S2011
Hormones in Plant Development

1. Introduction to Phytohormones

What are phytohormones?

Frits Went, 1903-1990

"……..characterised 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

Kenneth Thimann, 1904-1997

Dutch botanist

In 1928, he isolated **auxin** from plants

Known for the **Cholodny-Went model**

Develop synthetic plant hormones at Caltech labs.

Worked on the effects of air pollution on plant growth

English-American plant physiologist and microbiologist

Determined the structure of auxin

Phytohormones

chemical messengers that coordinate the cellular functions of multicellular organisms.

Phytohormones regulate:

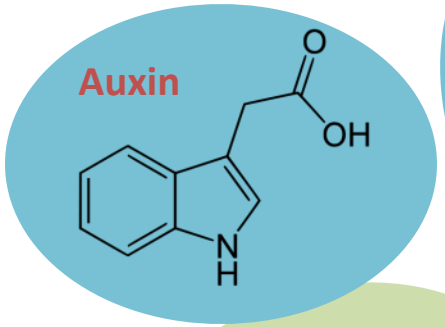
- **cellular activities (division, elongation and differentiation),**
- **pattern formation, organogenesis,**
- **reproduction, sex determination,**
- **responses to abiotic and biotic stress.**

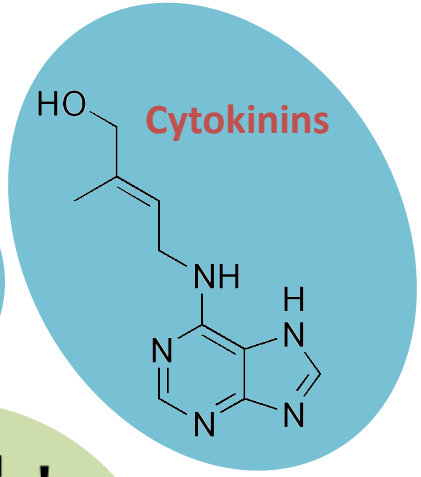


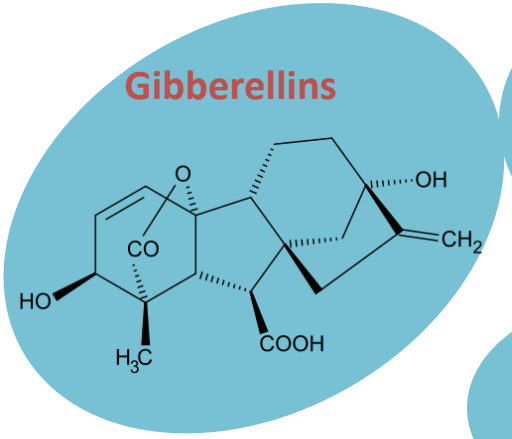


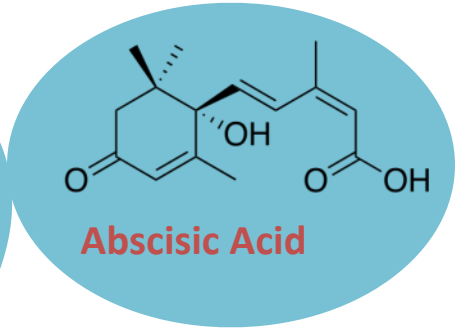
Notholaena standleyi © 2008 Carl Rothfels

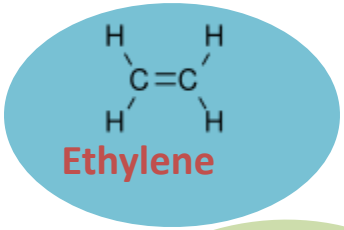
Phytohormones - Names and structures

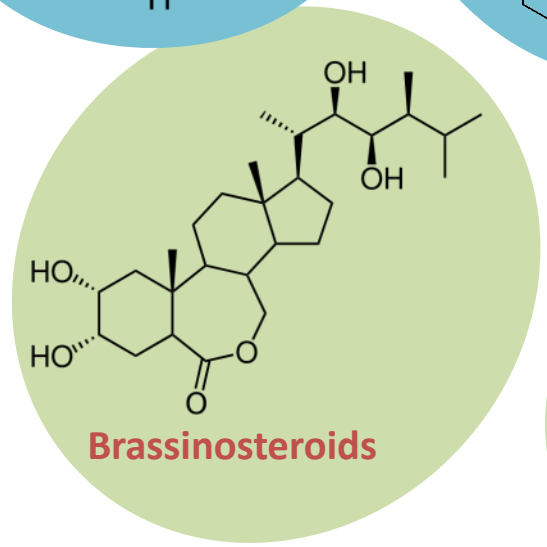


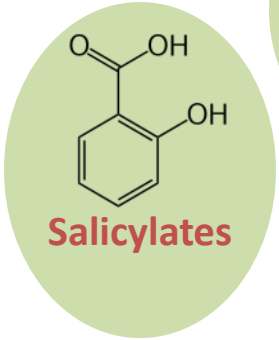


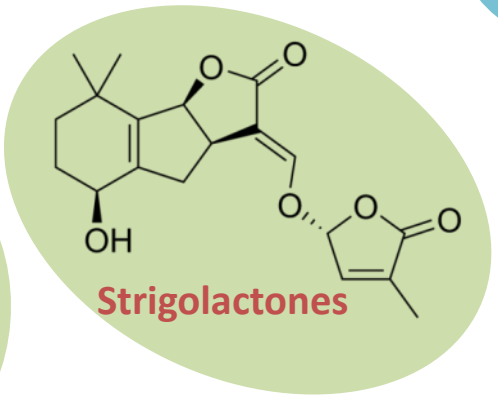


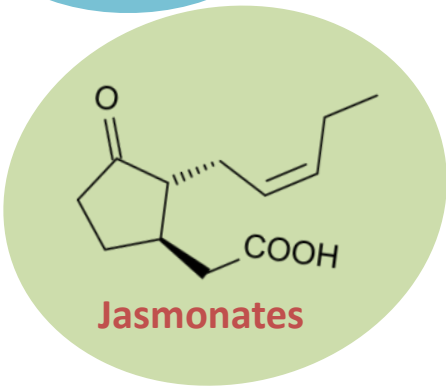












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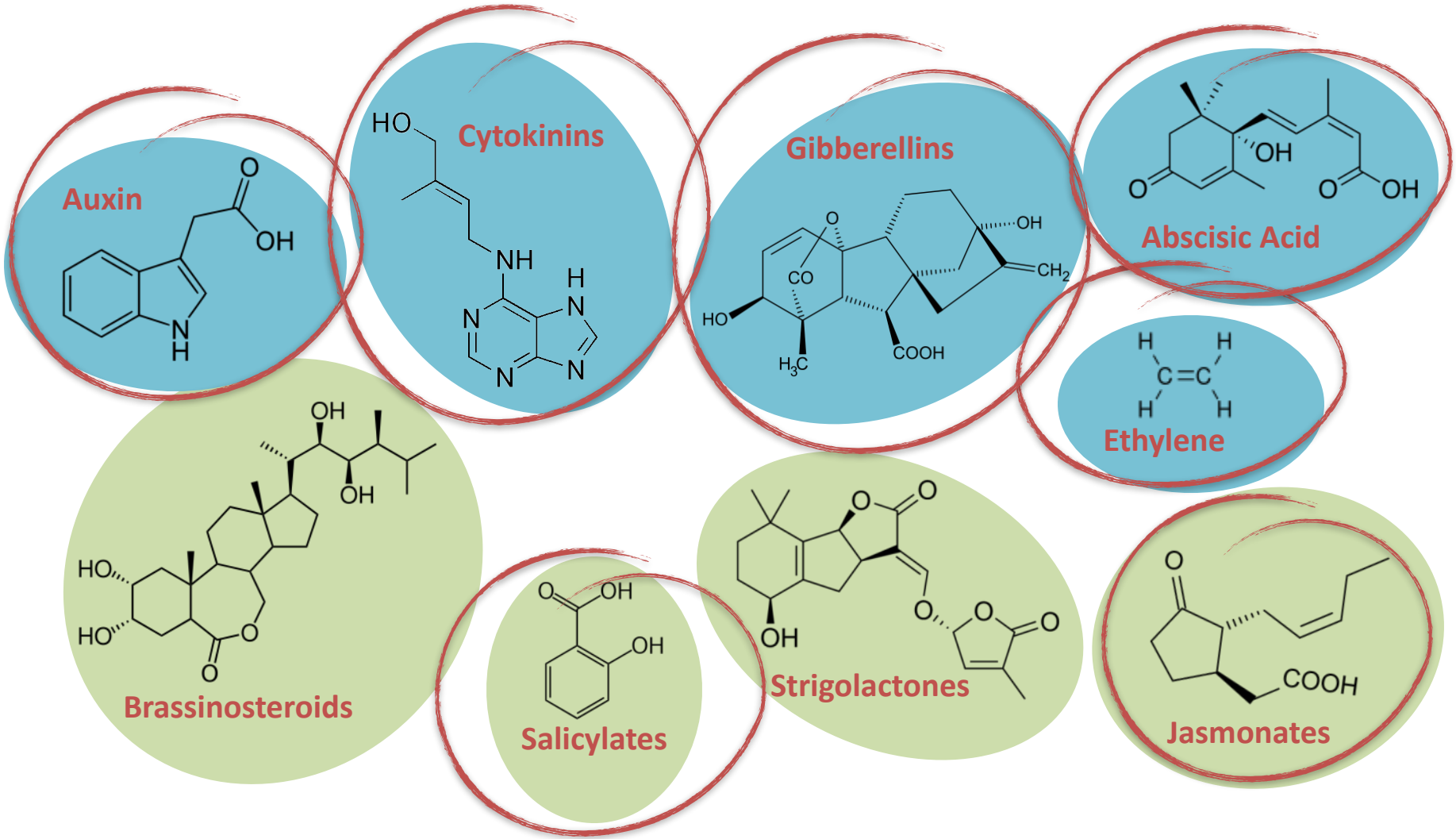
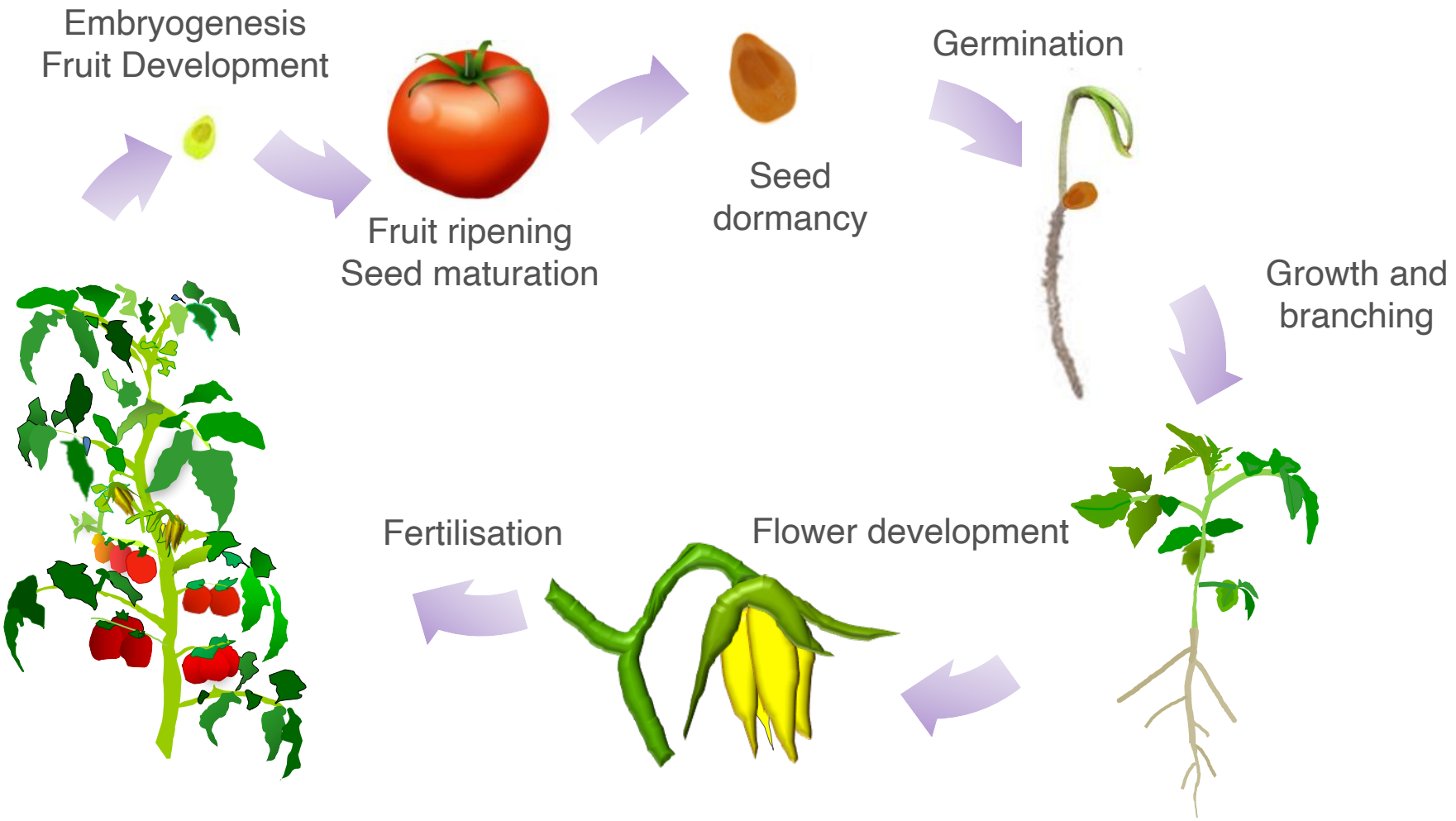
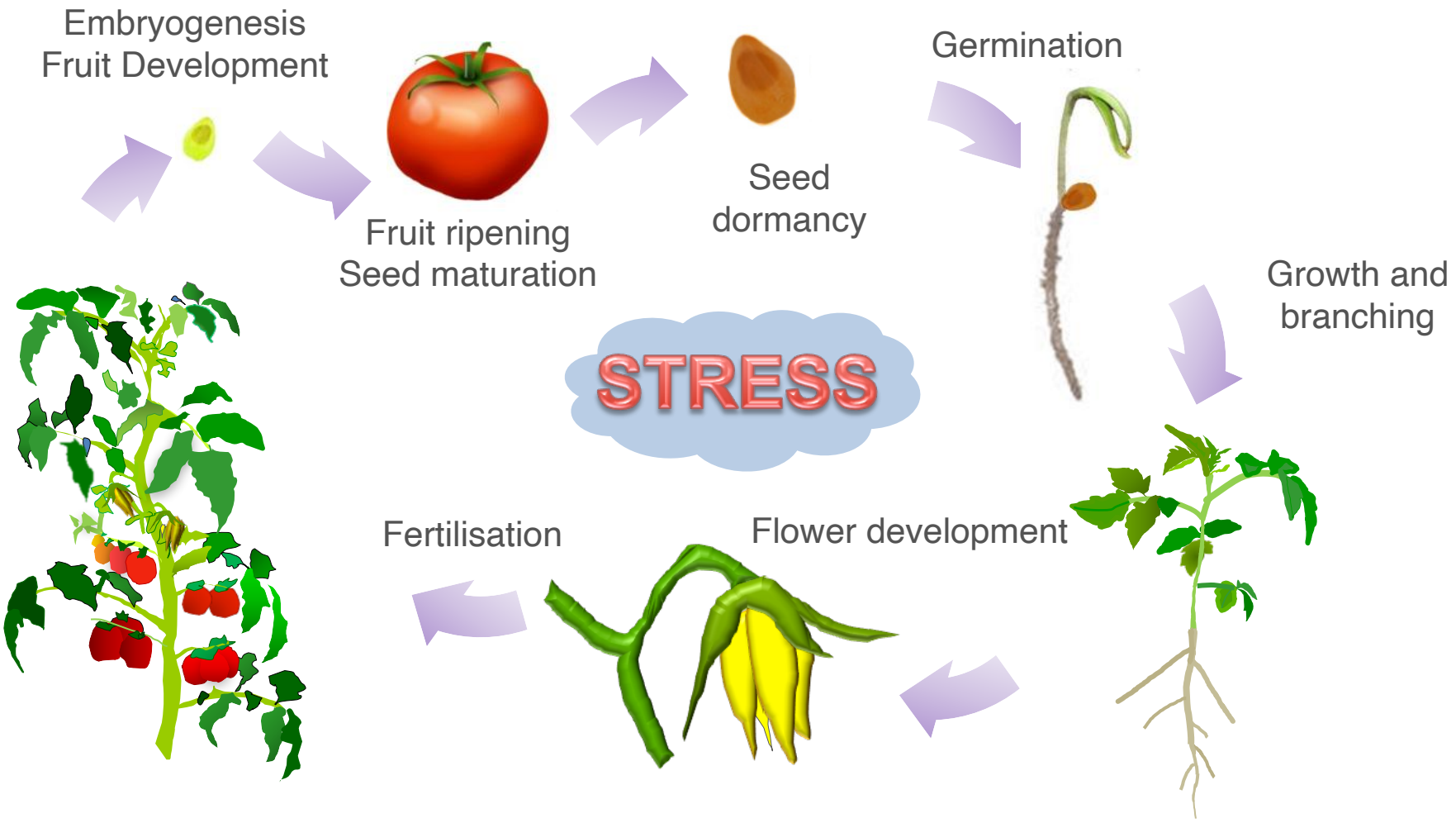


Phytohormones regulate all stages of the plant life cycle



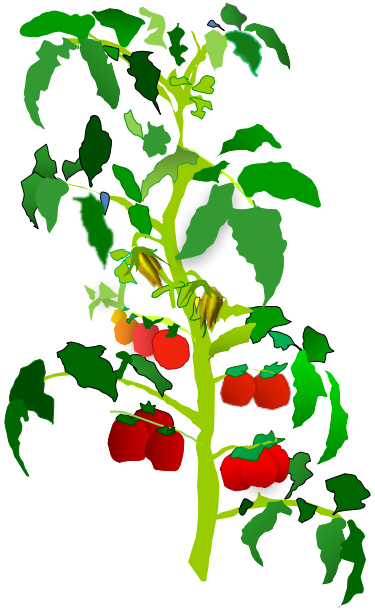
Phytohormones also help plants to cope with stress throughout their life

