Hormone

The physical traits, or **phenotype**, of a plant results from a complex interaction between its genetic instructions, or **genotype**, and the external **environment**. The growth and differentiation of cells in different parts of the plant are coordinated in response to these inputs.

Questions:

1) How does the plant receive and respond to environmental inputs or "signals"?

2) What communicating steps the plant use to adjust growth and development in response to the environment?

The answer lies in understanding the role of plant hormones.

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

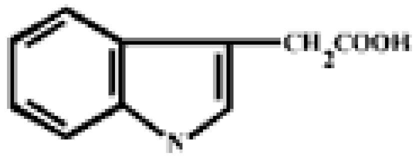
- Cell Division
- Cell Enlargement
- Cell Differentiation
- Flowering
- Fruit Ripening
- Movement (tropisms)
- Seed Dormancy
- Seed Germination
- Senescence
- Leaf Abscission
- Stomatal Conductance

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.

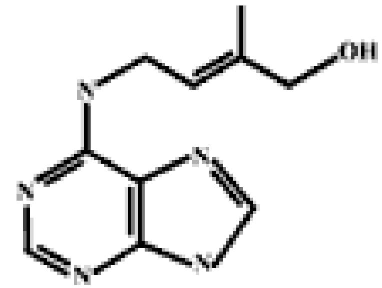
Plant Hormones	**Animal Hormones**
1.Small molecules only 2. Produced throughout the plant 3. Mainly local targets (nearby cells and tissues) 4. Effects vary depending on interaction with other hormones 5."Decentralized" regulation	1.Peptides/proteins and/or small molecules 2. Produced in specialized "glands" 3. Distant targets ("action at a distance") 4. Specific effects 5. Regulation by central nervous system

