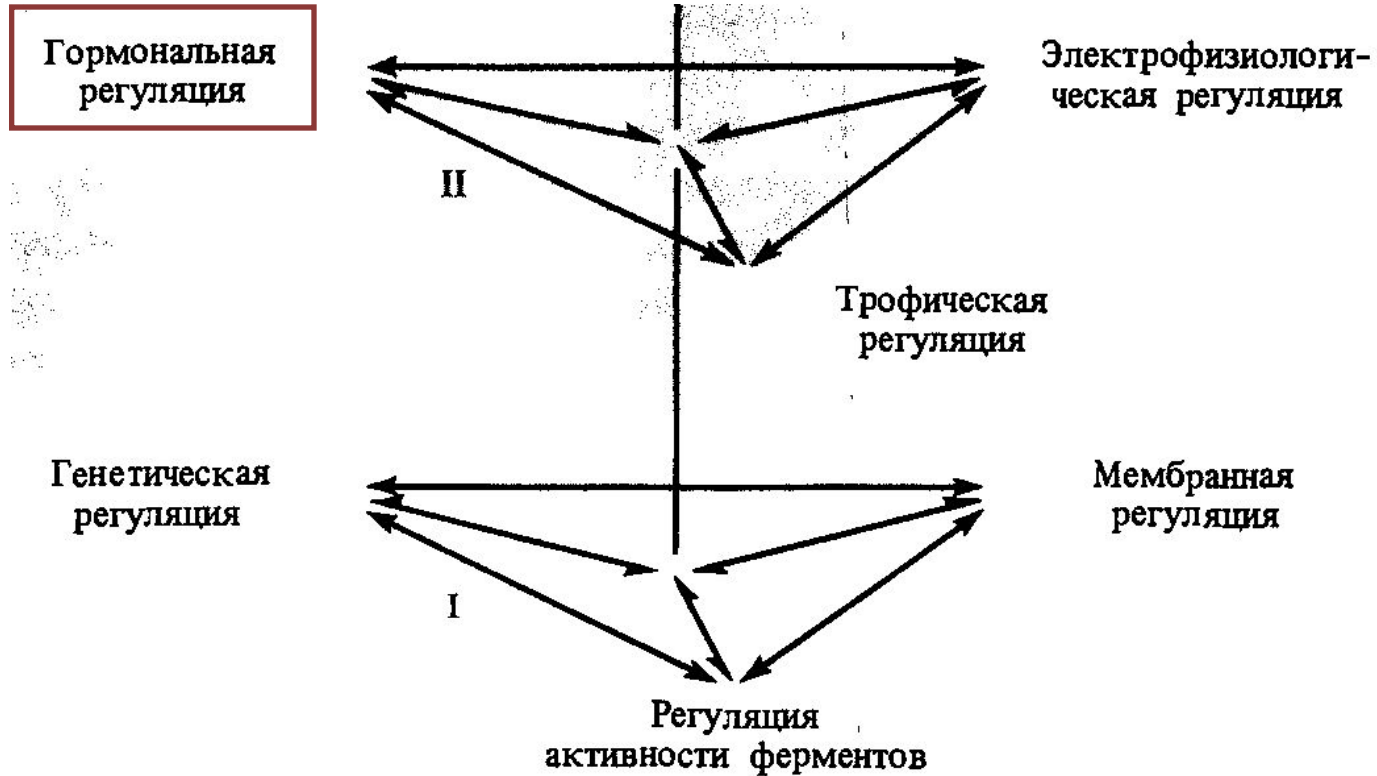


# Гормональная система растений

# Системы регуляции у растений



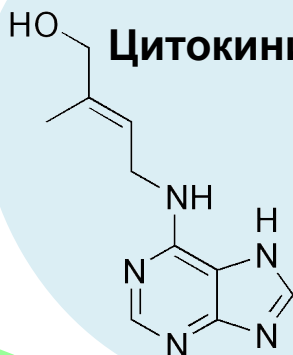
- (Полевой В.В., 1989)

# Основные гормоны растений

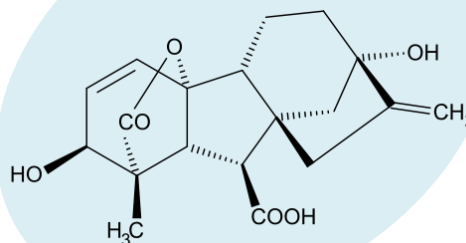
**Ауксины**



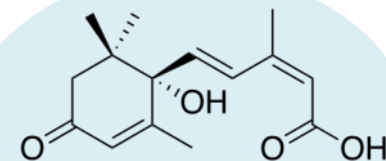
**Цитокинины**



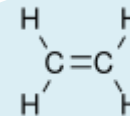
**Гиббереллины**



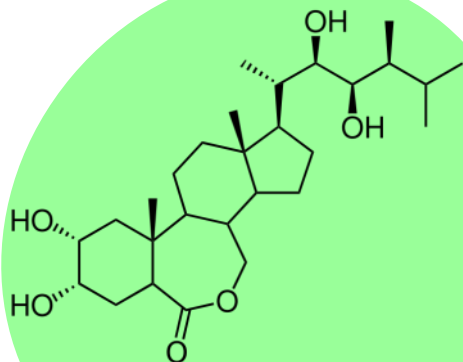
**Абсцизовая кислота**



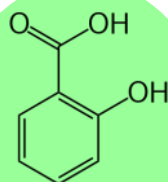
**Этилен**



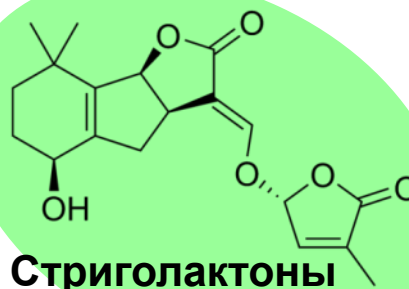
**Брассиностероиды**



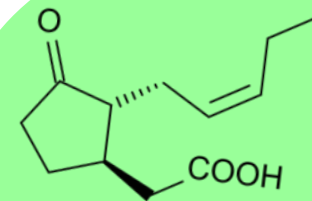
**Салицилаты**



**Стриголактоны**



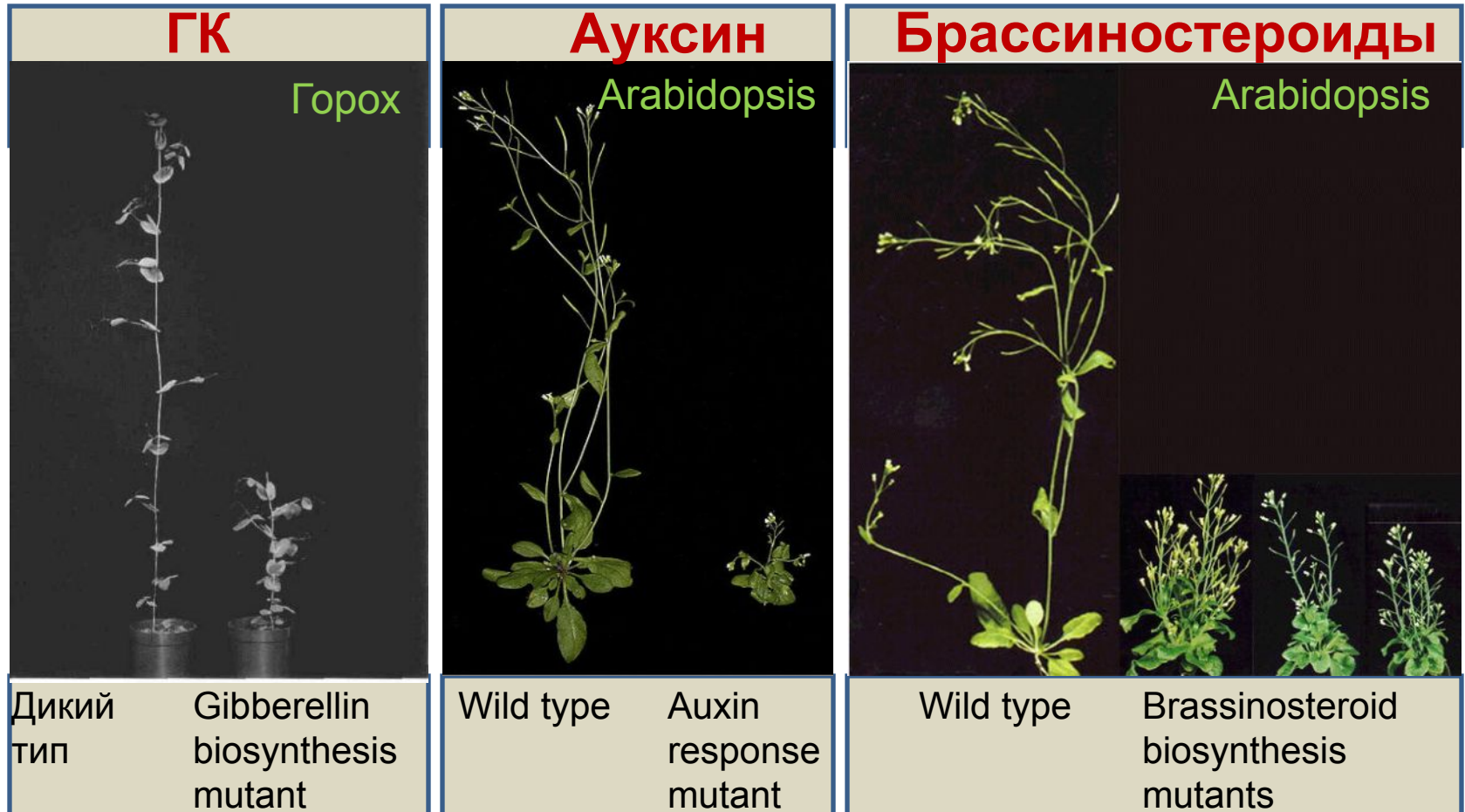
**Жасмонаты**



# Общие свойства гормонов растений

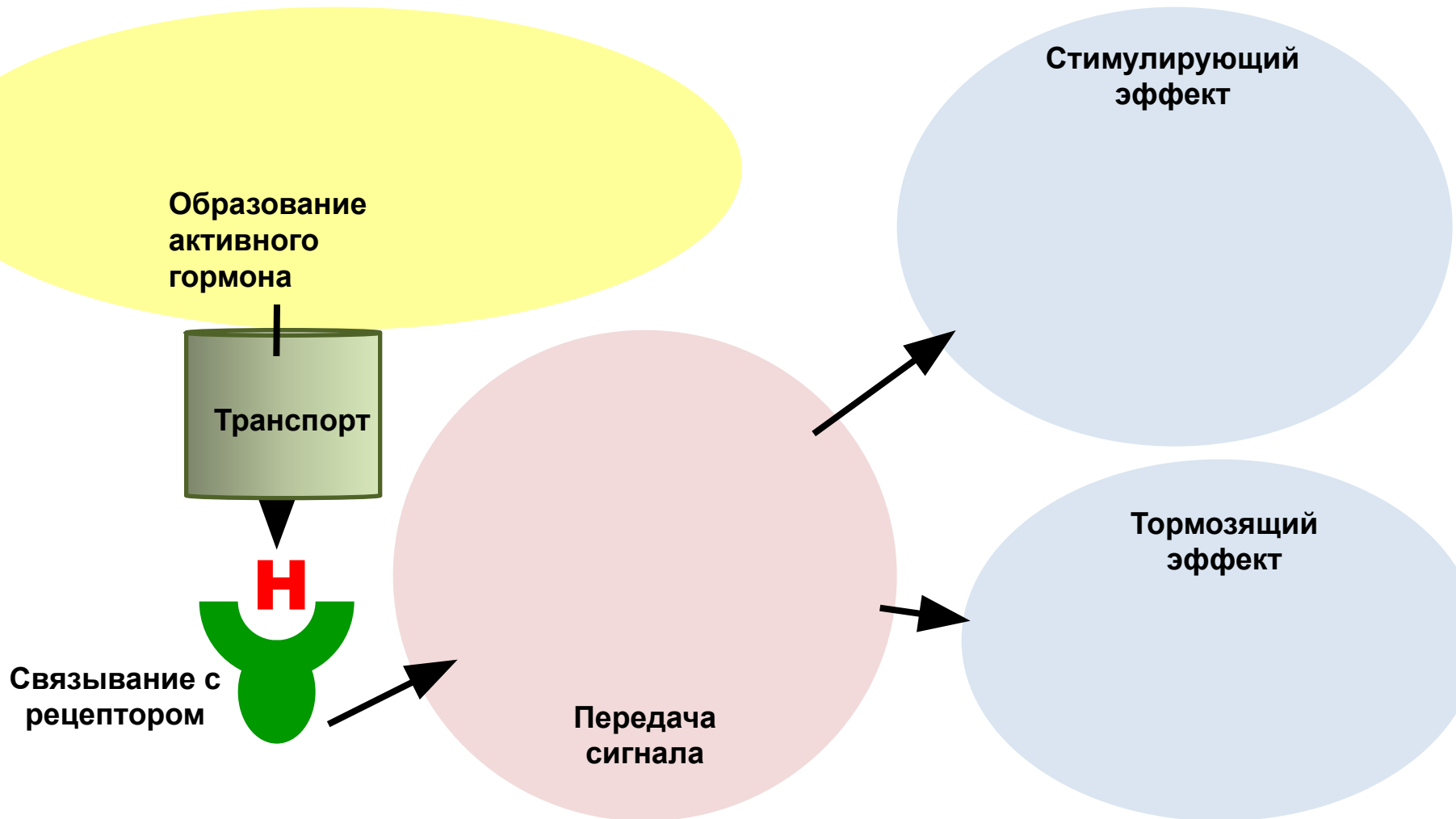
- Специфический ответ
- Наличие специфических рецепторов
- Концентрации  $10^{-6}$ - $10^{-12}$  М
- Мультифункциональность
- Потенциально могут быть образованы любой клеткой
- Не метаболизируются в регулируемых ими процессах
- Действуют не только дистанционно, но и в месте образования
- Эффект зависит от присутствия других гормонов и концентрации

# Нарушение синтеза некоторых гормонов отражается на росте растений

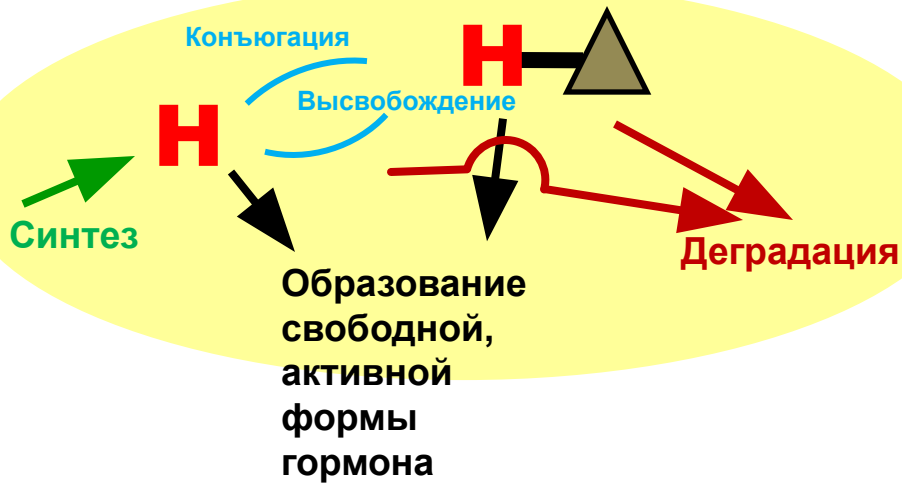


Lester, D.R., Ross, J.J., Davies, P.J., and Reid, J.B. (1997) Mendel's stem length gene (*Le*) encodes a gibberellin 3 $\beta$ -hydroxylase. *Plant Cell* 9: [1435-1443](#)-hydroxylase. *Plant Cell* 9: 1435-1443.; Gray WM (2004) Hormonal regulation of plant growth and development. *PLoS Biol* 2(9): [e311](#)-hydroxylase. *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

# Гормоны: синтез, транспорт, сигналинг



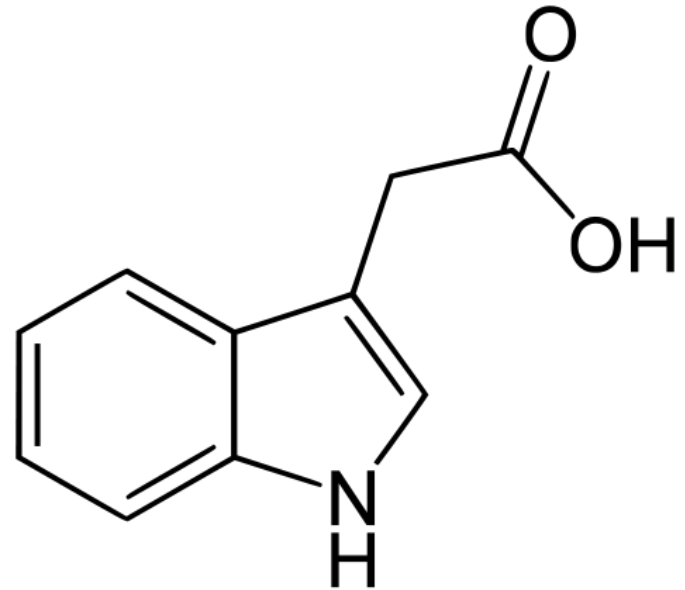
# Синтез



Многие регулируемые биохимические пути способствуют накоплению активной формы гормона. Конъюгат может временно хранить гормон в инертной форме, приводя к катаболическому распаду, или быть источником активного гормона.