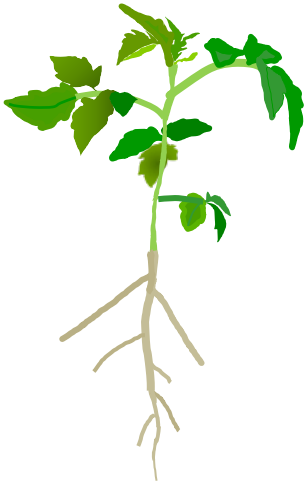


Phytohormones also help plants to cope with stress throughout their life

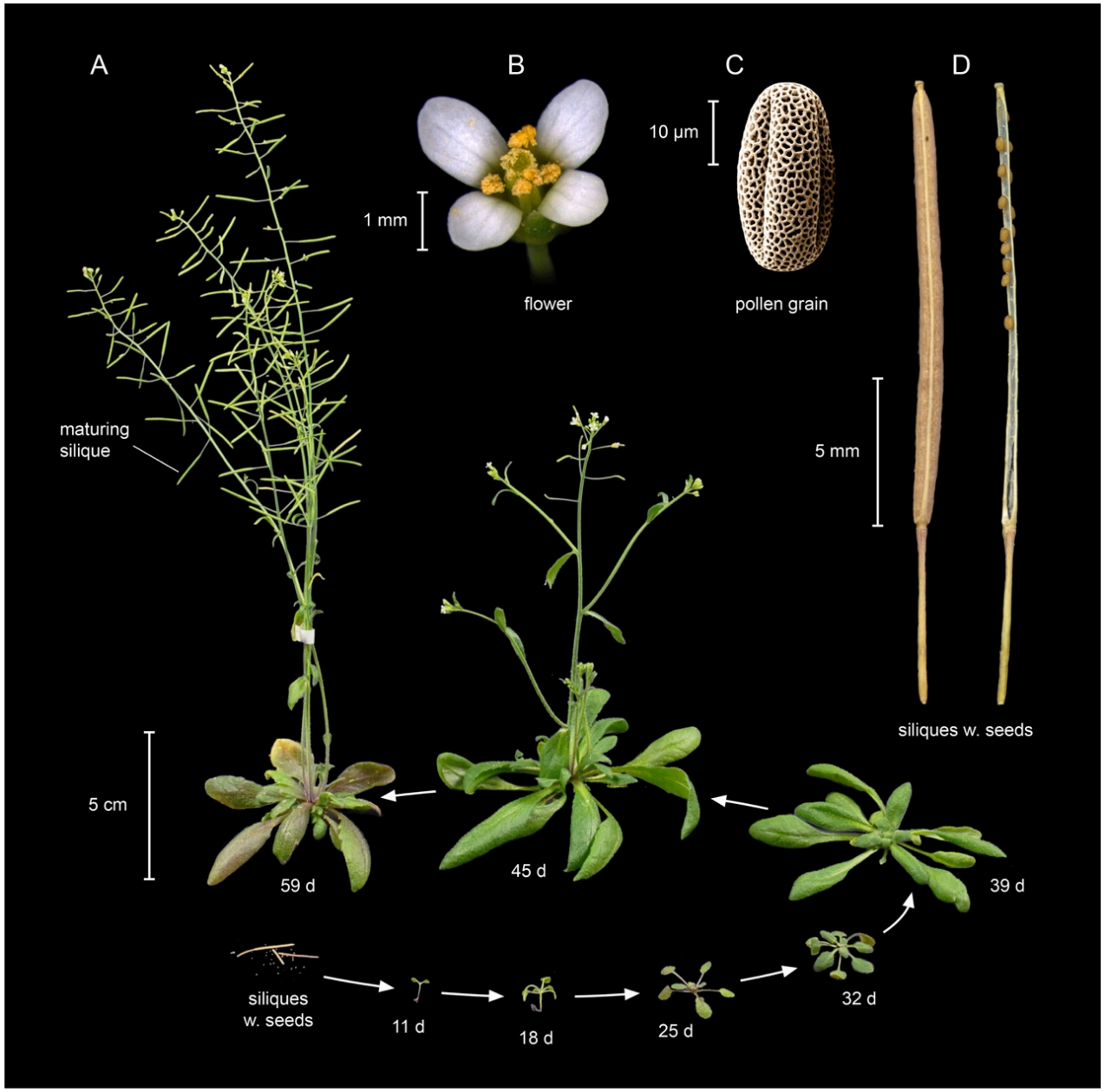
During this course, we will look at each hormones within the context of

- their role during development
- their crosstalk
- Their function during abiotic stress response

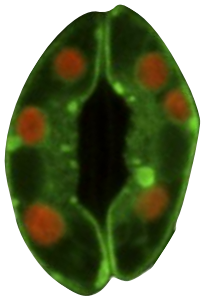




Arabidopsis thaliana life cycle



Lectures outline



How hormones work

Hormonal control of vegetative development

- Auxin
- Cytokinins
- Gibberellins

Hormonal control of reproduction

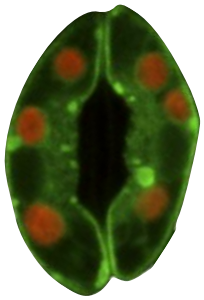
- Ethylene
- Abscisic Acid

Hormonal responses to stress

- Salicylates
- Jasmonates

Cross-regulation of hormonal effects

Lectures outline



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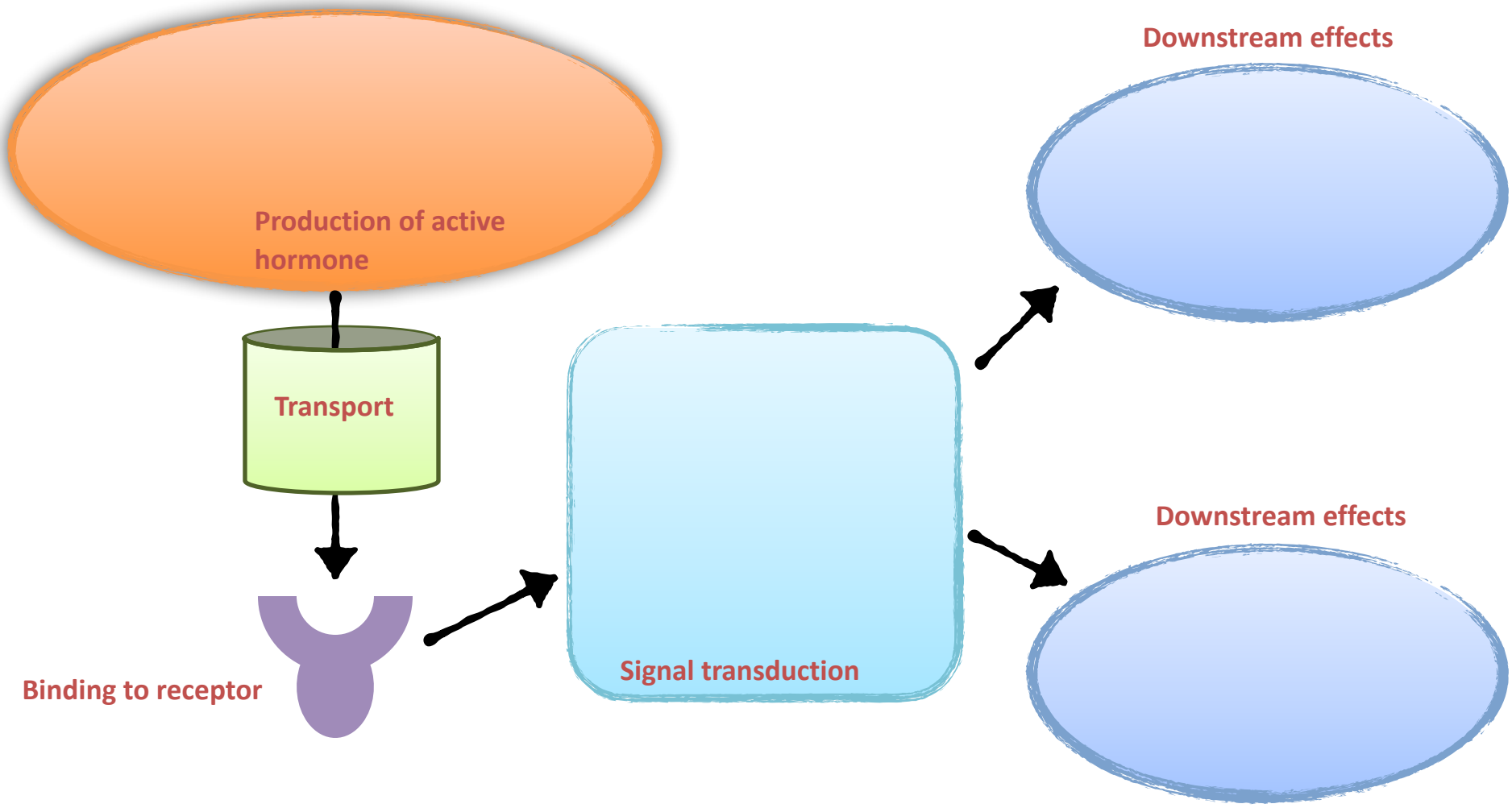
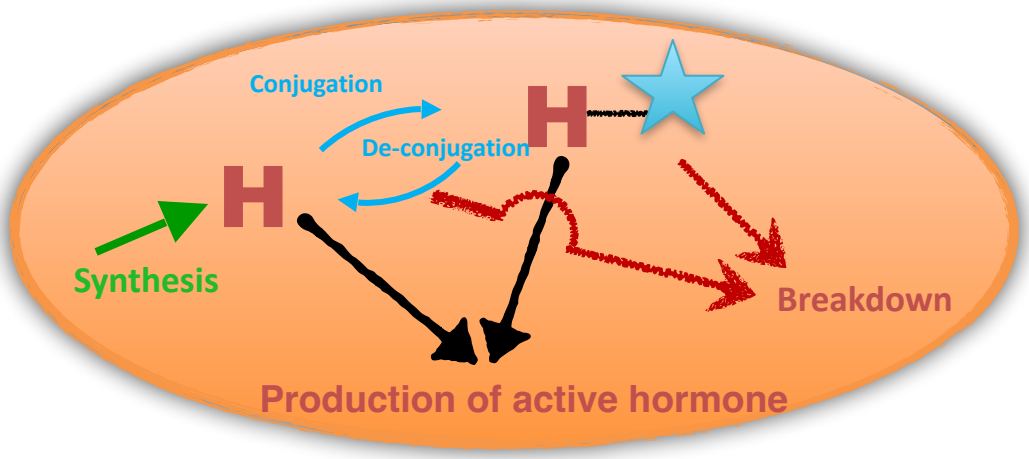
Cross-regulation of hormonal effects

Hormones: synthesis, transport, perception, signalling and responses



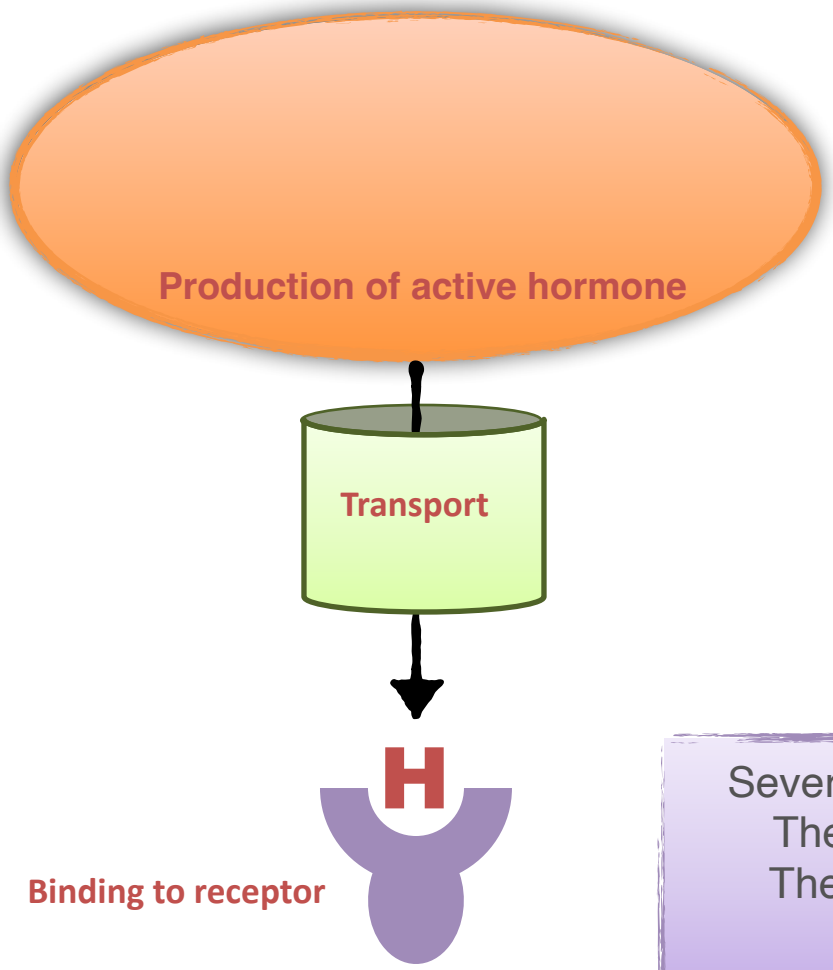
Hormones: synthesis



Many tightly regulated biochemical pathways contribute to active **hormone accumulation**.

Conjugation can **temporarily** store a hormone in an inactive form, lead to **catabolic breakdown**, or be the means for producing the **active hormone**.

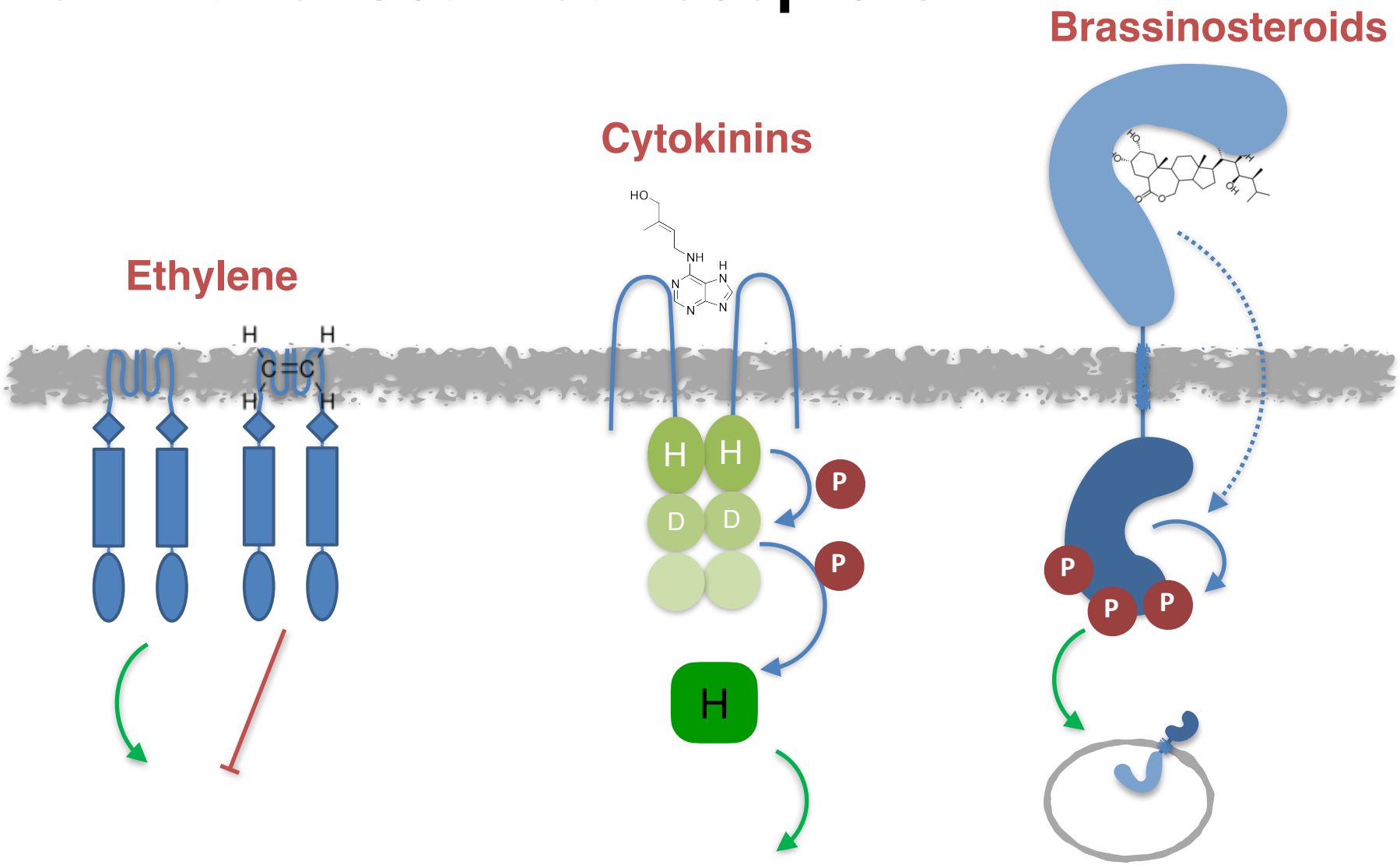
Hormones: transport and perception



Hormones can move:
- through the xylem or phloem
- across cellular membranes, or through apoplast
- through **regulated transport proteins**

Several hormone receptors have been identified.
They can be **membrane-bound** or **soluble.**
They can be at the **cell surface/organelles, cytosolic, nuclear.**

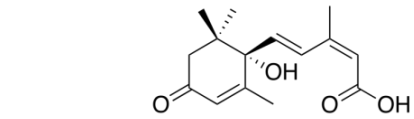
Membrane-localized receptors



Hormone binding initiates an information relay (**signalling**)

Soluble receptors: Binding to the hormone increases affinity to the co-receptor

Hormones can act like "**molecular glue**"



