Ethylene and Other Plant Hormones: Role in Senescence

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1

Definition of a "Hormone"

- Naturally occurring, organic substances that exert profound influences on physiological processes at very low concentrations
  - From the Greek "ho[illegible]n" = "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"

3

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

4

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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6

The 5 Major Plant Hormones

- Ethylene
- Auxin
- Gibberellin
- Cytokinin
- Abscisic Acid

7

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

8

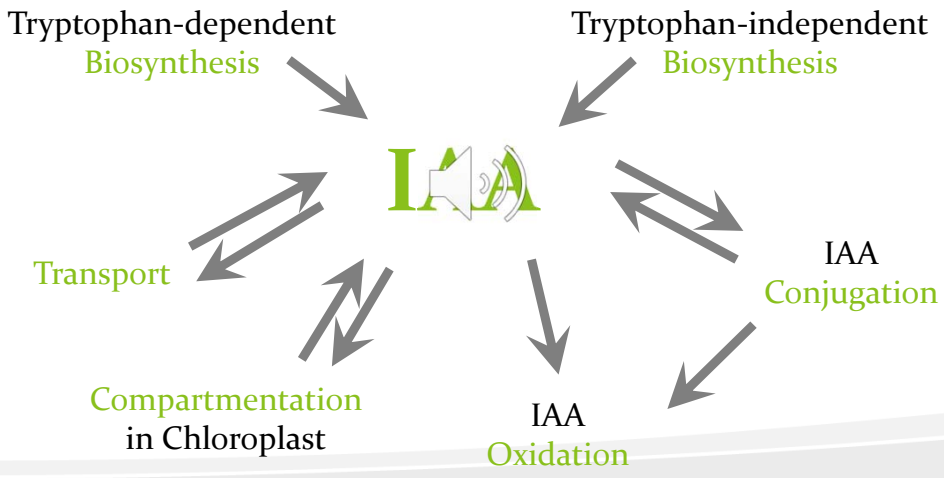
Additional Hormones?

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

  Defense against herbivores and pathogens
- Systemin – wound response
- Polyamines – stress tolerance