# Ауксин

- Аттракция
- Рост клеток делением
- Тропизмы
- Формирование проводящих пучков
- Апикальное доминирование побега
- Ризогенез
- Стимуляция выработки этилена



Индолил-3-уксусная кислота (ИУК), наиболее распространённый природный ауксин



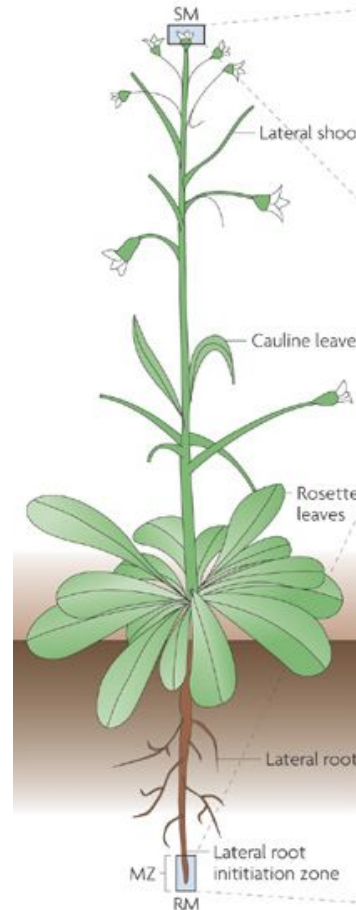
# Ауксины регулируют развитие растений

Инициация боковых органов в апикальной меристеме побега

Подавление ветвления побега

Развитие проводящей системы

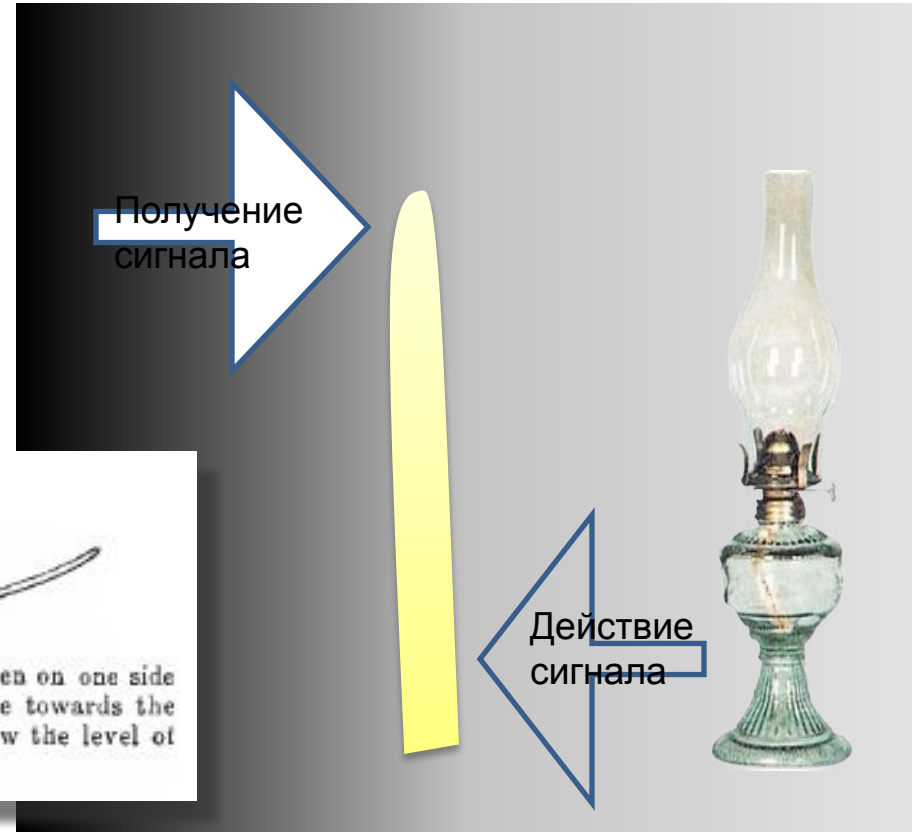
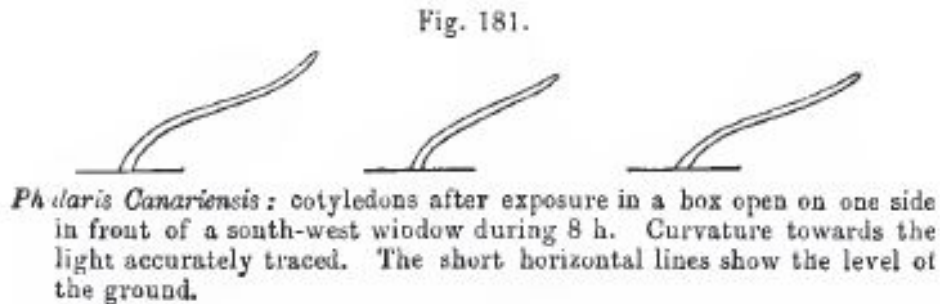
Поддержка инициальных клеток апикальной меристемы корня



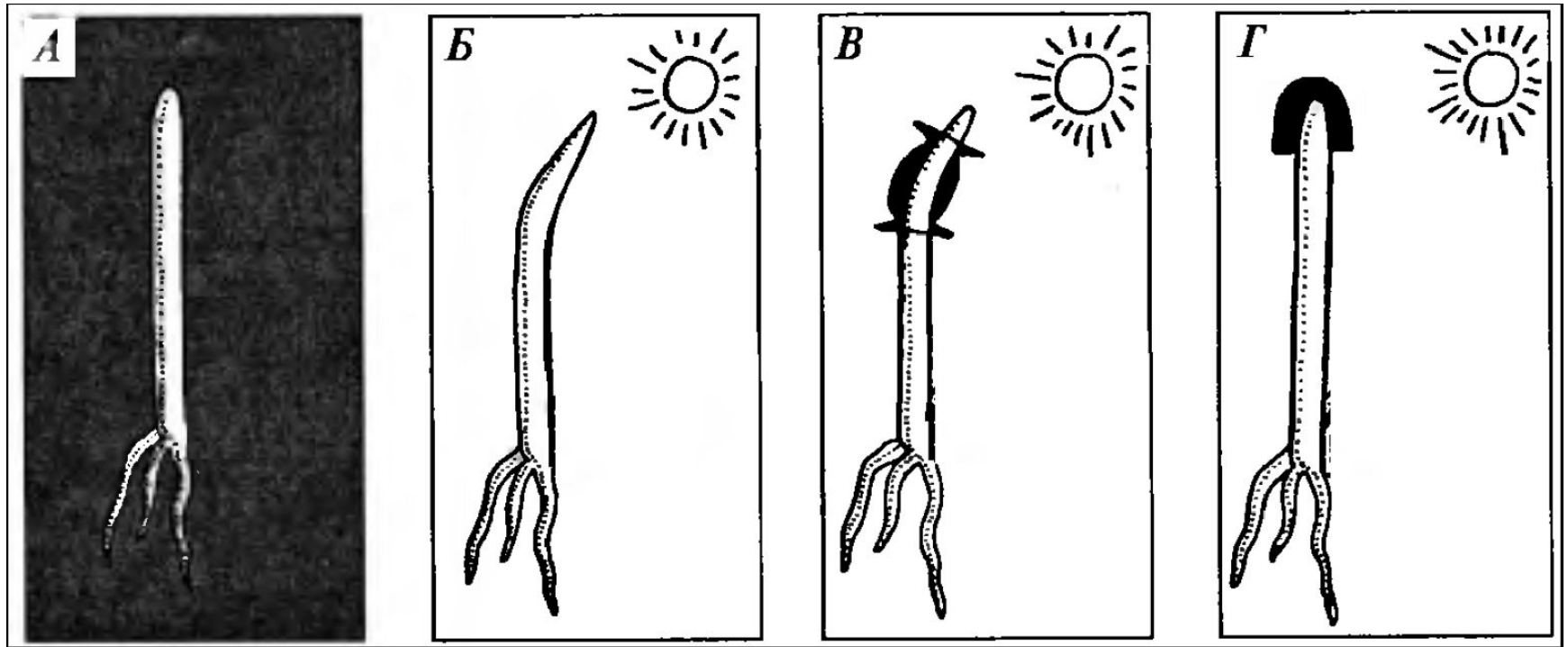
Поддержка ветвления корня

# Ростовой контроль

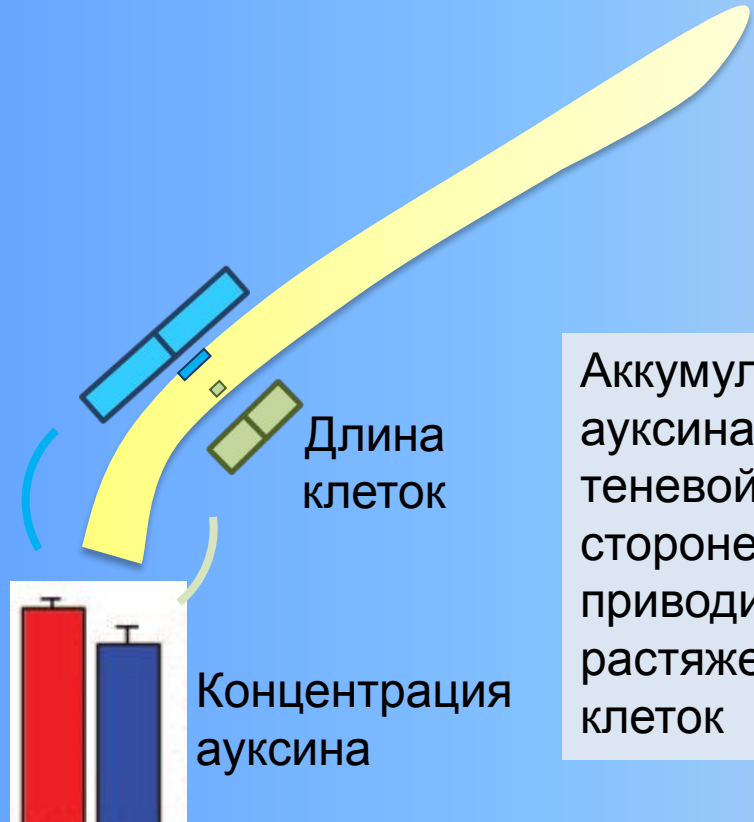
Опыт Ч. и Ф.  
Дарвинов



# Опыт Чарльза и Френсиса Дарвинов



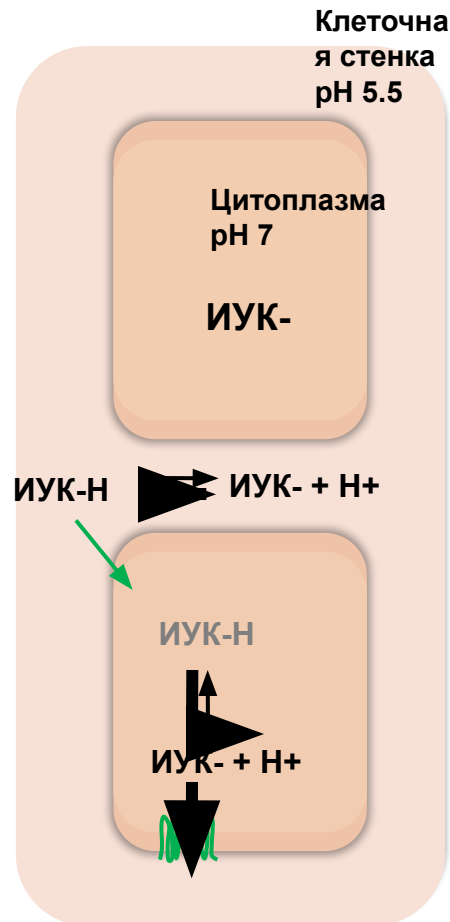
# Неравномерный рост клеток – результат перемещения ауксина на затененную сторону (Теория Холодного-Вента)



Аккумуляция ауксина на теневой стороне приводит к растяжению клеток



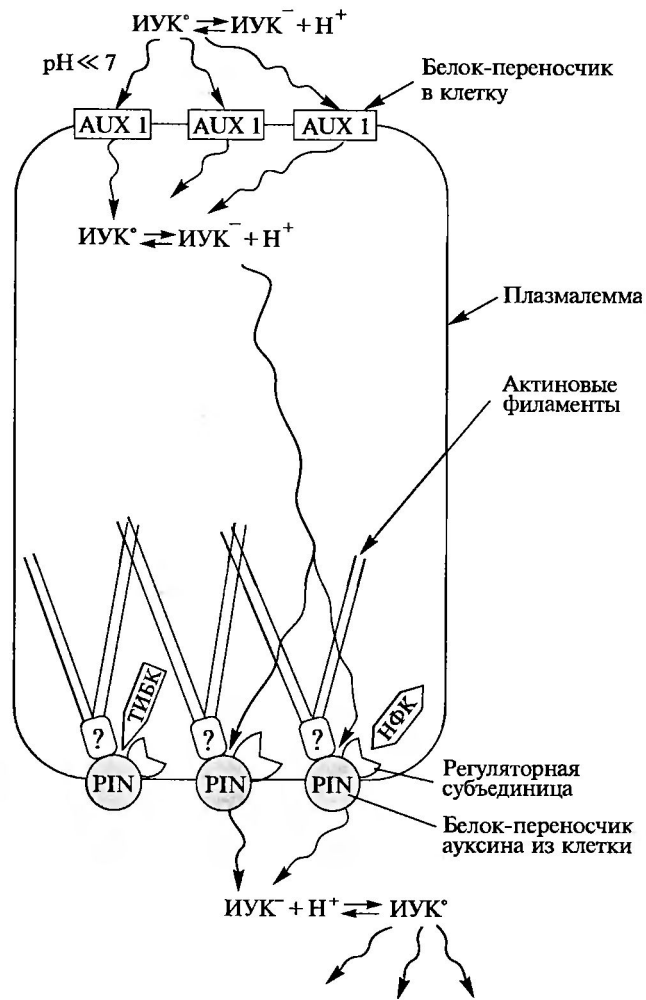
# Полярный, базипетальный транспорт ауксина



Ауксин - заряженный анион (ИУК<sup>-</sup>) в цитоплазме (pH 7).

В кислом матриксе кл. стенки (pH 5.5) молекула не заряжена (ИУК-Н). Незаряженная форма проникает через плазмалемму в клетку, где депротонируется и активно выводится из клетки специфическим переносчиком

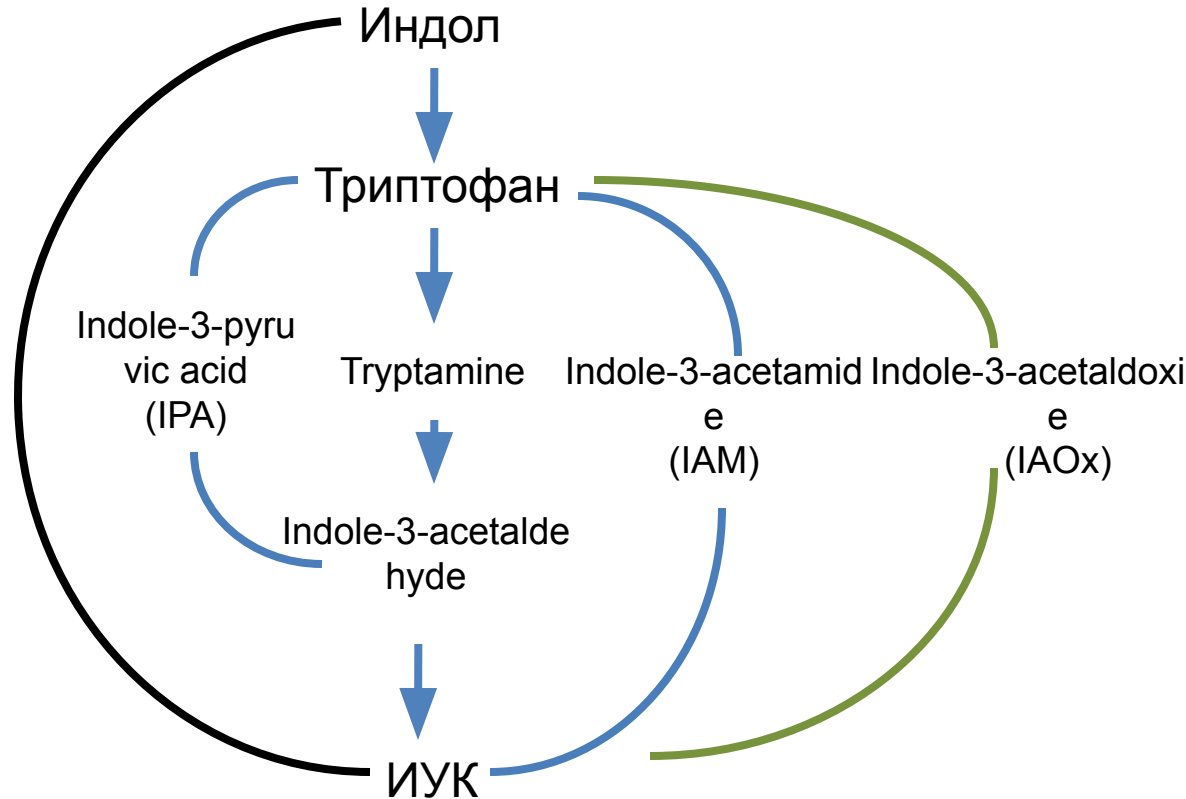
# Полярный транспорт ауксина



Транспорт ауксина сквозь клетки контролируется транспортными белками трех семейств, задающих направление транспорта молекулы.

# Биосинтез ауксина

ИУК синтезируется из триптофана (Trp) несколькими полу-независимыми путями и одним Trp-независимым путем.

