Ethylene and Other Plant Hormones: Role in Senescence

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Definition of a "Hormone"

- Naturally occurring, organic substances that exert profound influences on physiological processes at very low concentrations
  - From the Greek "ho[illegible]" = "to set in motion"
  - How a hormone is identified:
    1. Remove ⟶ the process does not occur
    2. Re-apply ⟶ the process occurs
    3. Works in isolated systems
    4. Other natural compounds don't cause similar effects (*e.g.*, nutrients)

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Definition of a "Hormone"

- Hormones help regulate processes and can either stimulate or inhibit them
- Hormones are also called "plant growth regulators" or "phytohormones"

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In Animals

- Hormones were originally described in animal systems
  - In animals, most hormones are produced in one part of the body and then transported to other body parts where they cause a response

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In Plants

- In plants, hormones are somewhat different
  - They can be produced by many (often all) plant tissues
  - The tissue where the hormone is produced can also respond to it
  - However, some plant hormones are transported to other parts of the plant, where they exert their influence

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In Plants

- Each hormone causes responses in many plant parts, but the specific response depends on:
  - Plant species and plant part
  - The plant's or tissue's developmental stage, which influences ***sensitivity*** to the hormone
  - Hormone concentration
  - Interaction with other hormones
  - Various environmental factors

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The 5 Major Plant Hormones

- Ethylene
- Auxin
- Gibberellin
- Cytokinin
- Abscisic Acid

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Interactions Among Plant Hormones

- Auxins (IAA)
- Gibberellins (GA)
- Cytokinins (CK)

→ Associated with growth & development by regulating cell division, enlargement & maturation

- Abscisic acid (ABA)
- Ethylene (C_2H_4)

→ Antagonize the activities of IAA, GA & CK; function mainly in senescence

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Additional Hormones?

- Brassinosteroids – promote stem elongation and cell division
- Jasmonic acid
- Salicylic acid

Defense against herbivores and pathogens

- Systemin – wound response
- Polyamines – stress tolerance

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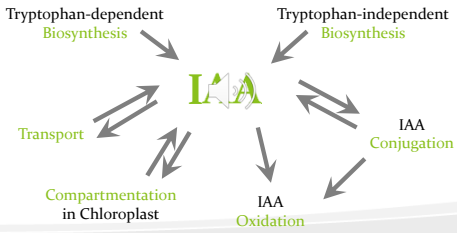
Breakdown/Conjugation



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Postharvest Application of Plant Hormones

- Treating climacteric fruits with ethylene hastens ripening
- Treating nonclimacteric fruits with ethylene hastens senescence
- Treating climacteric fruits and some nonclimacteric fruits with ABA also hastens ripening

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Postharvest Application of Plant Hormones

- Auxin, gibberellin or cytokinin applications can retard fruit senescence
  - GA delays chlorophyll loss in citrus fruits
  - 2,4-D (a synthetic auxin) is used to delay lemon "button" senescence

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Postharvest Application of Plant Hormones

- Auxin, gibberellin or cytokinin applications can retard vegetative senescence
  - 6-benzylamino purine (a synthetic cytokinin) delays senescence
  - Zeatin and dehydrozeatin (cytokinins) retard broccoli chlorophyll loss and senescence

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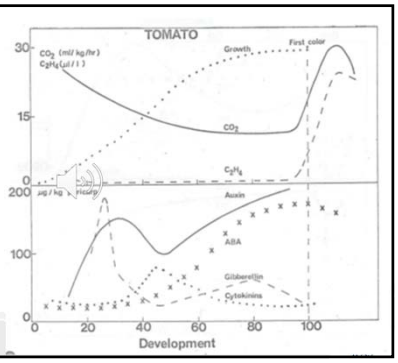
Trends in free hormone levels in tomato fruit pericarp tissue



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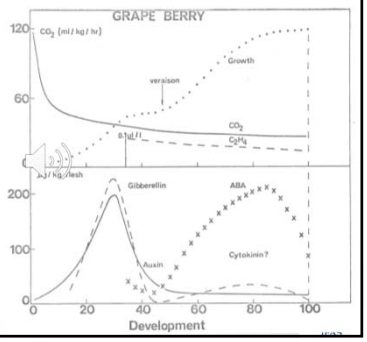
Trends in free hormone levels in grape berry pericarp tissue



