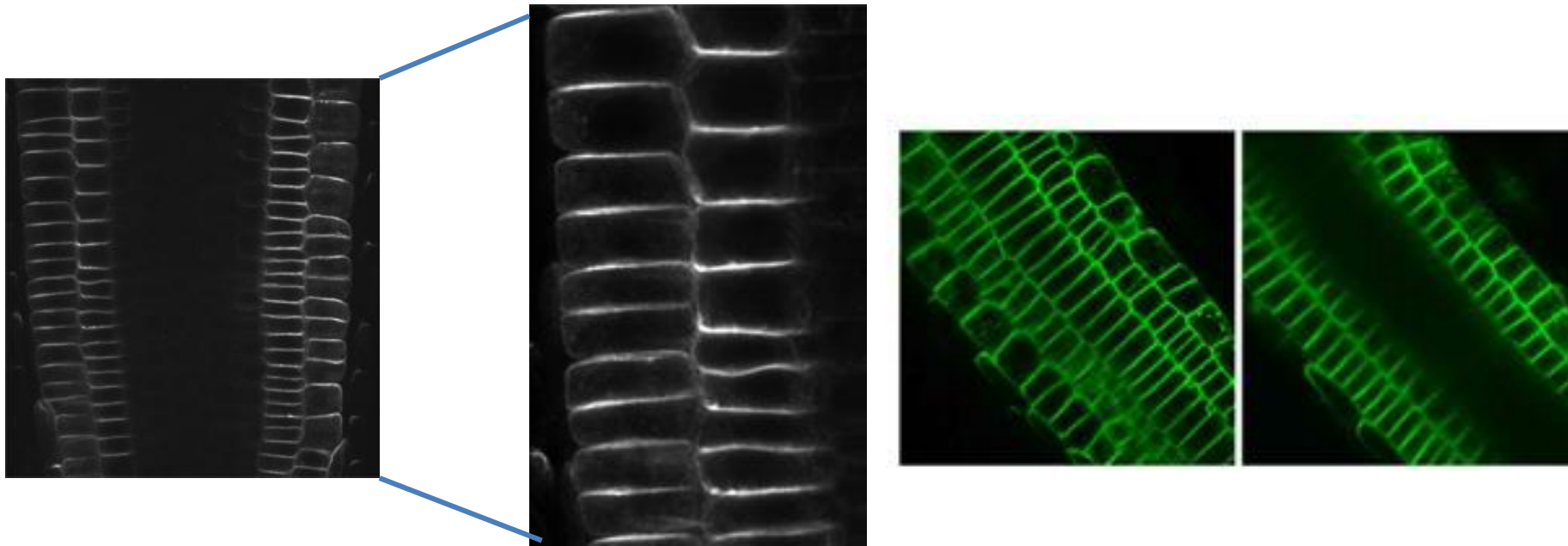


(B)



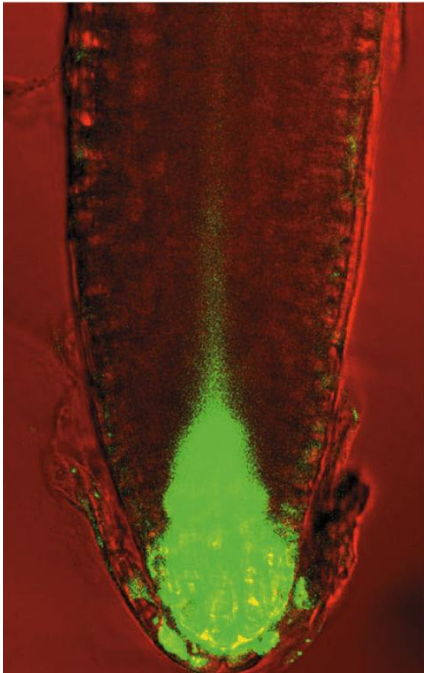
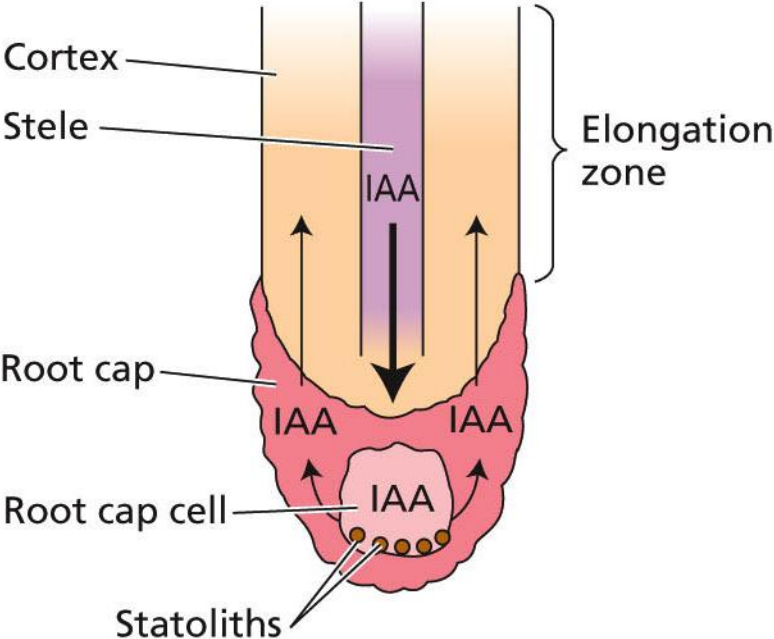
PIN1 mutant and cellular localization

eir1/agr1/pin2 (1998): roots are agravitropic but has a normal sensitivity to exogenous auxins. EIR1 gene of Arabidopsis is a member of family of plant genes with similarities to bacterial membrane transporters. The basipetal transport of auxin in this mutant was found to be less compared to wild-type. PIN2 is localized in the epidermal and cortical cell file of roots with a reverse polarity