9

Breakdown/Conjugation



10

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

11

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

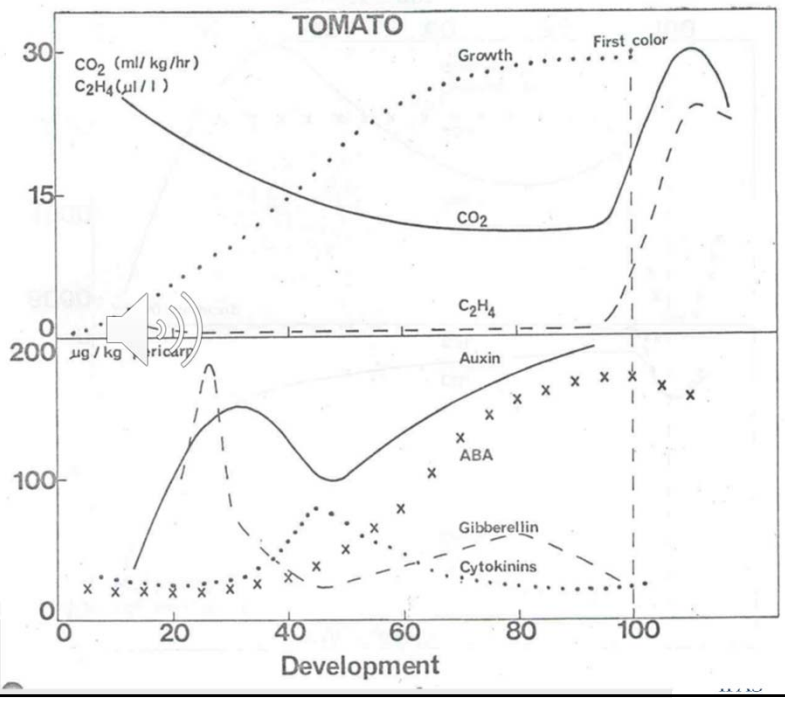
12

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

13

Trends in free hormone levels in tomato fruit pericarp tissue



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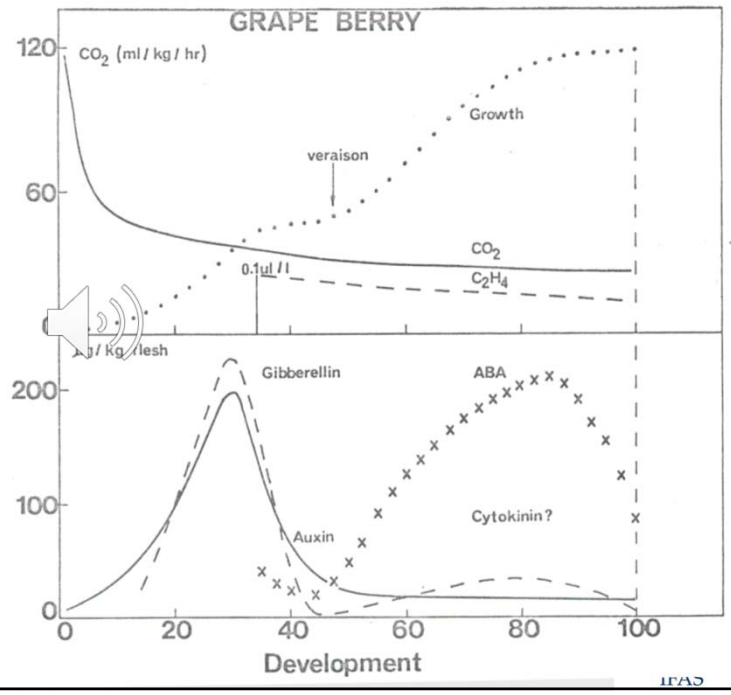
Trends in free hormone levels in grape berry pericarp tissue



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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***

16

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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17

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

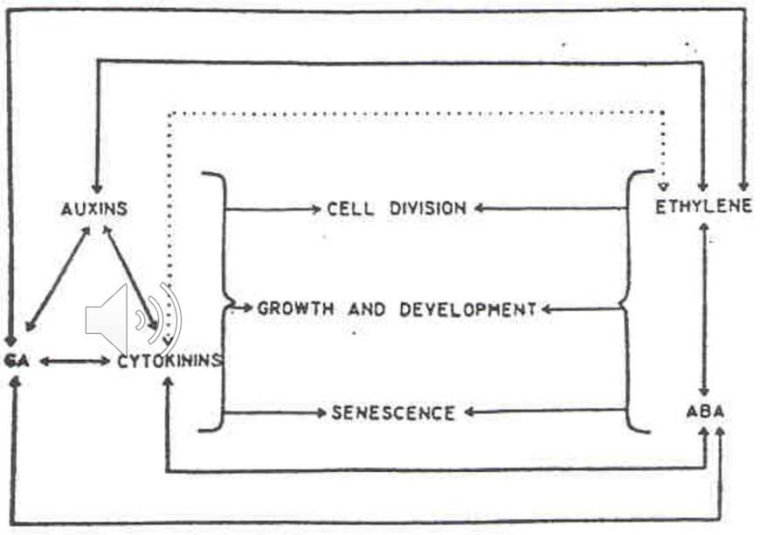


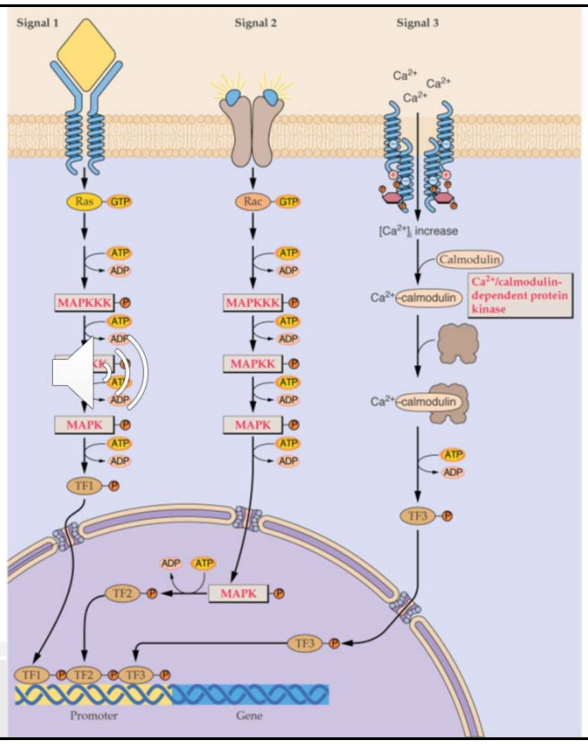
Figure 5. Hypothetical scheme of linkages and feedback relationships between category 1 and category 2 plant hormones related to their overall influences on growth, development, maturation, and senescence

18

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

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



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

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

'ACKER July 12, 1999

Tom Burfield/The Packer

One worker was killed and several others injured in an explosion and fire at Pan-American Banana Co., Los Angeles, on July 6. The cause of the explosion is unknown, but firefighters suspect ethylene gas or propane could be responsible.