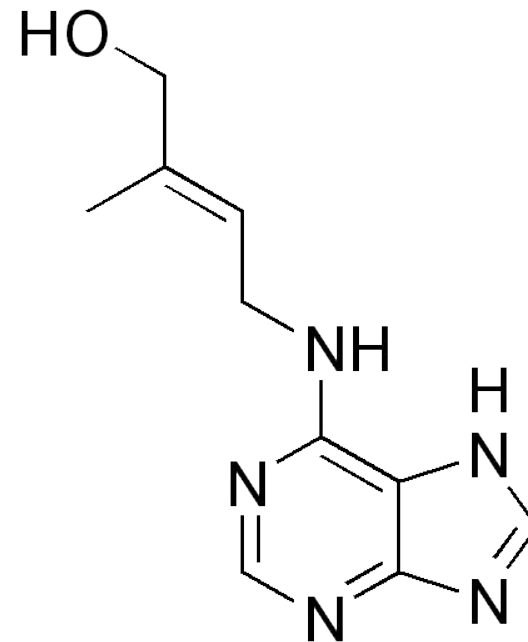






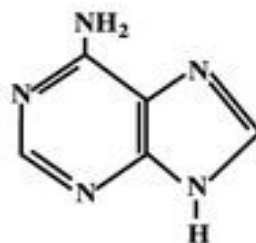
# ЦИТОКИНИН

- Деление клеток
- Контроль старения листьев
- Аттрагирующий эффект корня
- Апикальное доминирование корня
- Открывание устьиц



транс-зеатин

# Цитокинины - семейство аденин-подобных соединений



adenine

Изопентенил аденин

Транс-зеатин

Дигидрозеатин

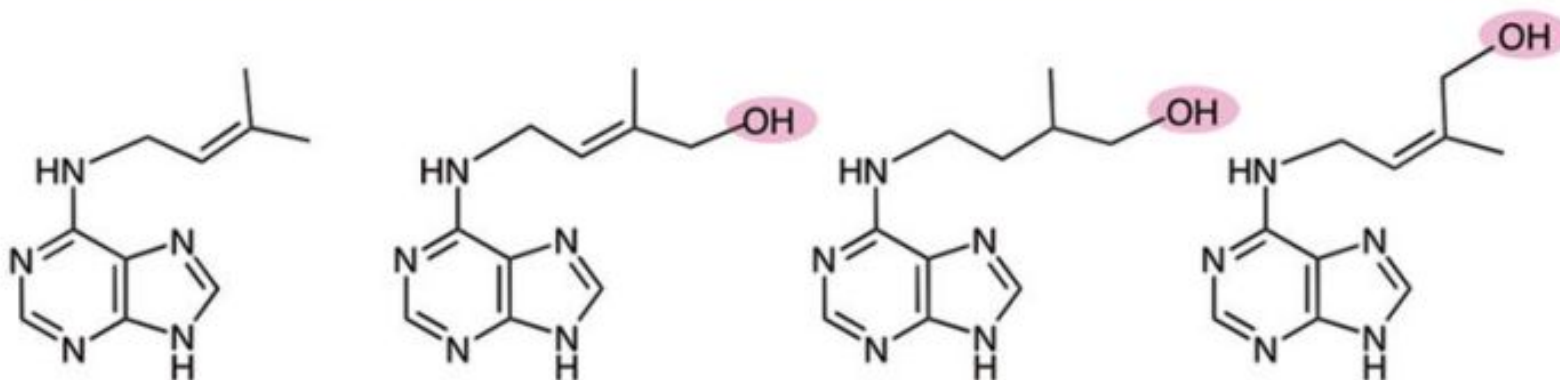
Цис-зеатин

iP

tZ

DZ

cZ



Hirose, N., Takei, K., Kuroha, T., Kamada-Nobusada, T., Hayashi, H., and Sakakibara, H. (2008). Regulation of cytokinin biosynthesis, compartmentalization and translocation. *J. Exp. Bot.* 59: [75–83](#).

# Синтез ЦК

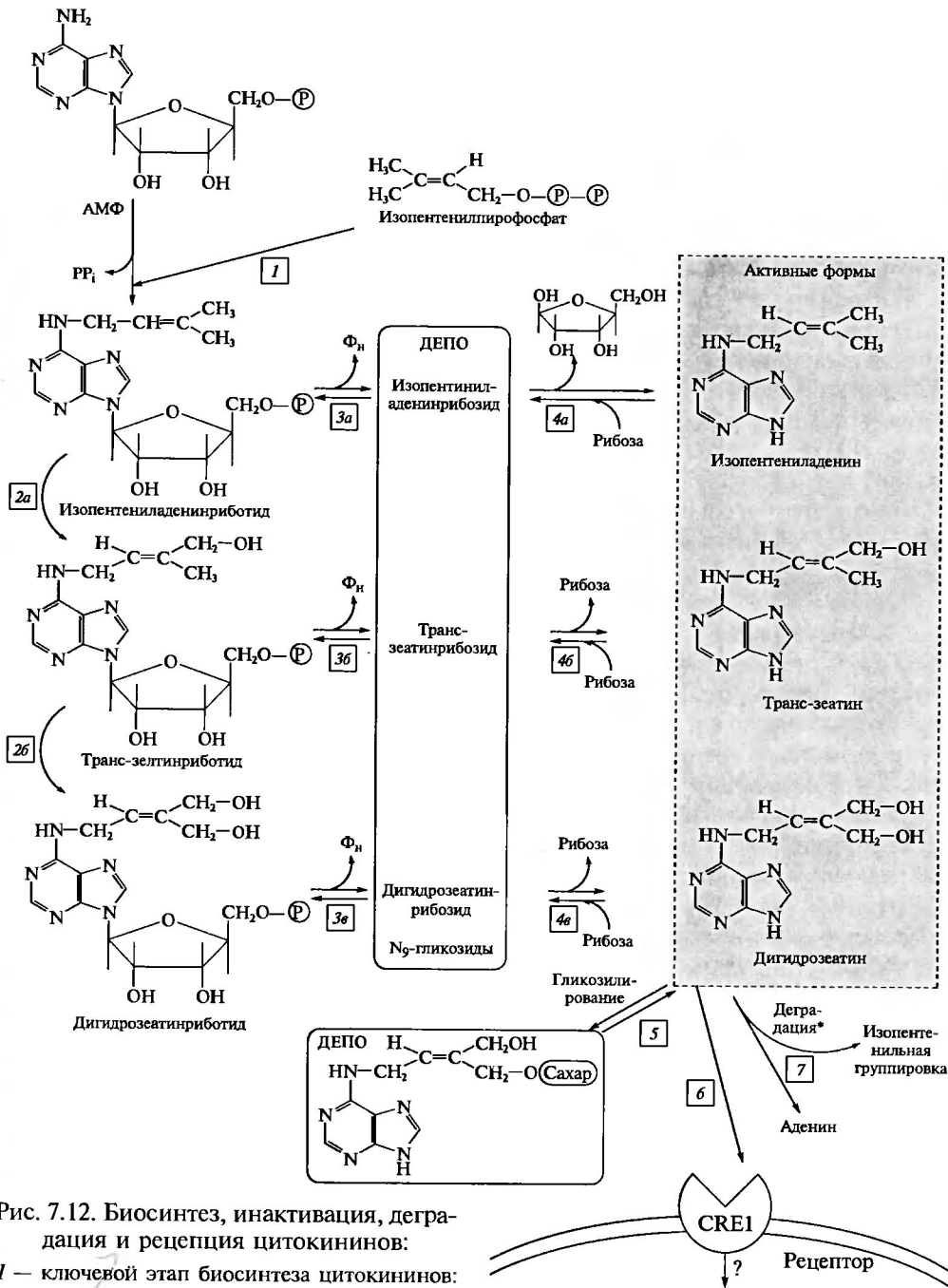


Рис. 7.12. Биосинтез, инактивация, дегградация и рецепция цитокининов:

**1** — ключевой этап биосинтеза цитокининов: трисоединение изопентенильной группировки-

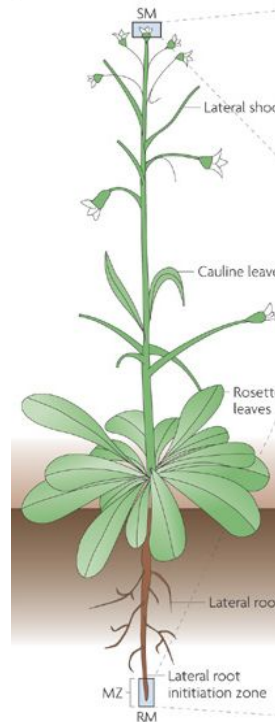
# Цитокинины – антагонисты

**Ауксин**

Подавляет  
ветвление  
побега

Поддерживает  
ветвление  
корней

**ауксина**

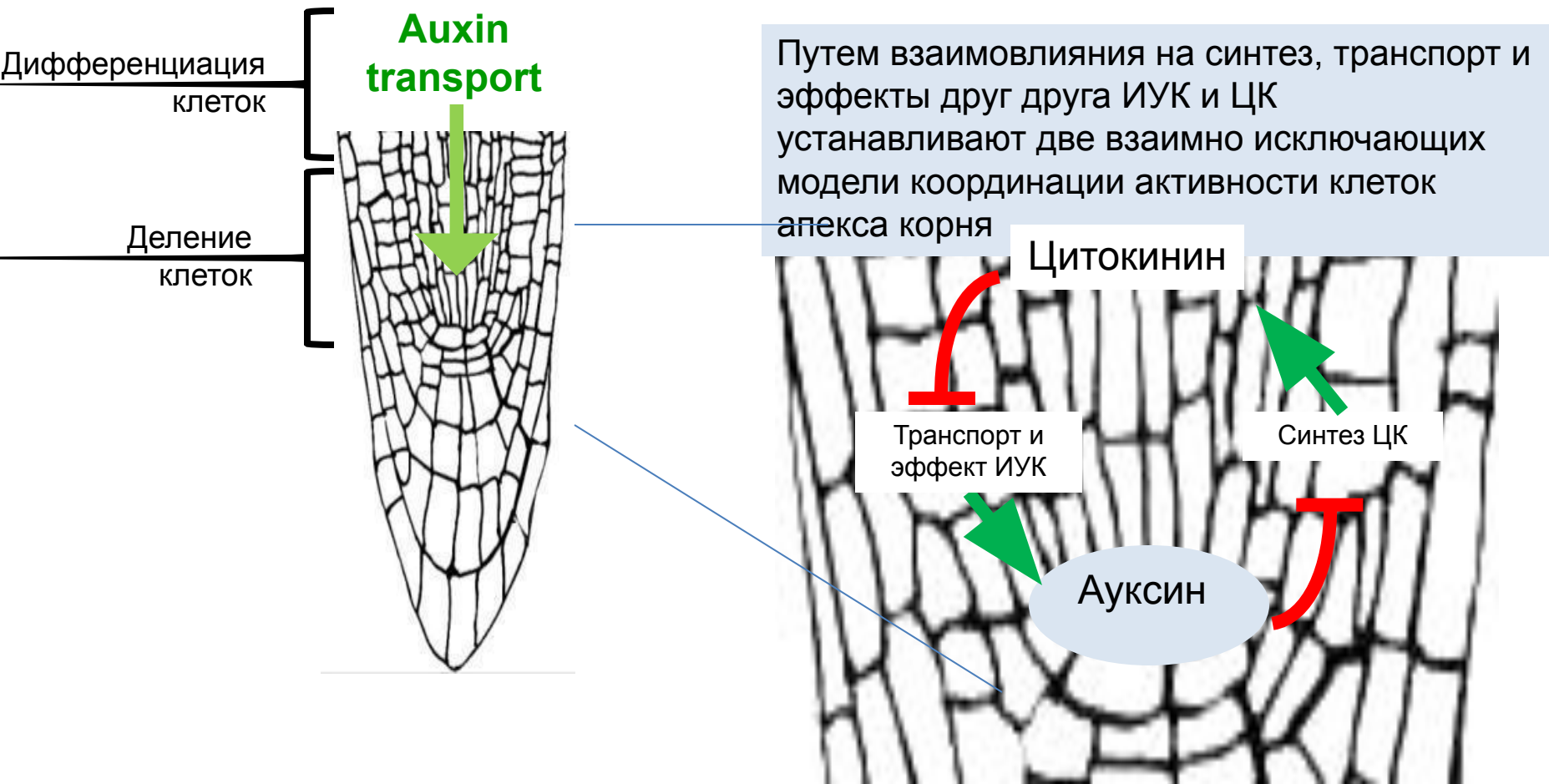


**цк**

Стимулирует  
ветвление  
побега

Подавляет  
ветвление  
корней

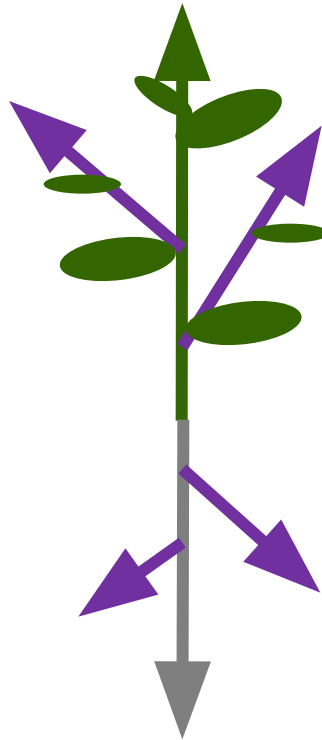
# Ауксин и цитокинин взаиморегулируются в апексе побега



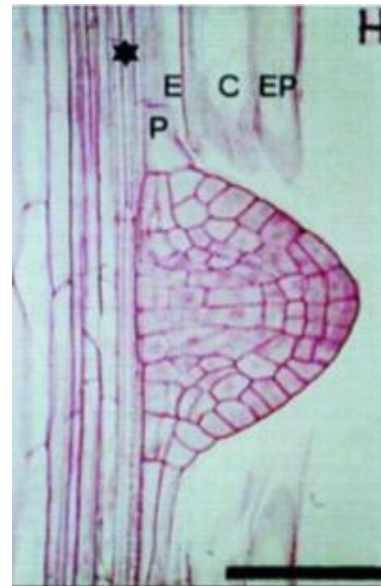
# Ауксин, цитокинин и стриголактон контролируют ветвление



Ветвление побега стимулируется ЦК и подавляется ИУК и стриголактоном



Рост боковых корней поддерживается ИУК и подавляется ЦК



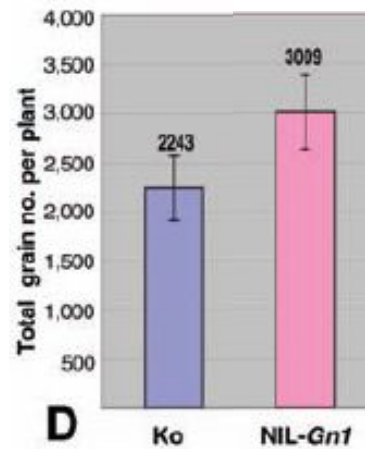
Ветвление контролирует все аспекты продуктивности растений от минерального питания до урожая зерна.

# Cytokinins affect grain production and drought tolerance



Koshihikari

NIL-*Gn1*



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-typ



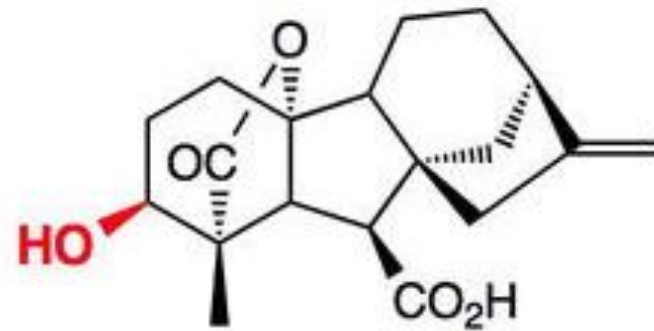
Elevated CK





# Гиббереллин

- Рост междоузлий
- Прорастание семян
- Цветение
- Определение пола у некоторых видов
- Стимуляция роста плодов

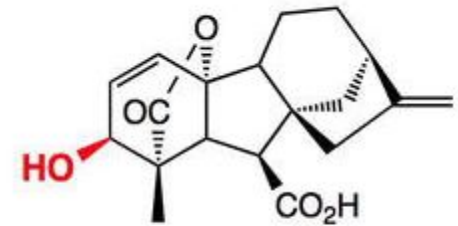
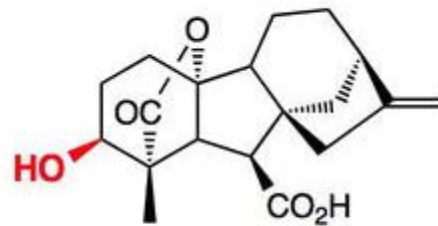


**A Gibberellin (GA<sub>4</sub>)**



# Гиббереллины – семейство веществ

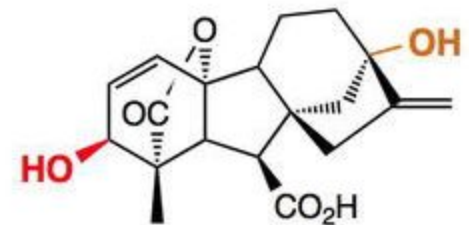
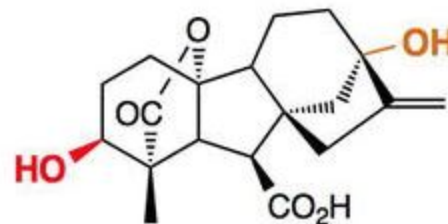
GA<sub>4</sub> – главная активная форма GA у *Arabidopsis*



GA<sub>4</sub>

GA<sub>7</sub>

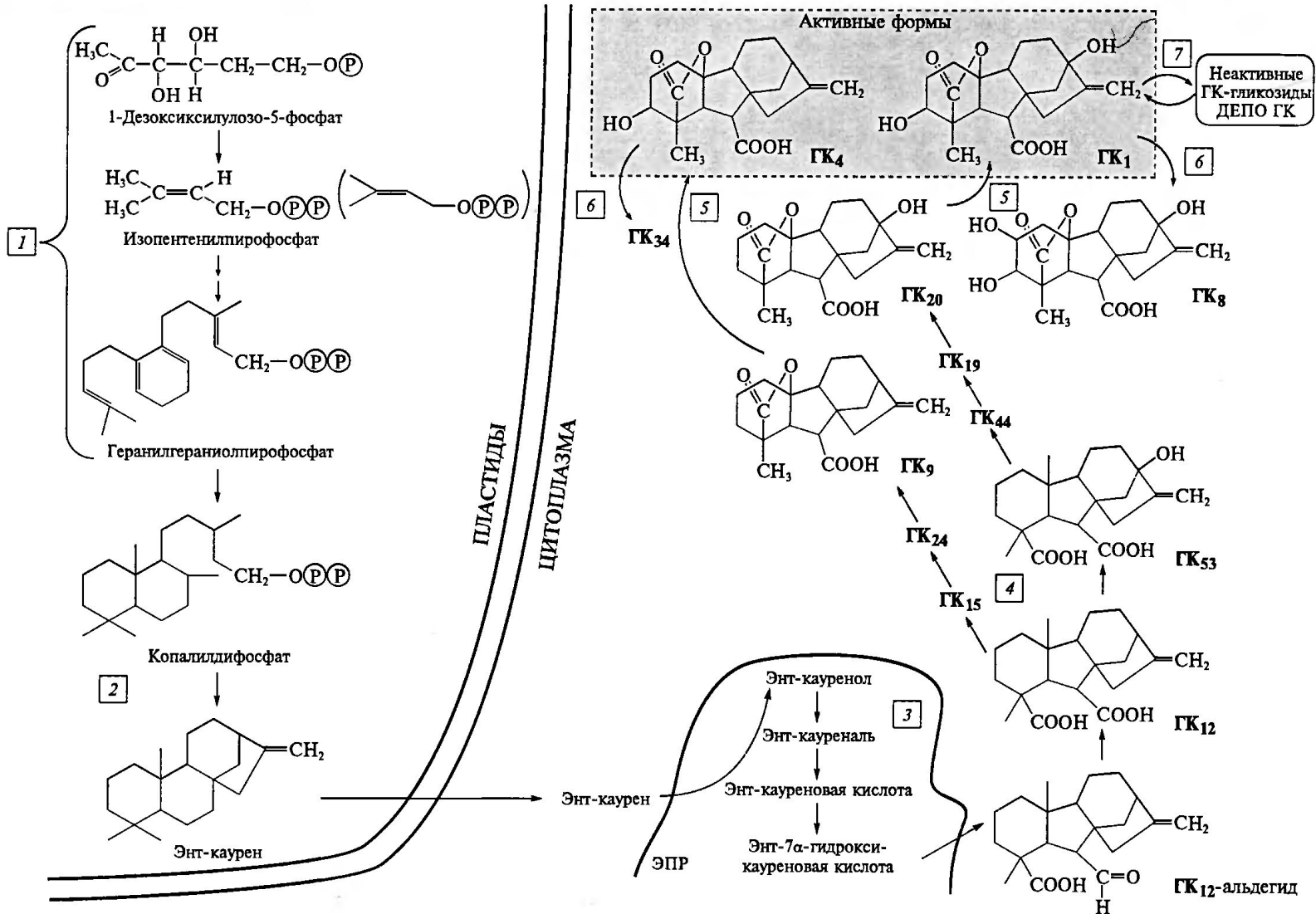
Активны только некоторые формы ГК.