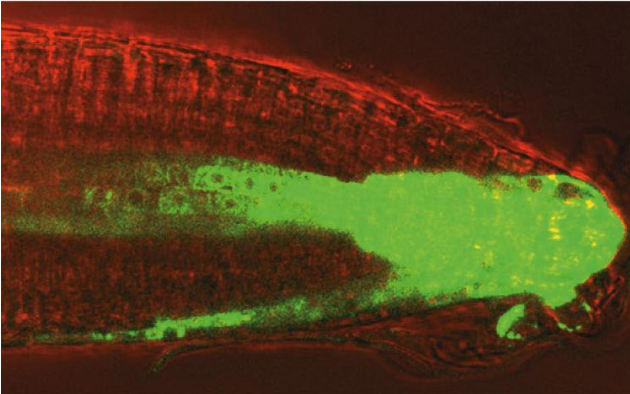
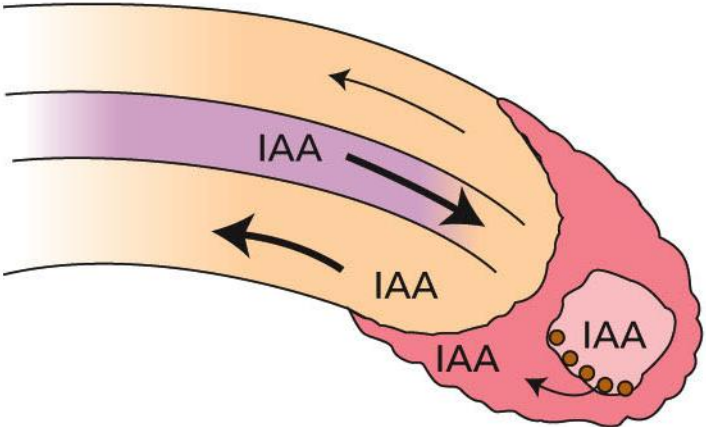


Cellular localization of PIN2

Vertical orientation



(B) Horizontal orientation



Genes involved in downstream auxin signaling pathway

ARF: auxin-response factors

23 member family in Arabidopsis

has DNA binding domains

can be either activators or repressors

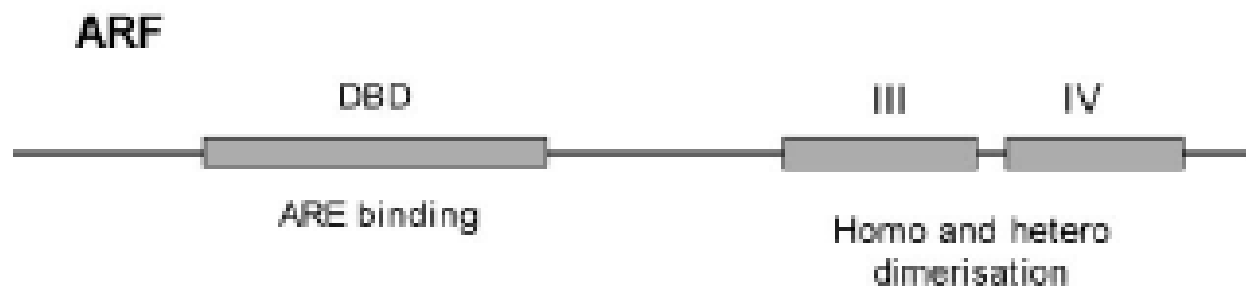
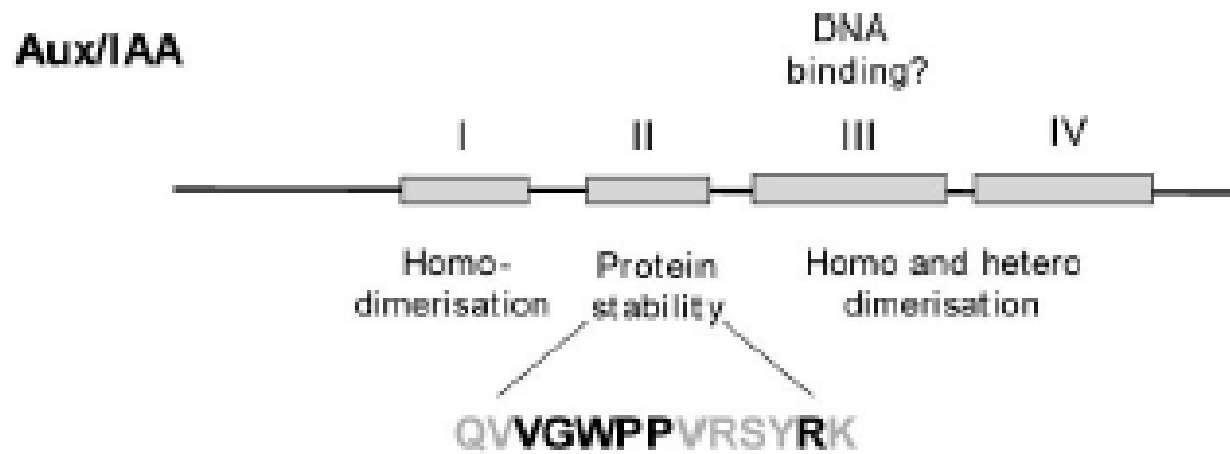
AUX/IAA: 29 member in Arabidopsis