$CH_2{=}CH_2$

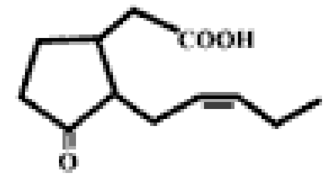
Ethylene



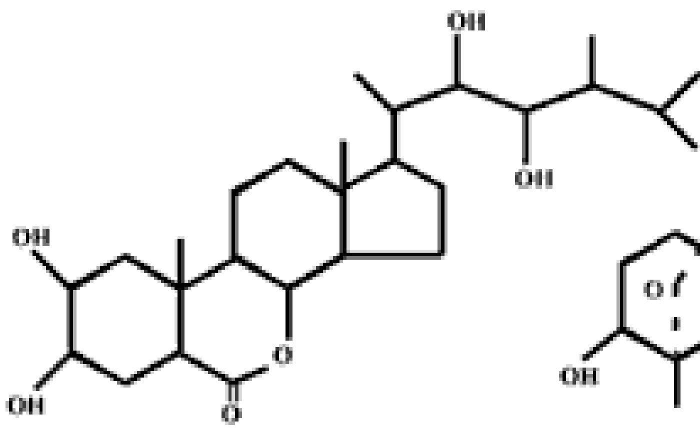
Auxin



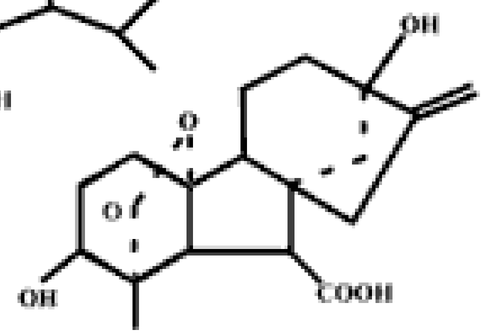
Cytokinins



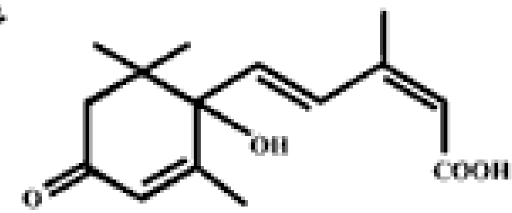
Jasmonic Acid



Brassinosteroids



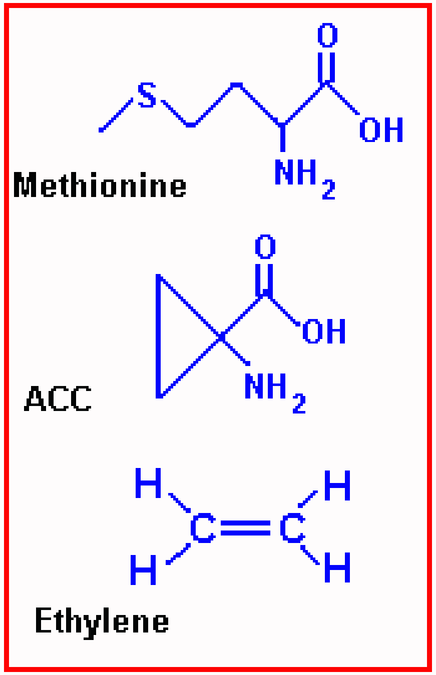
Gibberellins



Abscisic Acid

Ethylene

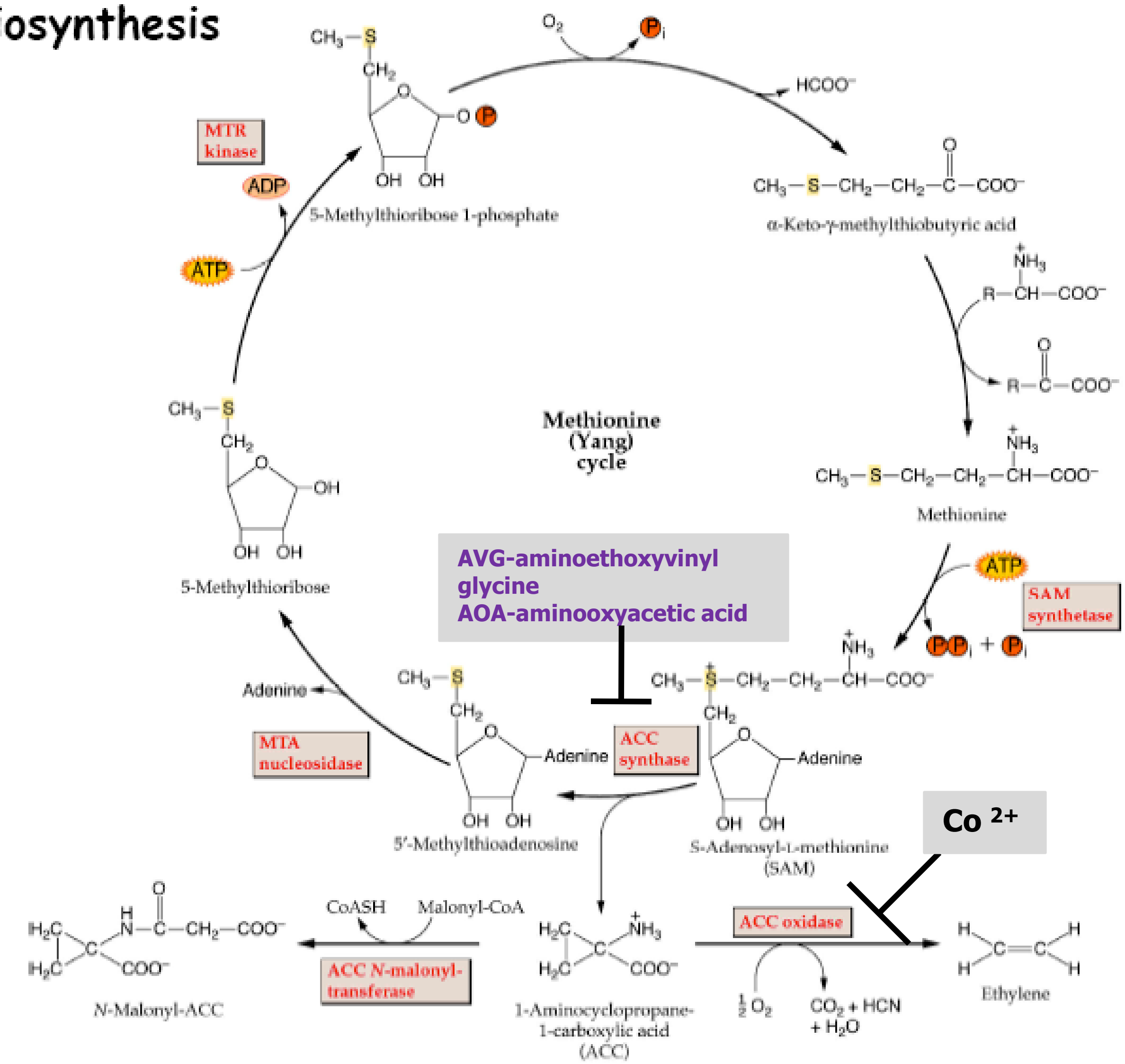
- Ethylene is a gaseous molecule produced in all parts of the plant
- made by most plants including angiosperms, gymnosperms, ferns, mosses and also synthesized by fungi and bacteria
- meristematic regions (shoot apex) and senescing tissues are rich sources
- ethylene production is stimulated by physiological 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