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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23

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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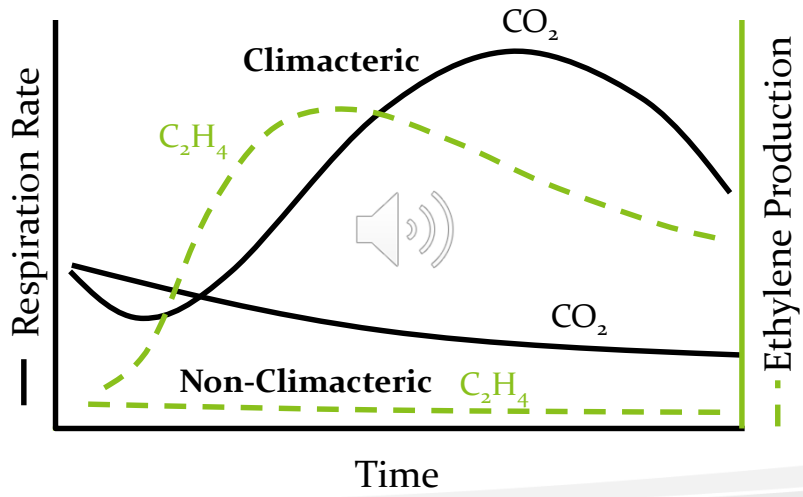
24



25

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

26

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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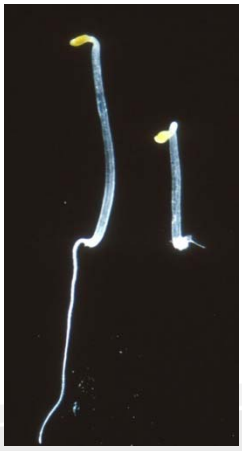
27

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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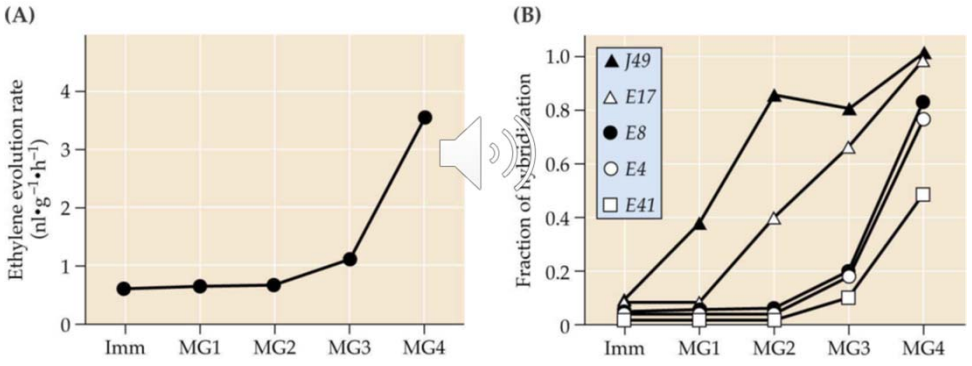
28

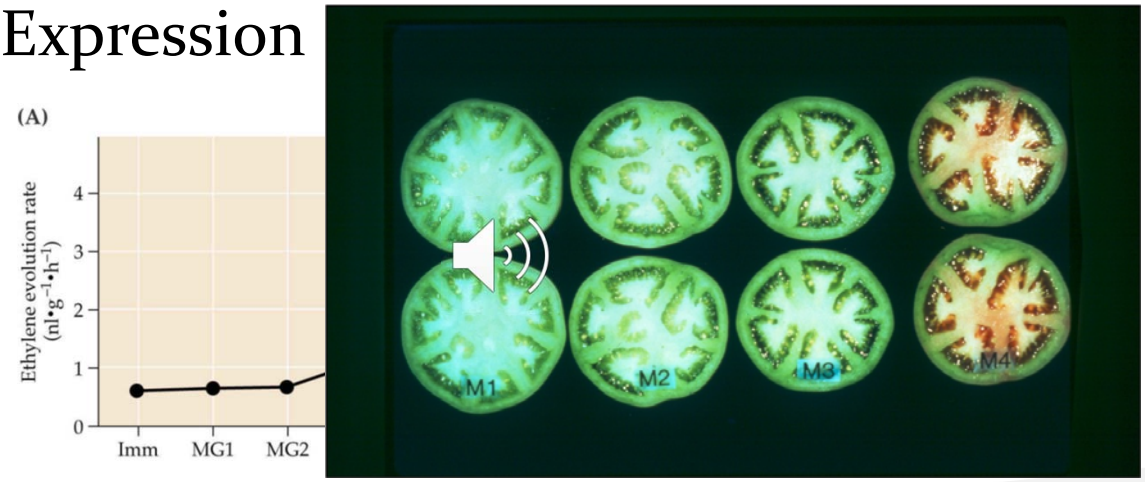
Ethylene-induced Gene Expression



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

29

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.