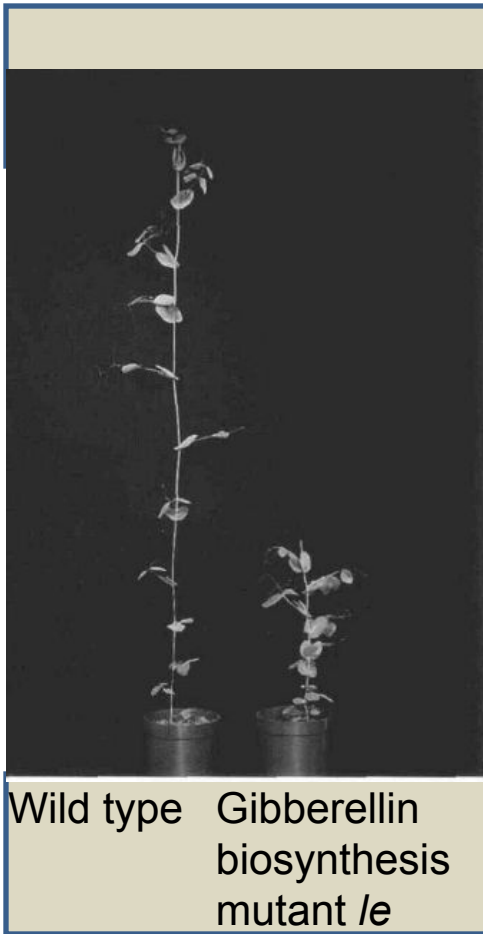
GA<sub>1</sub>

GA<sub>3</sub>

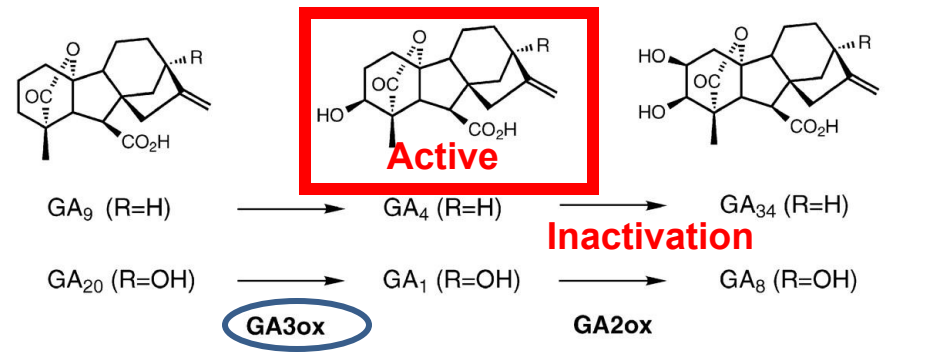
# Синтез гиббереллина



# Гиббереллин регулирует рост



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.



# Гены, контролирующие синтез ГК оказались важны для «зеленой

И»

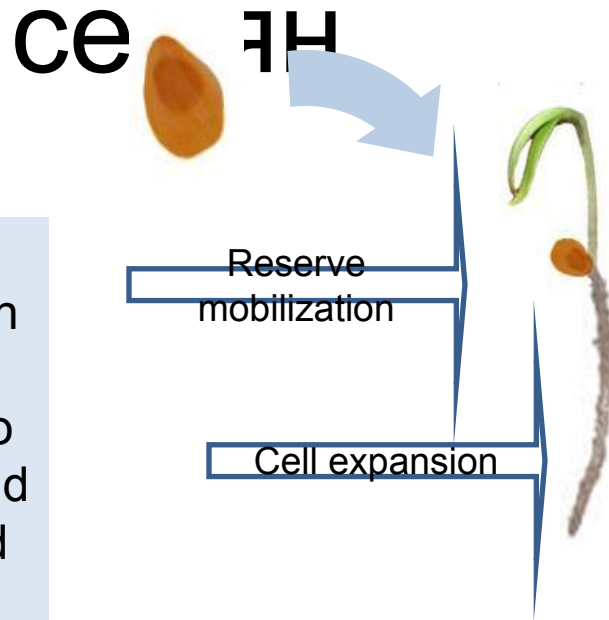
Tremendous increases in crop yields (the Green Revolution) during the 20<sup>th</sup> century occurred because of increased use of fertilizer and the introduction of semidwarf varieties of grains.

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

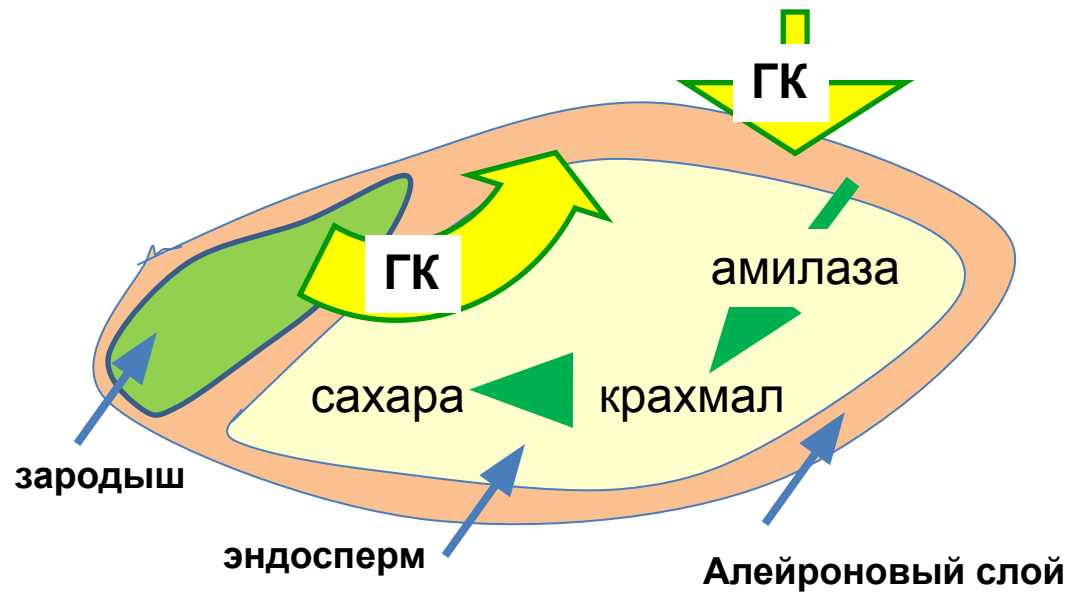
# ГК важна для прорастания



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



# Стимуляция прорастания зерна



# ИУК и ГК стимулируют деление и рост клеток плодов

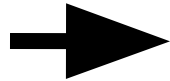
Seedless varieties of grapes and other fruits require exogenous application of GA for fruit development. Strawberry receptacles respond to auxin.



ИУК + ГК



ГК

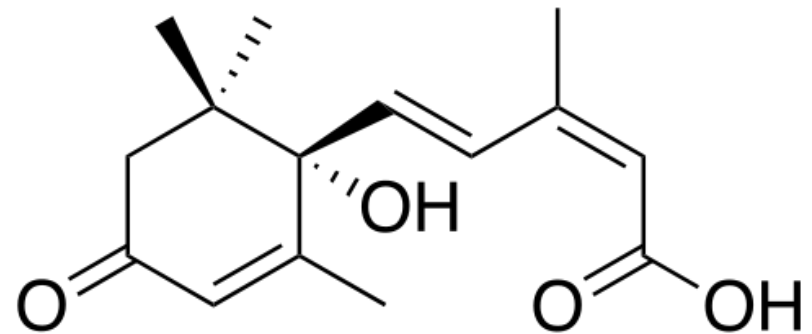


ИУК



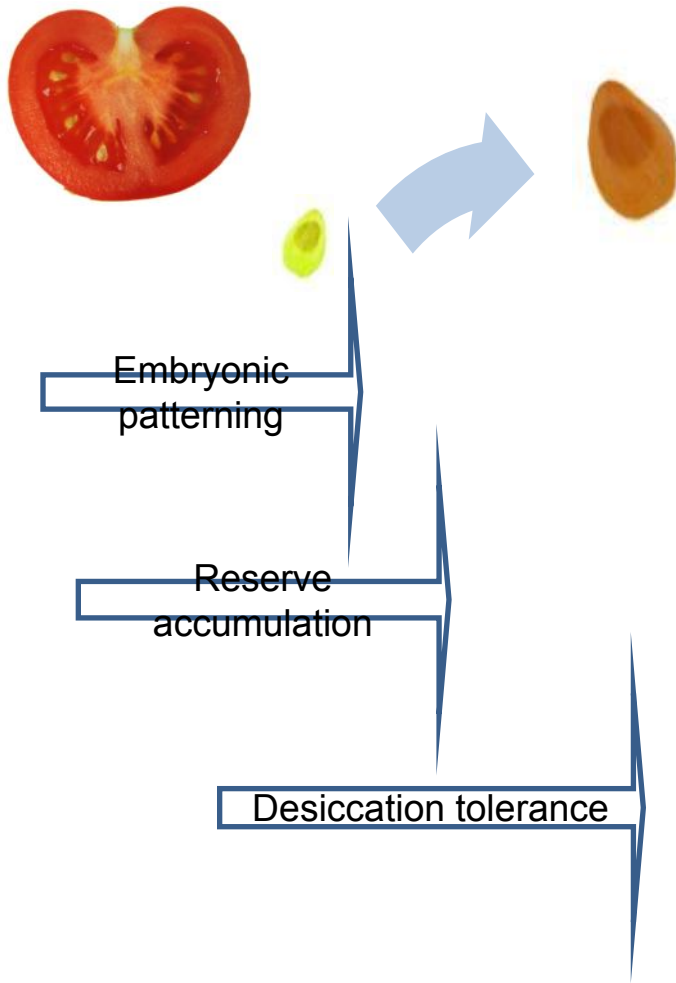
# Абсцизовая кислота

- Созревание и опадение семян
- Засухоустойчивость
- Стрессовый ответ
- Контроль открытия устьиц



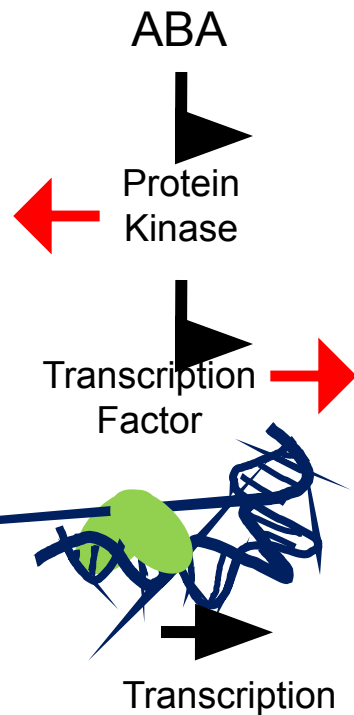
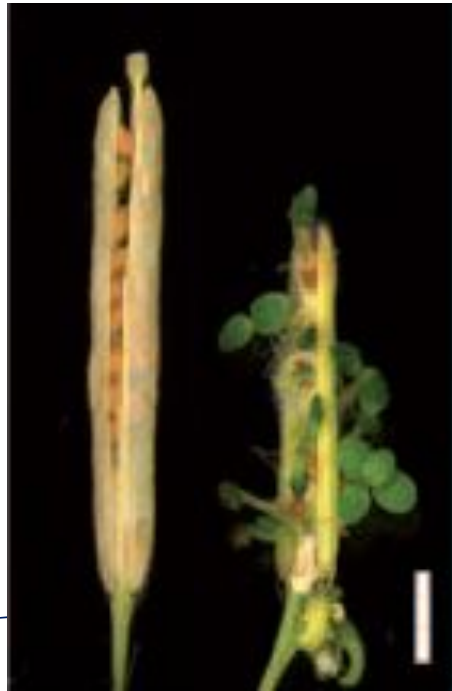


# ABA accumulates in maturing seeds



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

# ABA synthesis and signaling is required for seed dormancy



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

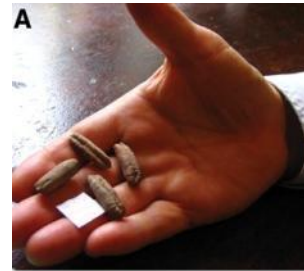
Nakashima, K., et al. (2009) Three Arabidopsis SnRK2 protein kinases, SRK2D/SnRK2.2, SRK2E/SnRK2.6/OST1 and SRK2I/SnRK2.3, involved in ABA signaling are essential for the control of seed development and Dormancy. *Plant Cell Physiol.* 50: [1345–1363](#)

Nakashima, K., et al. (2009) Three Arabidopsis SnRK2 protein kinases, SRK2D/SnRK2.2, SRK2E/SnRK2.6/OST1 and SRK2I/SnRK2.3, involved in ABA signaling are essential for the control of seed development and Dormancy. *Plant Cell Physiol.* 50: 1345–1363. Copyright (c) 2009 by the the Japanese Society of Plant Physiologists with permission from Oxford University Press.

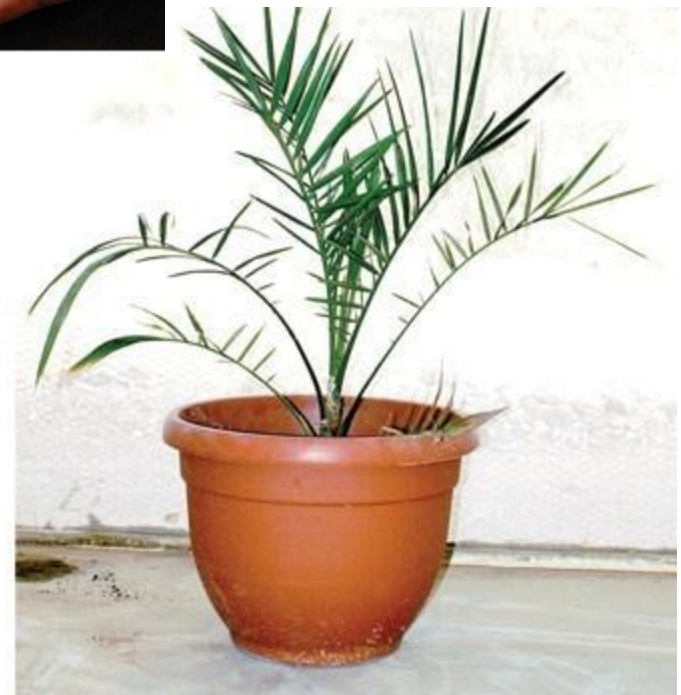
McCarty, D.R., Carson, C.B., Stinard, P.S., and Robertson, D.S. (1989) Molecular analysis of viviparous-1: An abscisic acid-insensitive mutant of maize. *Plant Cell* 1: [523–532](#).