Has protein binding domain

heterodimerize with ARFs

rapid auxin-dependent turn-over of AUX/IAA

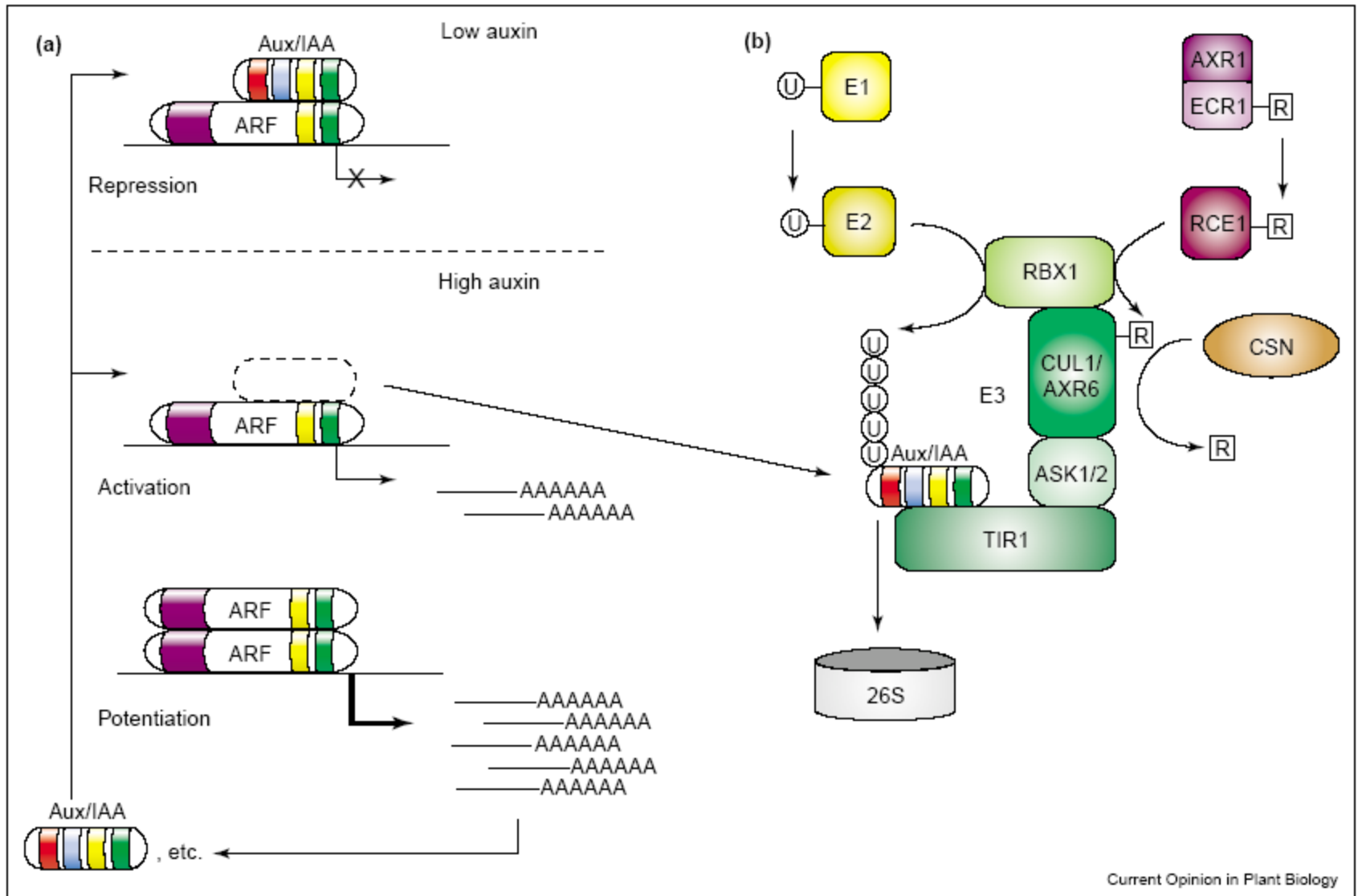
is dependent on ubiquitin-proteasome-pathway

