



## Introduction to Phytohormones

## What are phytohormones?



Frits Went, 1903-1990







Kenneth Thimann, 1904-1997


".....characterized by the property of serving as chemical messengers, by which the activity of certain organs is coordinated with that of others".  
 -Frits Went and Kenneth Thimann, 1937


## Phytohormones


Phytohormones control cellular activities (division, elongation and differentiation), and processes including pattern formation, sex determination, organogenesis, and responses to abiotic and biotic stress.








## Phytohormones – old timers and newcomers


  
Auxin


  
Cytokinin


  
Gibberellin


  
Abscisic Acid

  
Ethylene

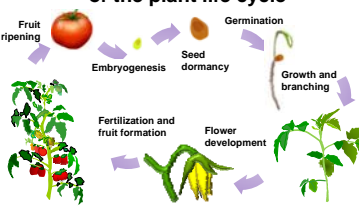
  
Brassinosteroid

  
Salicylic Acid

  
Strigolactone

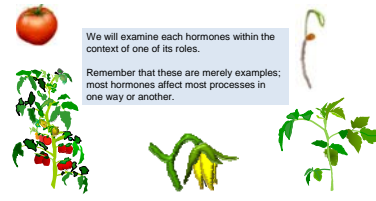
  
Jasmonic Acid

## Phytohormones regulate all stages of the plant life cycle



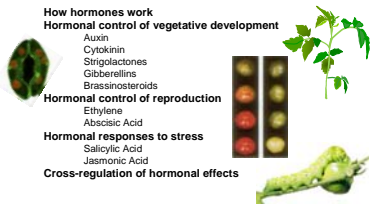
## Most hormones affect most stages of the plant life cycle

We will examine each hormone within the context of one of its roles.  
 Remember that these are merely examples; most hormones affect most processes in one way or another.

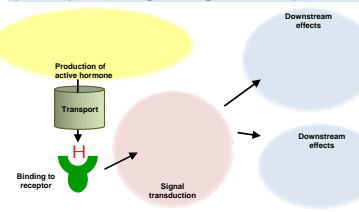


## Lecture outline

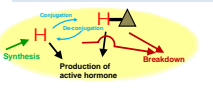
- How hormones work
- Hormonal control of vegetative development
  - Auxin
  - Cytokinin
  - Strigolactones
  - Gibberellins
  - Brassinosteroids
- Hormonal control of reproduction
  - Ethylene
  - Abscisic Acid
- Hormonal responses to stress
  - Salicylic Acid
  - Jasmonic Acid
- Cross-regulation of hormonal effects



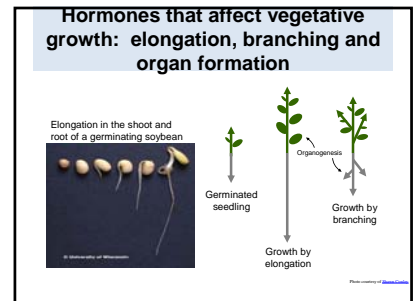
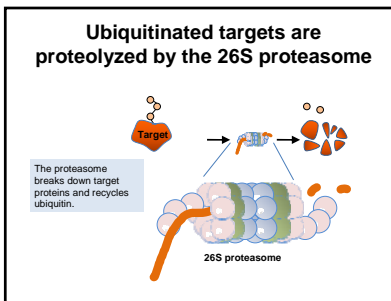
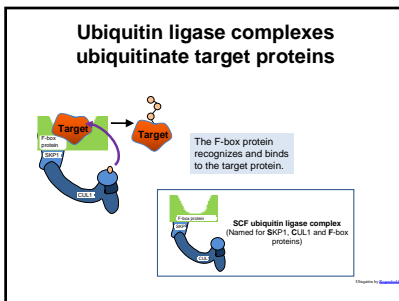
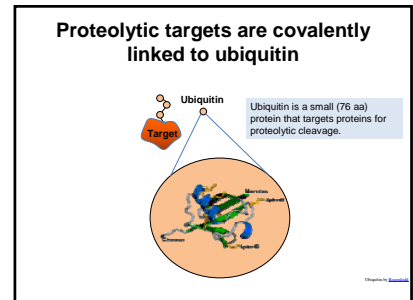
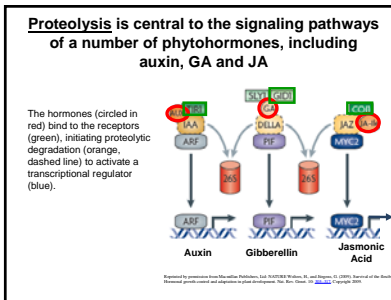
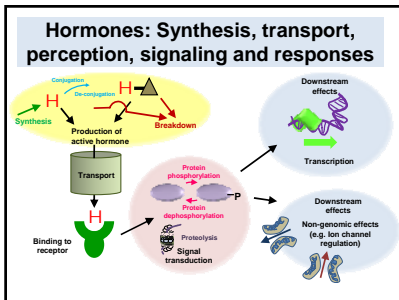
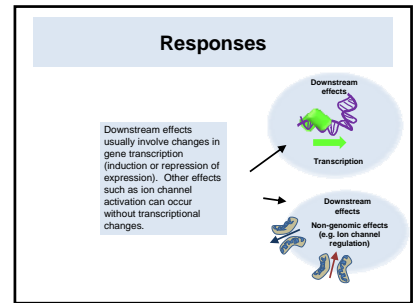
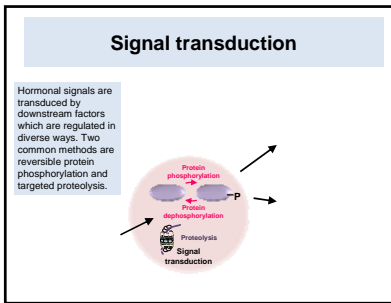
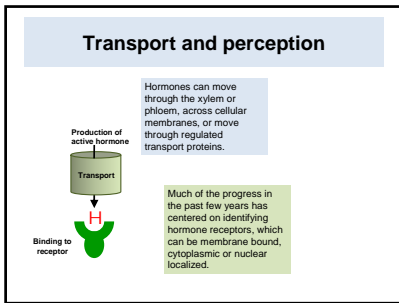
## Hormones: Synthesis, transport, perception, signaling and responses