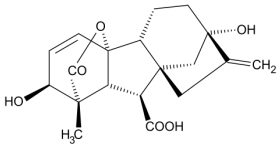
ABA

PYR1

PP2C

SnRK2

P



GID1

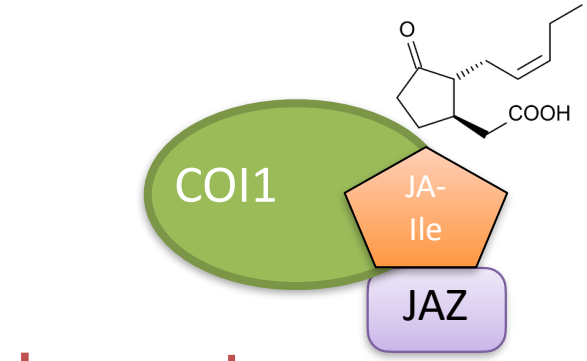
GA

DELLA

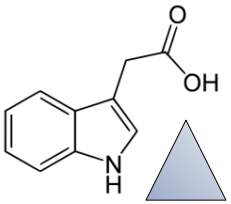
GID1

GA

DELLA



Jasmonates



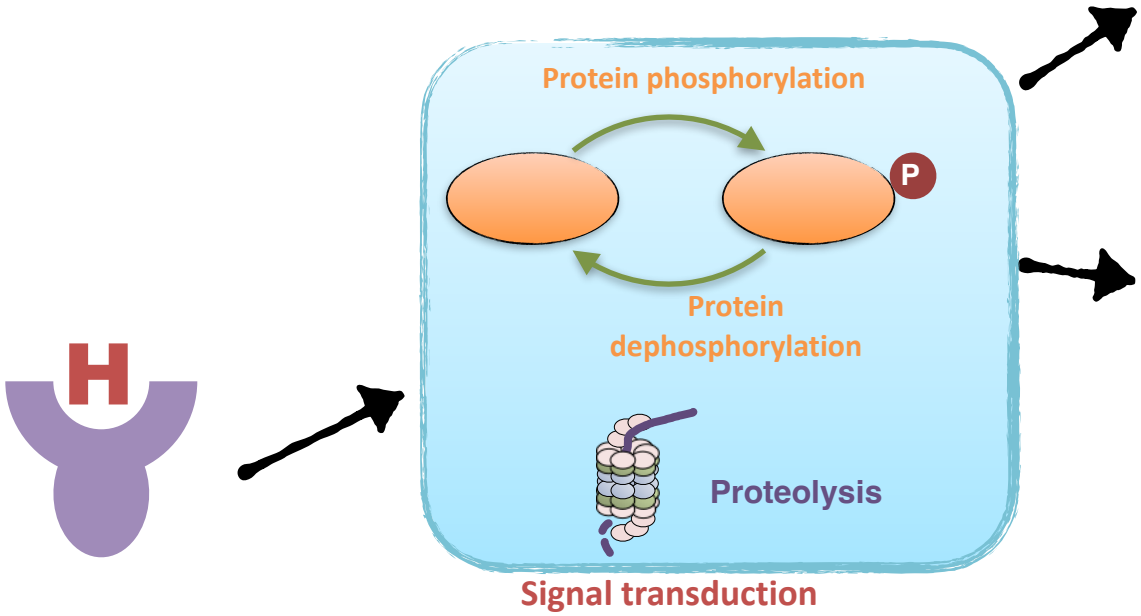
IAA

TIR1

Aux/IAA

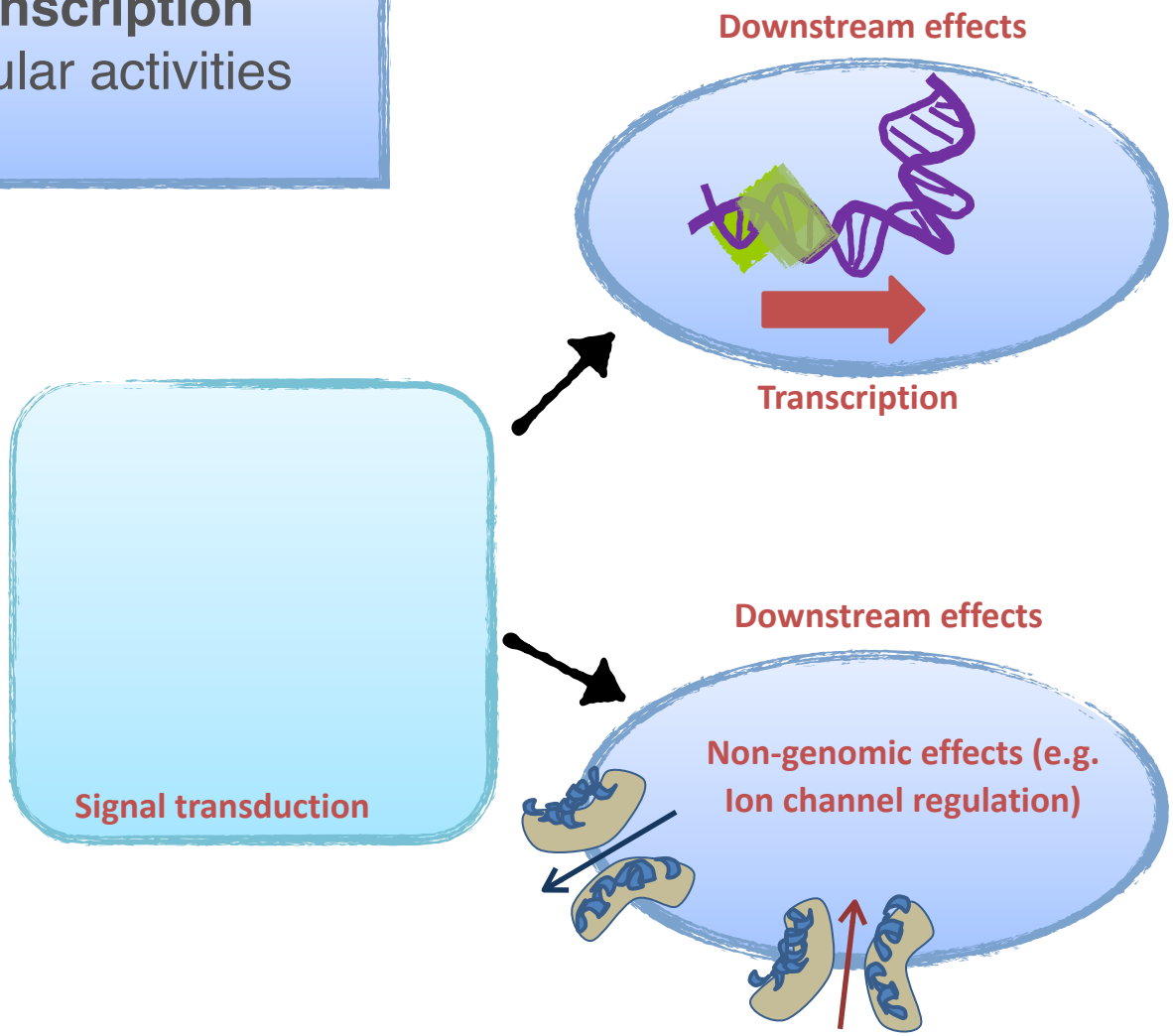
Signal transduction

Following binding to its receptor, the hormone induces a signalling cascade, that can be of diverse nature, mainly:
(1) reversible protein **phosphorylation**
(2) targeted **proteolysis**



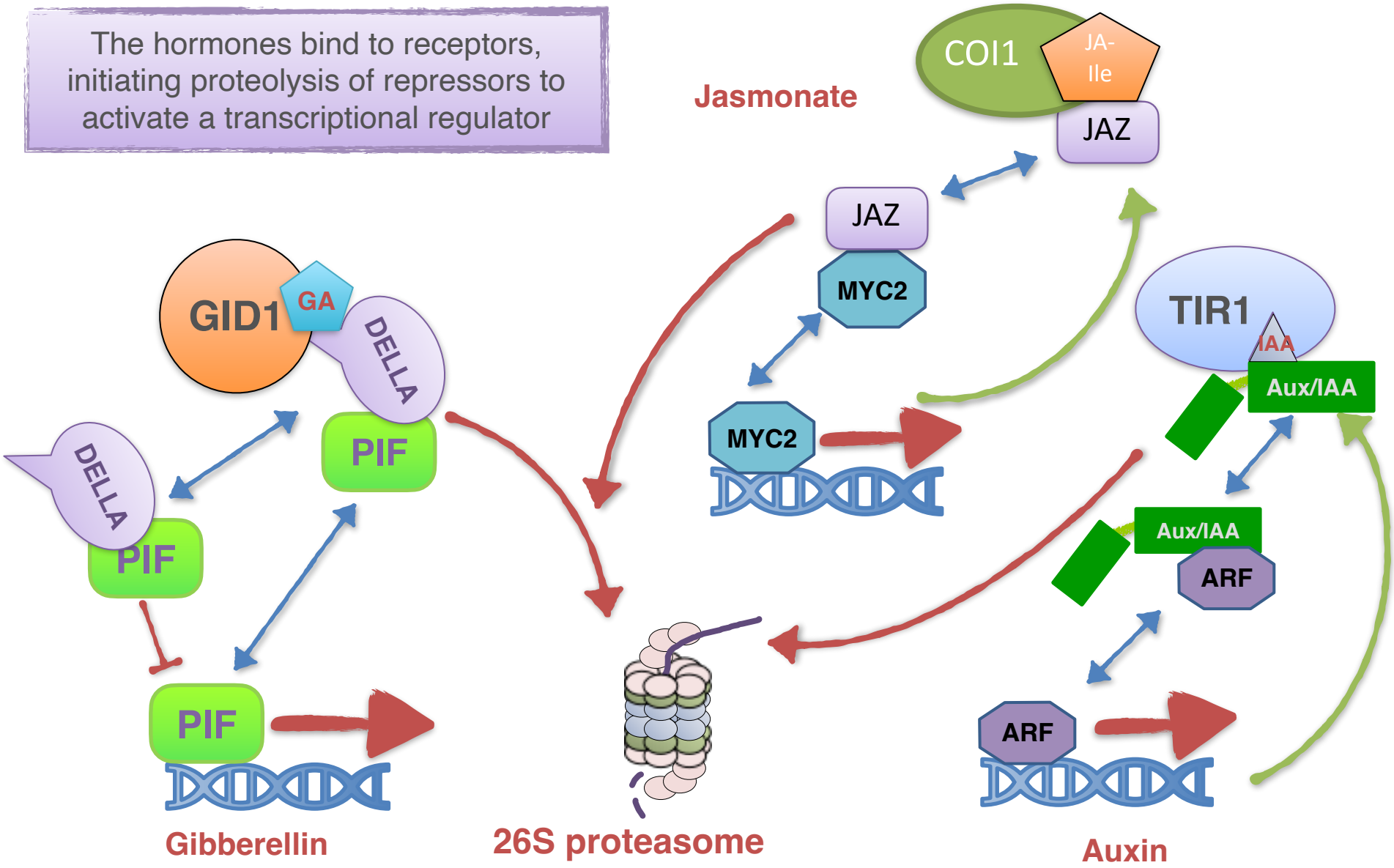
Hormones: Responses

Downstream effects can involve:
(1) **changes in gene transcription**
(2) changes in other cellular activities like **ion transport**

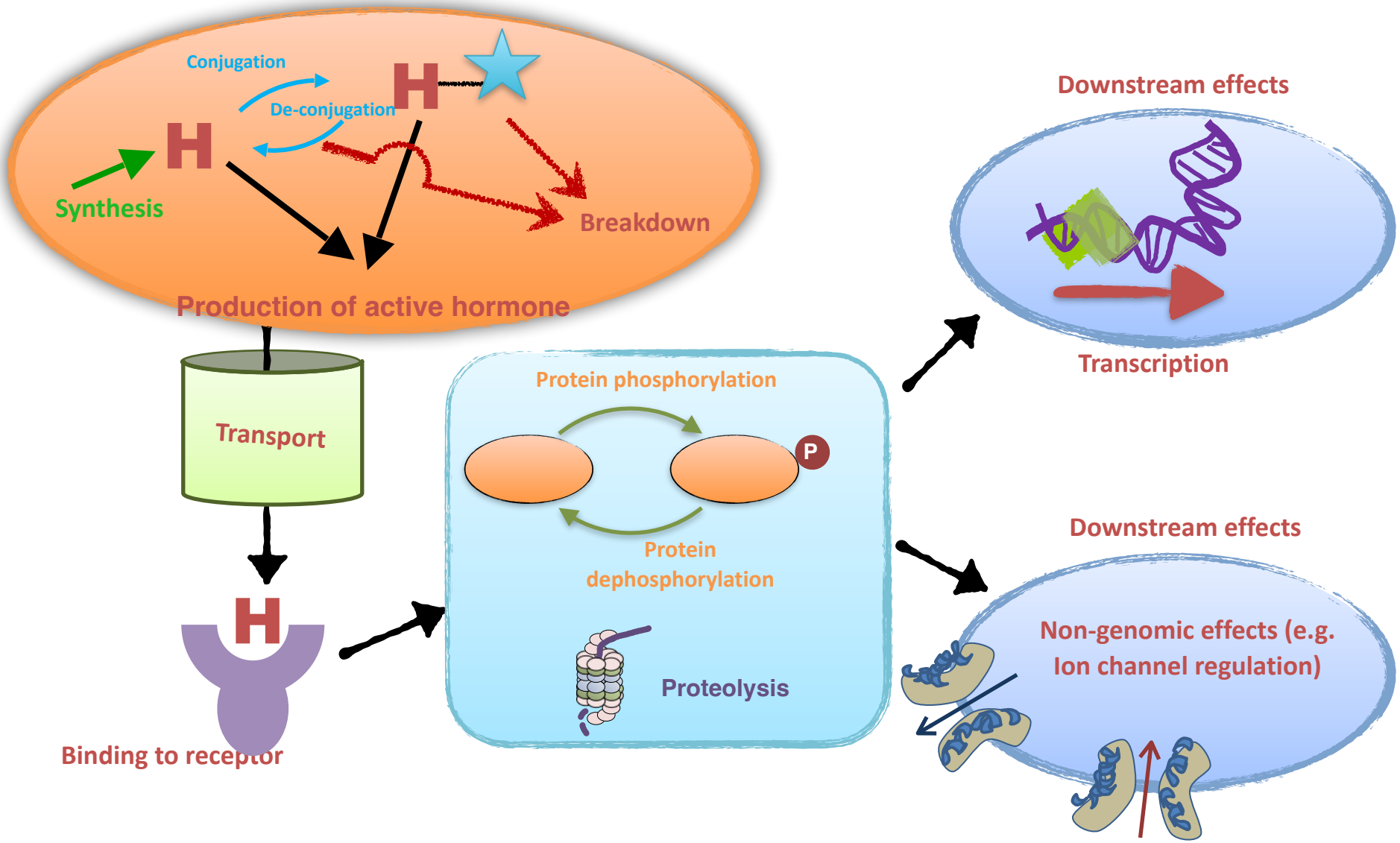


Signal transduction by targeted proteolysis

The hormones bind to receptors, initiating proteolysis of repressors to activate a transcriptional regulator



Hormones: synthesis, transport, perception, signaling and responses



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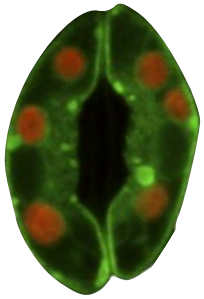

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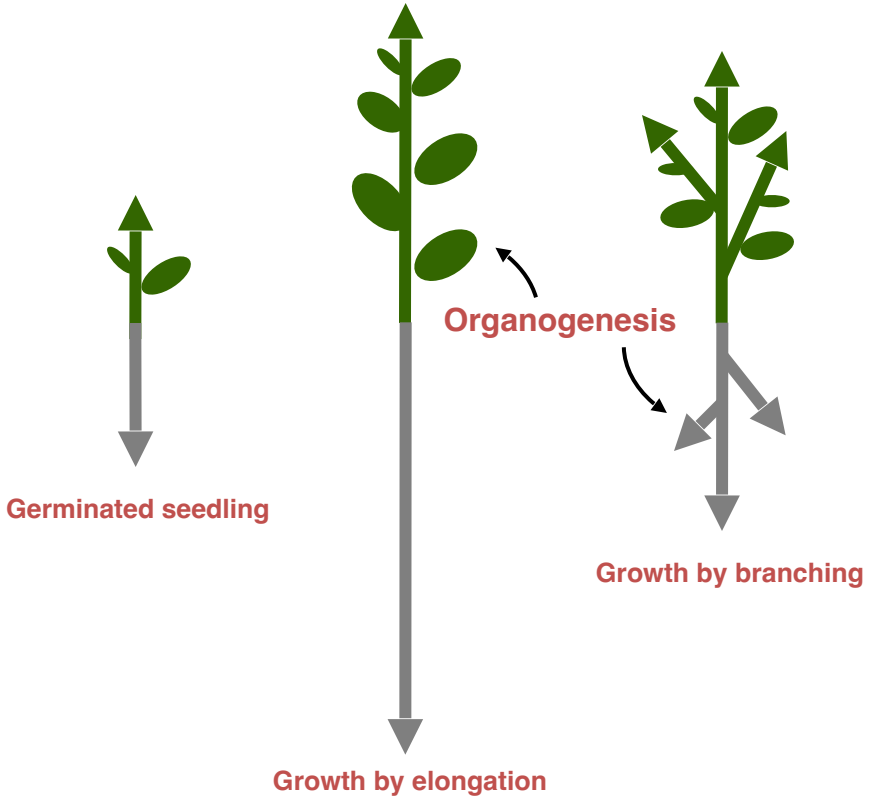
Cross-regulation of hormonal effects

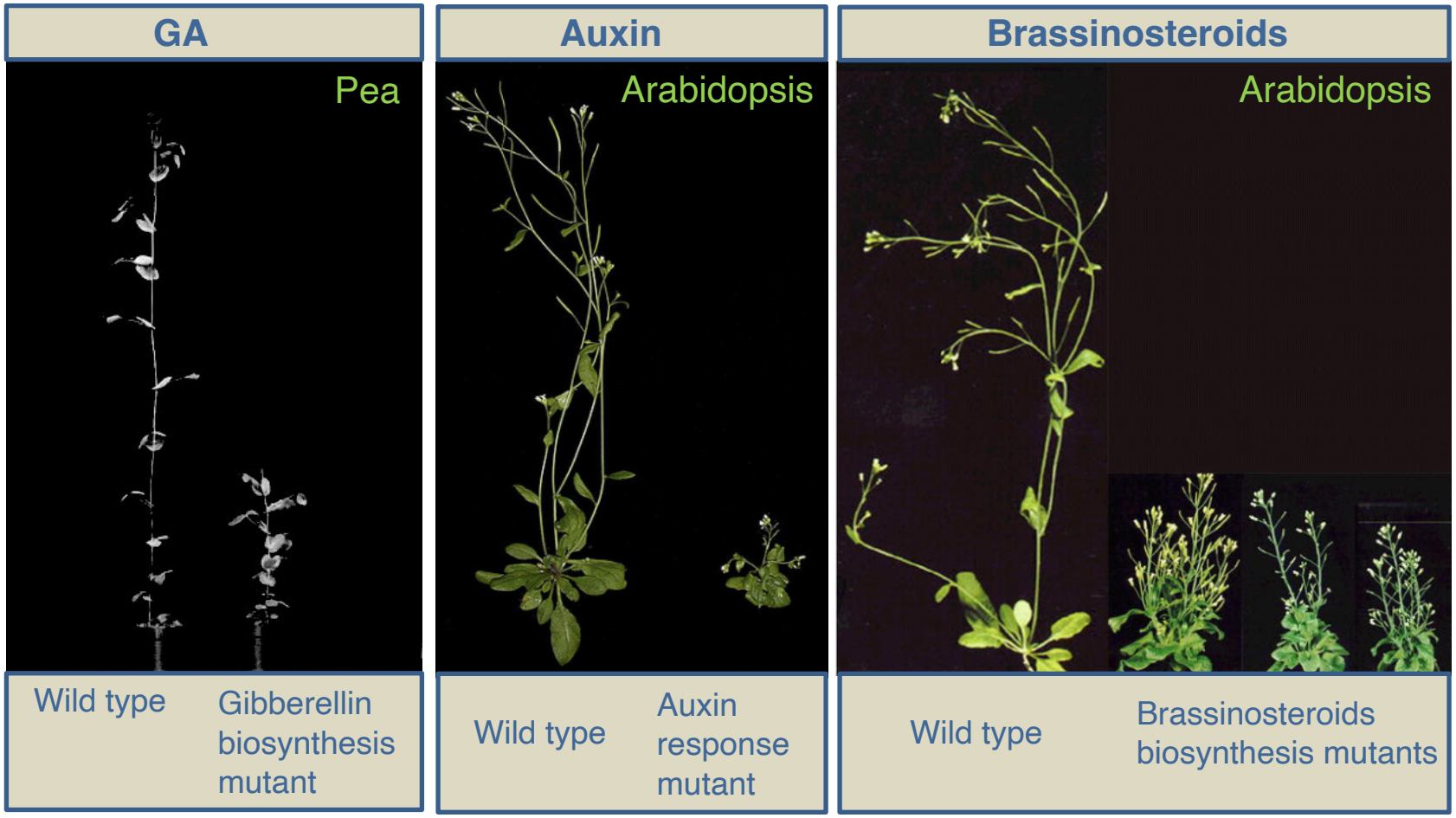
Hormones affect vegetative growth: elongation, branching and organogenesis

Elongation in the shoot and root of a germinating soybean

Photo courtesy of Shawn Conley

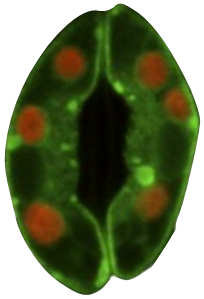


Disrupting hormone synthesis or response interferes with elongation



Lester, D.R., Ross, J.J., Davies, P.J., and Reid, J.B. (1997) Mendel's stem length gene (*Le*) encodes a gibberellin 3β-hydroxylase. Plant Cell 9: 1435-1443.
Gray WM (2004) Hormonal regulation of plant growth and development. PLoS Biol 2(9): e311
Clouse SD (2002) Brassinosteroids: The Arabidopsis Book. Rockville, MD: American Society of Plant Biologists. doi: 10.1199/tab.0009

Lectures outline



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Cross-regulation of hormonal effects

Auxin regulates plant development

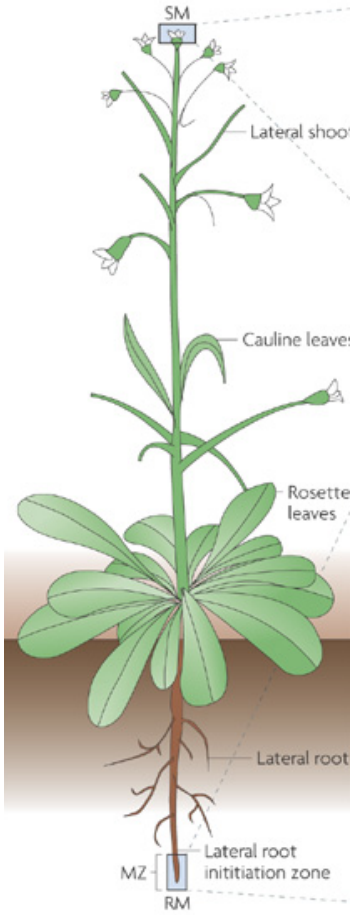
Lateral organ initiation at the shoot apical meristem

Inhibit branching in the shoot

Patterning and vascular development

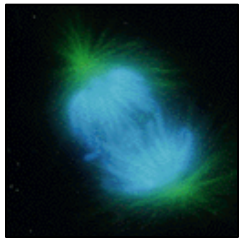
Maintain stem cell fate at the root apical meristem

Promote branching in the root



Wolters, H., and Jürgens, G. (2009). Survival of the flexible: Hormonal growth control and adaptation in plant development. Nat. Rev. Genet. 10: 305–317.