30

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

31

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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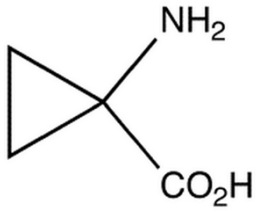
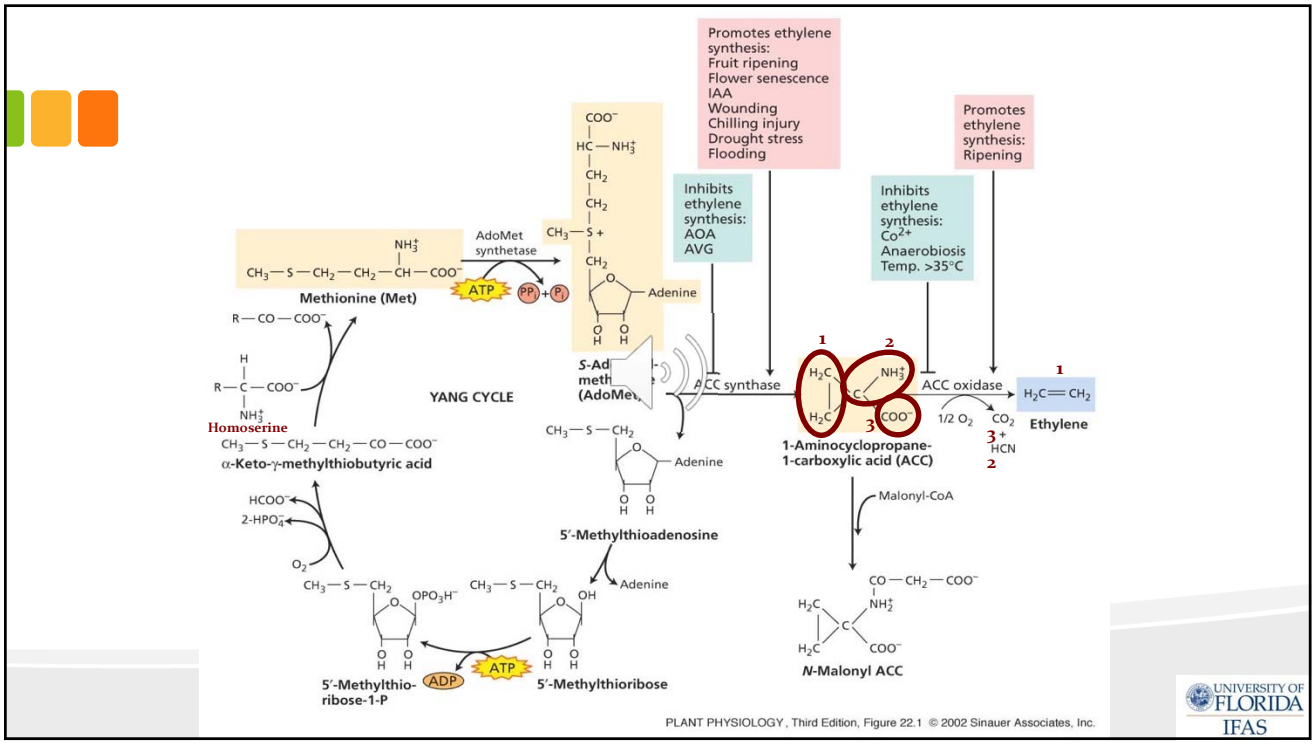
32

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





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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35

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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36