## Synthesis



Many biochemical pathways contribute to active hormone accumulation. These pathways are tightly regulated. Conjugation can temporarily store a hormone in an inert form, lead to catabolic breakdown, or in the case of jasmonic acid be the means for producing the active hormone.



### Disrupting hormone synthesis or response interferes with elongation

GA	Auxin	Brassinosteroid
Wild type Gibberellin biosynthesis mutant	Wild type Auxin response mutant	Wild type Brassinosteroid biosynthesis mutant

Went, F.W., Snow, C.S., Thimann, S.V., and Reed, D.B. (1940) Growth of pea roots in relation to gibberellin. *Journal of Experimental Botany* 11: 1-14.  
Went, F.W. (1948) Auxin and growth. *Journal of Experimental Botany* 19: 1-14.  
Went, F.W. (1949) Brassinolide, a growth substance from Brassica napus L. *Journal of Experimental Botany* 20: 1-14.

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### Auxin

- Growth
- Phototropism and gravitropism
- Branching
- Embryonic patterning
- Stem cell maintenance
- Organ initiation

Indole-3-acetic acid (IAA), the most abundant natural auxin

### Auxin controls growth

Charles Darwin studied the way seedlings bend towards light, a direct effect of auxin action.

Site of signal perception

Site of response

Charles Darwin, Darwin, C., and Darwin, F. (1880) The power of movement in plants. *Journal of Experimental Botany* 1: 1-14.

### Darwin concluded that a signal moves through the plant controlling growth

"We must therefore conclude that when seedlings are freely exposed to a lateral light some influence is transmitted from the upper to the lower part, causing the latter to bend."

Charles Darwin, Darwin, C., and Darwin, F. (1880) The power of movement in plants. *Journal of Experimental Botany* 1: 1-14.

### Differential cell growth is a result of auxin movement to the shaded side

Auxin concentration

Auxin accumulation on shaded side stimulates elongation and bending.

Went, F.W. (1926) A gradient of auxin in coleoptiles. *Journal of Experimental Botany* 17: 1-14.

### Auxin moves in part by a chemiosmotic mechanism

Auxin is a charged anion (IAA<sup>-</sup>) in the cytoplasm (pH 7). In the more acidic cell wall (pH 5.5) some is uncharged (IAAH). The uncharged form crosses the plasma membrane into the cell where it is deprotonated and unable to exit other than through specific transporters.

Reber, R., and Raven, J.H. (1978) Auxin and other signals in the stem of plants. *The Plant Cell* 1: 1-14.

### Polar auxin transport

Auxin transport out of cells is controlled by three families of transport proteins that collectively control the directionality of auxin movement. Asymmetric distribution of the transporters controls polar auxin transport.

Net flow of auxin

Reber, R., and Raven, J.H. (1978) Auxin and other signals in the stem of plants. *The Plant Cell* 1: 1-14.

### Auxin controls plant development

Promote and specify lateral organ initiation at the shoot apical meristem

Inhibit branching in the shoot

Control patterning and vascular development

Promote branching in the root

Went, F.W., and Skogerboe, G. (1949) Auxin and other signals in the stem of plants. *The Plant Cell* 1: 1-14.