Ethylene Biosynthesis



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

Tab. 1. Ethylene-related mutants.

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

axr2	Auxin resistant	Agravitropic root lacking root hairs, and insensitive to auxin, ethylene, and ABA; shoot agravitropic and dwarfed	Wilson et al. 1990
axr3	Auxin resistant	Increased apical dominance, increased root proliferation, seems to have an increased auxin response; root is insensitive to ethylene, auxin, and cytokinin	Leyser et al. 1996
rhd6	Root hair defective	Altered root hair initiation; phenotype can be rescued with exogenous ACC or auxin	Masucci and Schiefelbein 1994
Lycopersicon esculentum			
Nr	Never ripe	Ethylene insensitive; *Nr* is homologous to *ETR1* and *ERS*, structurally more similar to *ERS*	Hobson 1967, Wilkinson et al. 1995
dgt	Diageotropica	Horizontal shoot growth, hyponastic leaves, no lateral roots, auxin resistant; reduced levels of auxin-binding proteins; phenotype is partially rescued by ethylene treatment	Zobel 1973, Bradford and Yang 1980, Kelly and Bradford 1986, Hicks et al. 1989
Epi	Epinastic	Epinastic, swollen stems and petioles, excessive root branching	Fujino et al. 1988, Ursin and Bradford 1989
Medicago truncatula			
skl1	Sickle	Ethylene insensitive; hyperinfectable by rhizobial symbiont	Penmetsa and Cook 1997
Nicotiana plumbaginifolia			
aus1	Auxin sensitive	Mild leaf epinasty, short primary root, increased root branching, no root hairs; increased sensitivity to ethylene and auxin	de Souza and King 1991
Pisum sativum			
agt	Ageotropum	Agravitropic roots, shoots are only agravitropic in the dark; 2- to 5-fold less ethylene production, lesion in auxin transport or sensitivity?	Ekelund and Hemberg 1966, Olsen and Iversen 1980, Takahashi et al. 1991
lk	Erectoides	Reduced internode and petiole length, GA insensitive, higher ethylene biosynthesis	Reid 1986, Ross and Reid 1986