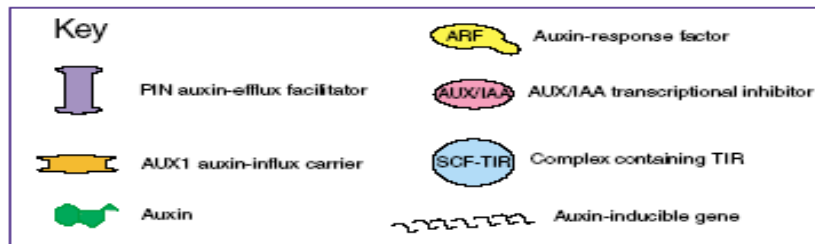
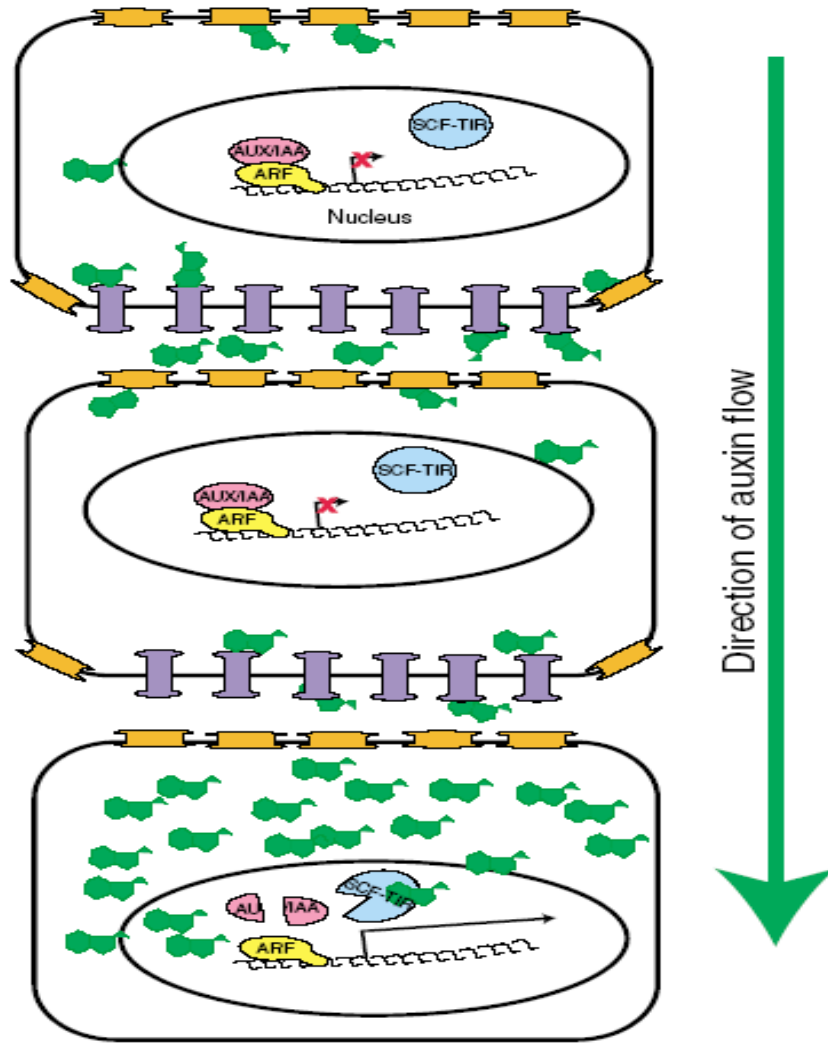


Functionally characterized genes.

Gene name	Gene identifier
Auxin-response factors	
<i>ARF3/ETT^a</i>	<u>AT2G33860</u>
<i>ARF5/MP</i>	<u>AT1G19850</u>
<i>ARF7/NPH4/TIR5/MSG1</i>	<u>AT5G20730</u>
Aux/IAA genes	
<i>IAA3/SHY2</i>	<u>AT1G04240</u>
<i>IAA6/SHY1</i>	<u>AT1G52830</u>
<i>IAA7/AXR2</i>	<u>AT3G23050</u>
<i>IAA12/BDL</i>	<u>AT1G04550</u>
<i>IAA14/SLR</i>	<u>AT4G14550</u>
<i>IAA17/AXR3</i>	<u>AT1G04250</u>
<i>IAA18</i>	<u>AT1G51950</u>
<i>IAA19/MSG2</i>	<u>AT3G15540</u>
<i>IAA28</i>	<u>AT5G25890</u>

Auxin signaling pathway





Auxin Inhibitors

Auxin influx inhibitors

Chromosaponin I
1-Naphthoxyacetic acid (1-NOA)

Auxin efflux inhibitors

Flavonoids
Triiodobenzoic acid (TIBA)
Naphthylphthalamic acid (NPA)

Auxin action inhibitor

p-chlorophenoxyisobutyric acid (PCIB)