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Available data on the natural levels of the various hormones in fruits point out:

- the diversity among species
- the large changes that occur during development and senescence
- the lack of close correlations between the levels of extractable hormones and the stage of development

➢ ***Something other than changes in hormone concentrations must be involved***

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Hormonal Action

- At different developmental stages or in different tissues, cells…
  - May be unresponsive to a particular hormone in the environment (*i.e.*, they are "blind" to it)
  - May become more sensitive to the hormone, so that the same low hormone concentration begins to elicit a response
  - May become less sensitive to the hormone
  - The same hormone concentration elicits a positive response in one tissue (*e.g.*, shoots) while eliciting a negative response in another (*e.g.*, roots).

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The role of each class of hormone may be direct or indirect through effects on other hormones

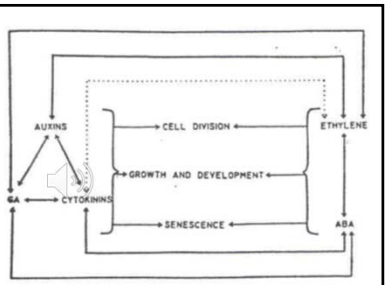

Figure 5. Hypothetical scheme of linkages and feedback relationships between category 1 and category 2 plant hormones related to their overall influences on growth, development, maturation, and senescence

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Hormone Action

- Hormone responses are transduced *via* binding to unique receptor sites
  - "Sensitivity" to hormones changes during development
    - changes in receptors
    - changes in receptor regulation
    - changes in receptor concentration
  - Balance between levels of different hormones changes

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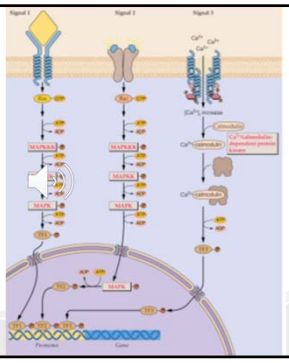
Many signals are transduced by protein kinase cascades that regulate gene expression.



Buchanan et al. 2000. Biochemistry and Molecular Biology of Plants. ASPP Press.

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What is Ethylene?

- A simple, gaseous hydrocarbon synthesized by all plant tissues and by some microorganisms – C_2H_4
- The natural aging and ripening hormone, it is physiologically active in trace amounts (≤0.1 ppm)
- Flammable limits in air = 3.1 to 32% by volume (≥31,000 ppm)

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Explosion, fire destroy banana ripening facility

The Packer July 12, 1999

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Ethylene as an Air Pollutant

- Natural sources: plants, soil, natural gas, burning vegetation
  - All plants, esp. fruits, and wounded or decaying tissues
- Human sources: refuse & biomass burning (61%), combustion of coal, oil and gas (28%)
- Also, an industrial byproduct, in cigarette smoke, produced by fluorescent ballasts and rubbers exposed to heat or UV light, etc.

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Ethylene Production by Fruits

- Levels of production and internal concentrations vary widely among different fruits
- Production is closely related to respiration in climacteric fruits
  - Ethylene increase with ripening may begin before or after climacteric rise in respiration (related to sensitivity/resistance)
  - Autocatalytic ethylene production

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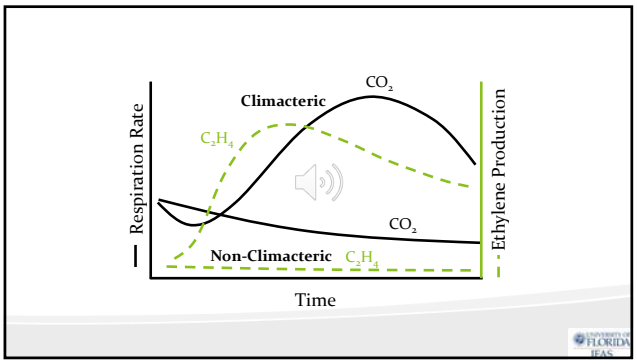

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Classification of Horticultural Commodities According to Their Ethylene Production