Ref: Smalle J and Straeten VD (1997); Physiologia Plantarum 100: 593-605

Classification of ethylene mutants

Type 1: constitutive response

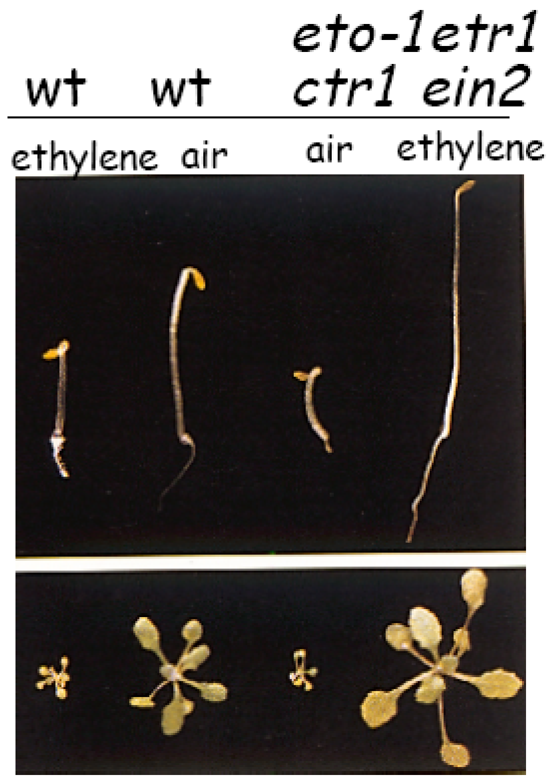
eto1 (ethylene over-producer)

ctr1 (constitutive ethylene response)

Type 2: ethylene insensitive

etr1 (ethylene resistance)

ein2, 3, 4,5 (ethylene insensitive)



eto1: phenotype can be blocked by ethylene synthesis inhibitors

ctr1: phenotype is unaffected by ethylene synthesis inhibitors

Epistasis pathway established by double mutant analysis

ctr1: constitutive responses

eto1: constitutive responses:

etr1: ethylene insensitive

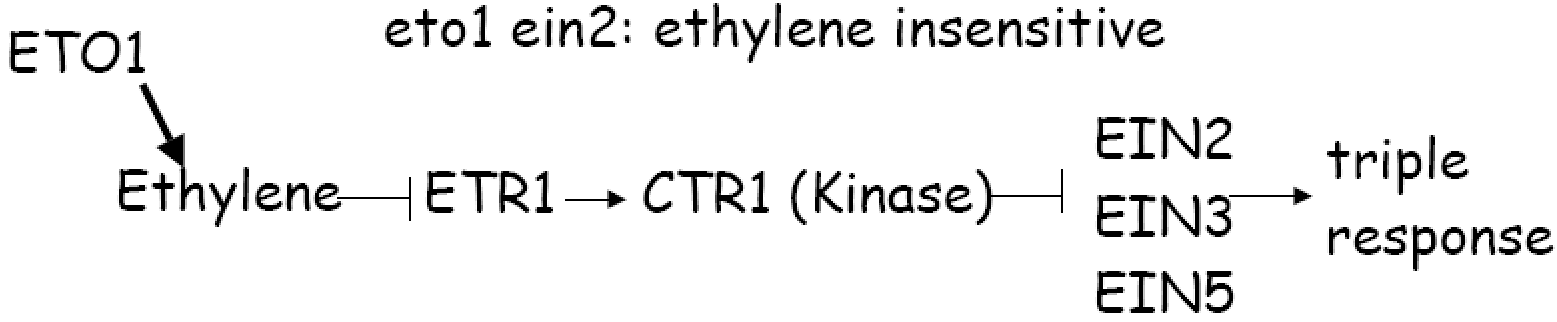
ein2: ethylene insensitive

etr1 ctr1: constitutive response

ein2 ctr1: ethylene insensitive

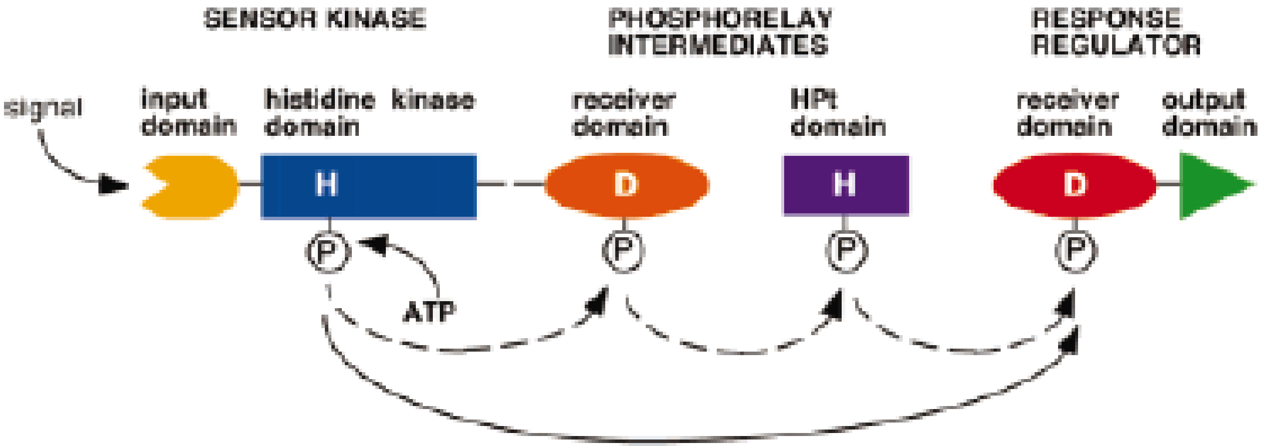
eto1 etr1: ethylene insensitive

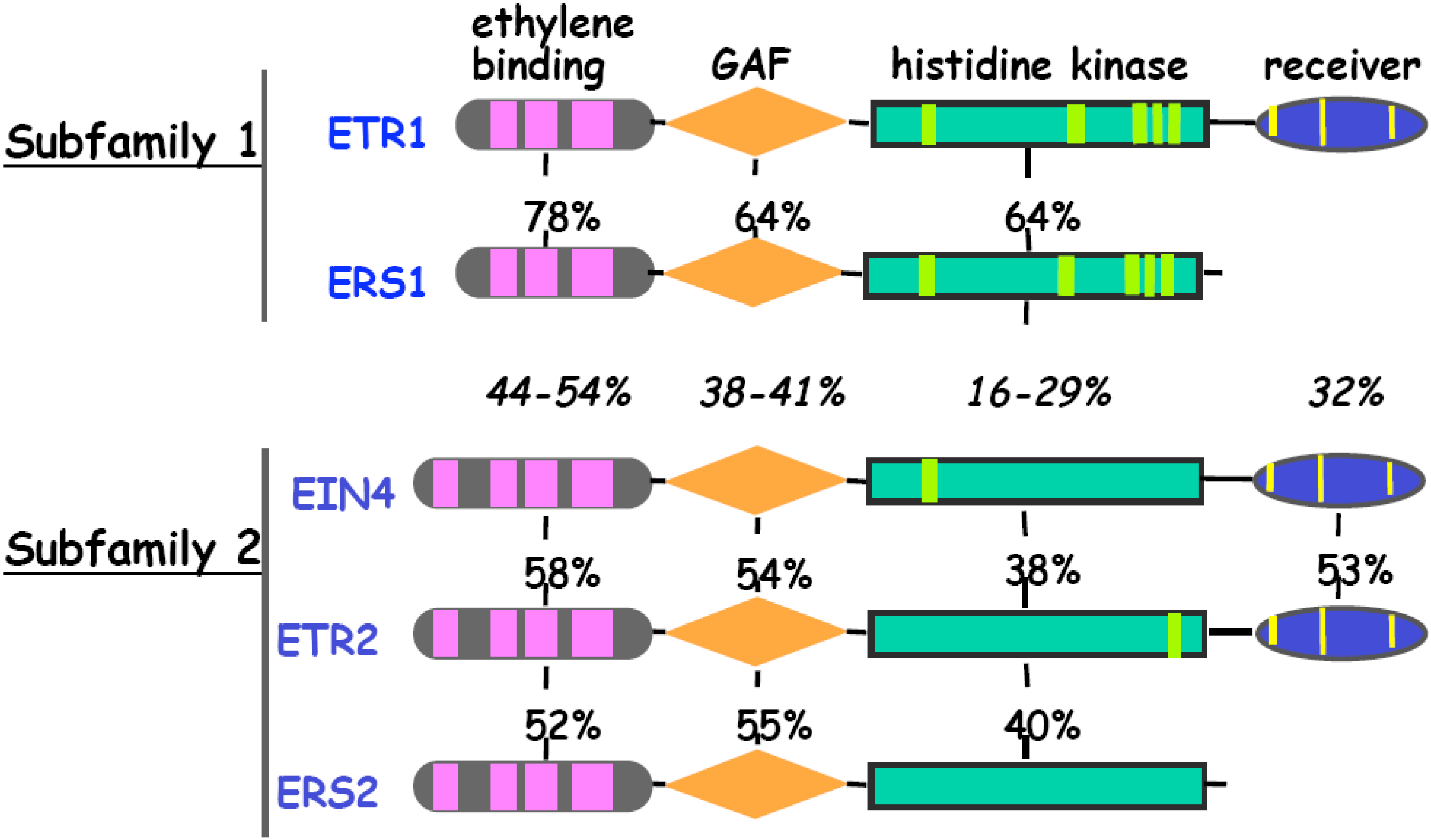
eto1 ein2: ethylene insensitive



In Arabidopsis ethylene is perceived by a family of five receptors that share a similarity with bacterial two-component regulators

ETR1
ETR2
ERS1
ERS2
EIN4




ethylene binding
GAF
histidine kinase
receiver
Subfamily 1
ETR1
78%
64%
64%
ERS1
44-54%
38-41%
16-29%
32%
Subfamily 2
EIN4
58%
54%
38%
53%
ETR2
52%
55%
40%
ERS2

Ethylene receptor family-

@ encodes a protein which has striking similarity with bacterial two component system
@ In yeast cell expression system it has been shown that ETR1 and ERS1 reversibly and saturably bind ethylene
@ The ethylene binding domain of ETR1 lies within the first 128 amino acids, and this domain is the most conserved region among the five arabidopsis ethylene receptors (44-54% identity)
@ A transition metal has been suggested to be necessary for ethylene binding and consistent with this hypothesis ETR1 was shown to bind ethylene only in presence of copper ions.
@ Recent findings suggest that ETR1 is localized in ER membrane

CTR1- @ encodes a protein with high sequence similarity to the raf family of mitogen activated protein kinases (MAPKKs). A number of MAP KKK and MAPKK genes have been isolated in plants, it is not yet known whether they are involved in ethylene signaling pathway.

@ A direct interaction has been found between both CTR1 and ETR1 and ERS1.

EIN2- @ encodes a protein which N terminal domain has sequence similarity to the Nramp family of the metal ion carriers. Ion transport activity has not been detected for EIN2.The biological function and the subcellular localization of this protein is still unknown.