Ethylene

★ Ethylene is a gaseous molecule produced in all parts of the plant

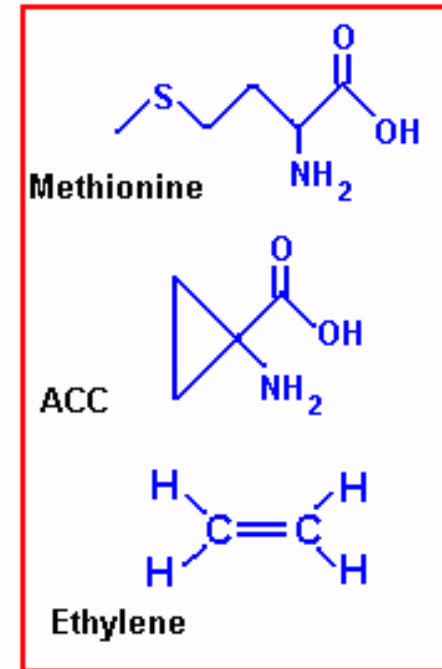
★ made by most plants including angiosperms, gymnosperms, ferns, mosses and also synthesized by fungi and bacteria

★ meristematic regions (shoot apex) and senescing tissues are rich sources

★ ethylene production is stimulated by physiological stresses including wounding, anaerobic conditions, flooding, chilling, disease and drought

in 1901, D. Neljubow realized that his dark-grown pea seedlings were short, fat and negatively gravitropic (**the triple response**) because of a component in "laboratory air" which he subsequently identified as ethylene

★ Cousins (1910) first reported that ethylene occurred in plants.