Auxin regulates plant development

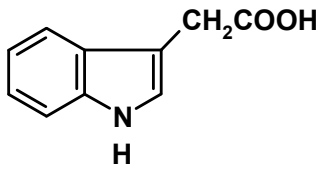


Embryogenesis

Fruit development

Phyllotaxis

Cell division



Indole-3-acetic acid
(IAA)

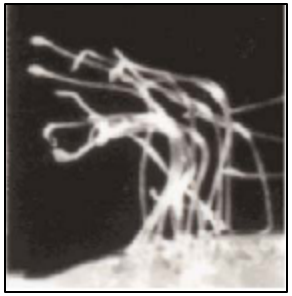
Cell elongation

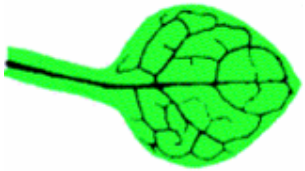
Branching

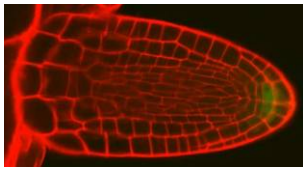
Tropic growth

Root development

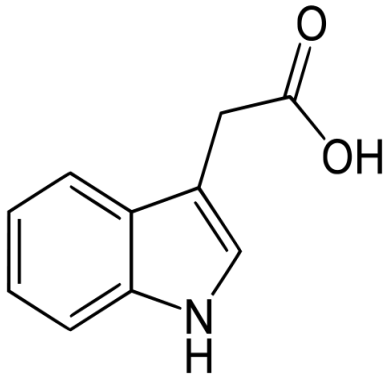
Vascular differentiation

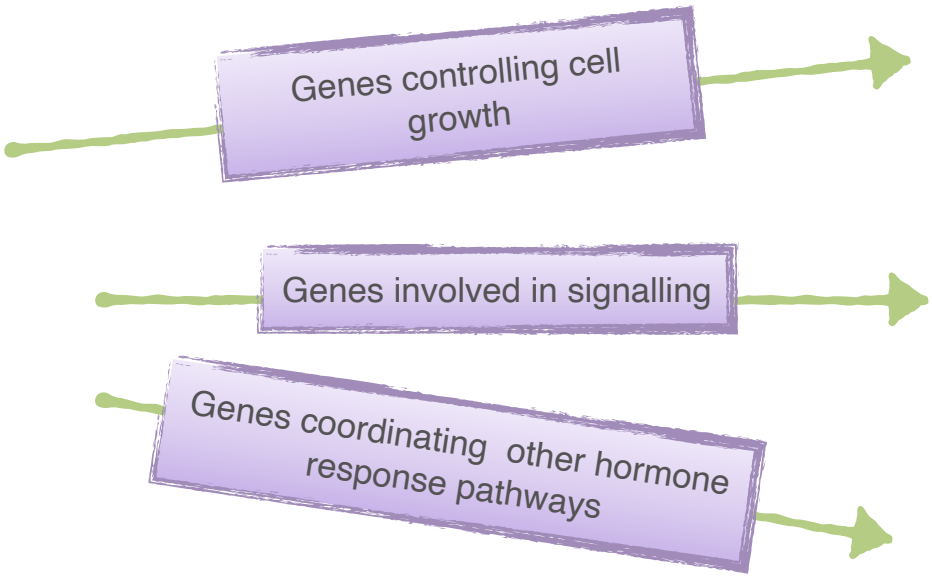


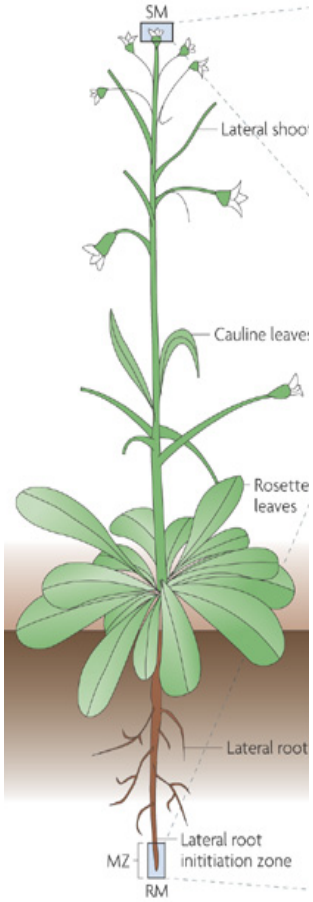




Many of auxin's effects are mediated by changes in gene expression







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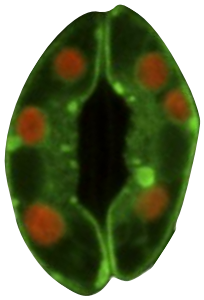

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Hormonal control of reproduction

- Ethylene
- Abscisic Acid

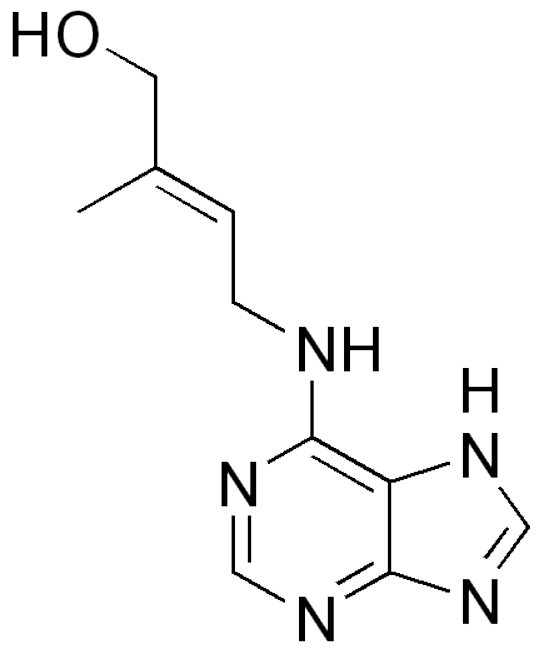
Hormonal responses to stress

- Salicylates
- Jasmonates

Cross-regulation of hormonal effects

Cytokinins

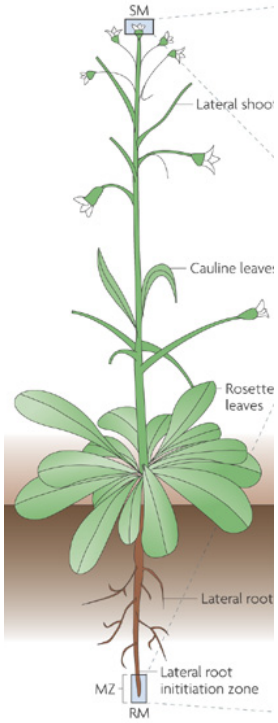
- ✓ Cell division
- ✓ Control of leaf senescence
- ✓ Control of nutrient allocation
- ✓ Root nodule development
- ✓ Stem cell maintenance
- ✓ Regulate auxin action
- ✓ Vascular formation



trans-zeatin, a cytokinin

Cytokinins act antagonistically to auxins

Cytokinin	Auxin
Promote stem cell fate at the shoot apical meristem	Promote lateral organ initiation at the shoot apical meristem
Promote differentiation at the root apical meristem	Maintain stem cell fate at the root apical meristem



Cytokinin	Auxin
Promote branching in the shoot	Inhibit branching in the shoot
Inhibit branching in the root	Promote branching in the root

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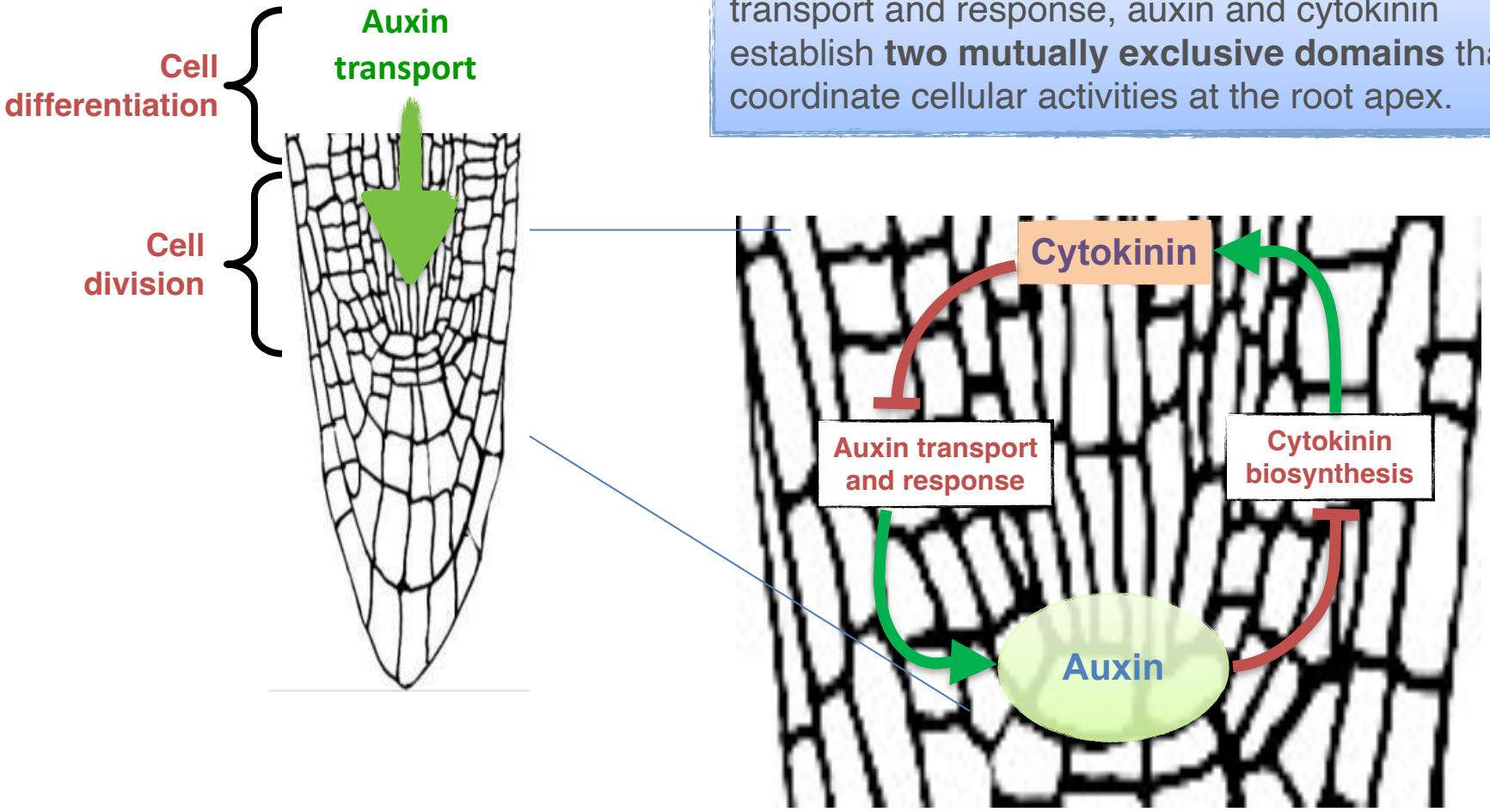
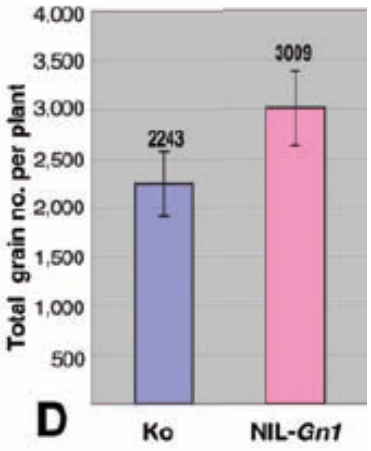
Auxin and cytokinin regulate each other's function at the root apex

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.



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.

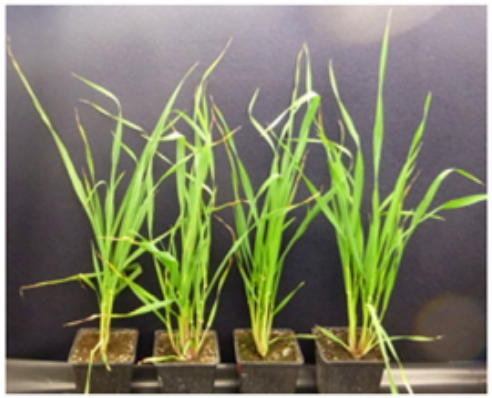
Wild-type

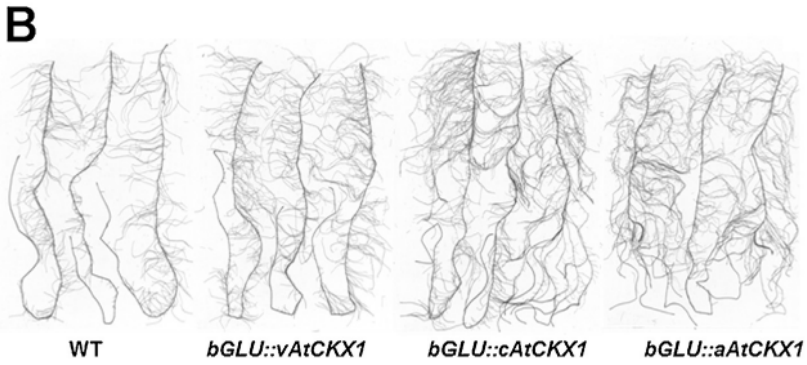
Elevated CK

Ashikari, M. et al. (2005) Cytokinin oxidase regulates rice grain production. Science 309: 741 – 745,
Rivero, R. M. et al. (2007) PNAS 104: 19631-19636.

Cytokinins affect root formation and drought tolerance in barley

Barley with less cytokinin, by overexpression of CKX in roots





Water content

	WT	bGLU::vAtCKX1	bGLU::cAtCKX1	bGLU::aAtCKX1
RWC (%)				
Drought stress	49	49	47	42
Revitalization	78	95*	98*	92*

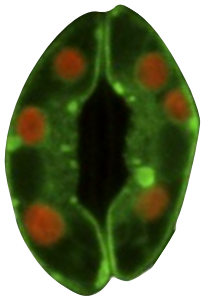
Dry weight

	WT	bGLU::vAtCKX1	bGLU::cAtCKX1	bGLU::aAtCKX1
Aerial part dry mass (%)				
Control conditions	100	88	114	53*
Drought and revitalization	100	125*	117*	74*

100%

Pospíšilová, H.; Jiskrová, E.; Vojta, P.; Mrízová, K.; Kokáš, F.; Čudejková, M. M.; Bergougnoux, V.; Plíhal, O.; Klimešová, J.; Novak, O.; Dzurová, L.; Frébort, I.; Galuszka, P. Transgenic barley overexpressing a cytokinin dehydrogenase gene shows greater tolerance to drought stress. N Biotechnol 2016, 33, 692–705.

Lectures outline



How hormones work

Hormonal control of vegetative development

- Auxin
- Cytokinins
- Gibberellins

Hormonal control of reproduction

- Ethylene
- Abscisic Acid

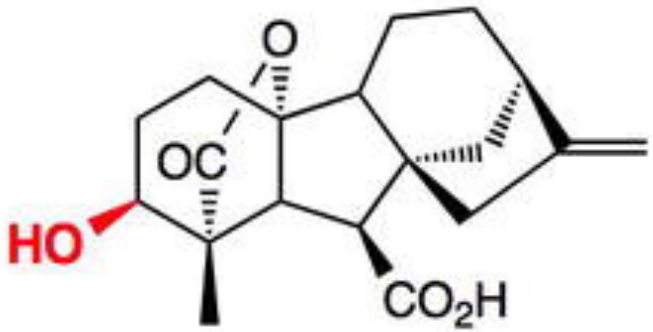
Hormonal responses to stress

- Salicylates
- Jasmonates

Cross-regulation of hormonal effects

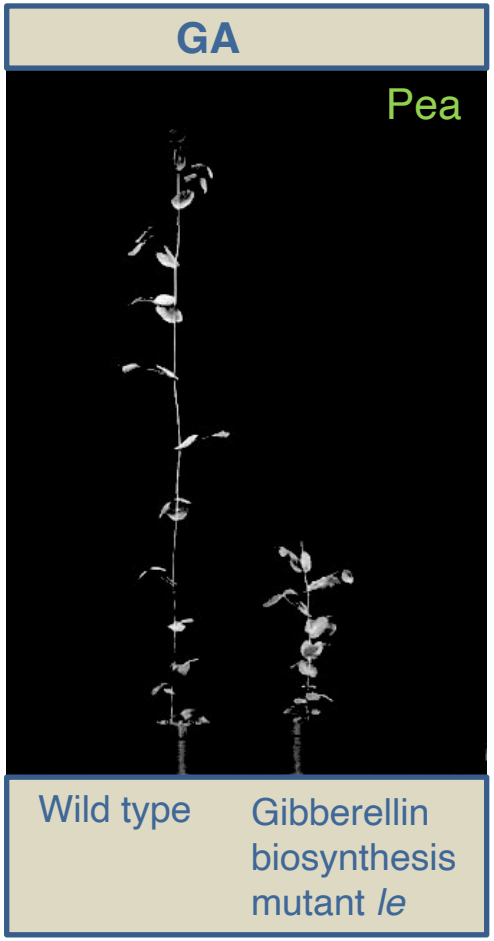
Gibberellins

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

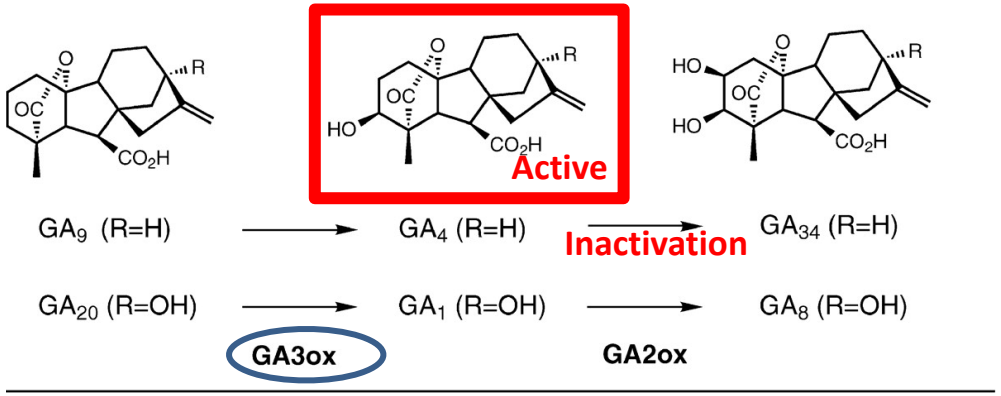


A Gibberellin (GA_4)

Gibberellins regulate growth



The pea mutant *le*, studied by Mendel, encodes **GA_3 oxidase**, which produces active GA. Loss of function of *le* reduces active GA levels and makes plants dwarfed.