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

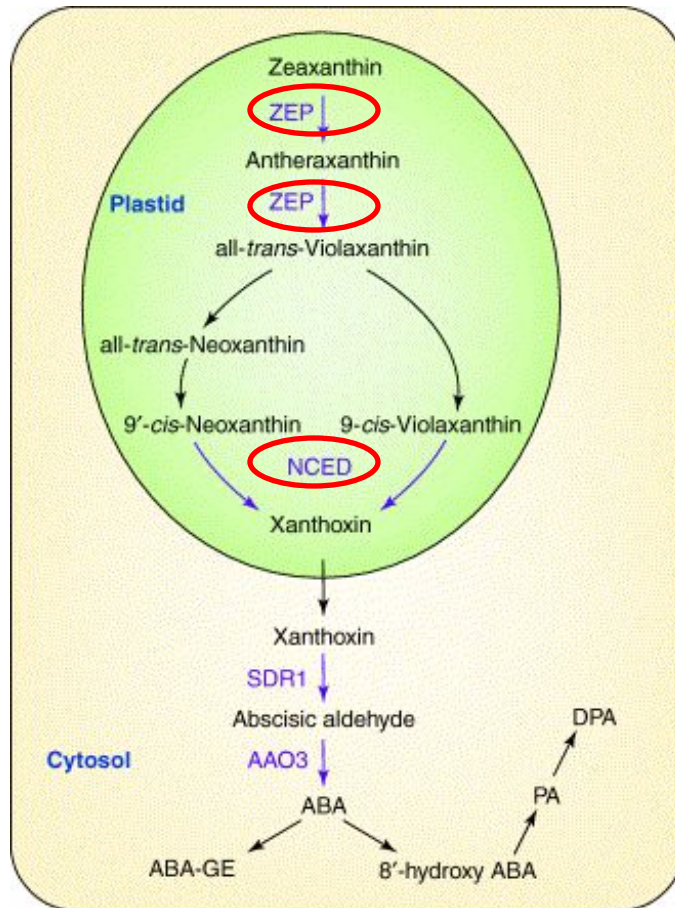
These date palm seeds are nearly 2000 years old, but still viable and capable of germination. Five hundred year old lotus seeds have also been successfully germinated. Having a thick seed coat may help these super seeds retain viability.



Date palm growing from 2000 year old seed.



# ABA biosynthesis is strongly regulated



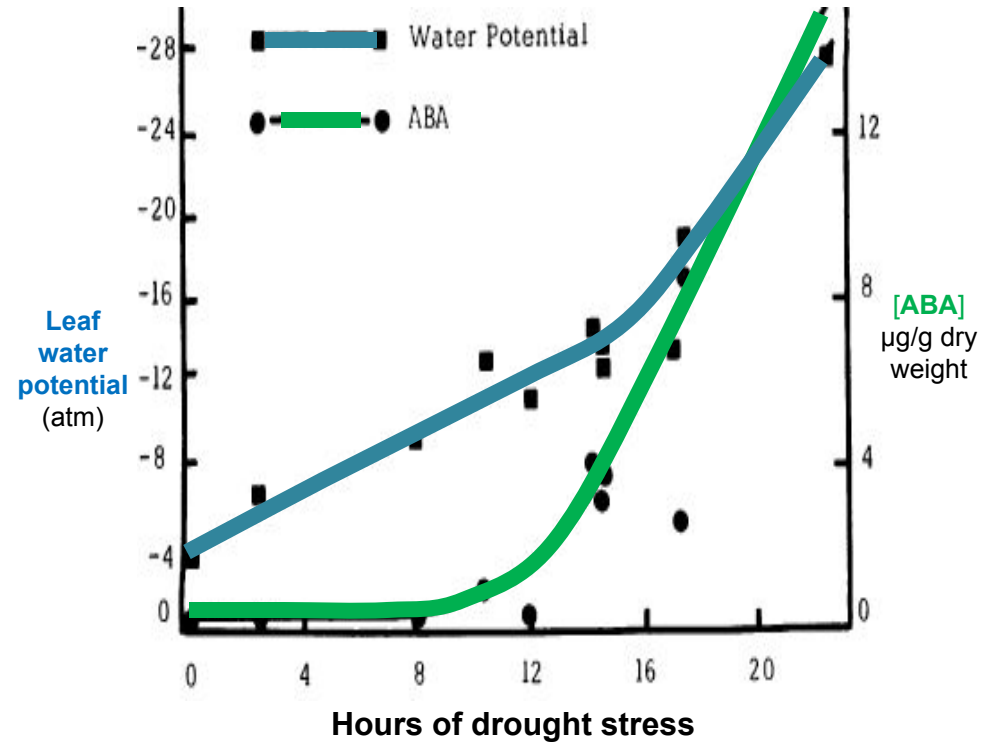
ABA levels are tightly controlled. Critical steps in ABA biosynthesis (circled in red) are encoded by multiple tightly regulated genes to ensure rapid and precise control.

TRENDS in Plant Science

Reprinted from Nambara, E., and Marion-Pol, A. (2003) ABA action and interactions in seeds. Trends Plant Sci. 8: [213-217](#) with permission from Elsevier.

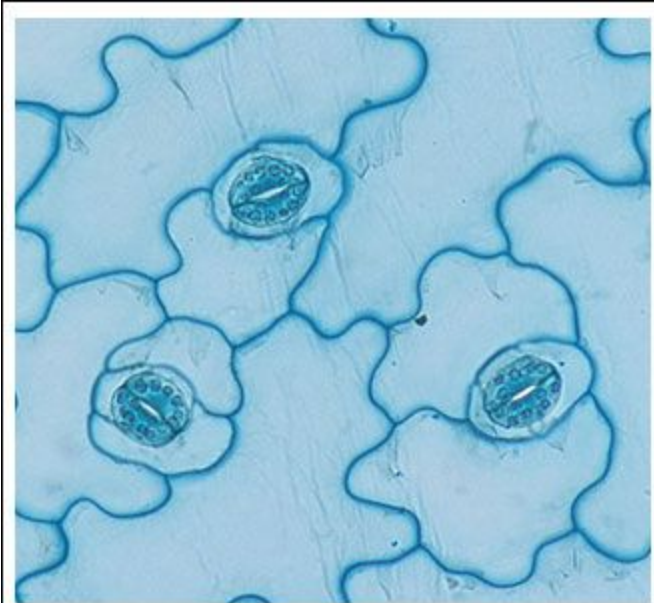


# ABA synthesis is strongly induced in response to stress



ABA levels rise during drought stress due in part to increased biosynthesis

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



© Image by John Addis

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

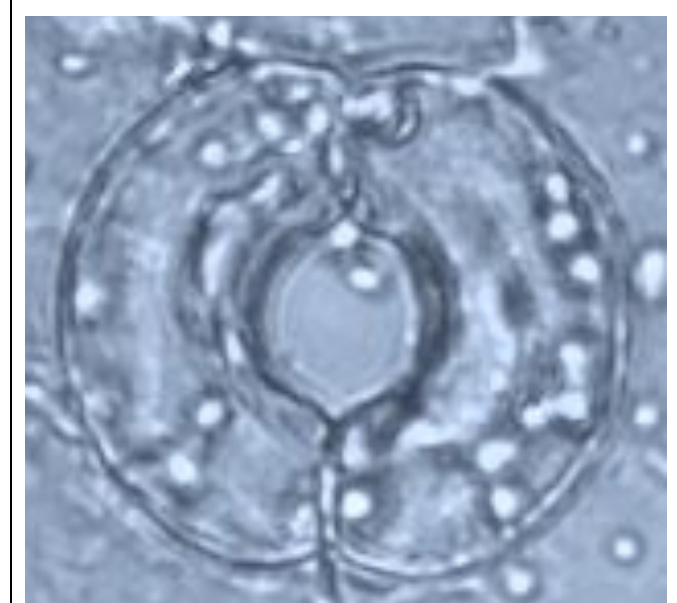
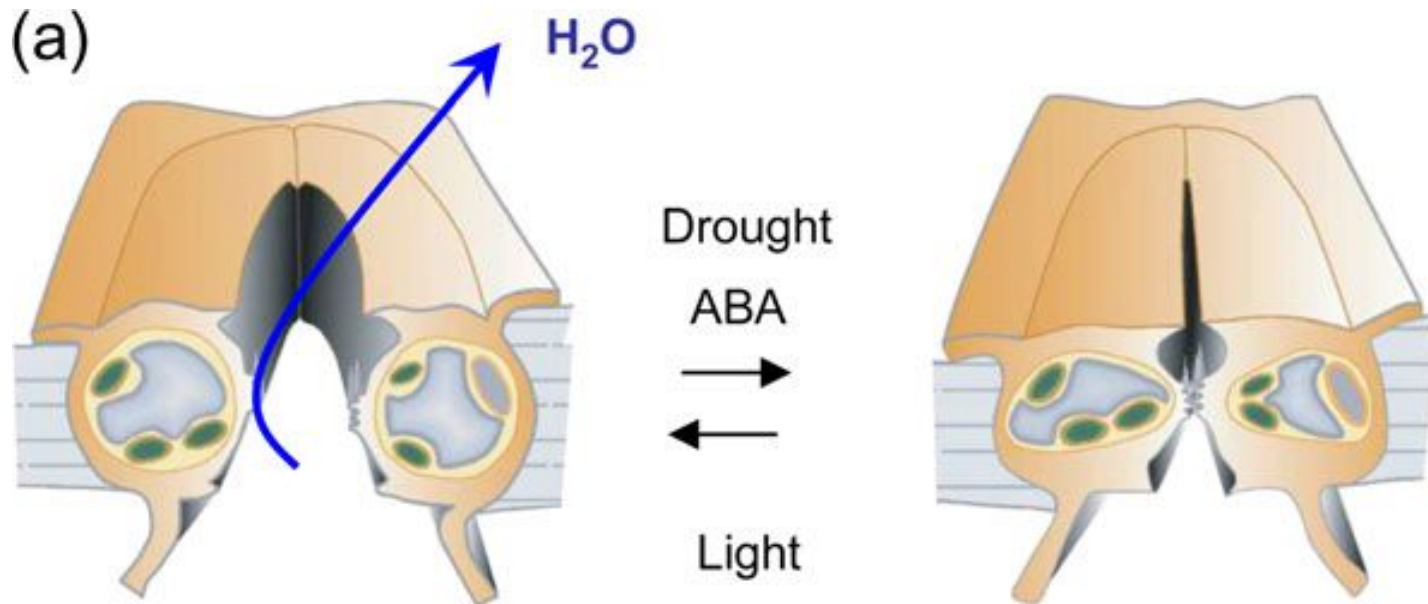


Image by Yizhou Wang, University of Glasgow

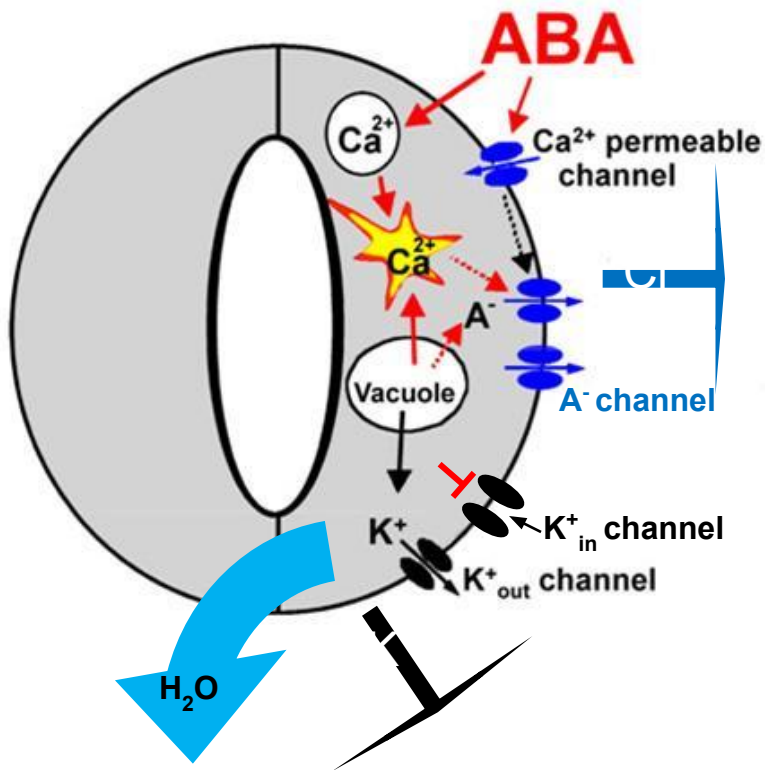
Guard cells control the opening and closing of stomata to regulate gas exchange: a fine balance is required to allow  $\text{CO}_2$  in for photosynthesis and prevent excessive water loss.

# 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.

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



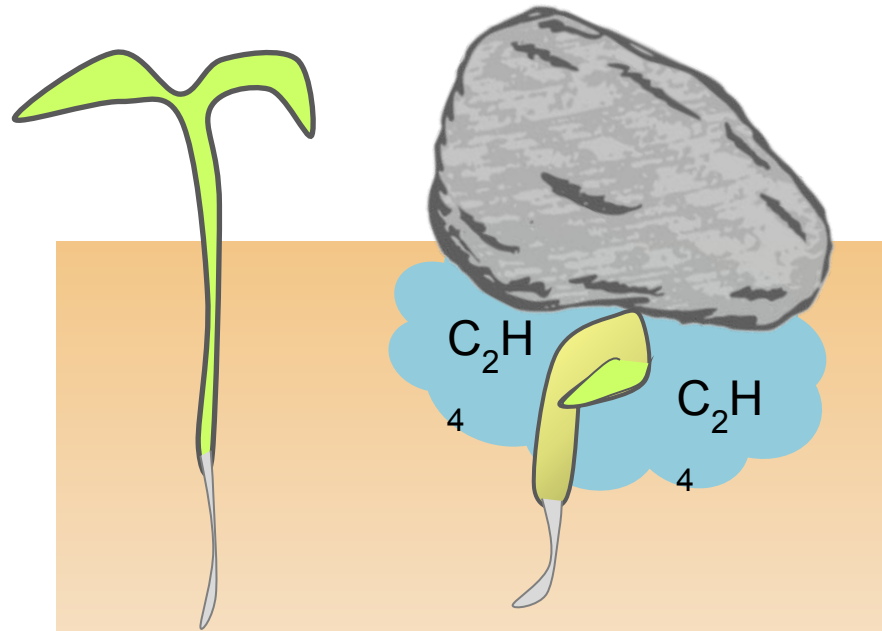
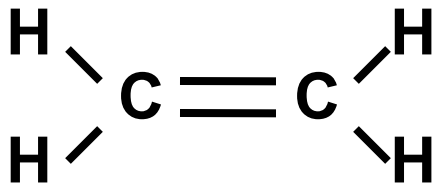
ABA triggers an increase in cytosolic calcium ( $\text{Ca}^{2+}$ ), which activates anion channels ( $\text{A}^-$ ) allowing  $\text{Cl}^-$  to leave the cell. ABA activates channels that move potassium out of the cell ( $\text{K}^+_{\text{out}}$ ) and inhibits channels that move potassium into the cell ( $\text{K}^+_{\text{in}}$ ). 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.



# 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

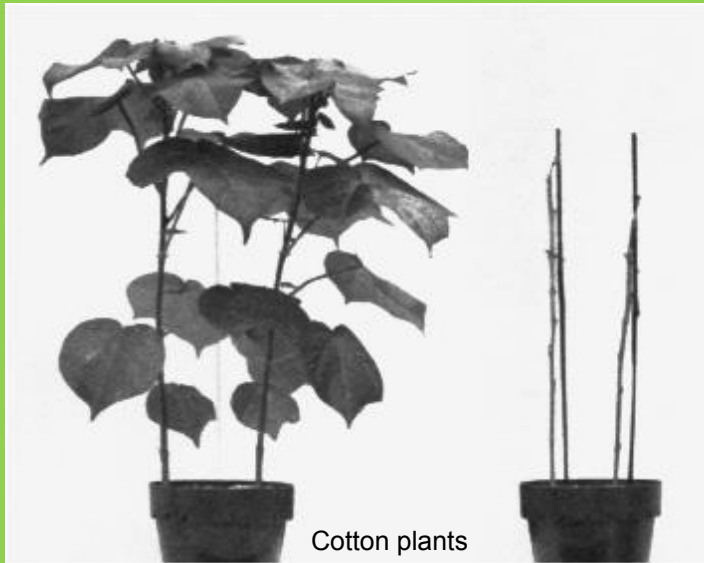


Ethylene induces the triple response:

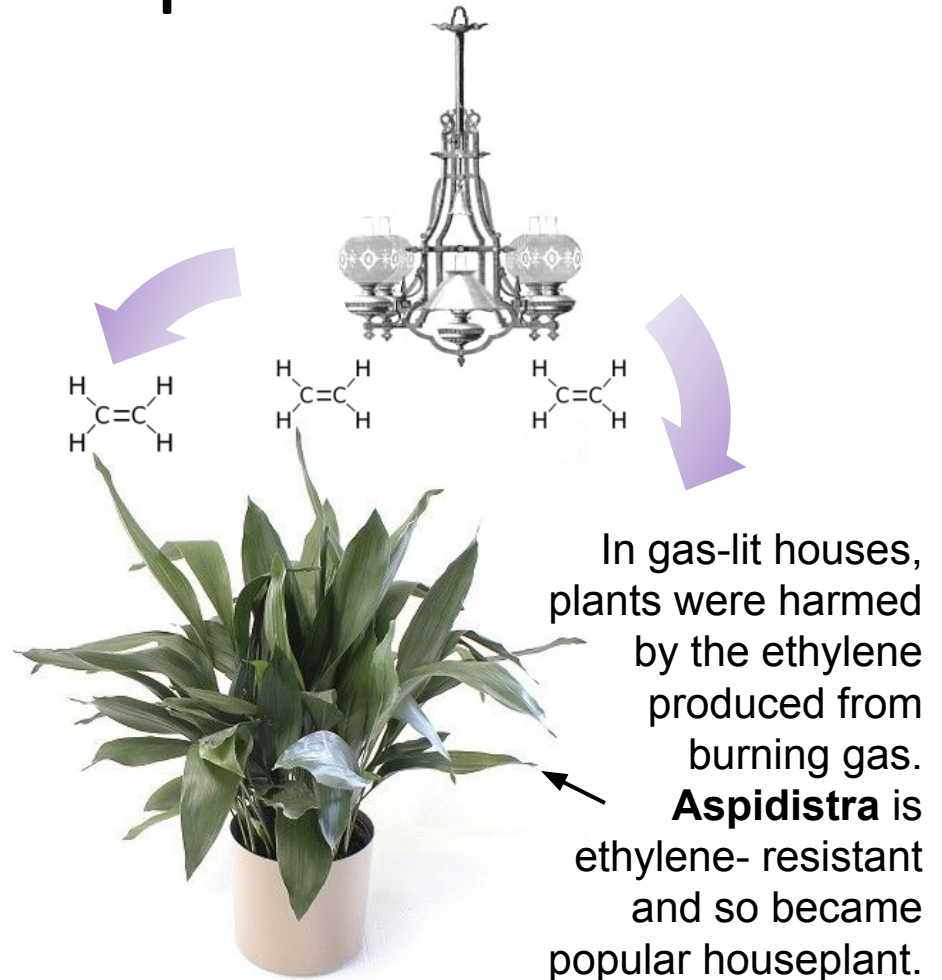
- reduced elongation,
- hypocotyl swelling,
- apical hook exaggeration.

