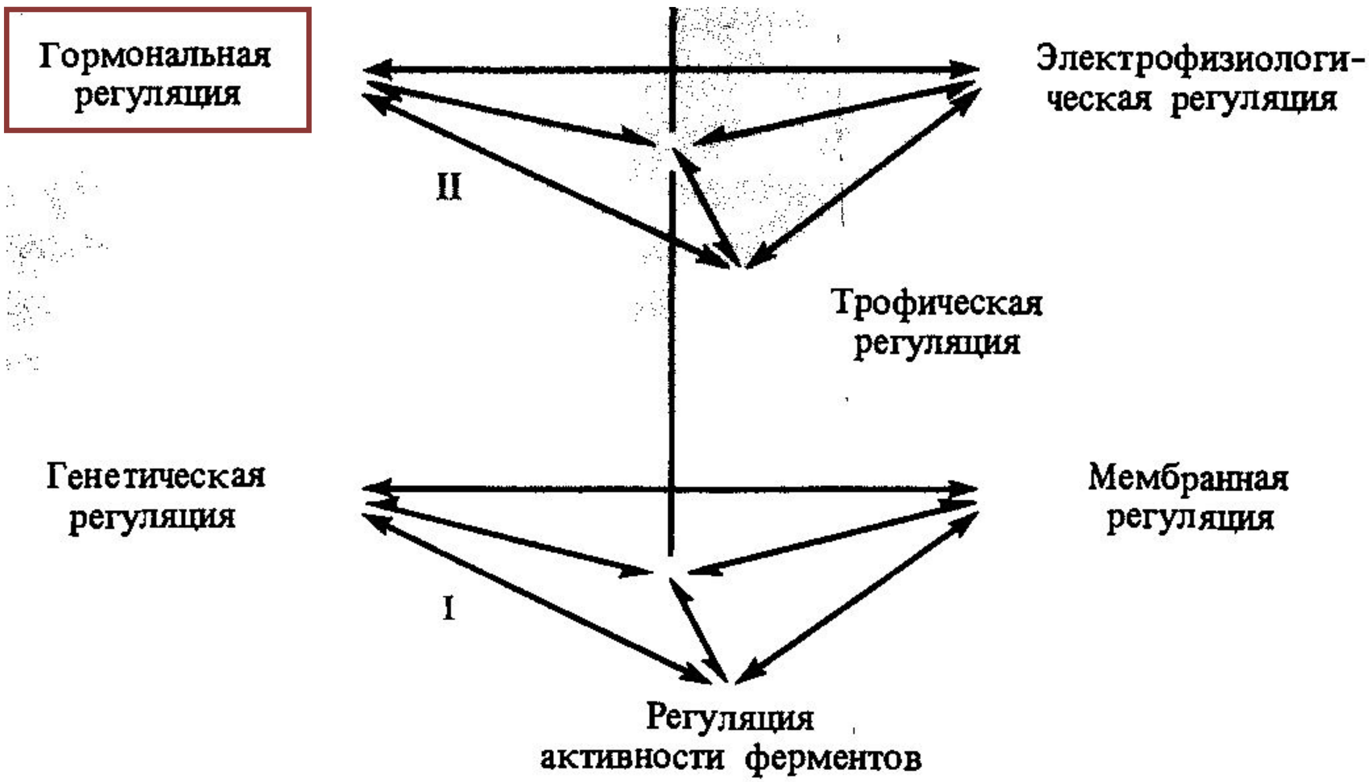
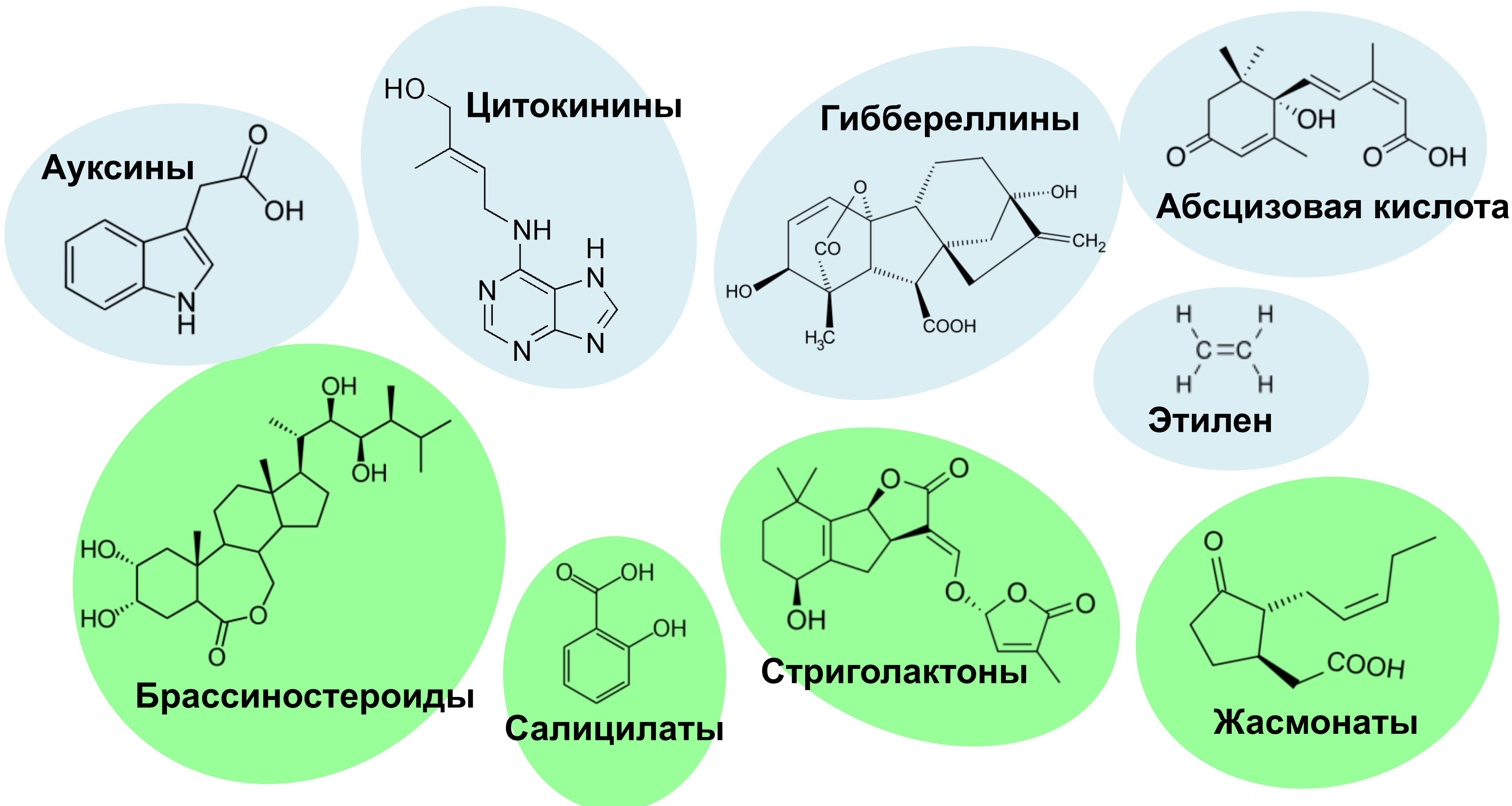
Гормональная система растений