Class	Range at 20°C (ul C_2H_4/kg-hr)	Commodities
Very Low	0.01 - 0.1	Cherry, citrus, grape, strawberry, pomegranate, leafy vegetables, root vegetables, potatoes, cut flowers
Low	0.1 - 1.0	Blueberry, cucumber, okra, peppers, persimmon, pineapple, raspberry
Moderate	1.0 - 10	Banana, fig, honeydew melons, mango, tomato
High	10 - 100	Apple, apricot, avocado, cantaloupe, feijoa, kiwifruit, nectarine, papaya, peach, pear, plum
Very High	>100	Cherimoya, passion fruit, sapote, mammee apple

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Ethylene Production by Pathogens

- Many species of bacteria & fungi that are plant pathogens produce ethylene, *e.g., Penicillium digitatum* ('green mold')
- Diseased plant tissues of all types produce elevated levels of ethylene
  - tulip bulbs infected by *Fusarium oxysporum* produce enough ethylene to cause gummosis and floral abortion in uninfected bulbs stored in the same room

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Ethylene Effects – the "Triple Response" of Seedlings

1. Inhibition of elongation growth in dark-grown seedlings
2. Promotion of radial growth swelling of the stem)
3. Mediates tight closure of the apical hook

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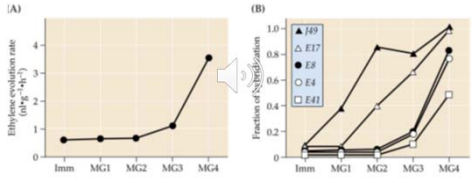
Ethylene-induced Gene Expression



Ethylene production (A) and ethylene-induced gene expression (B) in ripening tomato fruit. MG1 through MG4 refer to internal development of outwardly green fruit.

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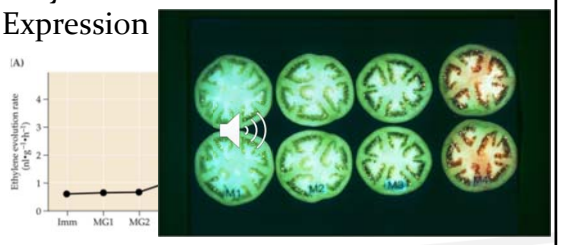
Ethylene-induced Gene Expression



Ethylene production (A) and ethylene-induced gene expression (B) in ripening tomato fruit. MG1 through MG4 refer to internal development of outwardly green fruit.

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Ethylene Effects in Postharvest Horticulture

Desirable	Undesirable
Promotes faster, more uniform fruit ripening	Promotes softening of fruits
Used for de-greening of citrus	Hastens senescence of plant tissues
Loosens fruits & nuts for mechanical harvest	Promotes abscission of leaves and flowers
	Promotes phenolic metabolism related to lignification and oxidative browning
	Causes/promotes some physiological disorders

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Ethylene Biosynthesis

- Synthesized from the amino acid methionine
  - requires ATP and O_2
  - *ACC Synthase* (ACS) is the rate-limiting step
  - *ACC Oxidase* (ACO) is constitutive
- Methionine is regenerated via the Yang cycle
  - methionine regeneration also requires ATP and O_2

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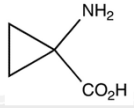
Ethylene Biosynthesis

- Aminocyclopropane carboxylic acid (ACC) is the unique precursor of ethylene
- ACC can be synthesized in one part of the plant and then be transported and exert its effect elsewhere through conversion to ethylene



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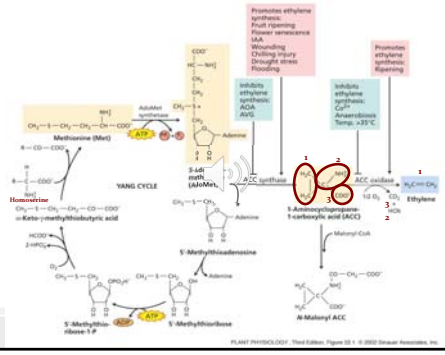

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Ethylene Biosynthesis Regulation - ACS

- The ethylene pathway is the same in all plant tissues, but the regulation differs
- ACS is rate-limiting and is
  - Induced by wounding and stress (anaerobiosis, heat, cold, drought, etc.) in all plant tissues
  - Induced by ethylene in climacteric tissues only
  - Induced by auxin in vegetative tissues

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Ethylene Biosynthesis Regulation - ACO