# Ethylene promotes senescence of leaves and petals

Air (control)    7 days ethylene



**Ethylene promotes leaf and petal senescence.**



# 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

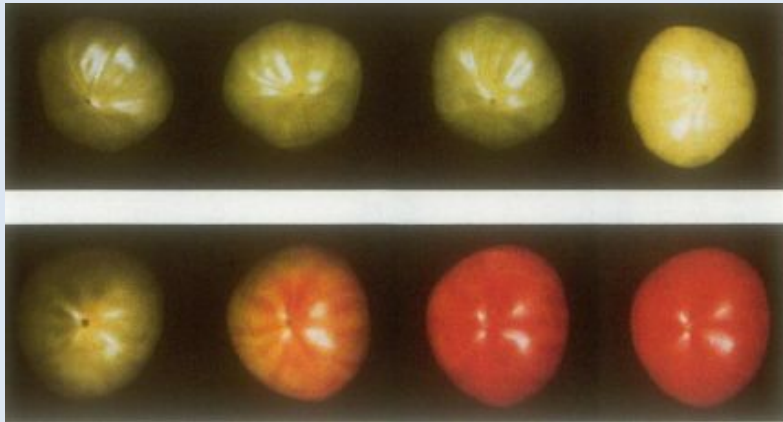
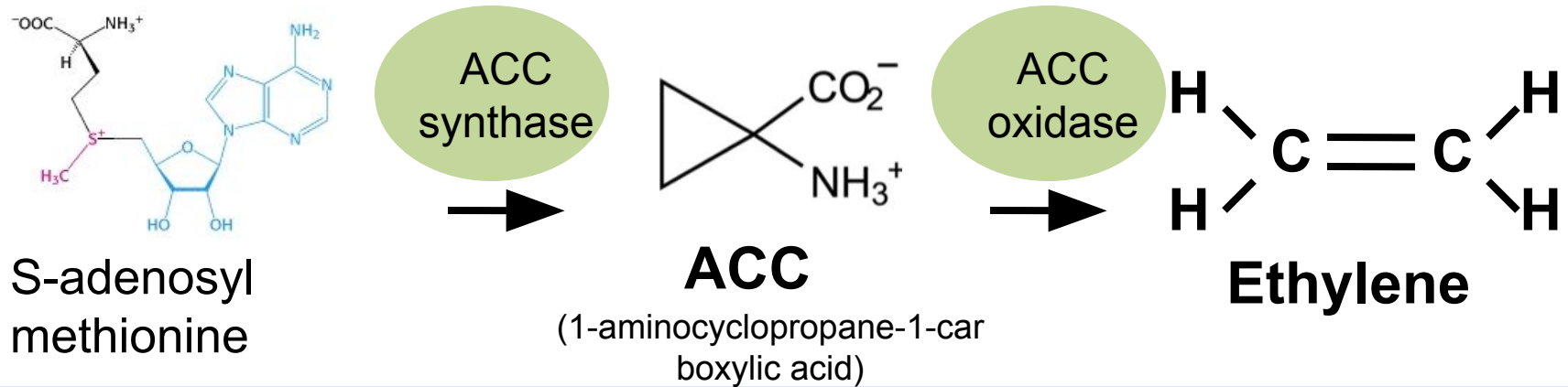
**Limit production** - high  $\text{CO}_2$  or low  $\text{O}_2$

**Removal from the air** -  $\text{KMnO}_4$  reaction, zeolite absorption

**Interfere with ethylene binding to receptor** - sodium thiosulfate (STS), diazocyclopentadiene (DACP), others



# Molecular genetic approaches can limit ethylene synthesis

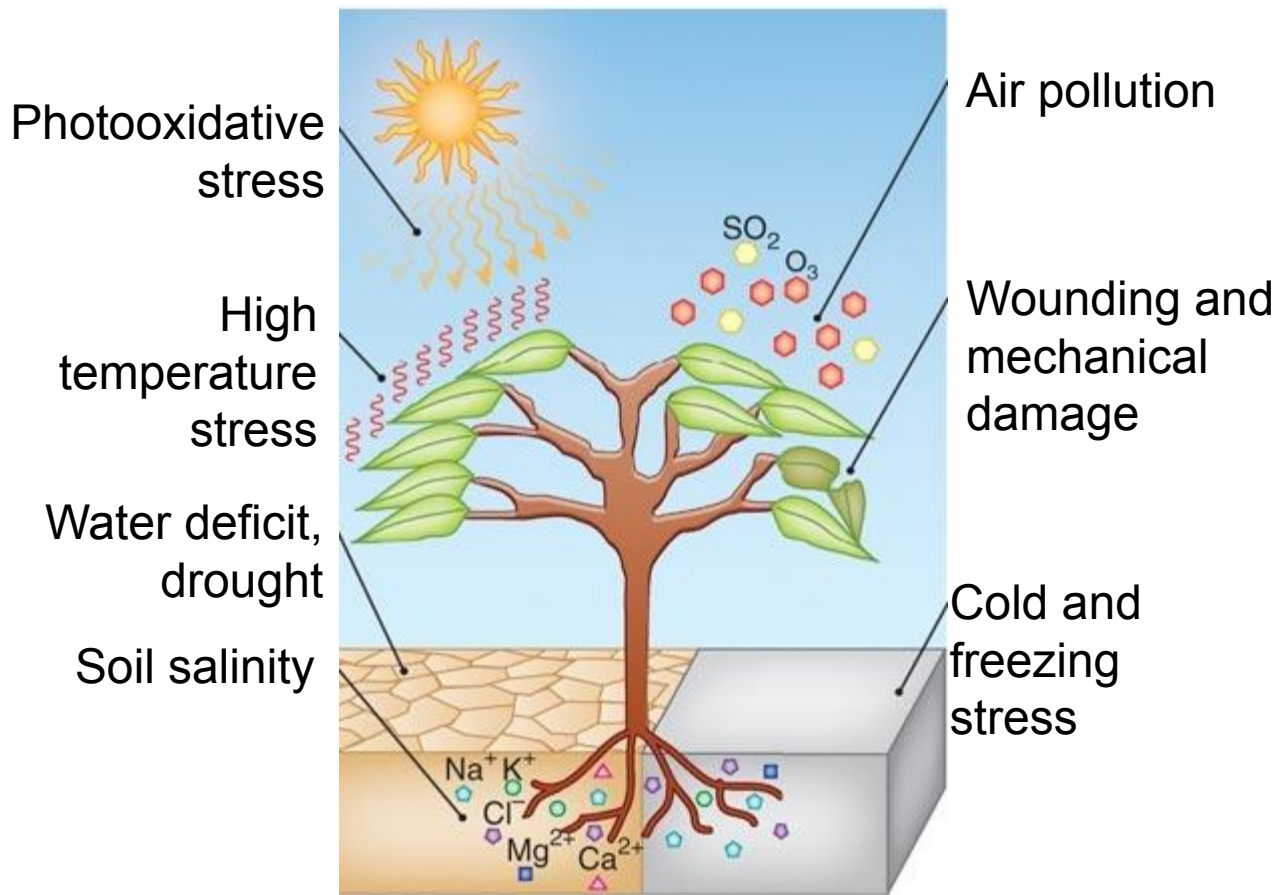


**Antisense  
ACC synthase**

**Control**

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

# Hormonal responses to abiotic stress

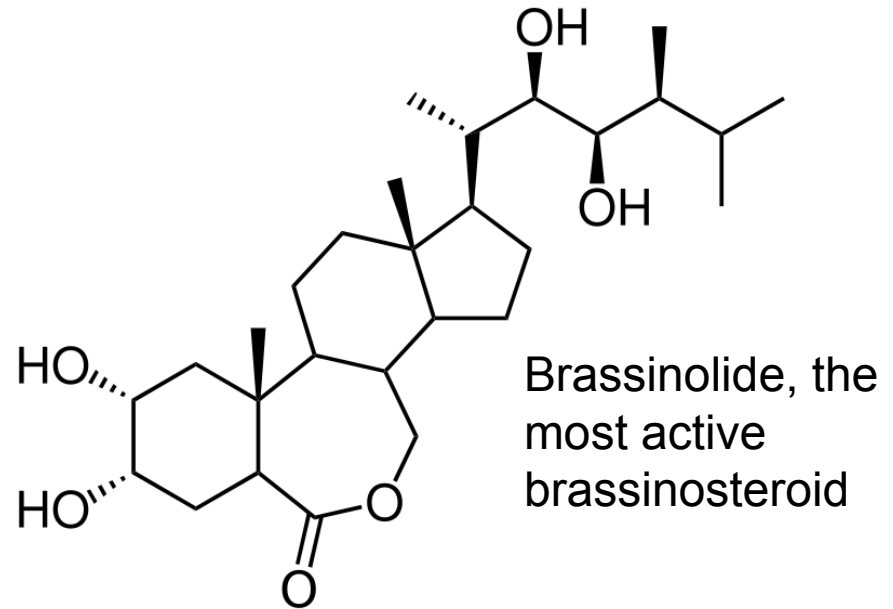


Plants' lives are very stressful.....

ABA and ethylene help plants respond to stress.

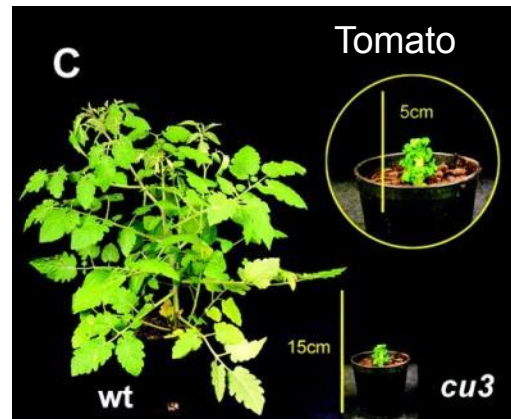
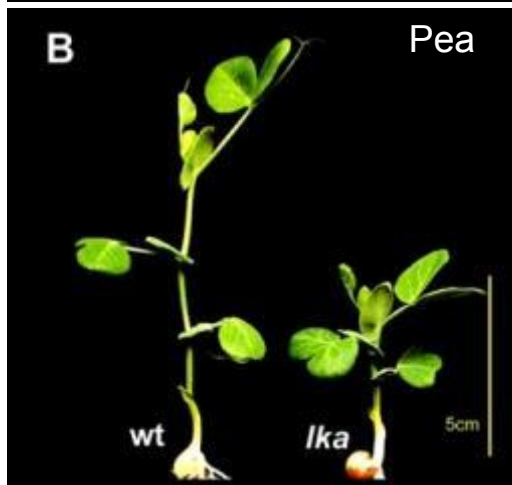
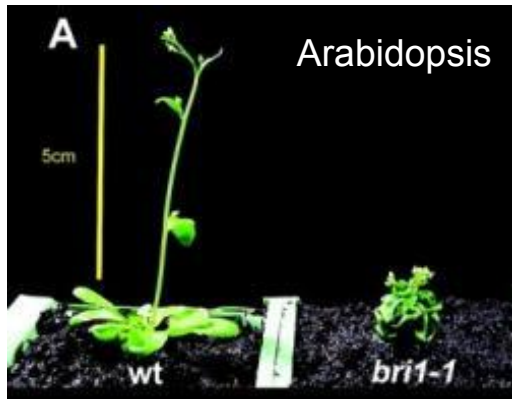
# Brassinosteroids

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





# 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

# Reducing BR signaling produces dwarf barley



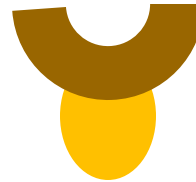
Wild-type



Cell  
elongation



H



*uzu*

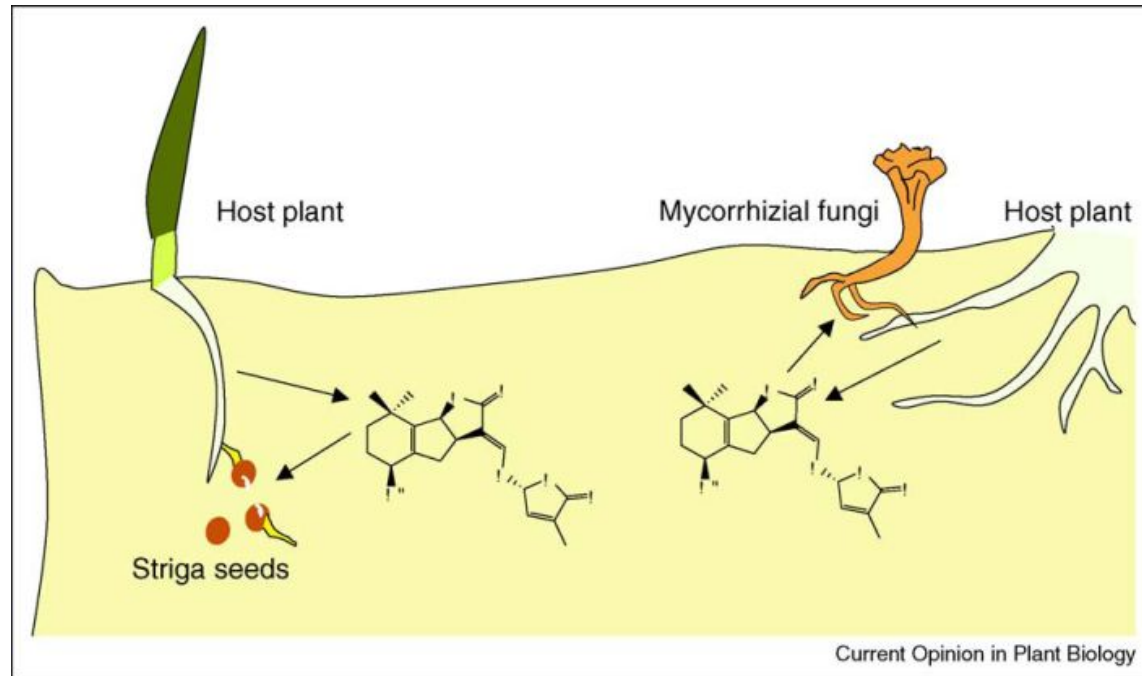


Less cell  
elongation

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.



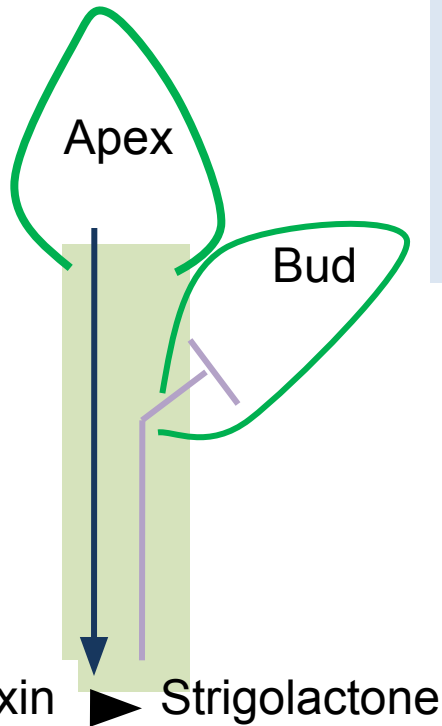
# Strigolactones



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

Image source [USDA APHIS PPQ Archive](#) ; Reprinted from Tsuchiya, Y., and McCourt, P. (2009). Strigolactones: A new hormone with a past. *Curr. Opin. Plant Biol.* 12: [556–561](#) with permission from Elsevier.

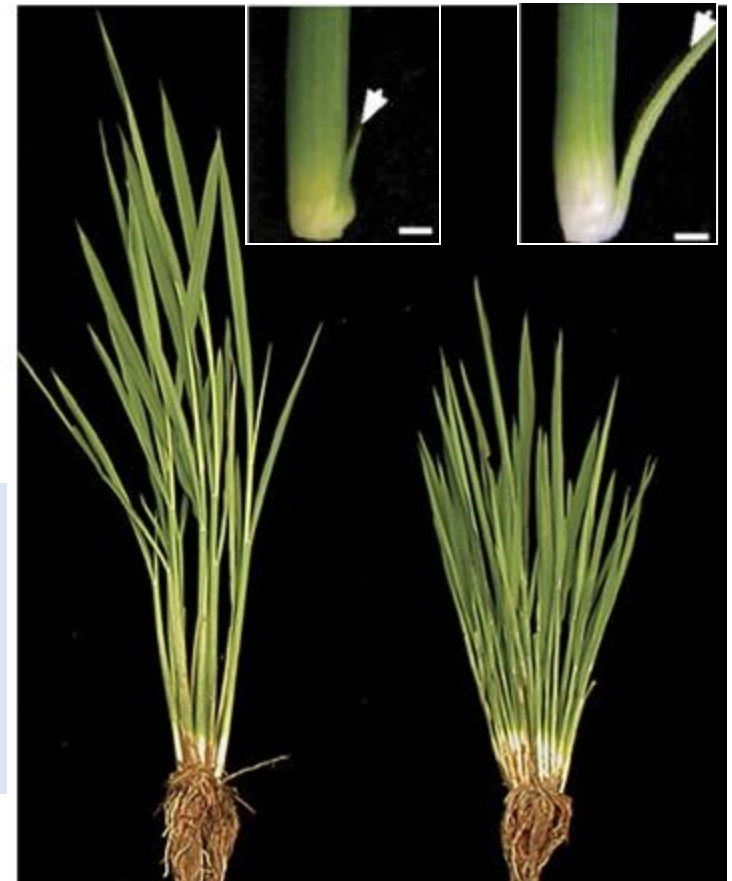
# Strigolactones inhibit branch outgrowth



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

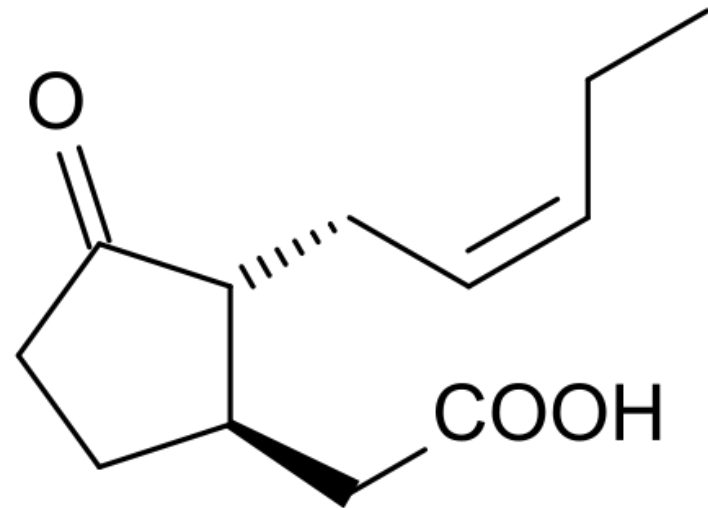
In a rice mutant that does not produce strigolactones, tillers (lateral branches) grow out as shown.