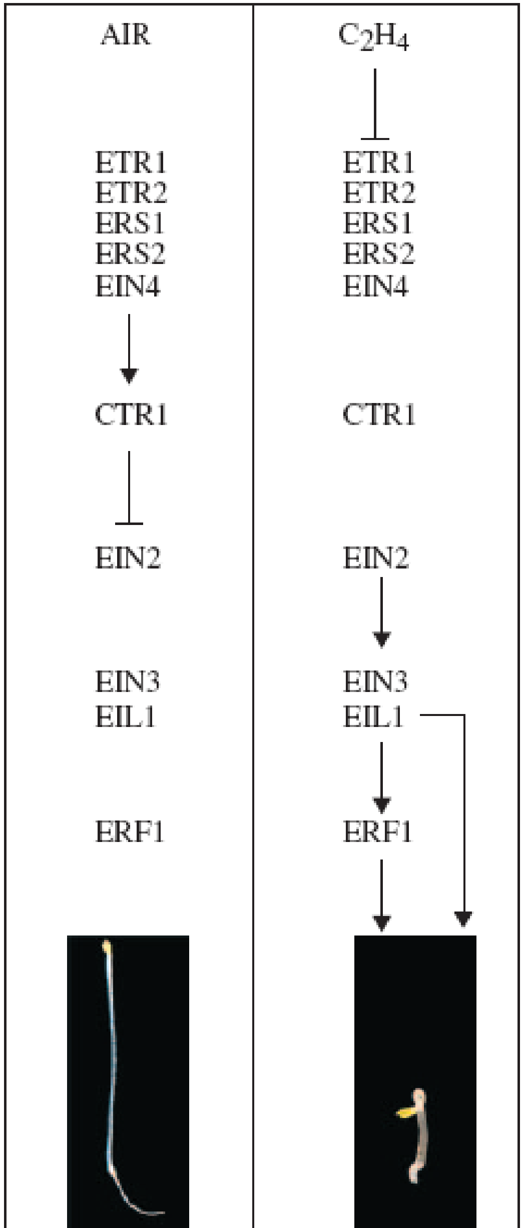
Transcriptional regulators-

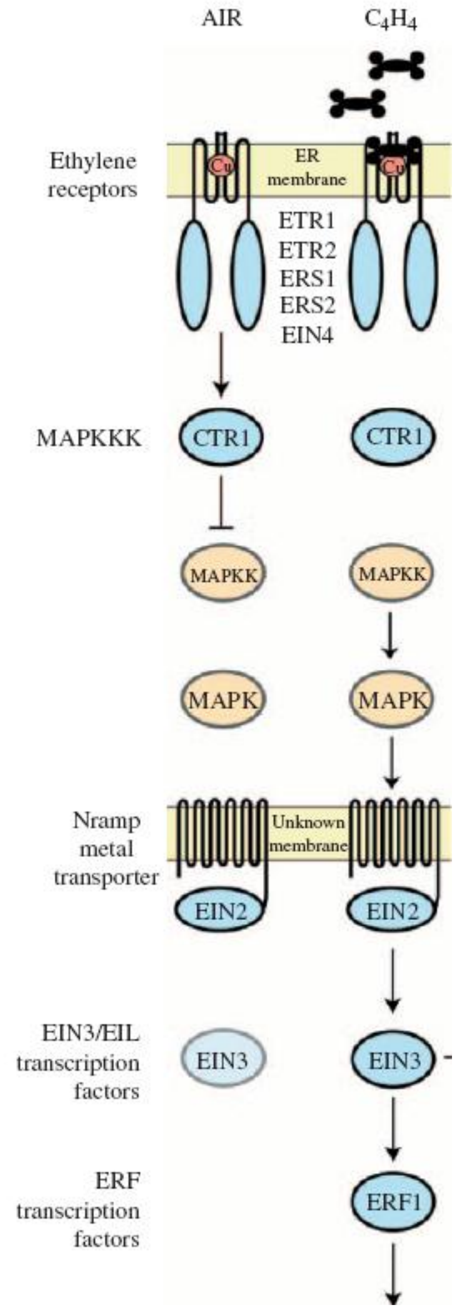
@ A common destination for cellular signaling pathway is the nucleus, where specific transcription factors control gene expression. Two –types of ethylene-responsive transcriptional regulators have been identified: the family of ETHYLENE INSENSITIVE MUTANT (EIN3)/EIN3 like proteins (EIL) and ETHYLENE RESPONSE ELEMENT BINDING PROTEINS (EREBPs).

@ EIN3 protein may be degraded inside the cell and this process could be mediated by a ubiquitin/proteasome pathway

@ several memebrs of the EIN3/EIL family have been shown to bind a conserved cis-element in the promoter of an EREBP-encoding gene called *ETHYLENE RESPONSE FACTOR (ERF1).*

@ EIN3 activates the transcription of ERF1 and ERF1 binds to the promoters of the target genes and activates them





Ethylene response

References:

Roman G, Lubarsky B, Kieber JJ, Rothenberg M, Ecker JR (1995) Genetic analysis of ethylene signal transduction in *Arabidopsis thaliana*: Five novel loci integrated into a stress response pathway. Genetics 139: 1393-1409

Blecker BA, Estelle MA, Somerville C, Kende H(1998) Insensitivity to ethylene conferred by a dominant mutation in *Arabidopsis thaliana.* Scinece 241: 1086-1088

Chang C and Stadler R (2001) Ethylene hormone receptor action in Arabidopsis. Bio Essays 23.7: 619-627

Guo H and Ecker JR (2004) The Ethylene signaling pathway: new insights. Curr.opin.plant biol 7: 40-49

Chen FY, Etheridge N, Schaller EG (2005) Ethylene signal transduction. Annals of Botany 95: 901-915