- ACC Oxidase is usually present in excess and rapidly converts ACC to ethylene
  - ACO activity (like ACS) also increases during climacteric fruit ripening
  - ACO activity is inhibited by low O_2 and high temperature (>35C)
  - ACO activity is dependent on presence of low levels of CO_2

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Ethylene Action

- Ethylene binds to a number of different copper-containing, protein receptors in several "families"
  - receptor-kinase complexes act to prevent constitutive ethylene responses in the absence of ethylene
  - ethylene binding "de-represses" the response pathways

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Ethylene Action

- In other words, ethylene responses are always ready to go, being held back by the receptors (negative regulators)
- Ethylene binding to the receptors is like pulling a plug, allowing an almost instantaneous cascade of responses to proceed

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Ethylene Action

- Ethylene binding activates a cascade of responses:
  - the ethylene-receptor membrane complexes interact with the kinase CTR1 in the membrane, which in turn negatively regulates a membrane transporter protein (EIN_2)
  - EIN_2 initiates a transcription cascade via two families of transcription factors (EIN_3/EIL → ERF_1) in the nucleus, leading to ethylene responses

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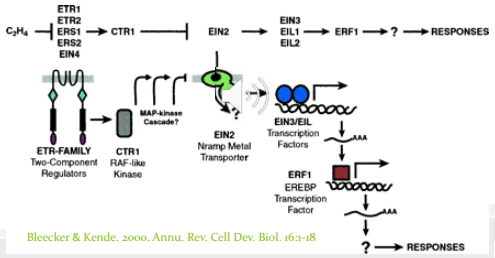
The Ethylene Signal Transduction Pathway



Bleecker & Kende. 2000. Annu. Rev. Cell Dev. Biol. 16:1-18

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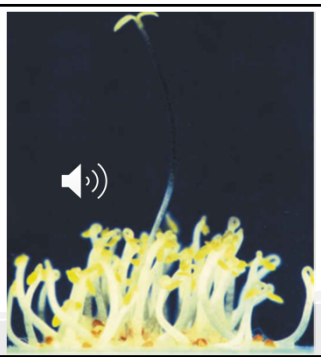
An ethylene-insensitive mutant of Arabidopsis is revealed by its lack of the triple response



Buchanan et al. 2000. Biochemistry and Molecular Biology of Plants. ASPP Press.

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Factors Affecting Ethylene Production & Action

- Genotype (species and cultivar)
  - avocado vs. apple vs. citrus vs. lettuce, etc.
  - *e.g.*, plum cultivars with different ethylene production & ripening rates
- Physiological age
  - ethylene production and response of climacteric fruits depends on their physiological age

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Factors Affecting Ethylene Production & Action

- Temperature
  - peak ethylene production at ~25C
  - ethylene production inhibited above 30C
- Oxygen level
  - reduced O_2 (<8%) reduces ethylene action and production rates
  - Elevated O_2 (>21%) stimulates ethylene production and action

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Factors Affecting Ethylene Production & Action

- CO_2 level
  - CO_2 competitively inhibits ethylene action, consequently, it can also inhibit autocatalytic ethylene production
  - However, CO_2 injury can induce elevated ethylene production
- Exogenous ethylene
  - ethylene exposure induces climacteric fruits to initiate autocatalytic ethylene production
  - No effect on nonclimacteric ethylene production

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Factors Affecting Ethylene Production & Action

- Other hydrocarbons
  - propylene, carbon monoxide, acetylene, etc. can enhance ethylene production by fruits because they mimic ethylene action
- Stresses
  - physical damage, diseases, fumigation, irradiation, etc. are all stresses that stimulate ethylene production

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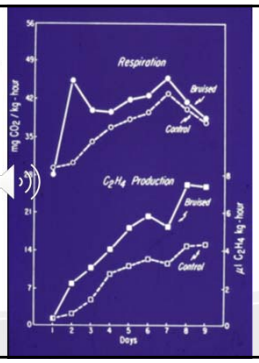
Effect of impacts (drops) on respiration and ethylene production of tomatoes damaged at the mature-green stage and held at 20°C



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Factors Affecting Ethylene Production & Action

- Growth regulators
  - may reduce or stimulate ethylene production depending on the growth regulator
- Inhibitors
  - biosynthesis inhibitors (AVG, AOA)
  - action inhibitors (CO_2, Ag^+, 1-MCP)

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