### Many of auxin's effects are mediated by changes in gene expression

Genes controlling cell growth

Genes involved in signaling

Genes coordinating other hormone response pathways

Went, F., and Thimann, G. (1937). *Hormonal Control of the Growth of Plants*. New York: McGraw-Hill.

### Auxin-induced changes in gene expression

**Low Auxin**

In low-auxin conditions, auxin responsive transcription factors (ARFs) are complexed with Aux/IAA proteins, which repress their function.

### In high auxin, the TIR1 auxin receptor binds Aux/IAA proteins

**Low Auxin**

**High Auxin**

### TIR1 is an F-box protein, part of the SCF ubiquitin ligase complex

SCF complex

### Auxin binding to TIR1 initiates proteolysis of Aux/IAA proteins

Ub

+ Auxin

Growth promotion

Removal of the repressors allows ARFs to regulate transcription.

### Lecture outline

**How hormones work**

**Hormonal control of vegetative development**

- Auxin
- Cytokinin
- Strigolactones
- Gibberellins
- Brassinosteroids

**Hormonal control of reproduction**

- Ethylene
- Abscisic Acid

**Hormonal responses to stress**

- Salicylic Acid
- Jasmonic Acid

**Cross-regulation of hormonal effects**

### Cytokinins

trans-zeatin, a cytokinin

- Cell division
- Control of leaf senescence
- Control of nutrient allocation
- Root nodule development
- Stem cell maintenance
- Regulate auxin action

### Cytokinins are a family of related adenine-like compounds

isopentenyl adenine (iP)

trans-zeatin (tZ)

dihydrozeatin (dZ)

zeatin (zZ)

adenine

Went, F., and Thimann, G. (1937). *Hormonal Control of the Growth of Plants*. New York: McGraw-Hill.

### Cytokinins act antagonistically to auxins

<b>CK</b>	<b>Auxin</b>	
Promote stem cell fate at the shoot apical meristem	Promote lateral organ initiation at the shoot apical meristem	Promote branching in the shoot
		Inhibit branching in the shoot
Promote differentiation at the root apical meristem	Maintain stem cell fate at the root apical meristem	Promote branching in the root
		Inhibit branching in the root

Went, F., and Thimann, G. (1937). *Hormonal Control of the Growth of Plants*. New York: McGraw-Hill.

### Auxin and cytokinin regulate each other's function at the root apex

Through effects on each other's synthesis, transport and response, auxin and cytokinin establish two mutually exclusive domains that coordinate cellular activities at the root apex.

### Auxin, cytokinin and strigolactones control branching

Shoot branches are promoted by CK and strigolactones and inhibited by auxin.

Root branches, called lateral roots, are promoted by auxin and inhibited by CK.

Branching controls every aspect of plant productivity from nutrient uptake to crop yields.

### Cytokinin signaling is mediated by a two-component system

A two-component system is a short signaling pathway that moves information from an input to an output. In bacteria it usually consists of two proteins, a histidine kinase (HK) with a conserved histidine residue (H) and a response regulator (RR) with a conserved aspartate residue (D).

### Information and phosphoryl groups are relayed between the components

Stimulation of the input domain activates the kinase activity, phosphorylating the transmitter domain. The phosphoryl group is subsequently relayed to the response regulator.

### Two component signaling in plants

Most plant HKs are hybrid histidine kinase, which transfer the phosphoryl group to a histidine phosphotransferase. The HPT transfers it to a response regulator.

### Cytokinin control of gene expression in Arabidopsis

Type B Arabidopsis response regulators (ARRs) are transcription factors. Type A or C ARRs interfere with CK signaling through as yet unknown means.

### Cytokinins affect grain production and drought tolerance

Rice plants that accumulate more CK can produce more grain per plant because of changes in inflorescence architecture.

Tobacco plants that produce more CK are more drought tolerant because of the delay in leaf senescence conferred by CK.

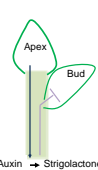
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### Strigolactones


Strigolactones, synthesized from carotenoids, are produced in plant roots. They attract mycorrhizal fungi and promote the germination of parasitic plants of the genus *Striga*.

### Strigolactones inhibit branch outgrowth



Auxin transported from the shoot to the root induces strigolactone synthesis, which inhibits bud outgrowth.

In a rice mutant that does not produce strigolactones, tillers (lateral branches) grow out as shown.