Lester, D.R., Ross, J.J., Davies, P.J., and Reid, J.B. (1997) Mendel's stem length gene (*Le*) encodes a gibberellin 3β-hydroxylase. Plant Cell 9: 1435-1443.

Genes controlling GA synthesis are important "green revolution" genes

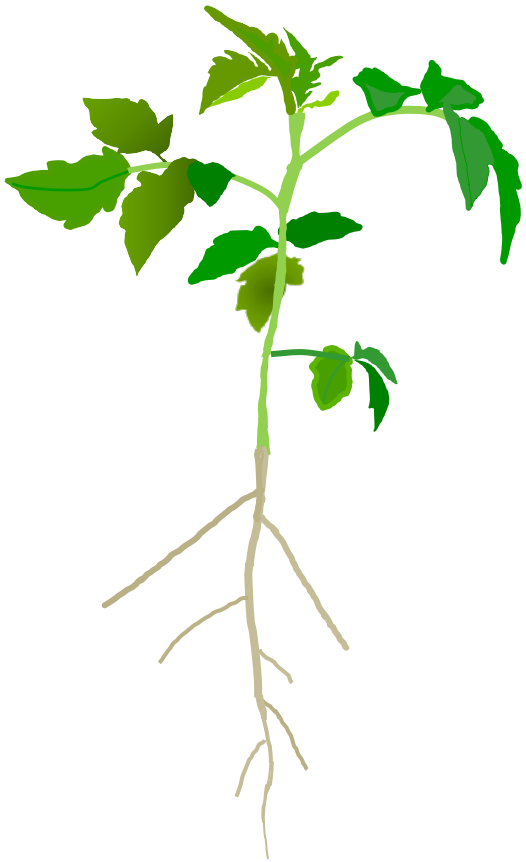
Distinguished plant breeder and Nobel Laureate Norman Borlaug 1914-2009

Tremendous increases in crop yields (the Green Revolution) during the 20th century occurred because of increased use of fertiliser and the introduction of semi-dwarf varieties of grains.

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

Photos courtesy of S. Harrison, LSU Ag center and The World Food Prize.

Summary – hormonal control of vegetative growth



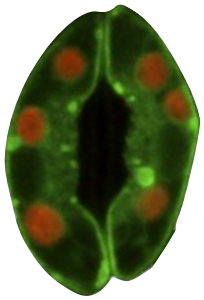
Plant hormones have diverse effects on plant growth.

Auxin, gibberellins and brassinosteroids contribute to elongation growth.

Auxin, cytokinins and strigolactones regulate branching patterns.

Growth and branching profoundly affect crop yields.

Lectures outline



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- Jasmonates

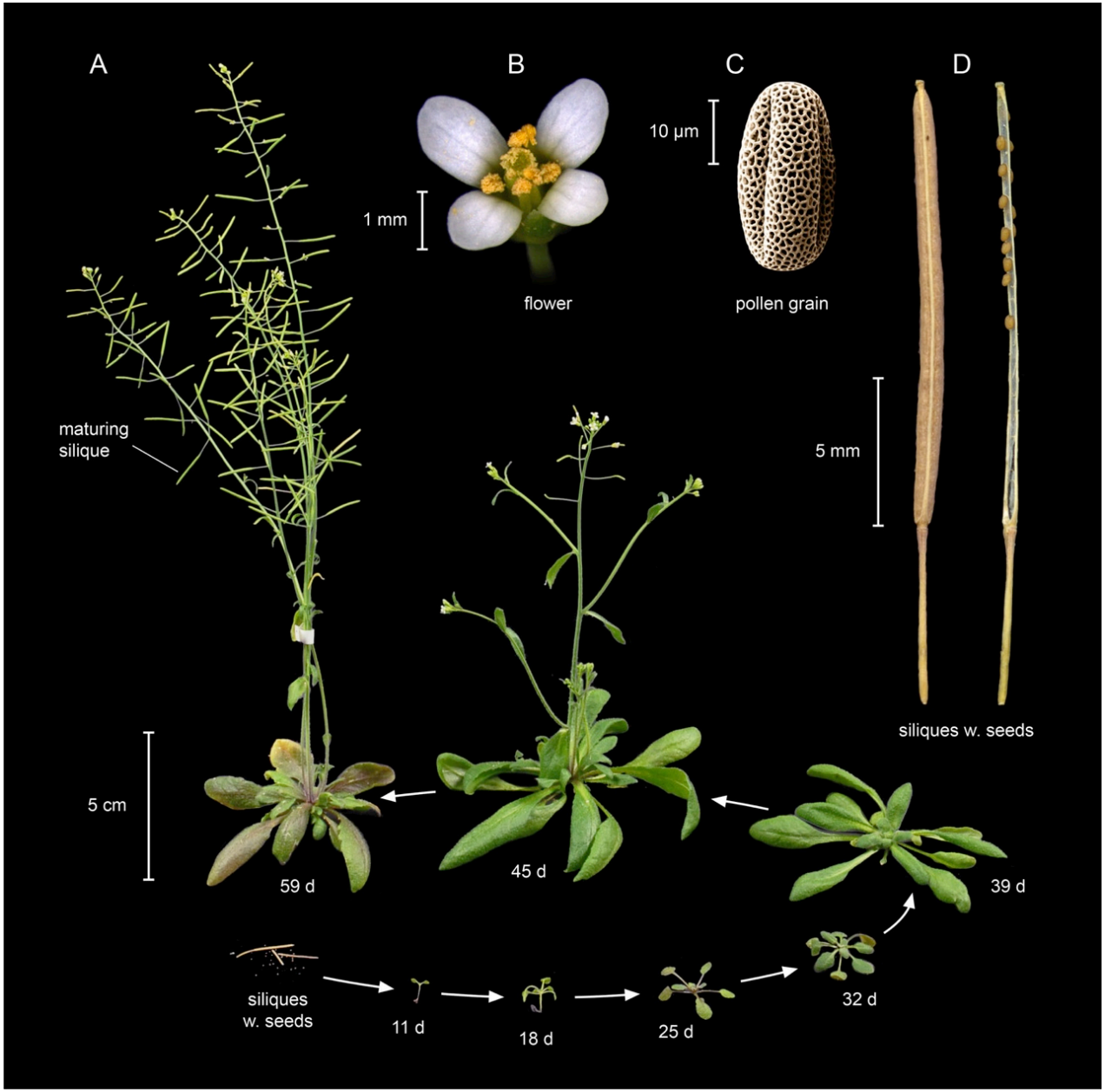
Cross-regulation of hormonal effects

Hormonal control of reproductive development

In angiosperms:

- ✓ transition from vegetative to reproductive growth
- ✓ flower development,
- ✓ fruit development and ripening
- ✓ seed development, maturation and germination

Arabidopsis thaliana life cycle



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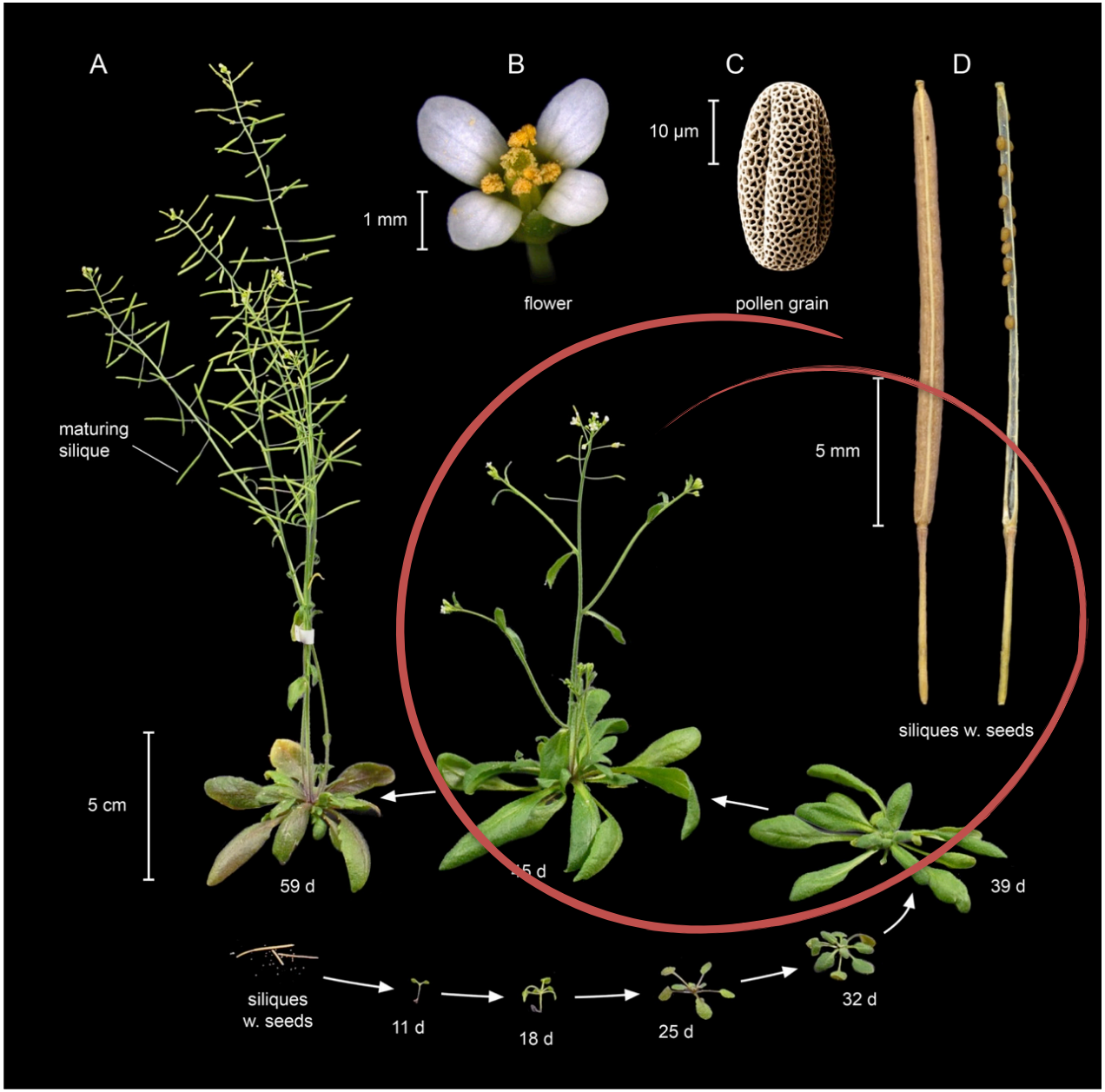


Kramer, eLife, 2015

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.

Photo credit: Early Crocus *(Crocus tommasinianus)* by anemoneprojectors via Flickr.
Photo credit: Sady Stary Liskovec, Brno
Photo credit: A. Bielach

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

Lolium temulentum
Annual temperate grass

GA promotes flowering?

Yes

Beta vulgaris
Biennial

Yes

Malus domestica
Perennial

No

Arabidopsis thaliana
Annual

Short Days
Yes

Long Days
No

Photos courtesy of Plate 271 from Anne Pratt's *Flowering Plants, Grasses, Sedges and Ferns of Great Britain* c.1878, by permission of Shrewsbury Museums Service; David Kuykendall ARS; Vincent Martinez; Takato Imaizumi.

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 synchronise flowering.

Flower development

Hormones contribute to flower development in many ways:

- ✓ Patterning of the floral meristem
- ✓ Outgrowth of organs
- ✓ Development of the male and female gametophytes
- ✓ Cell elongation

Ethylene and gibberellins are involved in sex determination

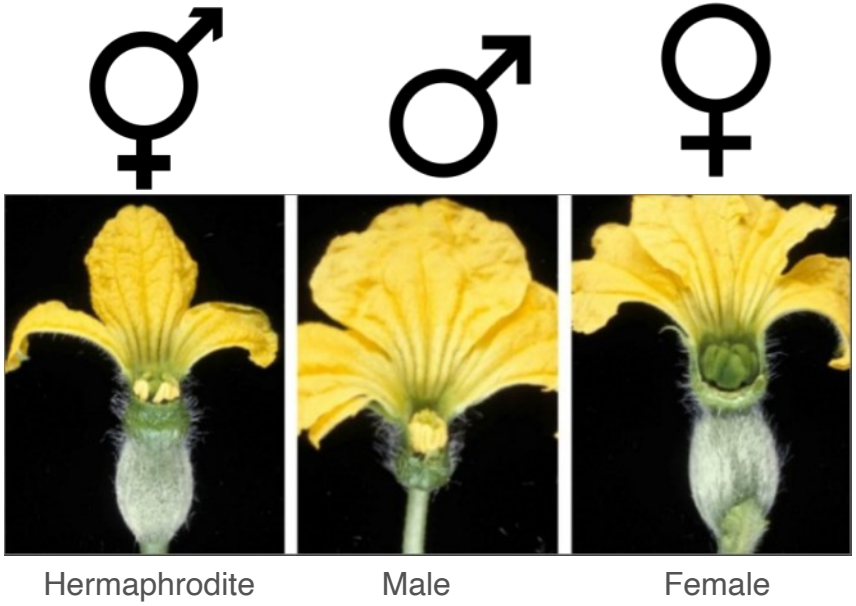
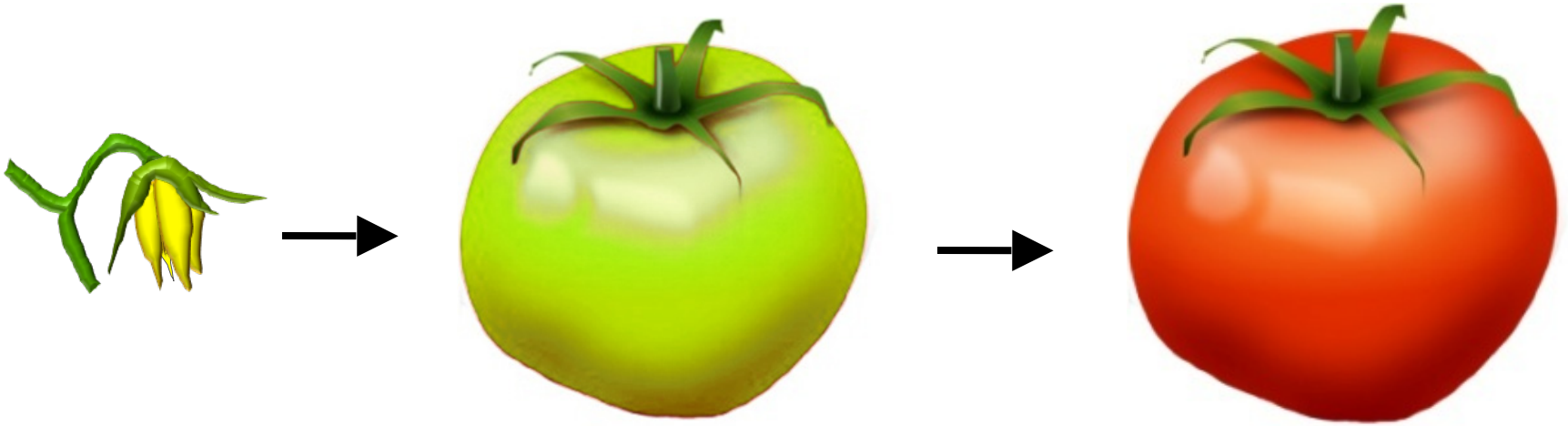


Image of Abdelhafid Bendahmane, URGV - Plant Genomics Research INRAE

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.

Auxin and GA promote cell division and growth of the fruit

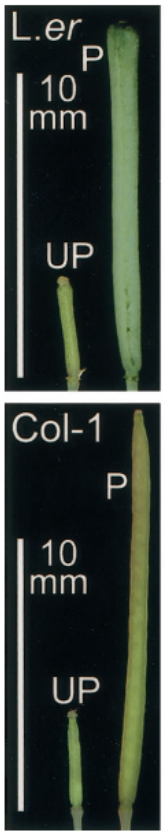
Seedless varieties of grapes and other fruits require exogenous application of GA for fruit development. Strawberry receptacles respond to auxin.

Auxin + GA

GA

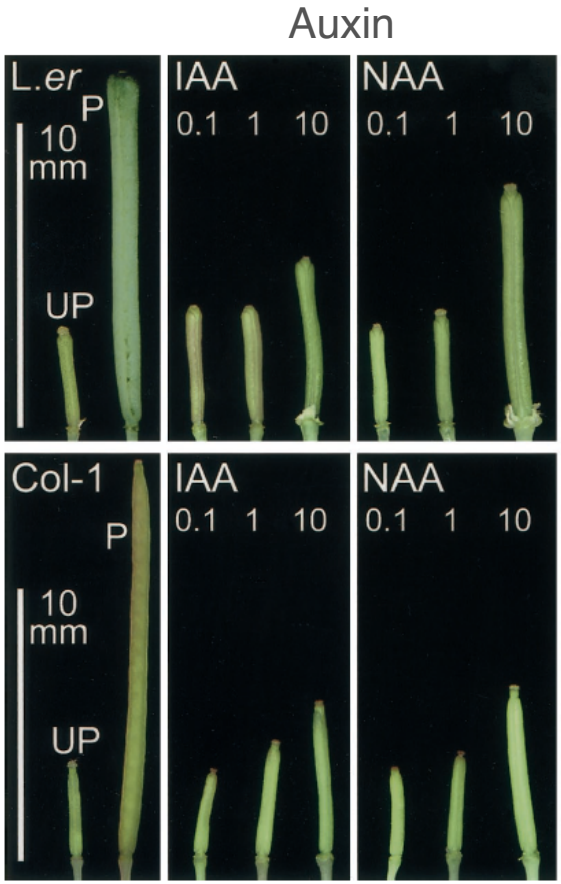
Auxin

Auxin and GA promote cell division and growth of the fruit



Vivian-Smith A & Koltunow AM (1999) Genetic analysis of growth-regulator-induced parthenocarpy in Arabidopsis. *Plant Physiol* **121**, 437–451.