WT Mutant

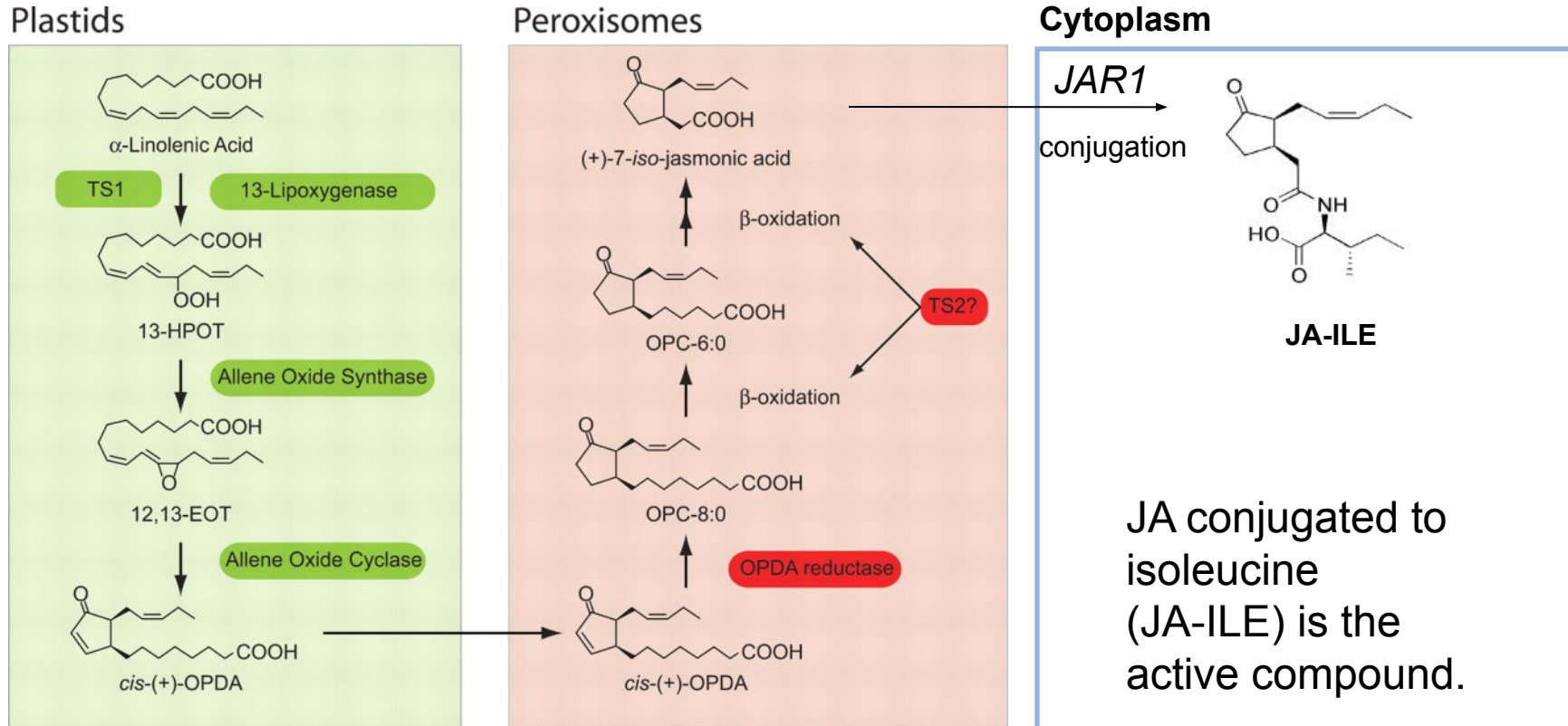


# Jasmonates

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



# JA biosynthesis



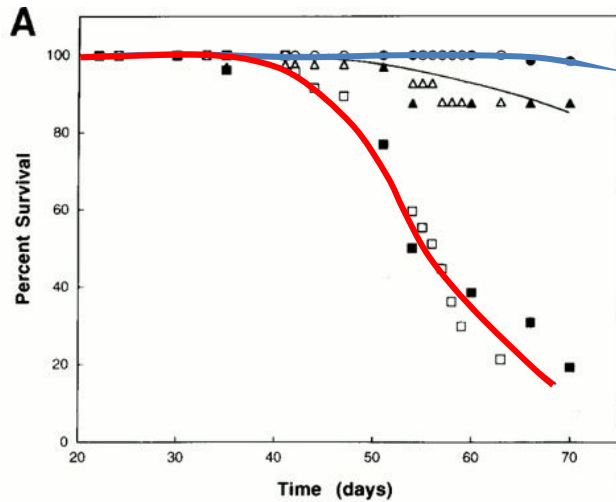
From Acosta, I., et al. (2009) *tasselseed1* is a lipoxygenase affecting jasmonic acid signaling in sex determination of maize. Science 323: 262–265. Reprinted with permission from AAAS.



# Jasmonate signaling contributes to defense against herbivory

WT

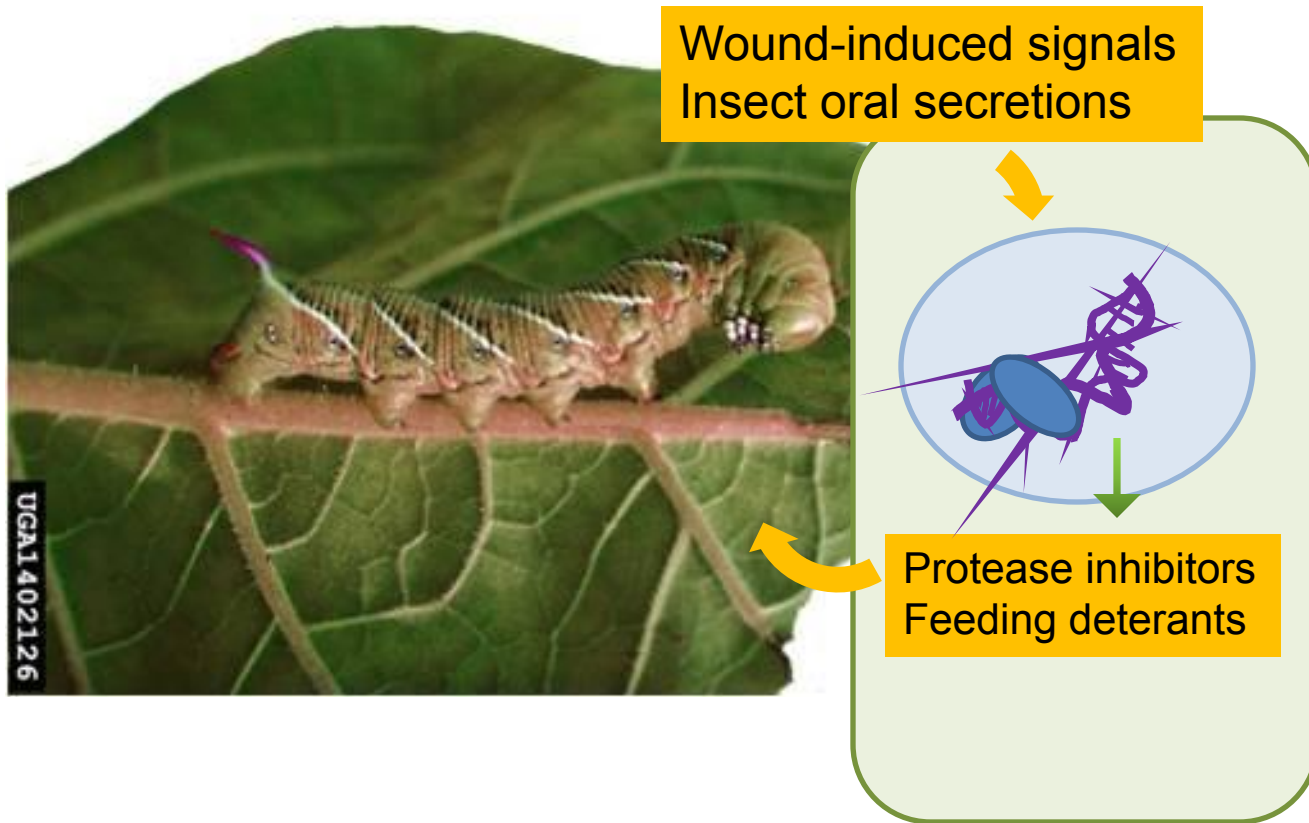
Mutant without JA



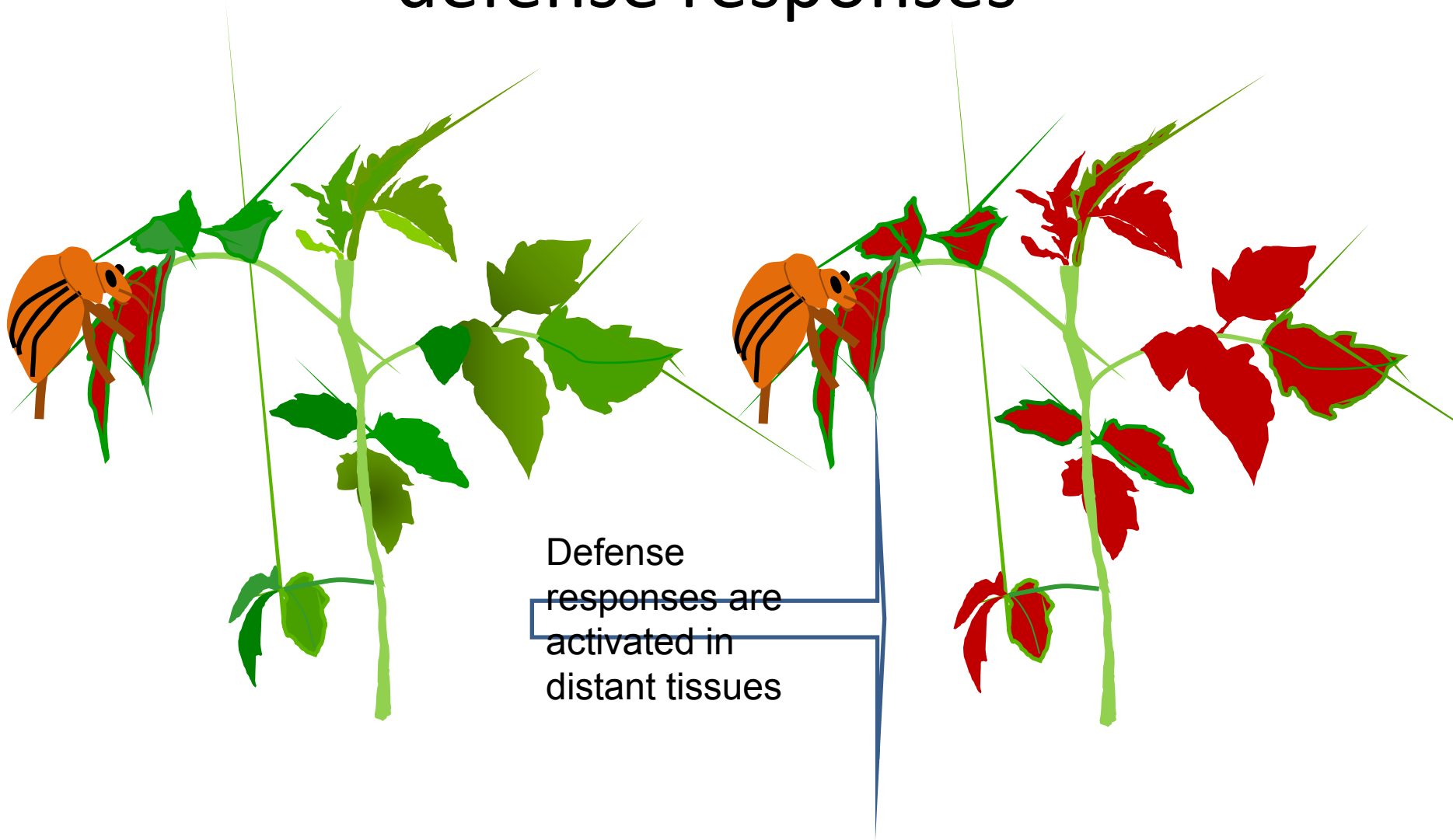
When exposed to hungry fly larvae, plants unable to produce JA have low rates of survival.



# Jasmonates induce the expression of anti-herbivory chemicals

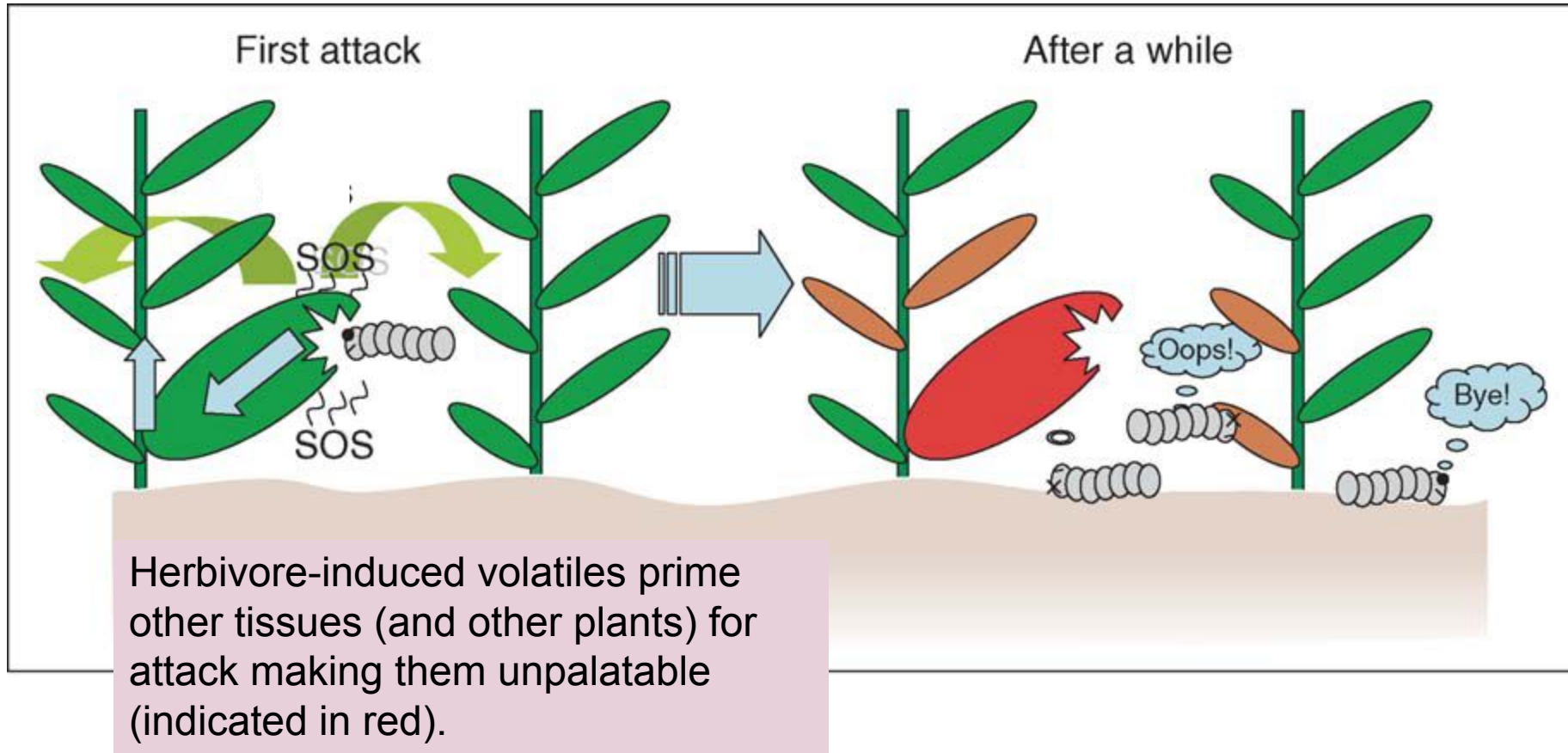


# Jasmonates contribute to systemic defense responses



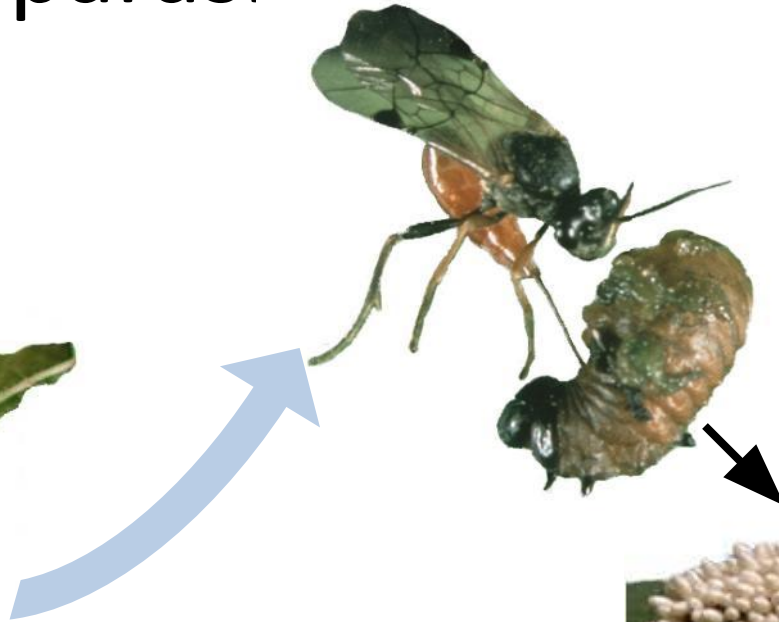
Defense responses are activated in distant tissues