WT Mutant

Lee, H., et al. (2008) BRB27, a rice mutant gene mapped for the repression of tiller outgrowth, regulates auxin root response. Plant Cell 20. [DOI: 10.1105/PC.107.2008](#)

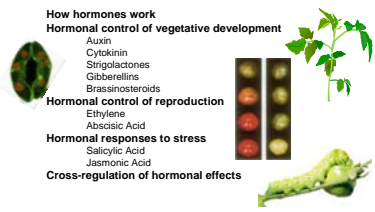
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**Hormonal control of reproduction**  
Ethylene  
Abscisic Acid

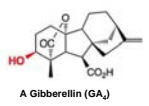
**Hormonal responses to stress**  
Salicylic Acid  
Jasmonic Acid

**Cross-regulation of hormonal effects**



### Gibberellins

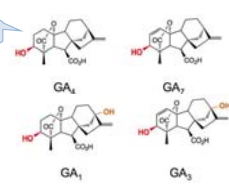
- Growth
- Seed germination
- Promote flowering
- Promote sex determination in some species
- Promote fruit growth



A Gibberellin (GA<sub>3</sub>)

### Gibberellins are a family of compounds

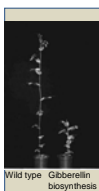
GA<sub>1</sub> is the major active GA in Arabidopsis



Only some GAs are biologically active. The major bioactive gibberellins are shown here.

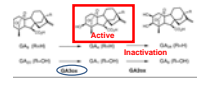
Lee, H. (2008) Gibberellins: biochemistry, genetics and signaling pathways in Arabidopsis. September 10, 2008. The Arabidopsis Book, Book 10. DOI: 10.1191/0950268808arab0101a

### Gibberellins regulate growth



Wild type: Gibberellin biosynthesis mutant: *le*


The pea mutant *le*, studied by Mendel, encodes GA<sub>3</sub> oxidase, which produces active GA. Loss of function of *le* reduces active GA levels and makes plants dwarfed.



Lee, H., Lee, J., Davis, P.J., and Reed, J.R. (1995) Dwarfed Lemnong pea (*L. sativum* L.) mutants. HortScience 26:1071-1072. [DOI: 10.1590/0013-738X-1995-26-1071](#)



### Genes controlling GA synthesis are important "green revolution" genes




Tremendous increases in crop yields (the Green Revolution) during the 20<sup>th</sup> century occurred because of increased use of fertilizer and the introduction of semidwarf varieties of grains.

The semidwarf varieties put more energy into seed production than stem growth, and are sturdier and less likely to fall over.

Distinguished plant breeder and Nobel Laureate **Norman Borlaug 1914-2009**

Photos courtesy of B. Borlaug. [DOI: 10.1007/978-1-4020-2242-9\\_10](#)

### Several of the green revolution genes affect GA biosynthesis

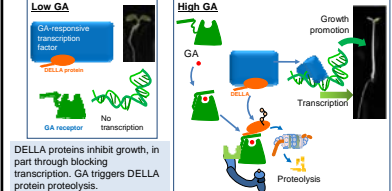


Wild-type Semidwarf

Semidwarf rice varieties underproduce GA because of a mutation in a the GA20 oxidase biosynthetic gene.

Reprinted by permission from Dordrecht Publishers Ltd., Oliver Smith, A., et al. (2002) Green revolution: a major genetic revolution. In: The Green Revolution: Genes and Genomes. Springer, New York, NY, pp. 1-10. [DOI: 10.1007/978-1-4020-2242-9\\_10](#)

### GA signaling pathway



**Low GA**  
GA-responsive transcription factor  
DELLA proteins  
GA receptor  
No transcription

**High GA**  
Growth promotion  
Transcription  
Proteolysis

DELLA proteins inhibit growth, in part through blocking transcription. GA triggers DELLA protein proteolysis.

Reprinted from Figure 1.18. In: Lee, H., and Reed, J.R. (2008) Gibberellin signaling pathways. In: The Green Revolution: Genes and Genomes. Springer, New York, NY, pp. 1-10. [DOI: 10.1007/978-1-4020-2242-9\\_10](#)

### A gene affecting DELLA protein stability is a "green revolution" gene

**Wild-type**  
GA binds to DELLA, leading to its degradation. The *Rht1* gene encodes a DELLA protein that lacks the DELLA domain and resists proteolysis, leading to a dwarf phenotype.

**Dwarf *rht1***  
The wheat *Rht1* locus encodes a DELLA protein. The dwarf allele lacks the DELLA domain and resists proteolysis.

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### Brassinosteroids

- Cell elongation
- Pollen tube growth
- Seed germination
- Differentiation of vascular tissues and root hairs
- Stress tolerance

Brassinolide, the most active brassinosteroid

### Brassinosteroid (BR) mutants are dwarfed

BRs promote cell elongation in part by loosening cell walls

Cell wall loosening

Lowered resistance to internal turgor pressure; cell expansion

Reid, M. J., and Evans, C. Brassinosteroid and plant growth hormone signaling. (2005) Plant Cell 17:115-125.

### Reducing BR signaling produces dwarf barley

Wild-type → Cell elongation

uzu → Less cell elongation

The uzu plants have a missense mutation in the BR receptor, making them less sensitive to BR. This is the first dwarf grain produced through modification of BR signaling.