Developmental processes regulated by ethylene

Promotion of seed germination

Inhibition or promotion of root growth

Inhibition of shoot growth

Promoting the elongation growth of submerged aquatic species

Inhibition/promotion of cell division and cell elongation

Induction of lateral cell expansion

Bud dormancy release

Initiation of adventitious roots and root hairs

Altering gravitropism in roots and stems

Promoting leaf epinasty

Inhibition/promotion of flowering

Abscission of leaves, flowers, fruits

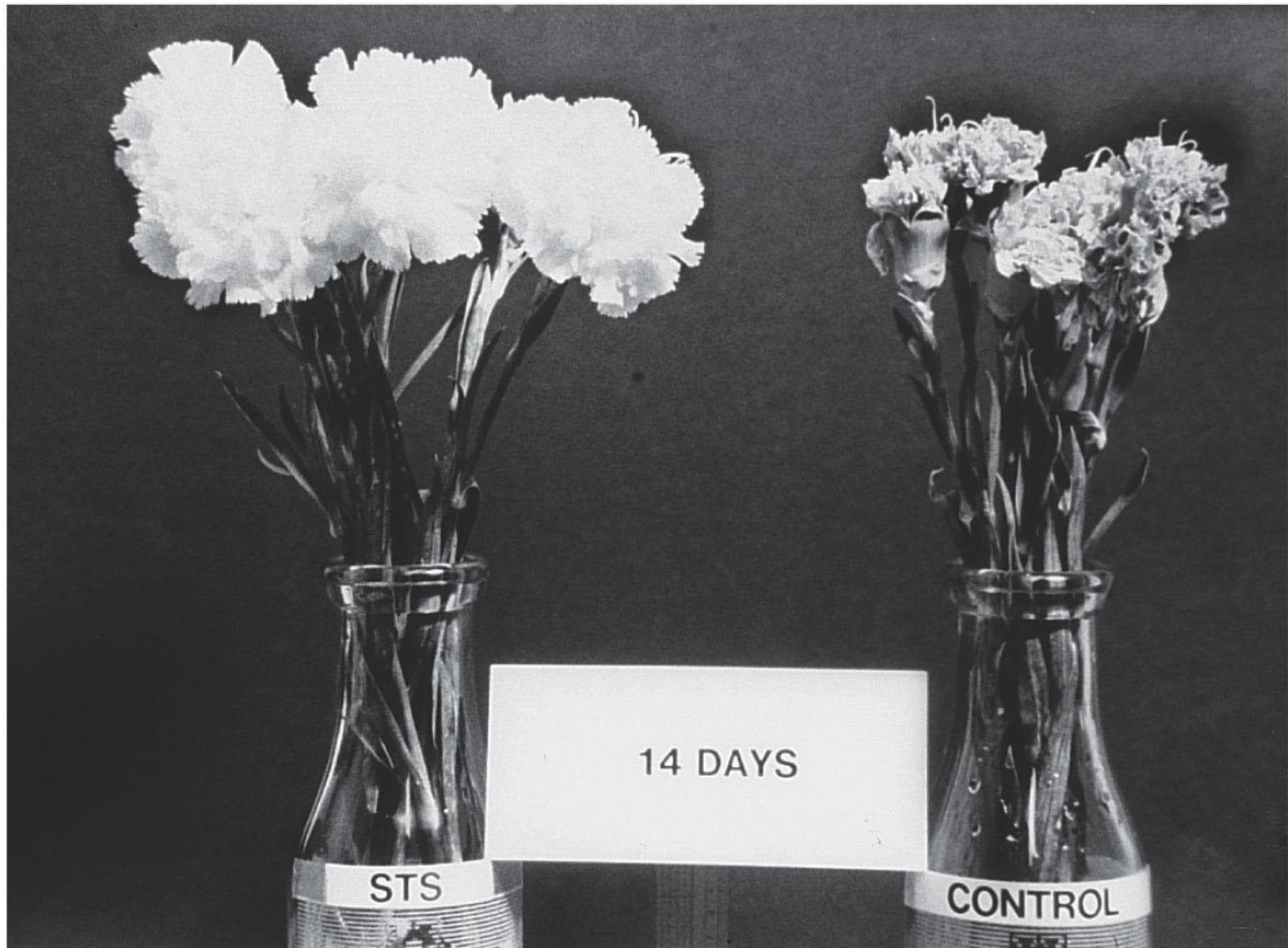
Promoting senescence of leaves, flowers

Involved in defense response pathway

Induction of phytoalexins and other disease resistance factors

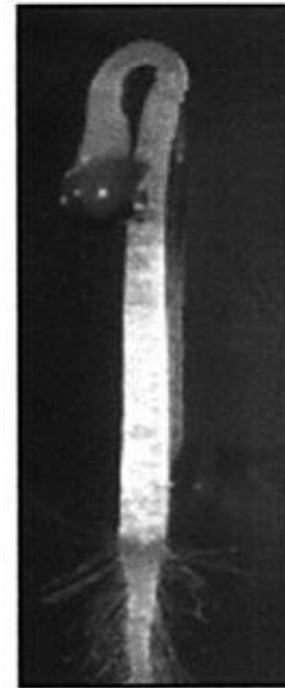
Fruit ripening

(C) Flower senescence

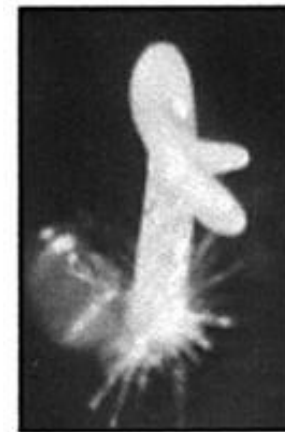


Triple response phenotypes

- ★ Reduced elongation of hypocotyl and root
- ★ Thickening of hypocotyl
- ★ Exaggeration of the apical hook curvature