Auxin and GA promote cell division and growth of the fruit



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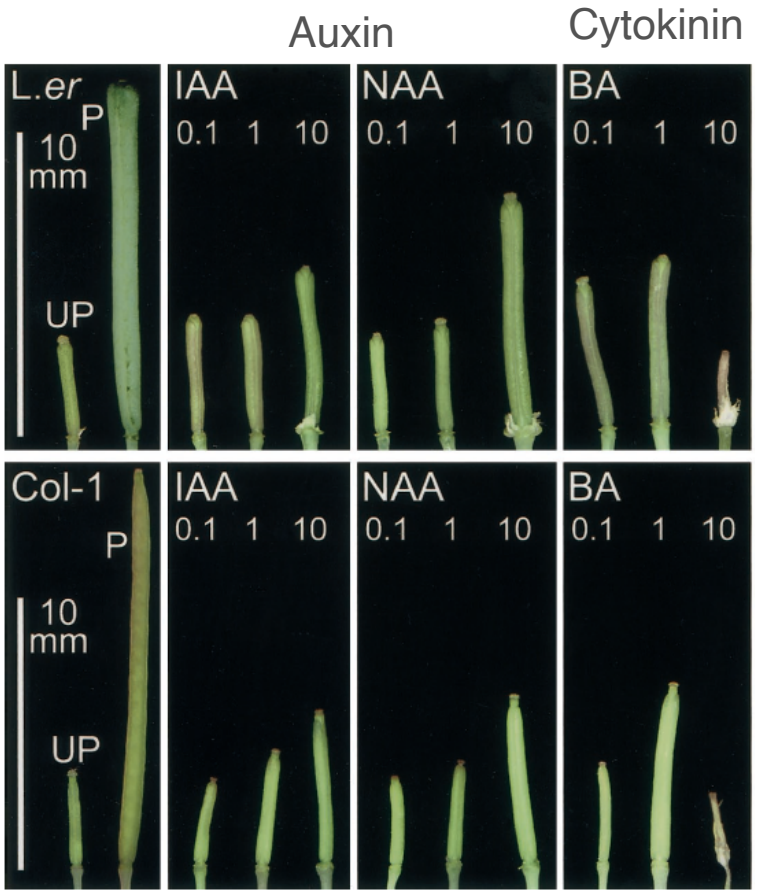

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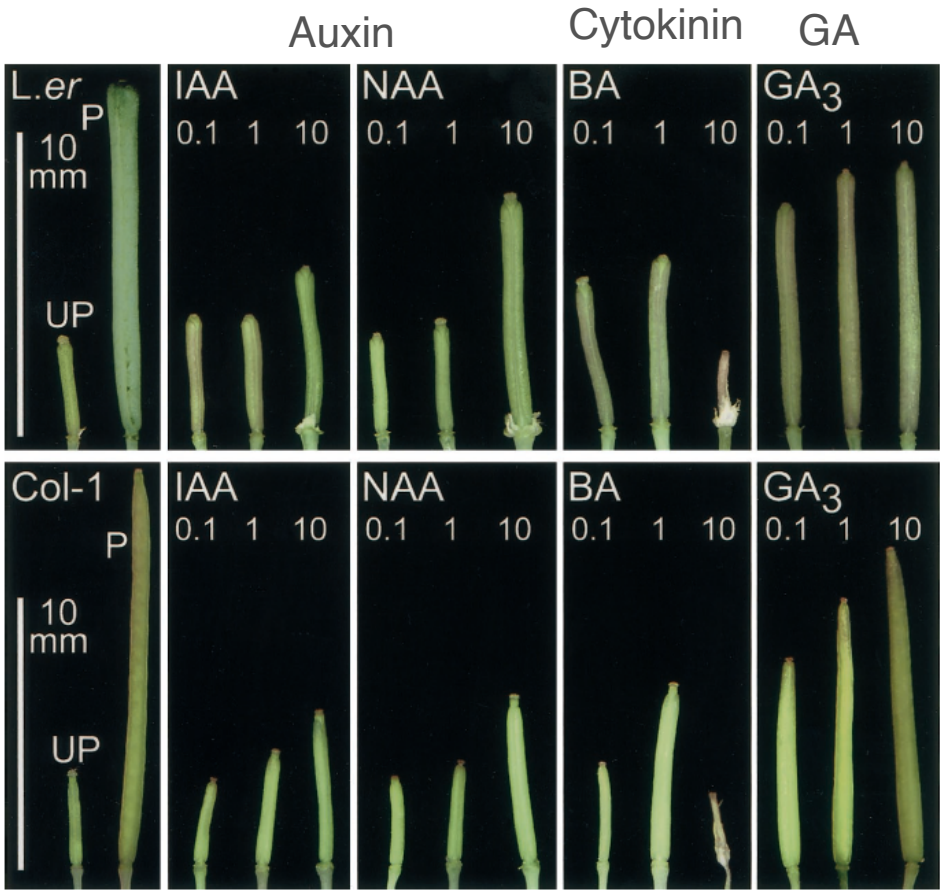

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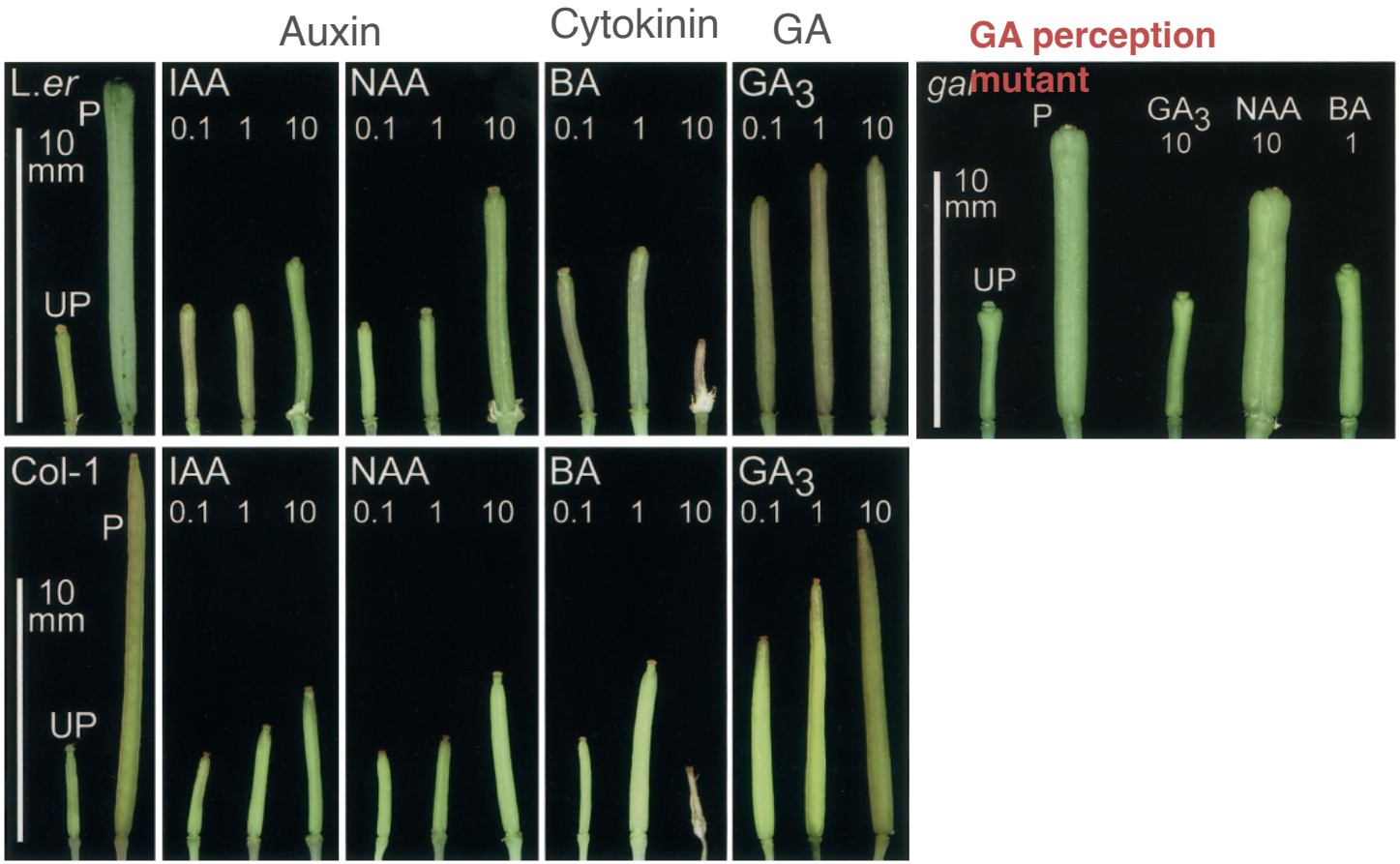

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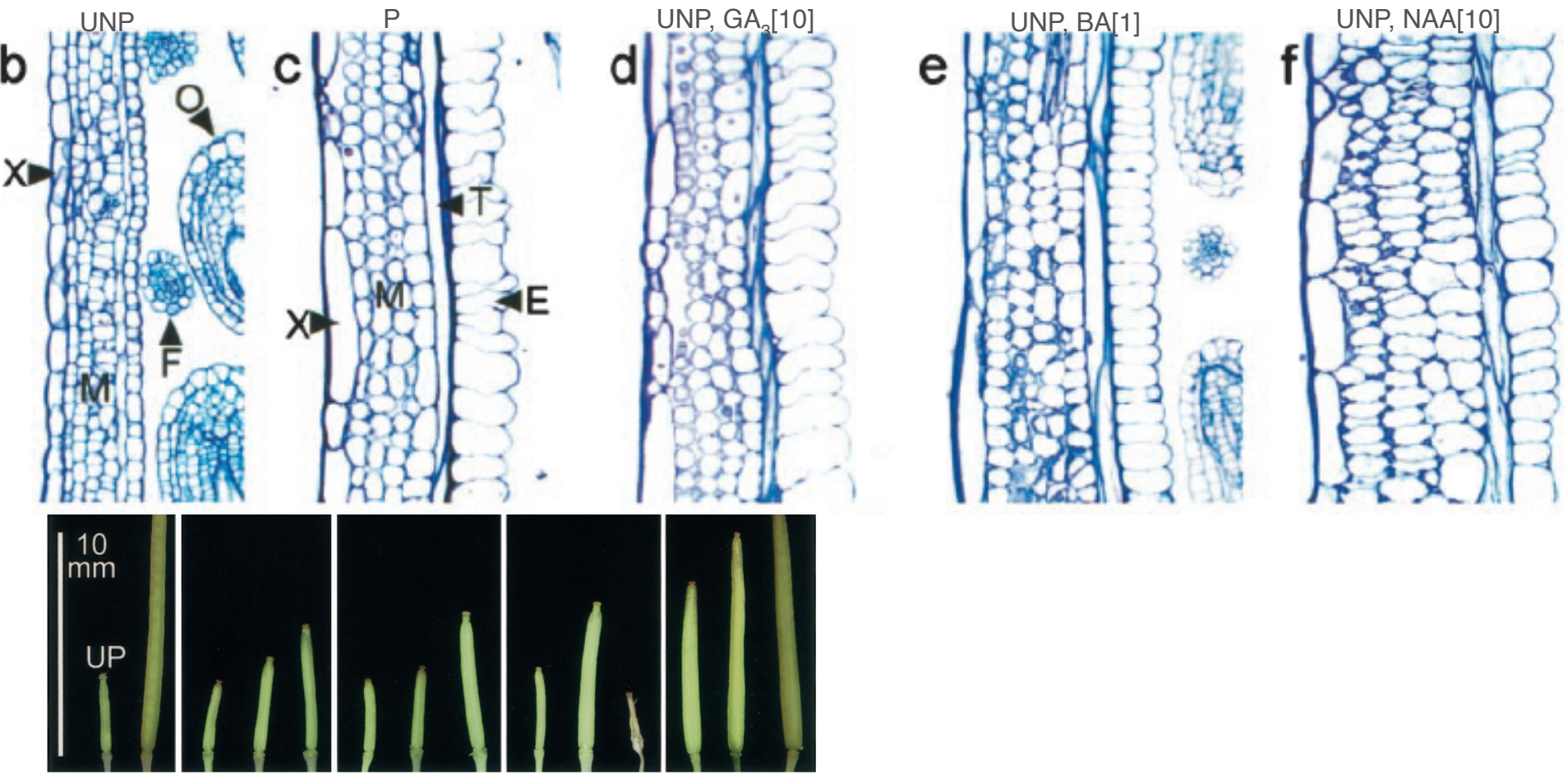
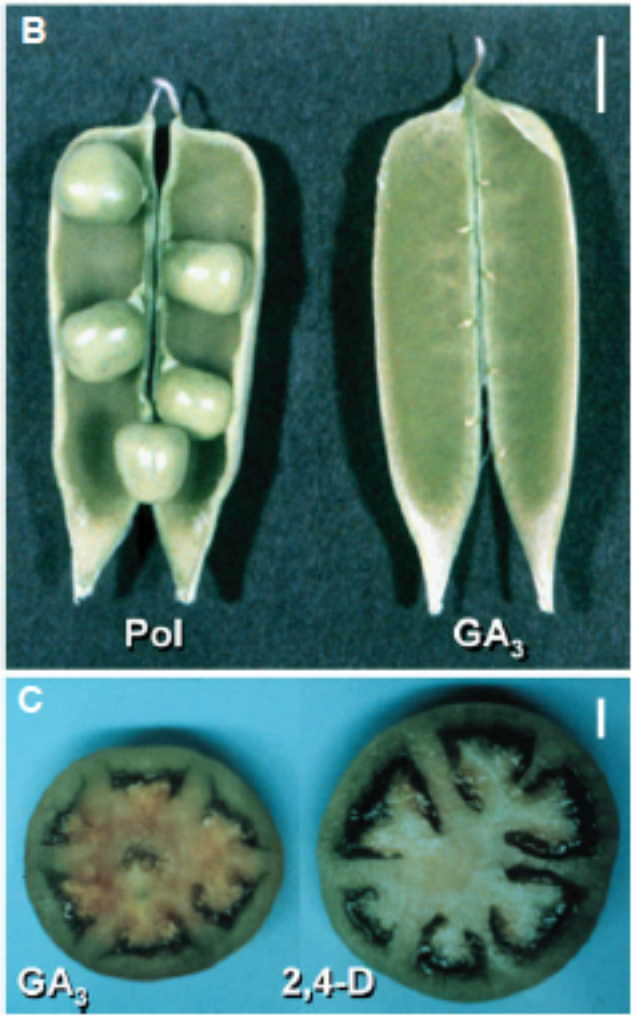
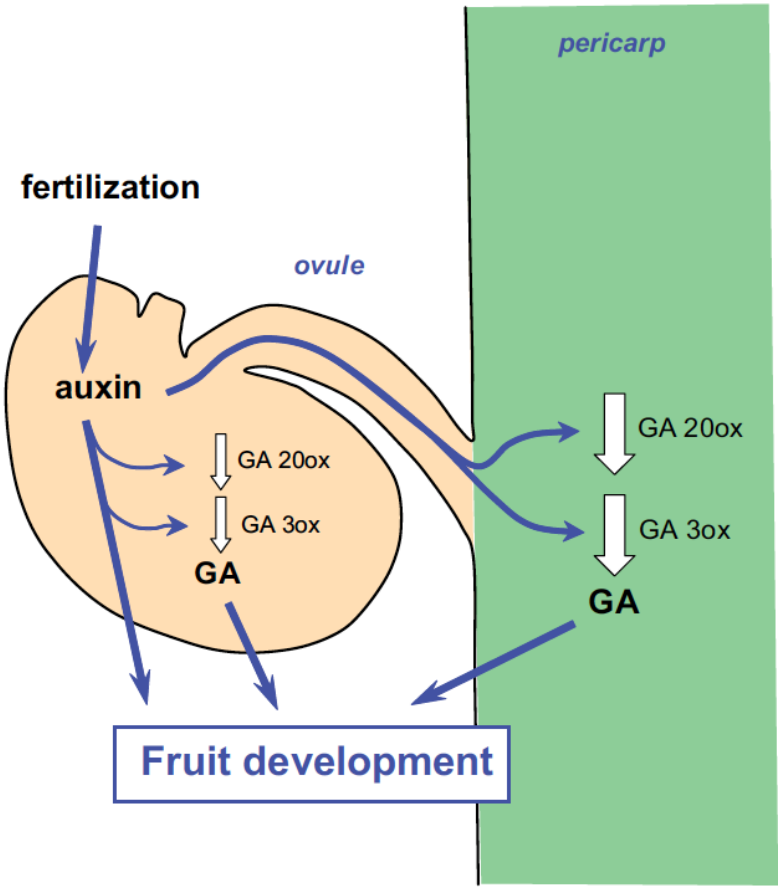


Vivian-Smith A & Koltunow AM (1999) Genetic analysis of growth-regulator-induced parthenocarpy in Arabidopsis. *Plant Physiol* **121**, 437–451.