Chen, M. et al. (2005) A mutation of barley grain yields from brassinosteroid signaling in wheat. (2005) Plant Cell 17:115-125.

### BR signaling

Without BR, the receptor (BR1) is bound to an inhibitor (BK1). The active BIN2 kinase phosphorylates and inactivates transcription factors.

### BR signaling

**Low BR**  
Receptor (BR1) is bound to inhibitor (BK1). BIN2 kinase is active and phosphorylates transcription factors, inactivating them.

**High BR**  
BR binds to the receptor (BR1), causing it to phosphorylate BAK1 and the BR1 receptor to phosphorylate each other and BSKs. BSKs phosphorylate and activate BSU1 phosphatase, which inactivates BIN2. When BIN2 is inactive, its target transcription factors are dephosphorylated and active.

Transcription

### Summary – hormonal control of vegetative growth

Plant hormones have diverse effects on plant growth.

Auxin, gibberellic acid and brassinosteroids contribute to elongation growth.


Auxin, cytokinin and strigolactones control branching patterns.

Growth and branching profoundly affect crop yields.

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### Hormonal control of reproductive development




In angiosperms, reproduction includes the transition from vegetative to reproductive growth, fruit development and ripening, and seed development, maturation and germination. All of these events are to some extent affected by hormonal signals.

Photos courtesy of [iStockphoto](#)

### Transition to flowering







The decision to reproduce is tightly controlled by environmental and hormonal factors. For many plants day-length is critical in this transition, but other plants are day-length neutral. Similarly, some plants absolutely require specific hormonal signals which have little or no effects on other plants.



Photos courtesy of [iStockphoto](#)


### GA's role in initiating flowering varies by species and growth-habit

<i>Lolium temulentum</i>	<i>Beta vulgaris</i>	<i>Malus domestica</i>	<i>Arabidopsis thaliana</i>
Annual temperate grass	Biennial	Perennial	Annual
Yes	Yes	No	Short Days
			Long Days
			No

Photos courtesy of [iStockphoto](#) (from New South Wales Primary Plant, Animal, and Food of Great Britain © 1978 by permission of Elsevier), [Science Source](#), [David Huxford](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)


### Ethylene promotes flowering in pineapples and other bromeliads





A pineapple is a fruit produced from pineapple flowers. Commercial growers treat the plants with ethylene to synchronize flowering.

Photos courtesy of [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)

### Fruit development and ripening are under hormonal control






Pollination initiates petal senescence, cell division and expansion in the ovary to produce a fruit, and fruit ripening.

Photos courtesy of [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)

### Auxin and GA promote cell division and growth of the fruit

Seedless varieties of grapes and other fruits require exogenous application of GA for fruit development. Strawberry receptacles respond to auxin.

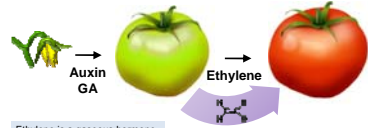
**Auxin + GA** → Apple

**GA** → Grape

**Auxin** → Strawberry

Photos courtesy of [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)

### Fruit ripening is induced by ethylene



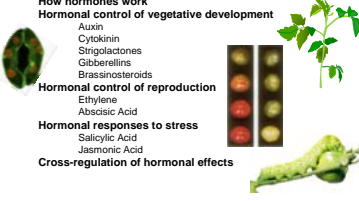
Auxin and GA promote fruit development. Ethylene then promotes ripening.

Ethylene is a gaseous hormone that promotes fruit softening and flavor and color development.

Photos courtesy of [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)

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    - Auxin
    - Cytokinin
    - Strigolactones
    - Gibberellins
    - Brassinosteroids
  - Hormonal control of reproduction
    - Ethylene
    - Abscisic Acid
  - Hormonal responses to stress
    - Salicylic Acid
    - Jasmonic Acid
  - Cross-regulation of hormonal effects



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### Ethylene

- Control of fruit ripening
- Control of leaf and petal senescence
- Control of cell division and cell elongation
- Sex determination in some plants
- Control of root growth
- Stress responses

$$\begin{array}{c}
 \text{H} & & \text{H} \\
 & \backslash & / \\
 & \text{C} = \text{C} \\
 & / & \backslash \\
 \text{H} & & \text{H}
 \end{array}$$

Photos courtesy of [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#), [iStockphoto](#)

### Ethylene promotes senescence of leaves and petals

**Air (control) 7 days ethylene**

**Ethylene promotes leaf and petal senescence.**

In gas-tight houses, plants were harmed by the ethylene produced from burning gas. *Aspidistra* is ethylene-resistant and so became popular houseplant.

Reed, C. E., et al. (1995) A gene mutation of ethylene action in plants. Plant Physiol. 109: 1043-1048.