# Jasmonates stimulate production of volatile signaling compounds



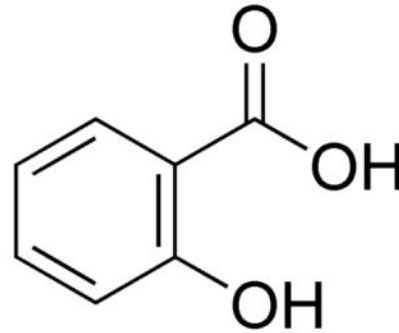


# Herbivore-induced volatiles are recognized by carnivorous and parasitoid insects



# Salicylic Acid – plant hormone and painkiller

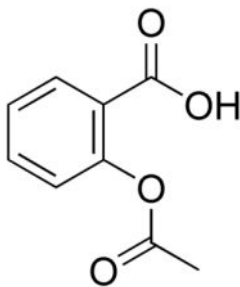
- Response to biotrophic pathogens
- Induced defense response
- Systemic acquired resistance



**Salicylic Acid**



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

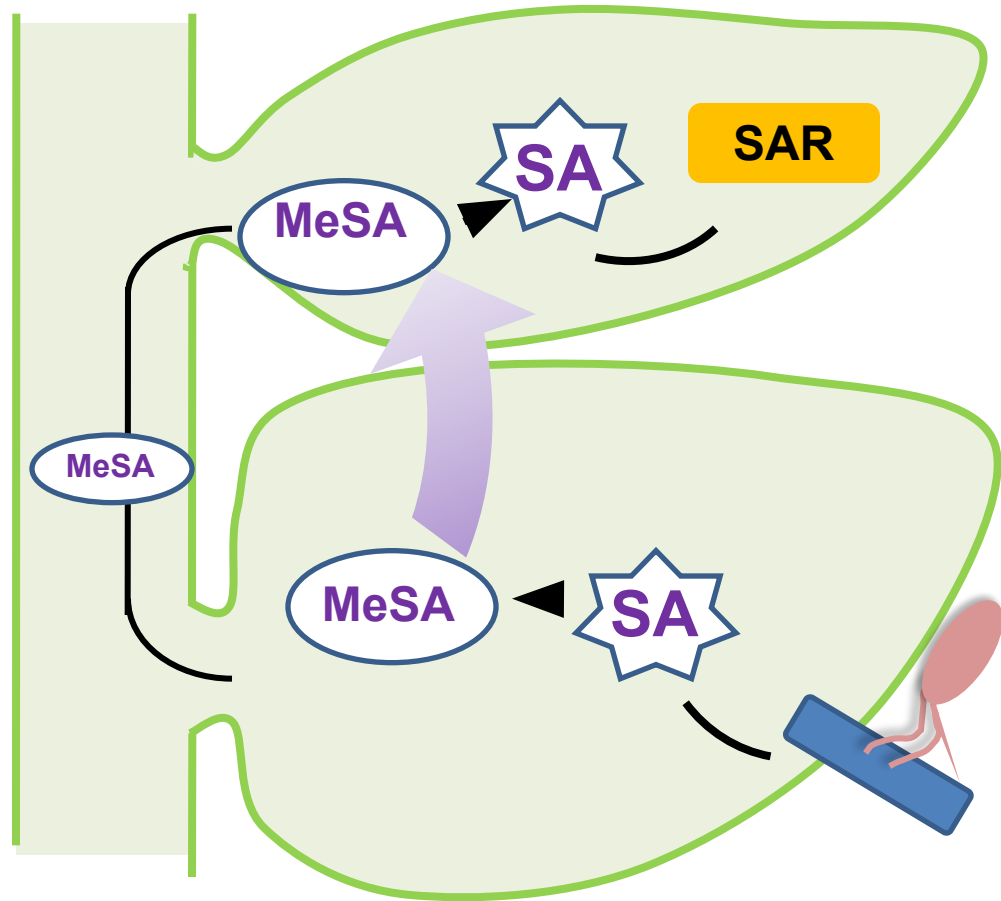


**Acetylsalicylic Acid - aspirin**

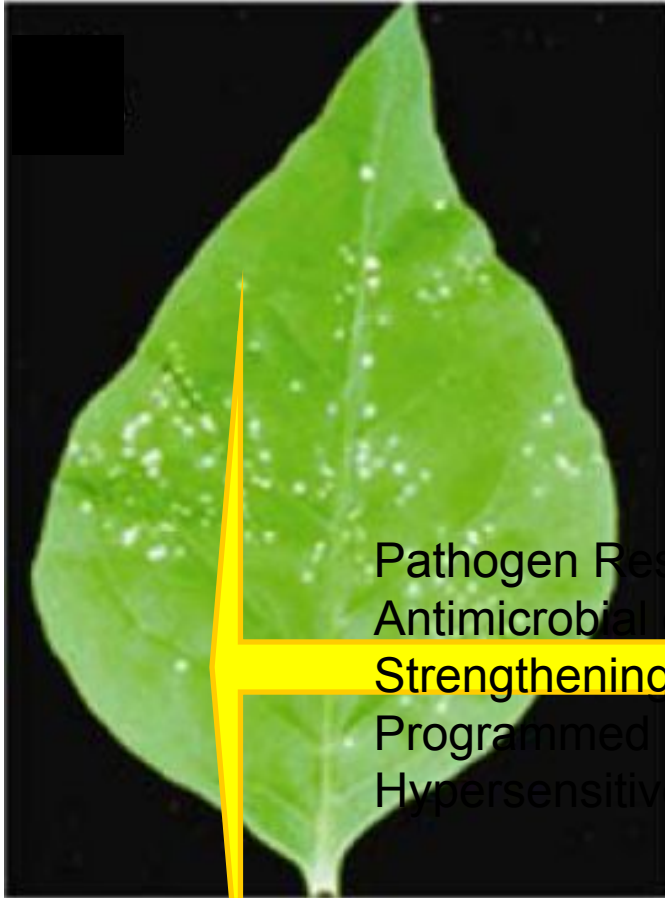
# Salicylates contribute to systemic acquired resistance

SA is necessary in systemic tissue for SAR, but the nature of the mobile signal(s) is still up in the air

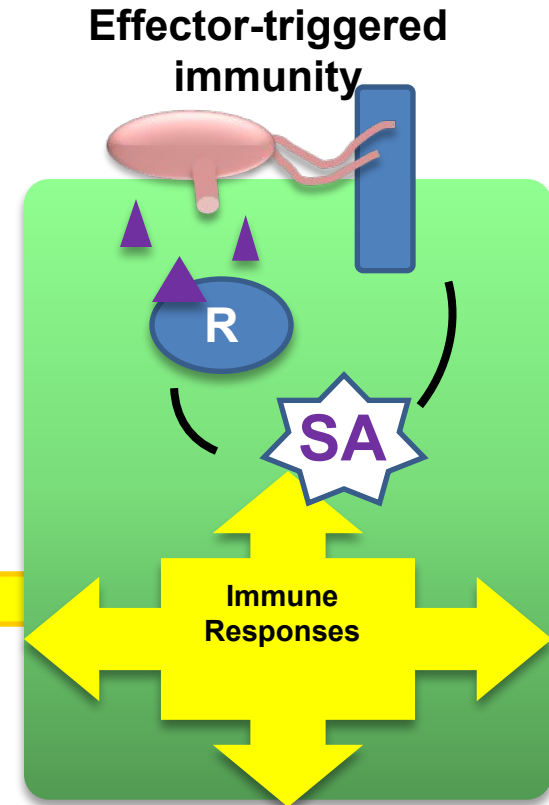
It is likely that multiple signals contribute to SAR



# The hypersensitive response involves cell death

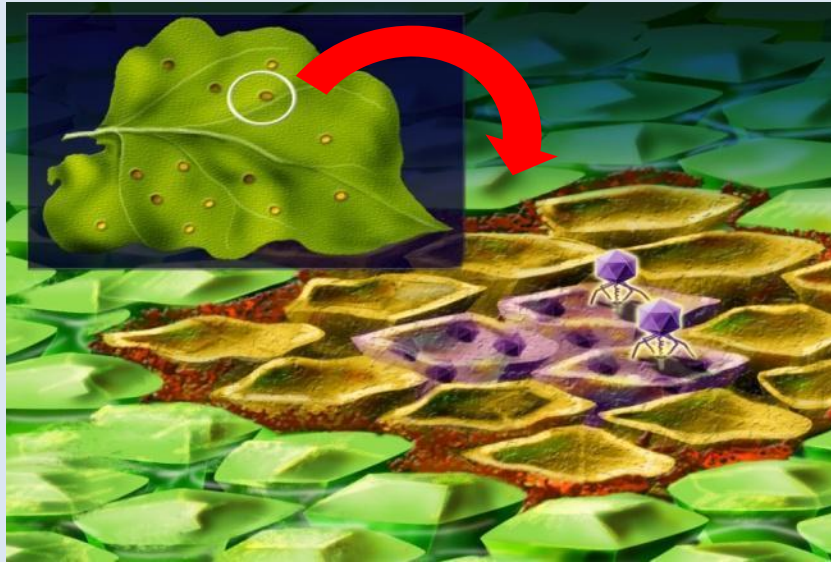


Pathogen Response (PR) genes  
Antimicrobial compounds  
Strengthening of plant cell walls  
Programmed cell death  
Hypersensitive response (HR)



From Cawly, J., Cole, A.B., Király, L., Qiu, W., and Schoelz, J.E. (2005) The plant gene *CCD1* selectively blocks cell death during the hypersensitive response to cauliflower mosaic virus infection. *MPMI* 18: [212-219](#) selectively blocks cell death during the hypersensitive response to cauliflower mosaic virus infection. *MPMI* 18: 212-219; Redrawn from Pieterse, C.M.J., Leon-Reyes, A., Van der Ent, S., and Saskia C M Van Wees, S.C.M. (2009) *Nat. Chem. Biol.* 5: [308-316](#).

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

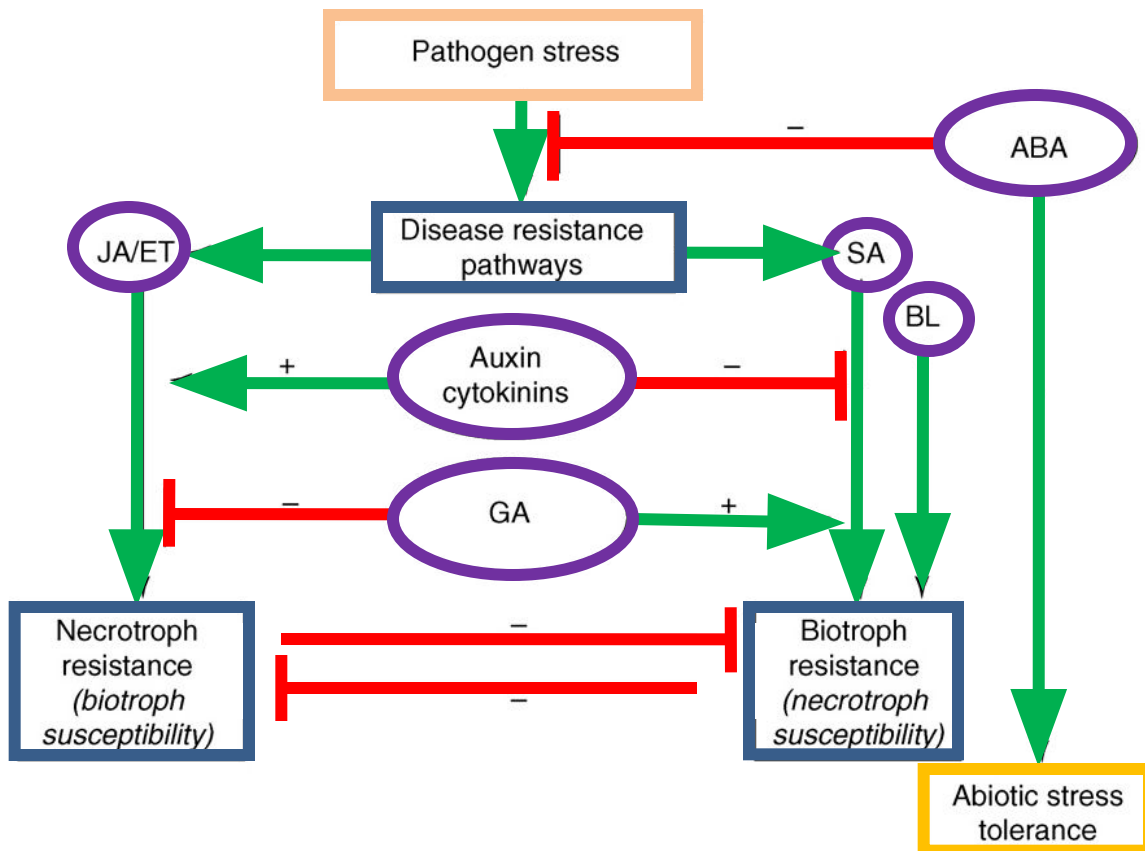


The HR kills the infected cells and cells surrounding them and prevents the pathogen from spreading.



Without a hypersensitive response, the pathogen can multiply.

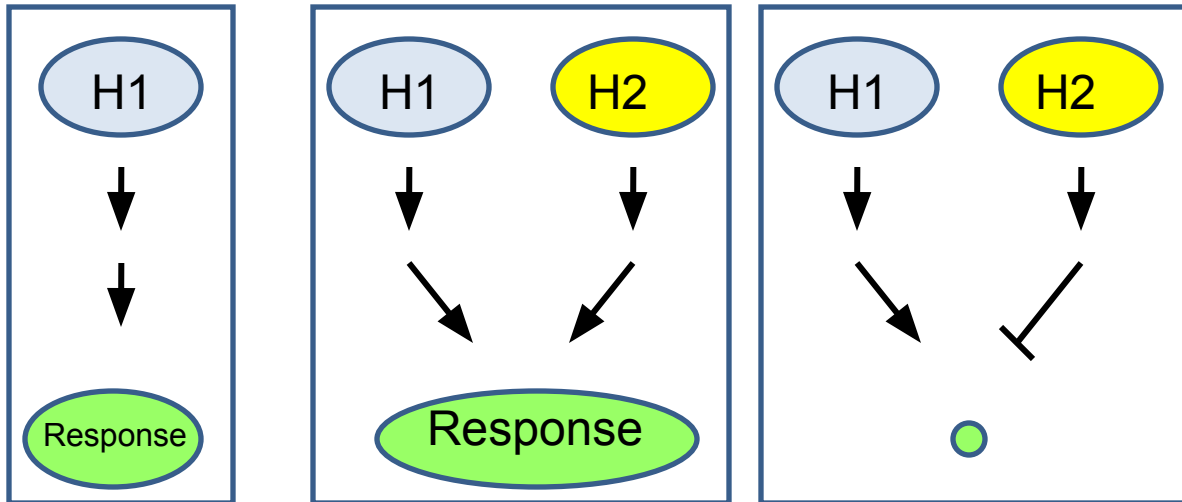
# Other hormones affect defense response signaling



Current Opinion in Plant Biology

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.

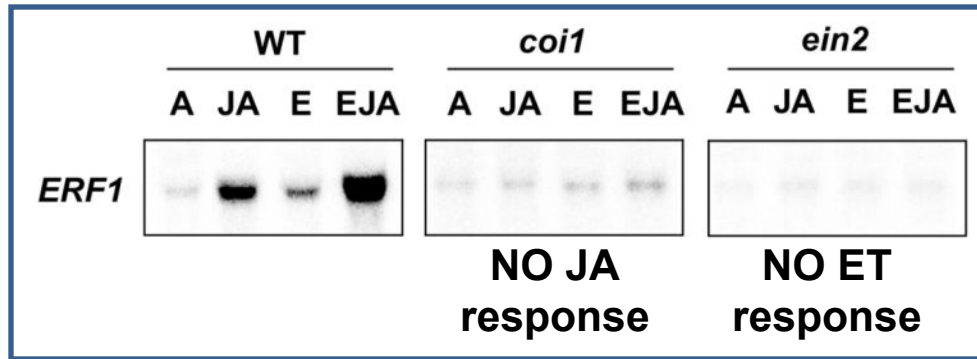
# Crosstalk between hormone signaling pathways



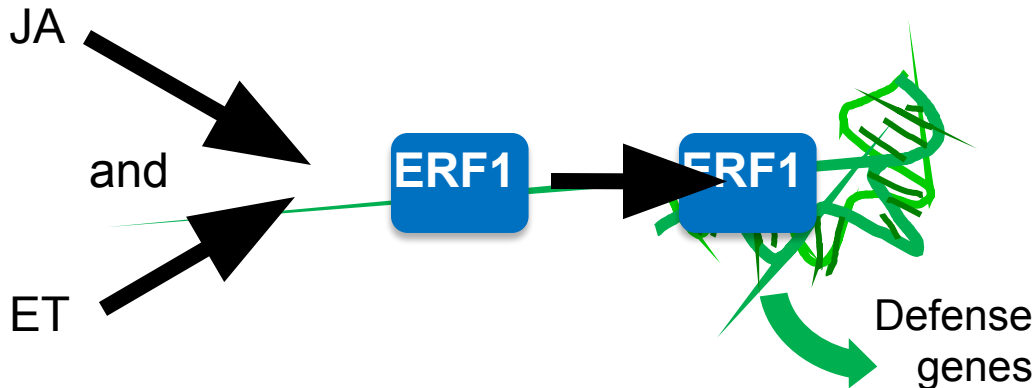
Crosstalk (or cross-regulation) occurs when two pathways are not independent. It can be positive and additive or synergistic, or negative.



# 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





# 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.