Auxin and GA promote growth of the fruit without seeds

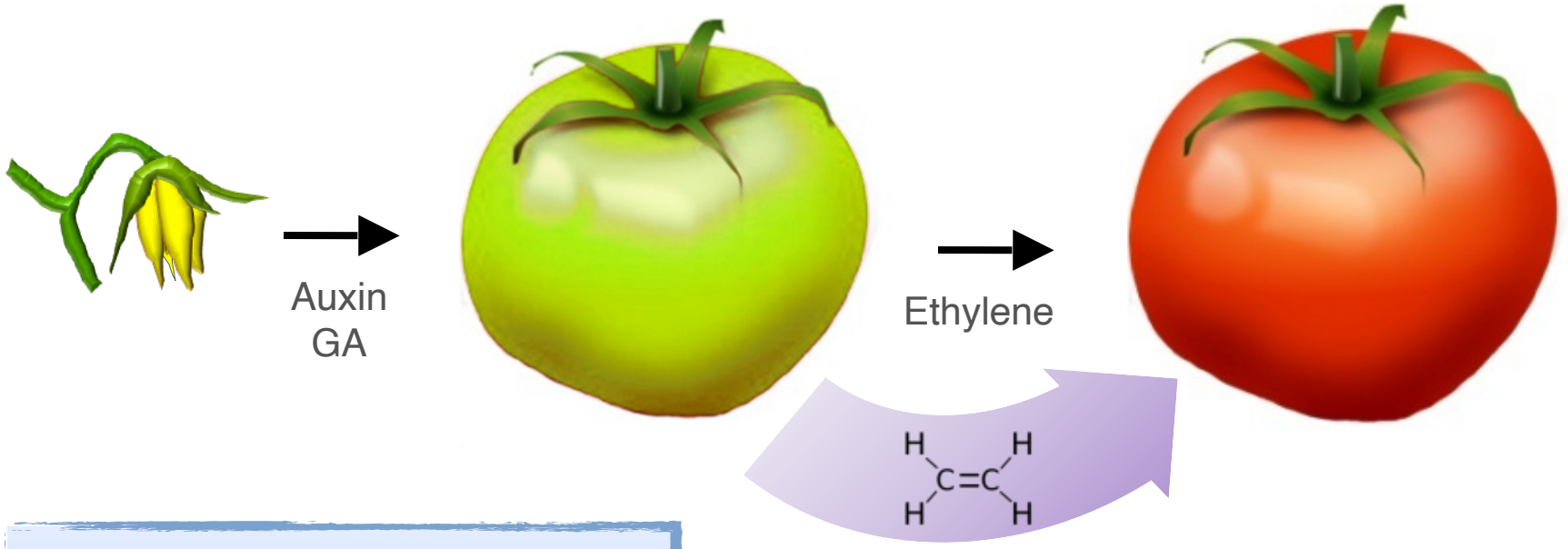
parthenocarpy





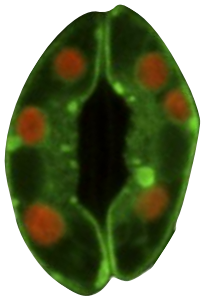
Alabadí D, Blázquez MA, Carbonell J, Ferrándiz C & Perez-Amador MA (2008) Instructive roles for hormones in plant development. *Int. J. Dev. Biol.*

Fruit ripening is induced by ethylene



Ethylene is a gaseous hormone that promotes fruit softening and flavour and colour development

Lectures outline



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Hormonal control of reproduction

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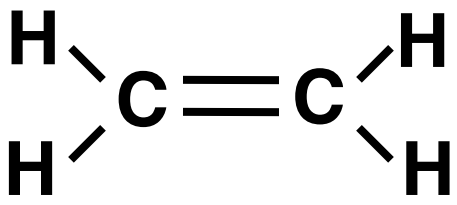
Hormonal responses to stress

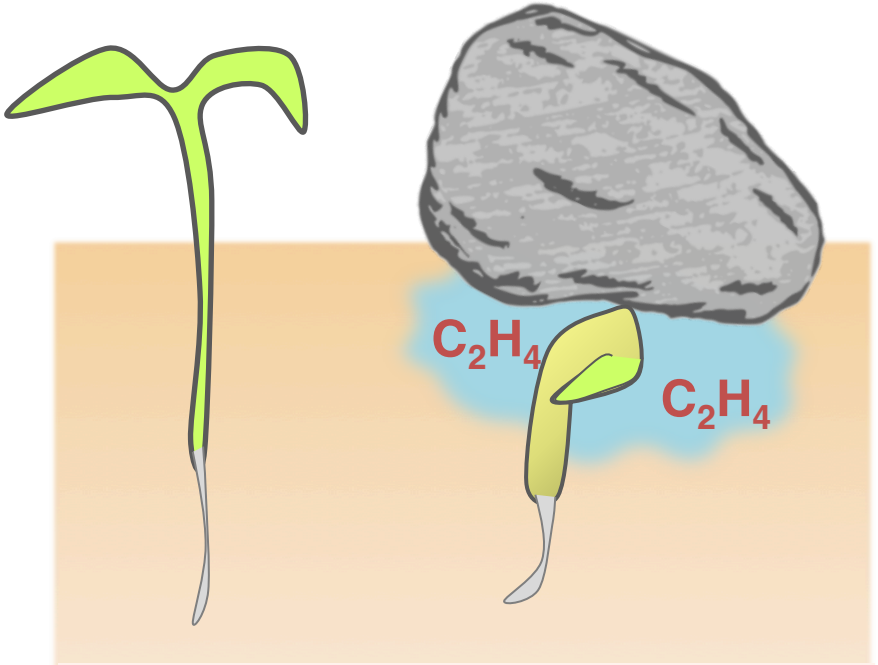
- Salicylates
- Jasmonates

Cross-regulation of hormonal effects

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

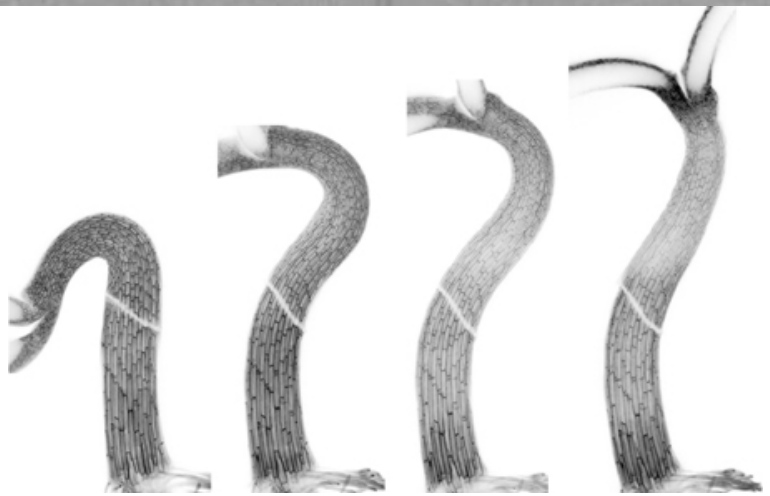




Ethylene induces the **triple response**:

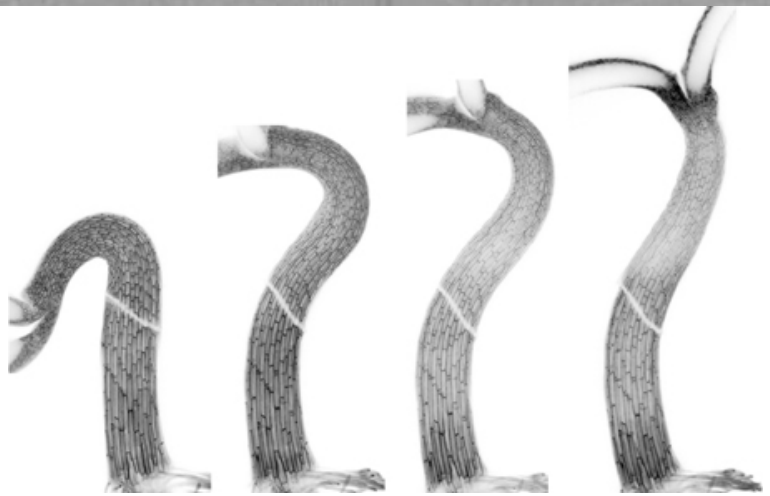
- ✓ reduced elongation,
- ✓ hypocotyl swelling,
- ✓ apical hook exaggeration.

Apical hook



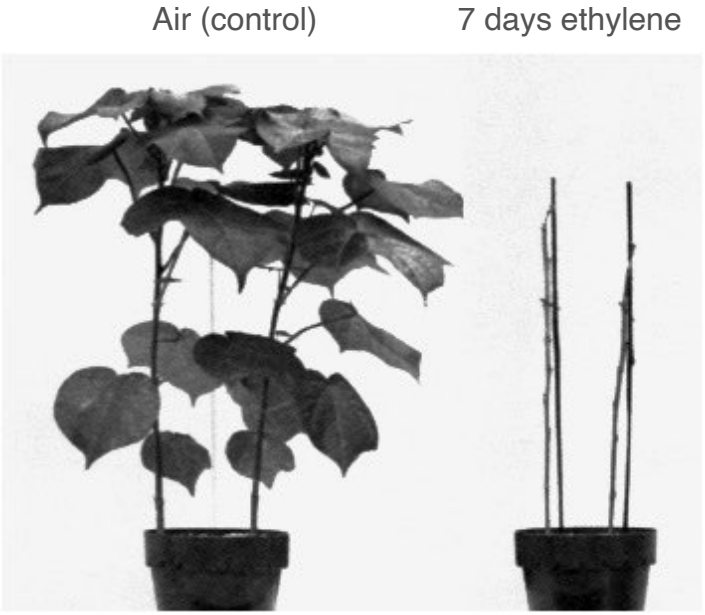
https://www.frontiersin.org/articles/10.3389/fpls.2013.00441/full

Apical hook



https://www.frontiersin.org/articles/10.3389/fpls.2013.00441/full

Ethylene promotes senescence of leaves and petals

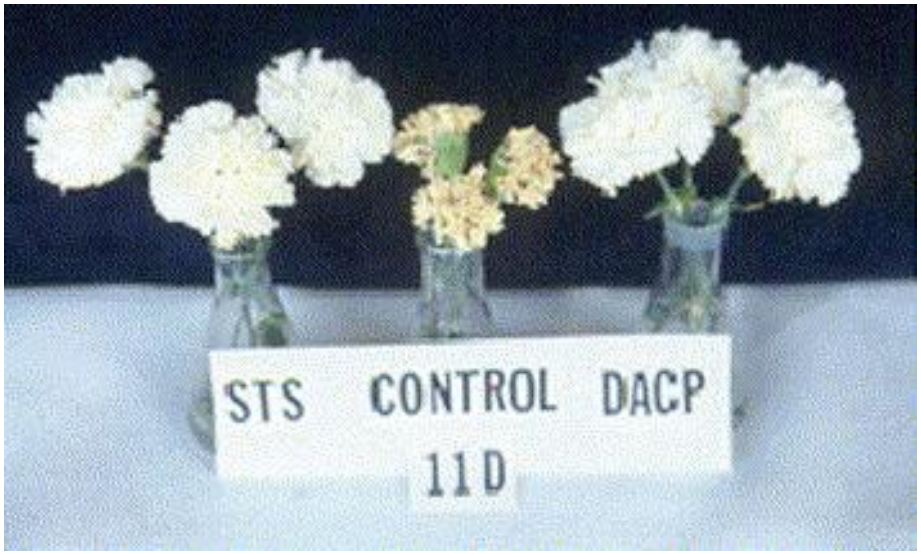


Ethylene promotes leaf and petal senescence.

Aspidistra is ethylene-resistant and so became popular houseplant.

Beyer, Jr., E.M. (1976) A potent inhibitor of ethylene action in plants. Plant Physiol. 58: 268-271.

Ethylene shortens the longevity of cut flowers and fruits



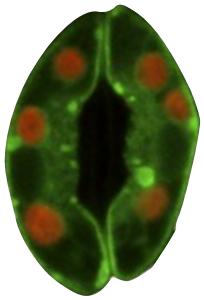
Ethylene levels can be managed to maintain fruit freshness, commercially and at home.

Strategies to limit ethylene effects

- ✓ Limit production - high CO_2 or low O_2
- ✓ Removal from the air -$KMnO_4$ reaction, zeolite absorption
- ✓ Interfere with ethylene binding to receptor - sodium thiosulfate (STS), diazocyclopentadiene (DACP), others

Serek, M., Woltering, E.J., Sisler, E.C., Frello, S., and Sriskandarajah, S. (2006) Controlling ethylene responses in flowers at the receptor level. Biotech. Adv. 24: 368-381

Lectures outline



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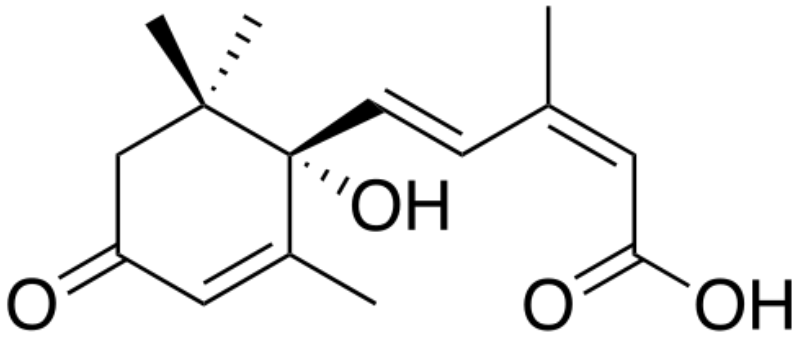
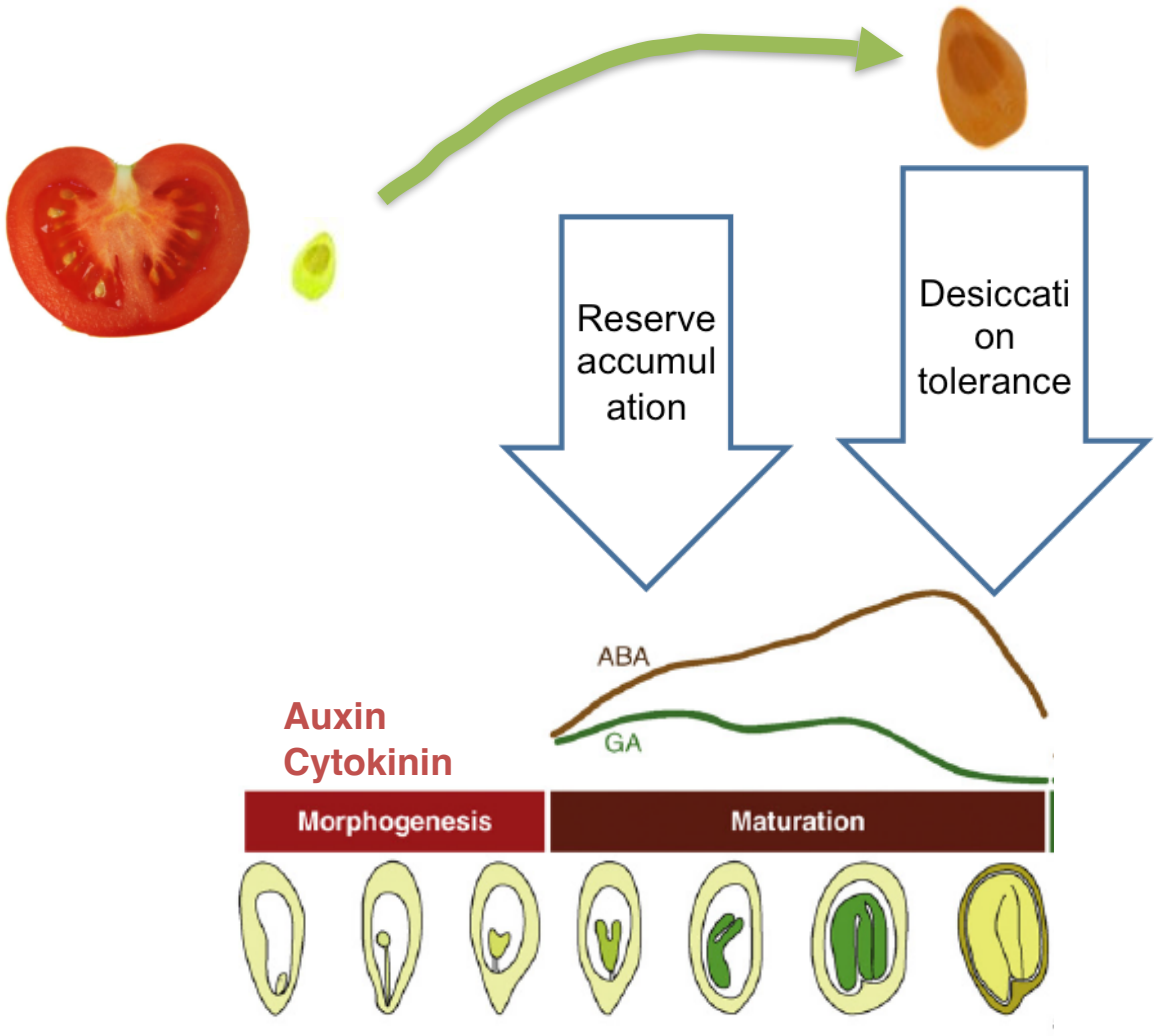
Cross-regulation of hormonal effects

Abscisic acid

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



ABA accumulates in maturing seeds



Seed maturation requires ABA synthesis and accumulation of **reserve nutrients** to confer **desiccation tolerance** to the seed.

Braybrook SA & Harada JJ (2008) LECs go crazy in embryo development. *Trends in Plant Science* 13, 624–630.

Developmental control of seed maturation

ABA promotes seed maturation.

ABA deficient mutants do not complete processes associated with maturation & dormancy

e.g. *abi3* ABA insensitive mutant from Arabidopsis undergoes:

- ✓ Precocious germination
- ✓ Retain chlorophyll
- ✓ Differentiate shoot meristem and vasculature

Seeds from Arabidopsis plants showing normal brown mature seeds (wild type Landsberg erecta ecotype, Ler) and mutant *abi3-5* seeds which are still green.

Precocious germination of maize seed in the maize *viviparous1* mutant.

Roschzttardtz et al., (2009) *Plant Physiology* 150:84-95

McCarty et al (1989) The Plant Cell, Vol. 1, 523-532,.

Once dormant and dry, seeds can remain viable for very long times

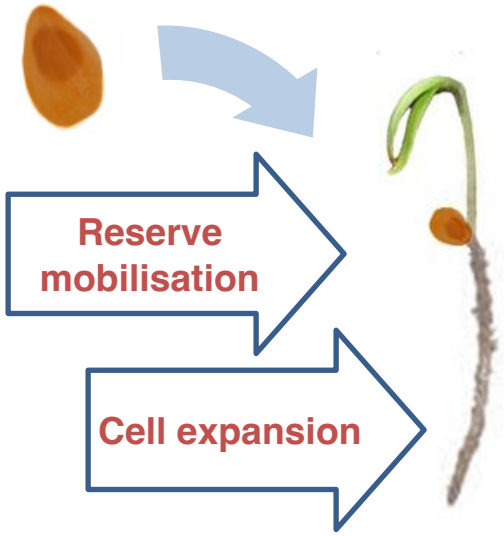
These date palm seeds are nearly 2000 years old, but still viable and capable of germination.
Five-hundred year old lotus seeds have also been successfully germinated.
Having a thick seed coat may help these super seeds retain viability.

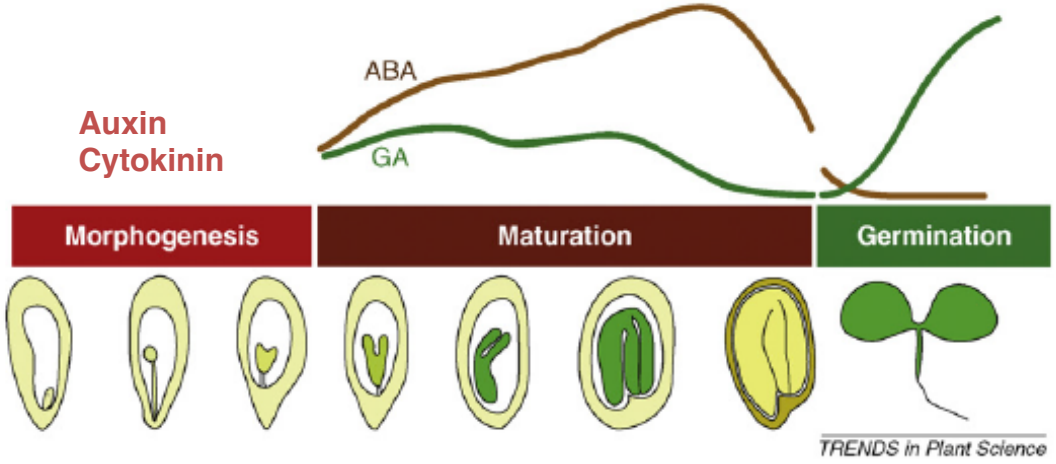
Date palm growing from 2000 year old seed.

Sallon, S., et al. (2008). Germination, genetics, and growth of an ancient date seed. Science 320: 1464,
Lotus picture by Peripitus

GA is required for seed germination

Seed germination requires **elimination of ABA** and **production of GA** to promote growth and breakdown of seed storage products.





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Summary – hormonal regulation of reproductive development

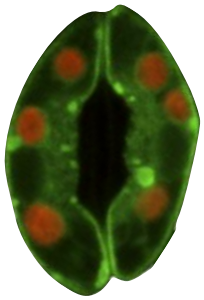
GA and ethylene promote flowering in some plants.

Fruit growth, maturation and ripening are regulated by auxin, GA and ethylene.

Seed maturation and germination are regulated by ABA and GA.

Understanding the roles of hormones in plant reproduction is important for food production, because most of our caloric intake is derived from seeds.