### Ethylene shortens the longevity of cut flowers and fruits

**STS CONTROL DACP 110**

Ethylene levels can be managed to maintain fruit freshness, commercially and at home.

**Strategies to limit ethylene effects**

- Limit production - high CO<sub>2</sub> or low O<sub>2</sub>
- Removal from the air - KMnO<sub>4</sub> reaction, zeolite absorption
- Interfere with ethylene binding to receptor - sodium thiosulfate (STS), diazocyclopentadiene (DACP), others

Reprinted from Reed, C. E., et al. (1995) Ethylene action in plants. Plant Physiol. 109: 1043-1048.

### Molecular genetic approaches can limit ethylene synthesis

**ACC synthase**  
S-adenosyl methionine → ACC (1-aminocyclopropane-1-carboxylic acid)

**ACC oxidase**  
ACC → Ethylene

**Antisense ACC synthase**  
Introduction of antisense constructs to interfere with expression of biosynthesis enzymes is an effective way to control ethylene production.

Shelton, A., Benedito, S. I., Gallo, P. M., Kang, S., and Gallo, J. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.

### Ethylene-regulated gene expression is negatively regulated

**Receptor**  
**CTR**

In the absence of ethylene, CTR binds the receptor and prevents transcription. Ethylene binding to the receptor releases CTR, permitting transcription.

Reed, C. E., et al. (1995) Ethylene action in plants. Plant Physiol. 109: 1043-1048.

### Ethylene perception mutants interfere with ripening

**Receptor**  
**CTR**

Several mutations that affect ethylene perception and signaling interfere with fruit ripening.

Wild type  
Green-ripe  
*Never-ripe2*  
*Never-ripe*

Reed, C. E., et al. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.

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Reed, C. E., et al. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.

### Abscisic acid

- Seed maturation and dormancy
- Desiccation tolerance
- Stress response
- Control of stomatal aperture

Reed, C. E., et al. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.

### ABA accumulates in maturing seeds

Embryonic patterning  
Reserve accumulation  
Desiccation tolerance

Seed maturation requires ABA synthesis and accumulation of specific proteins to confer desiccation tolerance to the seed.

Reed, C. E., et al. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.

### ABA synthesis and signaling is required for seed dormancy

ABA  
Protein Kinase  
Transcription Factor  
Transcription

Loss of function of ABA signaling (protein kinase or transcription factor function) interferes with ABA-induced dormancy and causes precocious germination.

Reed, C. E., et al. (2003) Molecular approaches to limit ethylene synthesis in plants. Plant Physiol. 133: 1043-1048.



### ABA binding to an intracellular receptor initiates transcriptional responses

**PYL1 is an ABA receptor.** When PYL1 binds ABA, it also binds the protein phosphatase PP2C, inhibiting its function.

Reprinted by permission of Elsevier Publishers Ltd. Hirasawa, K. et al. (2007) Structural basis of stress and signaling. *Trends Pl* 34: 102-110.

### ABA signal transduction affecting gene expression

When ABA is present, inactivation of the PP2C phosphatase permits a protein kinase (e.g. SnRK) to phosphorylate and activate ABA-inducible TFs, promoting transcription of ABA-inducible genes.

Reprinted by permission of Elsevier Publishers Ltd. Hirasawa, K. et al. (2007) Structural basis of stress and signaling. *Trends Pl* 34: 102-110.

### ABA controls stomatal aperture by changing the volume of guard cells

Pairs of guard cells surround the openings of plant pores called stomata.

Guard cells control the opening and closing of stomata to regulate gas exchange: a fine balance is required to allow CO<sub>2</sub> in for photosynthesis and prevent excessive water loss.

Reprinted by permission of Elsevier Publishers Ltd. Hirasawa, K. et al. (2007) Structural basis of stress and signaling. *Trends Pl* 34: 102-110.

### ABA controls stomatal aperture by changing the volume of guard cells

When stomata are open, plants lose water through transpiration. ABA induced by drought causes the guard cells to close and prevents their reopening, conserving water.

Reprinted by permission of Elsevier Publishers Ltd. Hirasawa, K. et al. (2007) Structural basis of stress and signaling. *Trends Pl* 34: 102-110.

### ABA-induced stomatal closure is extremely rapid and involves changes in ion channel activities

ABA triggers an increase in cytosolic calcium (Ca<sup>2+</sup>), which activates anion channels (A<sup>-</sup>) allowing Cl<sup>-</sup> to leave the cell. ABA activates channels that move potassium out of the cell (K<sub>out</sub>) and inhibits channels that move potassium into the cell (K<sub>in</sub>). The net result is a large movement of ions out of the cell.

As ions leave the cell, so does water (by osmosis), causing the cells to lose volume and close over the pore.