-Ethylene

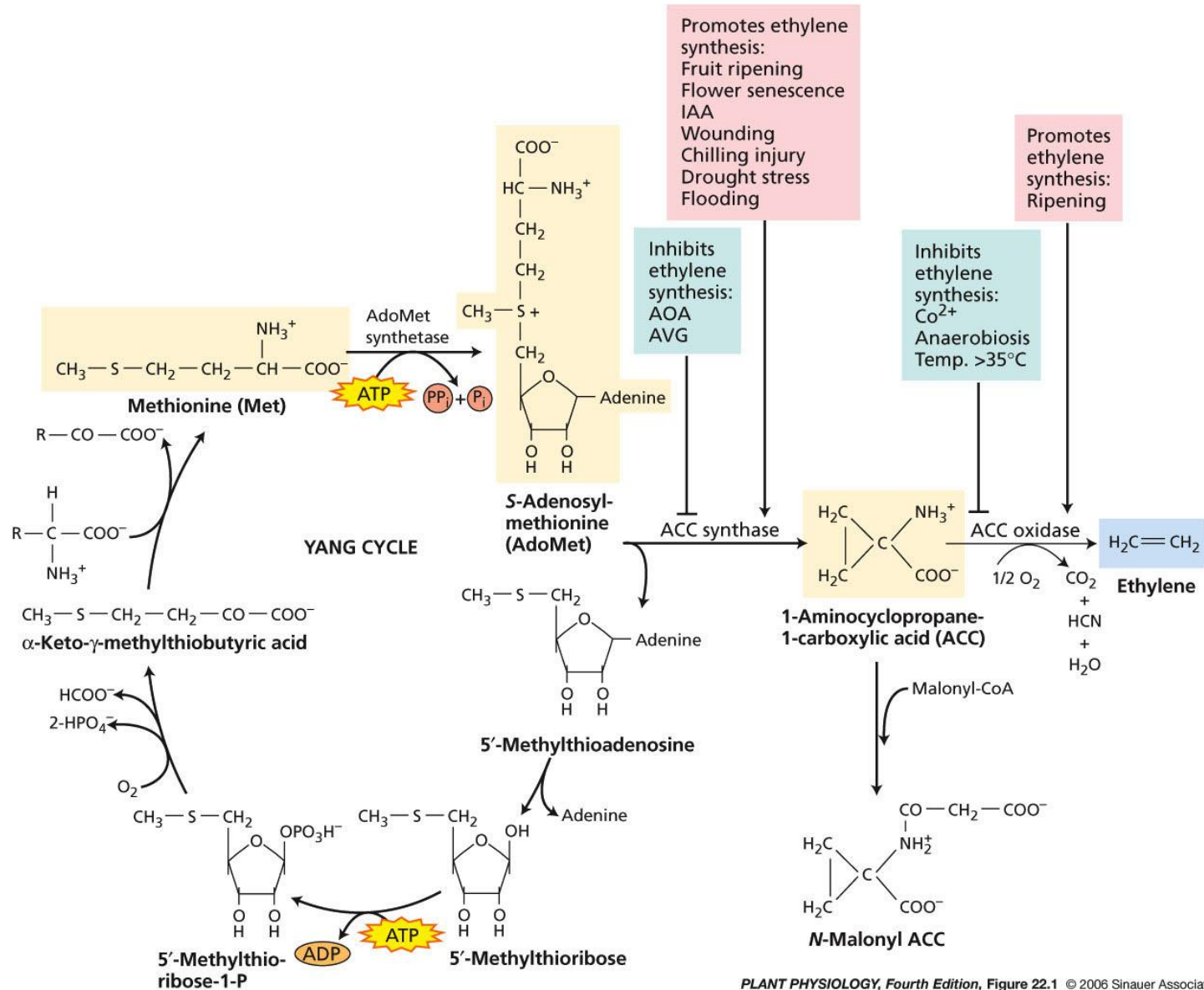


+Ethylene

In 1988, on the basis of triple response screening, the first ethylene mutant was isolated and reported



Ethylene Biosynthesis



Tab. 1. Ethylene-related mutants.

Locus	Name	Phenotype and comments	References
<i>Arabidopsis thaliana</i>			
<i>etr1</i>	Ethylene resistant	Ethylene insensitive; delay in bolting time; increase in rosette size; <i>ETR1</i> is homologous to two-component regulators	Bleecker et al. 1988, Chang et al. 1993
<i>ers</i>	Ethylene response sensor	Ethylene insensitive; <i>ERS</i> is homologous to <i>ETR1</i> ; mutation was induced with reverse genetics	Hua et al. 1995
<i>ein2</i>	Ethylene insensitive	Ethylene insensitive; delay in bolting time; increase in rosette size	Guzmán and Ecker 1990
<i>ein3</i>	Ethylene insensitive	Ethylene insensitive	Kieber et al. 1993
<i>ein4</i>	Ethylene insensitive	Ethylene insensitive	Roman et al. 1995
<i>ein6</i>	Ethylene insensitive	Ethylene insensitive	Roman et al. 1995
<i>ein7</i>	Ethylene insensitive	Ethylene insensitive	Roman et al. 1995
<i>ain1</i>	ACC insensitive	Ethylene insensitive; increase in rosette size	Van Der Straeten et al. 1993
<i>eti</i>	Ethylene insensitive	Ethylene insensitive	Harpham et al. 1991
<i>eto1</i>	Ethylene overproducer	Constitutive ethylene response in etiolated seedlings, due to higher ethylene biosynthesis level	Guzmán and Ecker 1990
<i>eto2</i>	Ethylene overproducer	Constitutive ethylene response in etiolated seedlings, due to higher ethylene biosynthesis level	Kieber et al. 1993
<i>eto3</i>	Ethylene overproducer	Constitutive ethylene response in etiolated seedlings, due to higher ethylene biosynthesis level	Kieber et al. 1993
<i>ctr1</i>	Constitutive triple response	Constitutive ethylene responses at all developmental stages tested, not due to higher ethylene biosynthesis; phenocopied by ethylene treatment; <i>CTR1</i> is homologous to Raf kinases	Kieber et al. 1993
<i>hls1</i>	Hookless	No differential growth in apical hook of etiolated seedlings; phenocopied by treatments with auxins or auxin transport inhibitors; <i>HLS1</i> is homologous to <i>N</i> -acetyltransferases	Guzmán and Ecker 1990, Lehman et al. 1996
<i>eir1</i>	Ethylene-insensitive root	Root is ethylene insensitive and agravitropic	Roman et al. 1995
<i>aux1</i>	Auxin insensitive	Root is agravitropic and insensitive to ethylene and auxin; apical hook slightly ethylene insensitive; <i>AUX1</i> is homologous to amino acid permeases	Maher and Martindale 1980, Pickett et al. 1990, Roman et al. 1995, Bennett et al. 1996
<i>axr1</i>	Auxin resistant	Root is agravitropic and insensitive to ethylene, auxin and cytokinin; the shoot is short and bushy; etiolated seedlings have a short hypocotyl and are defective in apical hook formation; <i>AXR1</i> is homologous to ubiquitin-activating enzyme E1	Estelle and Somerville 1987, Lincoln et al. 1990, Leyser et al. 1993

Epistasis pathway established by double mutant analysis

ctr1: constitutive responses

eto1: constitutive responses:

etr1: ethylene insensitive

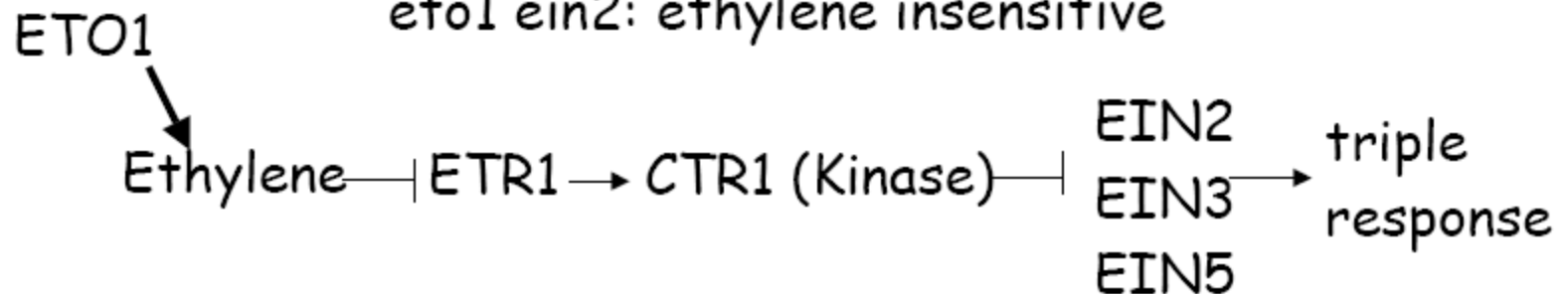
ein2: ethylene insensitive

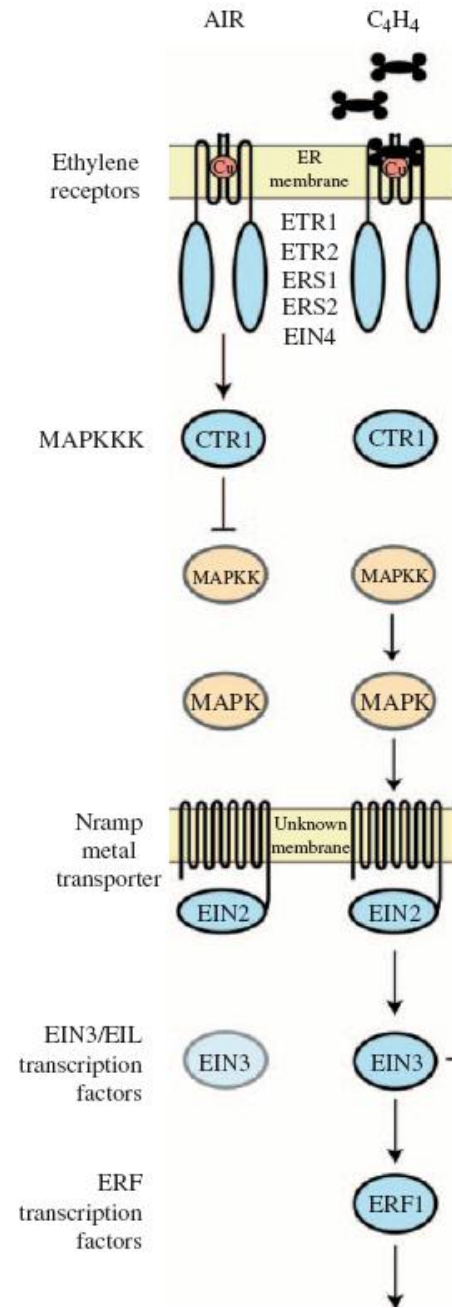
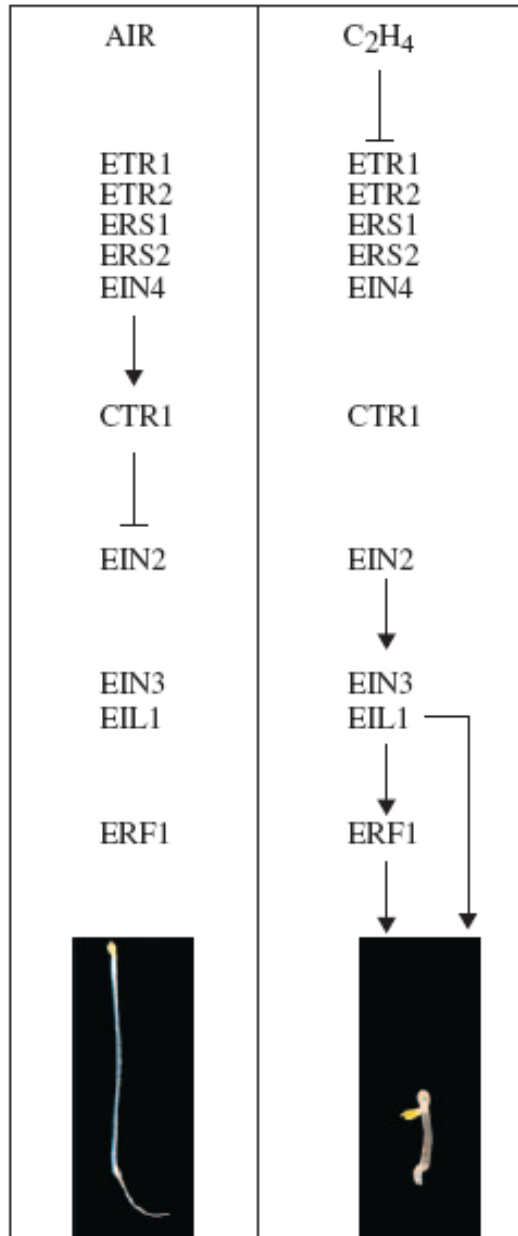
etr1 ctr1: constitutive response

ein2 ctr1: ethylene insensitive

eto1 etr1: ethylene insensitive

eto1 ein2: ethylene insensitive





Ethylene response