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

37

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

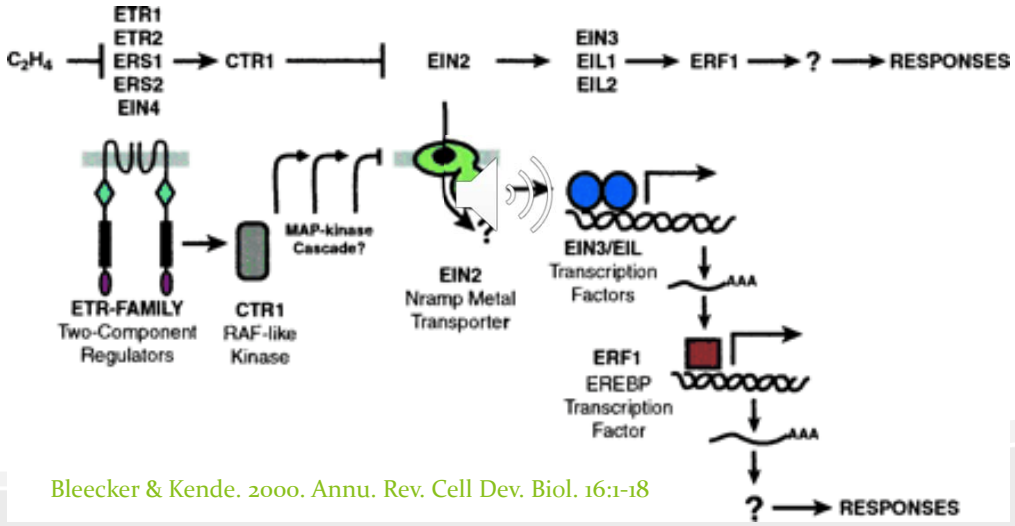
38

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 (EIN2)
  - EIN2 initiates a transcription cascade via two families of transcription factors (EIN3/EIL → ERF1) in the nucleus, leading to ethylene responses

39

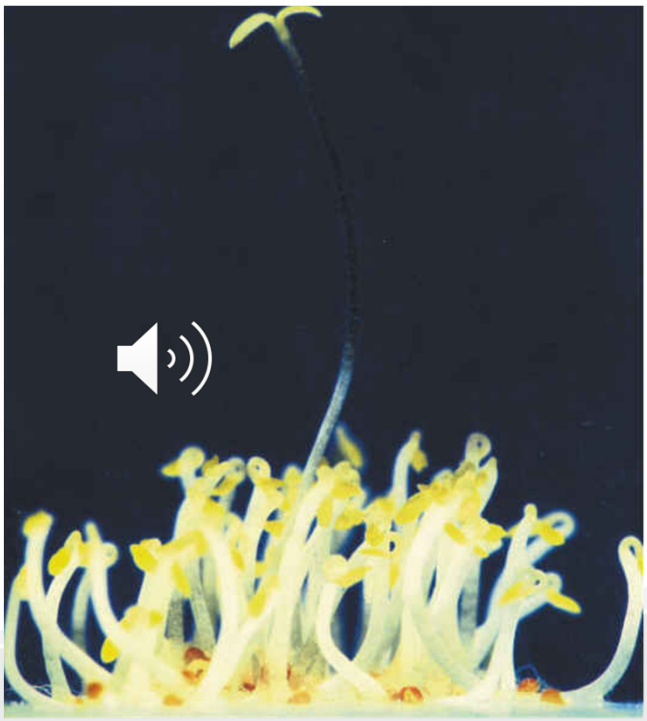
The Ethylene Signal Transduction Pathway



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

40

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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41

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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42

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

43

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

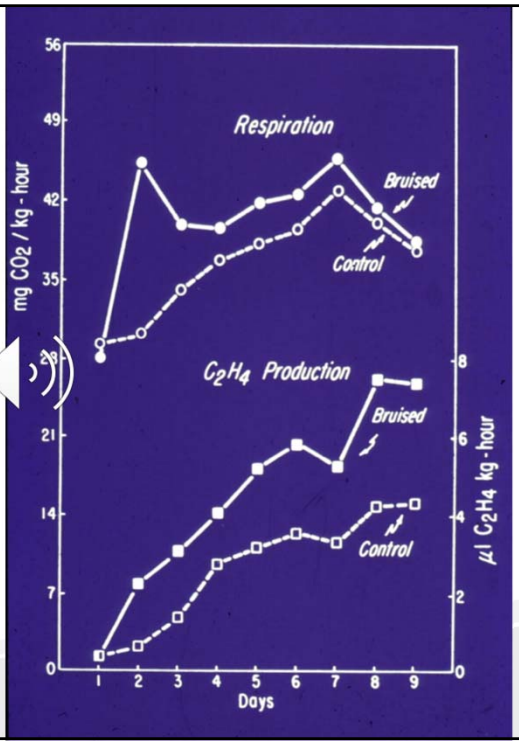
44

Factors Affecting Ethylene Production & Action

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

45

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



46

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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47