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### Hormonal responses to biotic stress

**Salicylic Acid**  
Bacteria, fungi, viruses – Biotrophic organisms

**Jasmonic Acid**  
Herbivores – insects, other animals, fungi – Necrotrophic organisms

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Reprinted by permission of Elsevier Publishers Ltd. Hirasawa, K. et al. (2007) Structural basis of stress and signaling. *Trends Pl* 34: 102-110.

### Salicylic Acid – plant hormone and painkiller

- Response to biotrophic pathogens
- Induced defense response
- Systemic acquired resistance

**Salicylic Acid**

Acetylsalicylic Acid – aspirin

Salicylic acid is named for the willow *Salix* whose analgesic properties were known long before the chemical was isolated.

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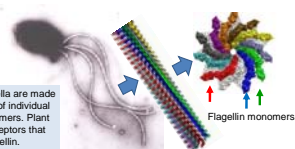
### Plants recognize PAMPs (pathogen-associated molecular patterns)

Flagellin is a conserved bacterial protein recognized by plants, also known as a pathogen-associated molecular pattern (PAMP).

Recognition of PAMPs by a plant cell triggers a set of immune responses that are mediated by salicylic acid.

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### Flagellin is an abundant bacterial protein recognized by plant cells



Bacterial flagella are made of thousands of individual flagellin monomers. Plant cells have receptors that recognize flagellin.

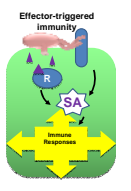
Flagellin monomers

Reprinted by permission of Macmillan Publishers Ltd. Chapman, P. V. and Staples, R. J. (2007) Controlling severity of a bacterial necrotrophic infection. *Nat Rev Microbiol* 5: 202-210. © 2007 Macmillan Publishers Ltd. All rights reserved.

### Some pathogens elicit a stronger defense response

Many plants express resistance genes (R genes) that recognize some specific bacterial proteins (effector proteins).

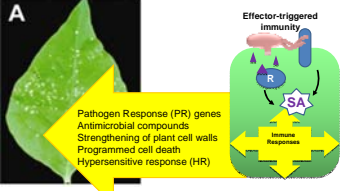
The interaction of an R protein with an effector protein promotes a stronger immune response, including the Hypersensitive Response, and SA is involved in transducing this signal.



Effector-triggered immunity

Reprinted from Pridmore, C.M., Lee-Ruff, A., Yeadon, R., and Bostock, P.M. (2005) The plant cell wall. *Plant Cell* 17: 200-210.

### The hypersensitive response involves cell death




Pathogen Response (PR) genes  
Antimicrobial compounds  
Strengthening of plant cell walls  
Programmed cell death  
Hypersensitive response (HR)

Effector-triggered immunity

Reprinted from C. Chen, A.B. Mody, L. Guo, W., and Roberts, C.B. (2005) The plant gene *EDD* enhances death of cells during the hypersensitive response to a necrotrophic fungus. *Plant Cell* 17: 211-220. © 2005 The American Society of Plant Biologists. All rights reserved.

### The hypersensitive response seals the pathogen in a tomb of dead cells



HR

No HR

The HR kills the infected cells and cells surrounding them and prevents the pathogen from spreading.

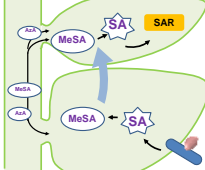
Without a hypersensitive response, the pathogen can multiply.

Reprinted with credit. [Smith-Beckler, 2004](#). *Natural Science*. Photo courtesy of Macmillan Publishers Ltd. Photo: R.J. Bostock, et al. (2005) Plant growth control and pathogen resistance. *Nat Rev Microbiol* 5: 202-210.

### Systemic Acquired Resistance (SAR)

The infected site sends signals, methyl salicylic acid (MeSA) and azelaic acid (AZA) through the veins and through airborne compounds that prime other tissues, making them resistant to pathogen attack.

This effect is called Systemic Acquired Resistance (SAR).



MeSA

AZA

SAR

Reprinted from Liu, Y.C., Meng, S.P., and Park, S.W. (2005) Systemic acquired resistance: The future is bright. *Plant Cell* 17: 110-120.