Lectures outline



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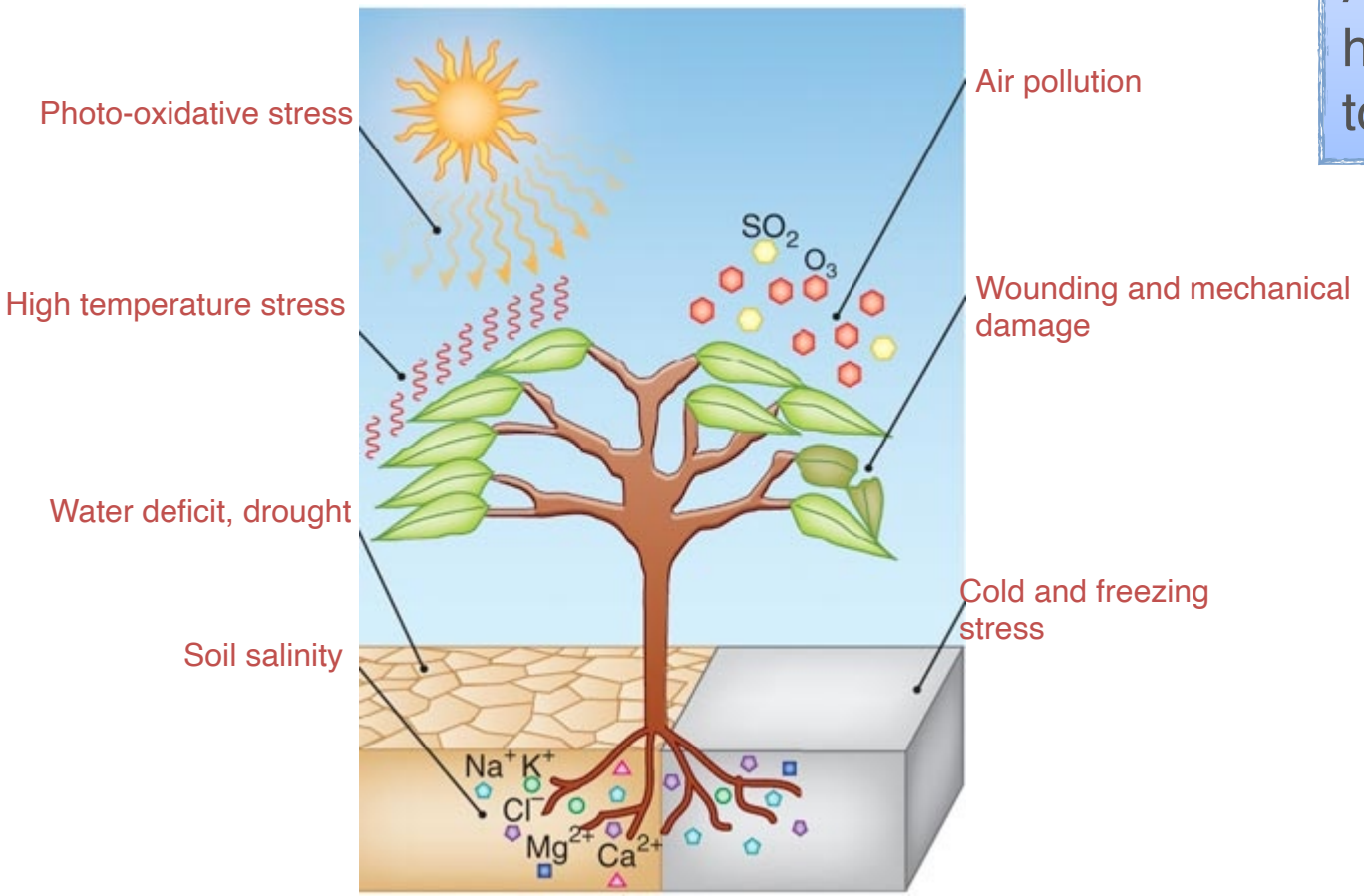
Cross-regulation of hormonal effects

Hormonal responses to abiotic stress

Plants' lives are very stressful.....

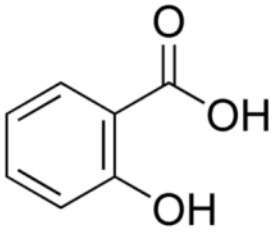
ABA and ethylene help plants respond to stress.



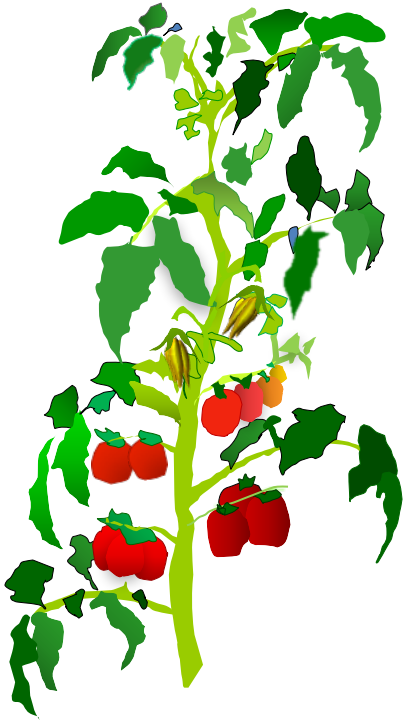
Vickers, C.E., Gershenzon, J., Lerdau, M.T., and Loreto, F. (2009) A unified mechanism of action for volatile isoprenoids in plant abiotic stress Nature Chemical Biology 5: 283 - 291

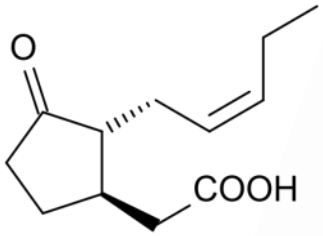
Hormonal responses to biotic stress

Bacteria, fungi, viruses – Biotrophic organisms



Salicylic Acid



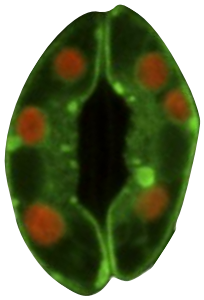


Jasmonates

Herbivores – insects, other animals, fungi – Necrotrophic organisms

Photo credits: A. Collmer, Cornell University; Salzbrot.

Lectures outline



How hormones work

Hormonal control of vegetative development

- Auxin
- Cytokinins
- Gibberellins

Hormonal control of reproduction

- Ethylene
- Abscisic Acid

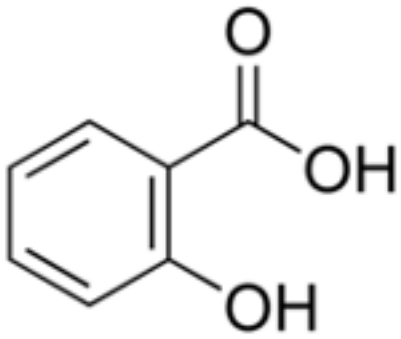
Hormonal responses to stress

- Salicylates
- Jasmonates

Cross-regulation of hormonal effects

Salicylic acid

- ✓ Response to biotrophic pathogens
- ✓ Induction of defense responses
- ✓ Systemic acquired resistance



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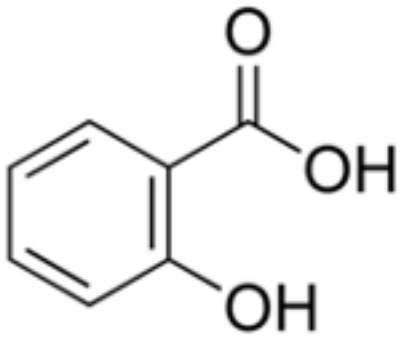
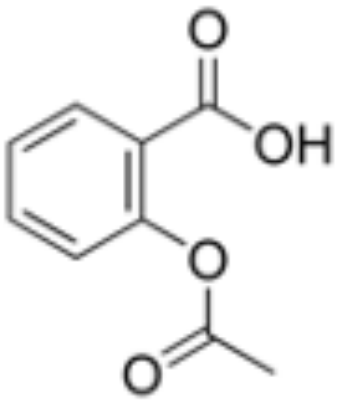
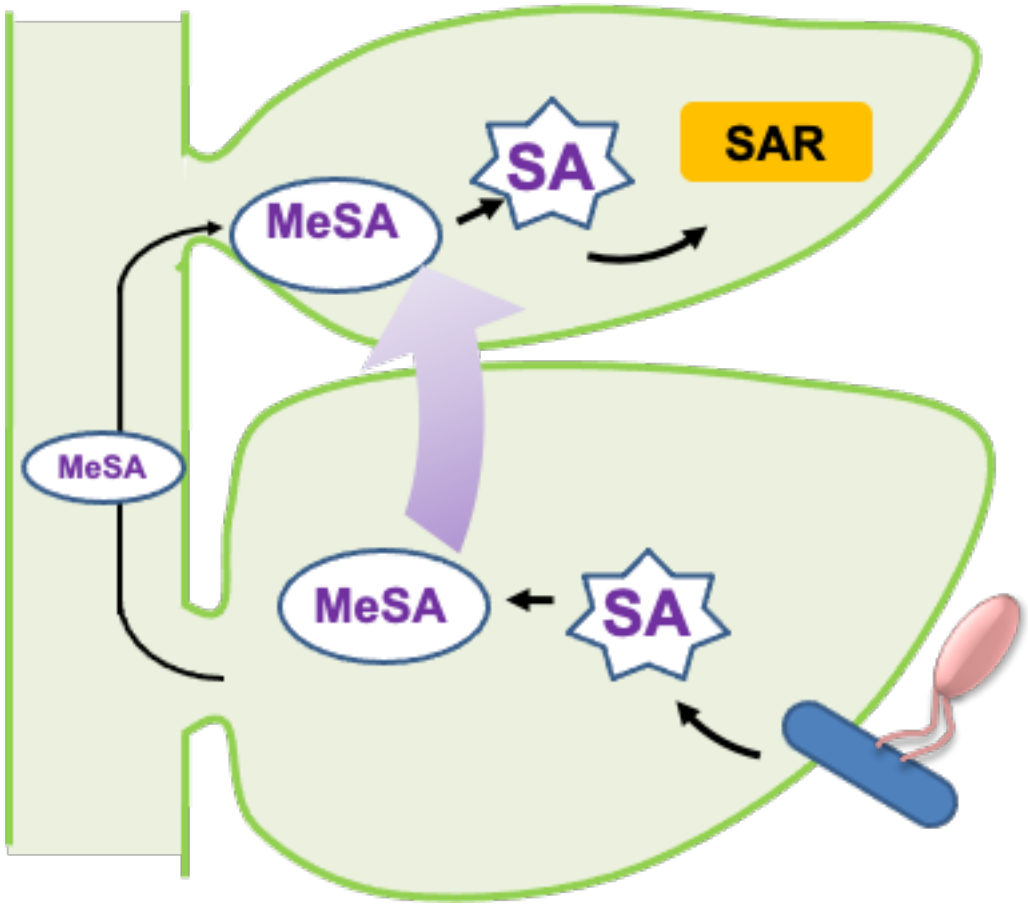




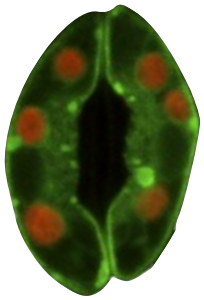
Acetylsalicylic Acid - aspirin

Salicylates contribute to Systemic Acquired Resistance



- ✓ SA production is induced by pathogen attack
- ✓ A mobile signal is produced for SAR
- ✓ Activation of an immunity response
- ✓ Hypersensitive response involves cell death of infected cells to prevent pathogens from spreading

Lectures outline



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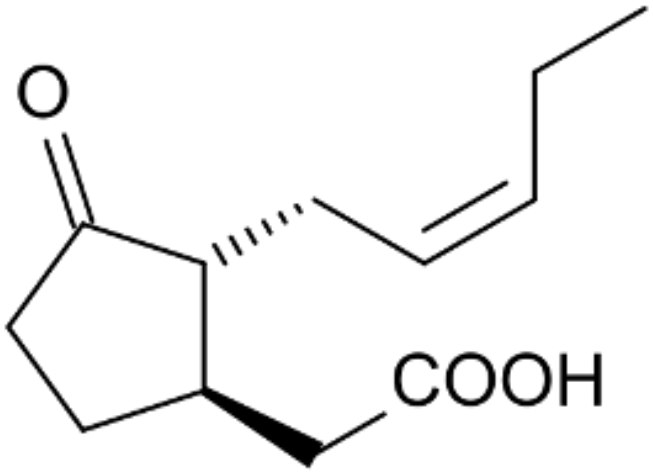
Cross-regulation of hormonal effects

Jasmonates

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



Jasmonate signaling contributes to defense against herbivory

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

McConn, M., et al. (1997) Jasmonate is essential for insect defense in *Arabidopsis.* Proc. Natl. Acad. Sci. USA 94: 5473-5477.

Jasmonates induce the expression of anti-herbivory chemicals

Wound-induced signals
Insect oral secretions

JA signaling

production of protease inhibitors
Feeding deterrents

➡ Contributes to systemic responses

R.J. Reynolds Tobacco Company, Bugworld.org

Summary – hormonal regulation of the stress response

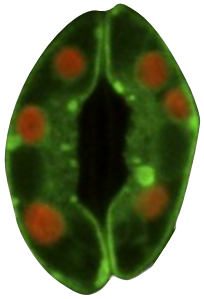
Hormonal signaling is critical for plant defenses against biotic and abiotic stresses

Auxin, cytokinin, 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 agriculture yields. Abiotic and biotic stresses are major causes of crop losses.

Lectures outline



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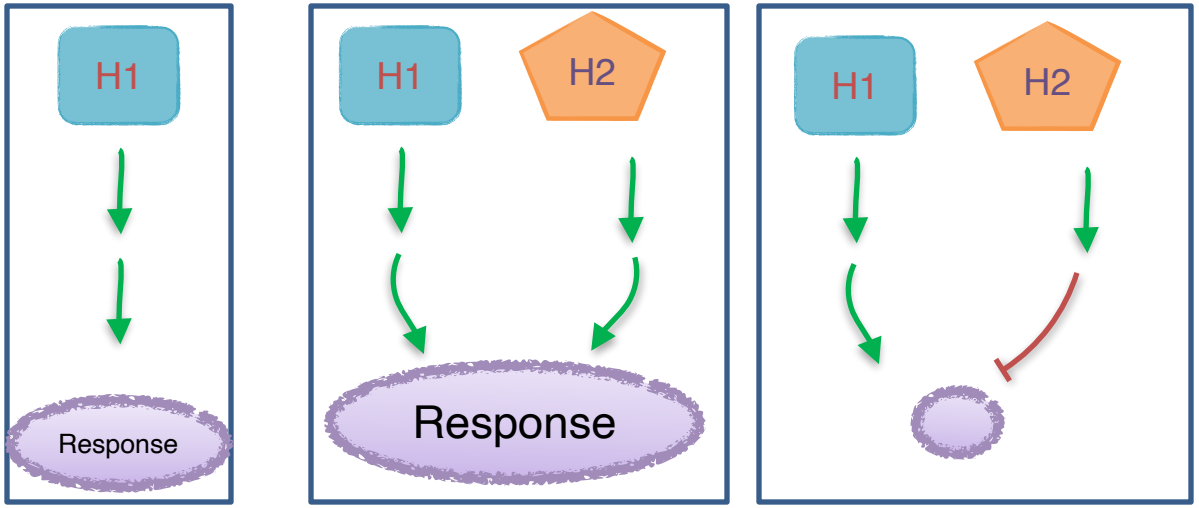
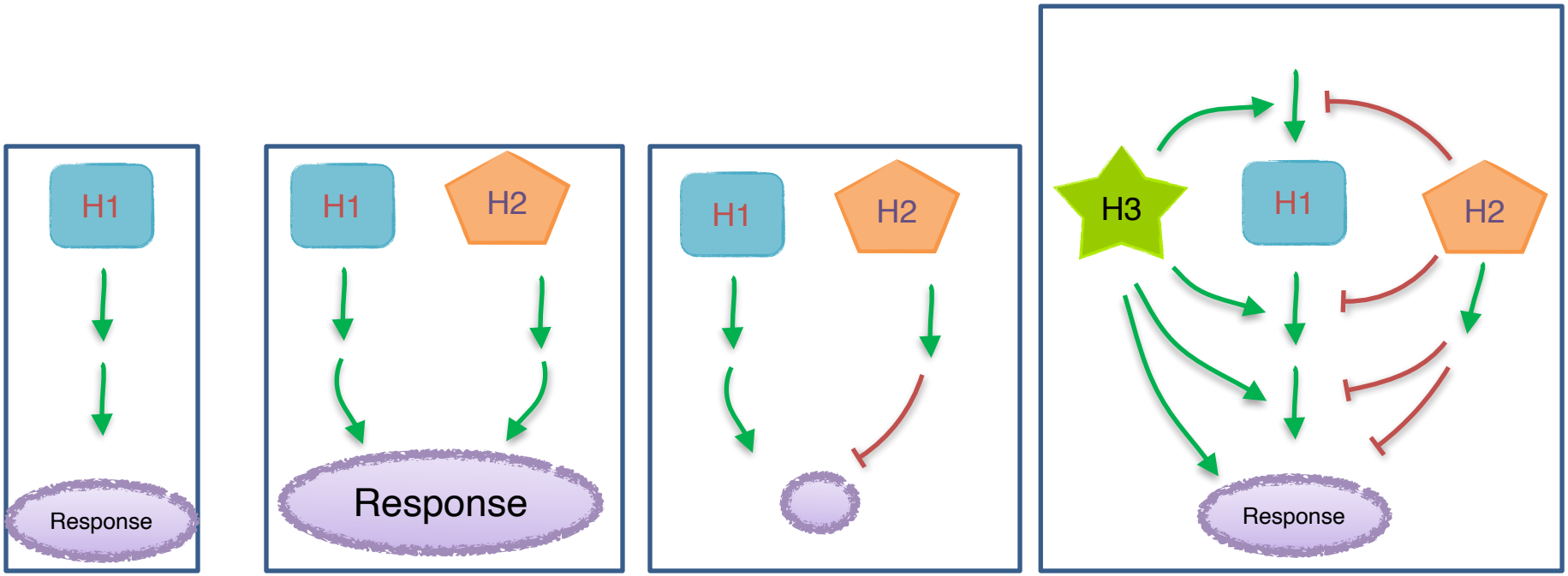
Cross-regulation of hormonal effects

Crosstalk between hormone signalling 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 signalling pathway of another hormone.

S2011 course outline

(2) 26/2 - **AUXIN** - production, transport, signalling; discovery of the hormone; tropism (physiology, genetics)

(3) 5/3 - **AUXIN** - root meristem and root-derived organs; Shoot organogenesis (differences and similarity with root), correlation with local auxin gradients, transport and organ formation.

(4) 12/3 - **AUXIN** - Embryogenesis - pattern formation during embryogenesis, Arabidopsis mutants, gene identities.

(5) 19/3 - **CYTOKININ** - production, degradation, perception, signal transduction, isolation and verification of the receptors and downstream components.

(6) 26/3 - **CYTOKININ** - Function in plant development.

(7) 2/4 - **ETHYLENE** - Genetic dissection of ethylene signalling; Molecular characterisation and arrangement of the pathway.

(8) 9/4 – **ABSCISIC ACID** - production and signalling; role in drought stress responses, root development and seed desiccation and dormancy

(9) 16/4 – **GIBBERELLIC ACID** – production and signalling; role in development, stress responses and seed development

(10) 23/4 — **SALICYLIC ACID** - an immunity response

(11) 30/4 — **JASMONATES** - A systemic response

(12) 7/5 – Illustration of **HORMONAL CROSSTALK**

(13) 14/5 - Hormones and **ABIOTIC STRESS**

(14) 21/5 - Round table, discussion, questions

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