### Lecture outline

**How hormones work**

**Hormonal control of vegetative development**

- Auxin
- Cytokinin
- Stimulocines
- Gibberellins
- Brassinosteroids

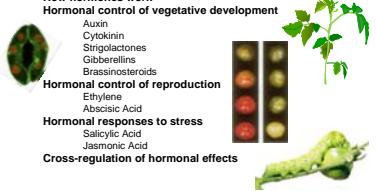
**Hormonal control of reproduction**

- Ethylene
- Abscisic Acid

**Hormonal responses to stress**

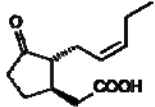
- Salicylic Acid
- Jasmonic Acid

**Cross-regulation of hormonal effects**



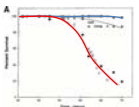
### Jasmonic Acid

- Response to necrotrophic pathogens
- Induction of anti-herbivory responses
- Production of herbivore-induced volatiles to prime other tissues and attract predatory insects



© 2005 American Chemical Society


### Jasmonic Acid signaling contributes to defense against herbivory



WT

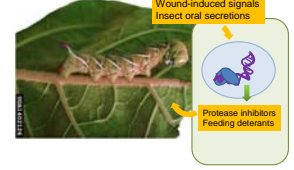
Mutant without JA

When exposed to hungry fly larvae, plants unable to produce JA have low rates of survival.



McClure, M. et al. (2007) Evidence is needed for causal effects in herbivory. *Plant Cell* 19: 100-101.

### JA induces the expression of anti-herbivorous chemicals and volatiles



Wound-induced signals  
Insect oral secretions

Protease inhibitors  
Feeding deterrents

© 2005 American Chemical Society

### JA stimulates production of volatile signaling compounds

Herbivore-induced volatiles prime other tissues (and other plants) for attack making them unpalatable (indicated in red).

Reprinted from Kliebenstein, J. 2004. The role of volatile signaling compounds in plant defense. *Plant Cell* 16: 1105-1114. doi:10.1105/PC.101105

### Herbivore-induced volatiles are recognized by carnivorous and parasitoid insects

Reprinted from Kliebenstein, J. 2004. The role of volatile signaling compounds in plant defense. *Plant Cell* 16: 1105-1114. doi:10.1105/PC.101105

### JA-induced changes in gene expression

### Other hormones affect defense response signaling

As part of their immune responses, plants modulate synthesis and response to other hormones. Some pathogens exploit the connections between growth hormones and pathogen-response hormones to their own advantage, by producing "phytohormones" or interfering with hormone signaling.

Reprinted from Boller, T., and G. Pieterse. 2004. Induced systemic resistance in plants. *Plant Cell* 16: 1105-1114. doi:10.1105/PC.101105

### Summary – stress responses

Hormonal signaling is critical for plant defenses against abiotic and biotic stresses.

ABA and ethylene are produced in stressed plants and critical for activating their defense pathways.

JA and SA contribute to local and systemic defenses against pathogens.

Understanding plant hormonal responses to stress is needed to improving agricultural yields. Abiotic and biotic stresses are major causes of crop losses and reduced yields and which must be minimized.

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### Crosstalk between hormone signaling pathways

Crosstalk (or cross-regulation) occurs when two pathways are not independent. It can be positive and additive or synergistic, or negative.

### Crosstalk between hormone signaling pathways

Crosstalk (or cross-regulation) occurs when two pathways are not independent. It can be positive and additive or synergistic, or negative.

Crosstalk can affect the synthesis, transport or signaling pathway of another hormone.

### Synergistic requirement for JA and ET signaling in defense response

JA and ET signaling are both required for high-level expression of ERF1, a TF that induces defense gene expression.

Reprinted from G. Pieterse, J. van der Meulen, and J. van der Meer. 2004. Induced systemic resistance in plants. *Plant Cell* 16: 1105-1114. doi:10.1105/PC.101105

### Negative interaction between JA and SA in defense responses

In defense signaling, the JA and SA pathways are mutually antagonistic (locally), and both are antagonized by ABA.

Why does ABA reduce SA and JA signaling? Perhaps a plant that is already stressed and producing high levels of ABA may be better off temporarily restricting its responses to pathogens.

Reprinted from Smith, C.K., and Pees, S. (2008) Making sense of hormone crosstalk during plant defense responses. *Trends Plant Sci.* 13: 102-109.

### GA and DELLAs interact extensively with other signaling pathways

Just about every stage of the plants life is coordinated by GA and its effects on the other hormone signaling pathways.

Although it is clear that GA's effects on DELLA proteins are very important, we don't yet understand what these proteins do.

Went, G. and Paolillo, G. (2007) The regulation of plant cell division and growth. *Plant Physiol.* 145: 100-108.

### GA and DELLAs interact extensively with other signaling pathways

Went, G. and Paolillo, G. (2007) The regulation of plant cell division and growth. *Plant Physiol.* 145: 100-108.

### Ongoing research

Hormones are critical signaling molecules that coordinate all aspects of plant growth and defense. Many aspects of hormone synthesis, homeostasis and signaling are still being discovered. Knowledge of these processes provides tremendous opportunities for agricultural improvements including the development of stress-resistant and pathogen-resistant plants, plants with greater abilities to take up nutrients, foods that stay fresh longer, and increased crop yields.

### The field of plant hormones is blossoming and fruitful