Системы регуляции у растений



- (Полевой В.В., 1989)

Основные гормоны растений



Общие свойства гормонов растений

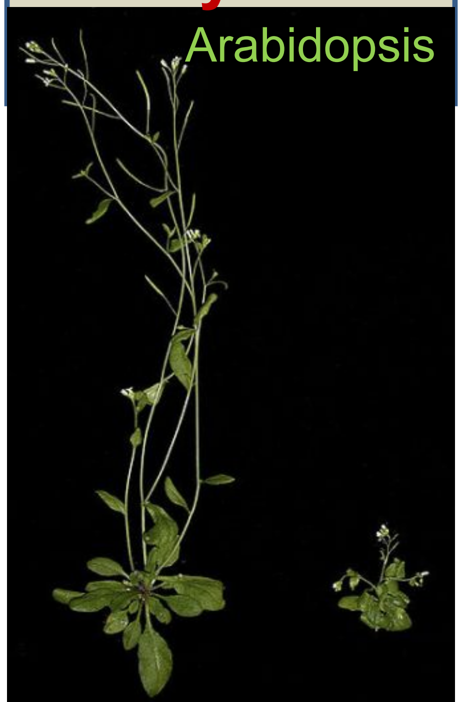
- Специфический ответ
- Наличие специфических рецепторов
- Концентрации 10^{-6}-10^{-12} М
- Мультифункциональность
- Потенциально могут быть образованы любой клеткой
- Не метаболизируются в регулируемых ими процессах
- Действуют не только дистанционно, но и в месте образования
- Эффект зависит от присутствия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

Нарушение синтеза некоторых гормонов отражается на росте растений

ГК

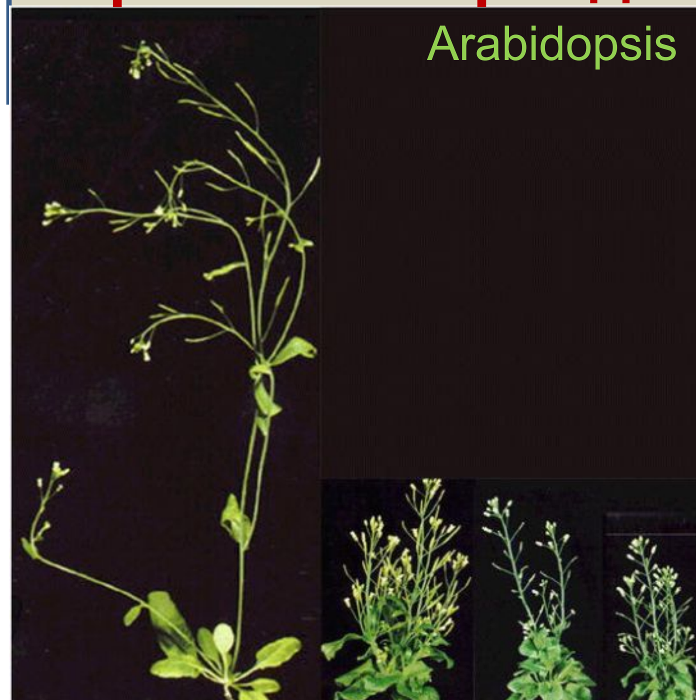
Дикий тип — Gibberellin biosynthesis mutant

Ауксин



Wild type — Auxin response mutant

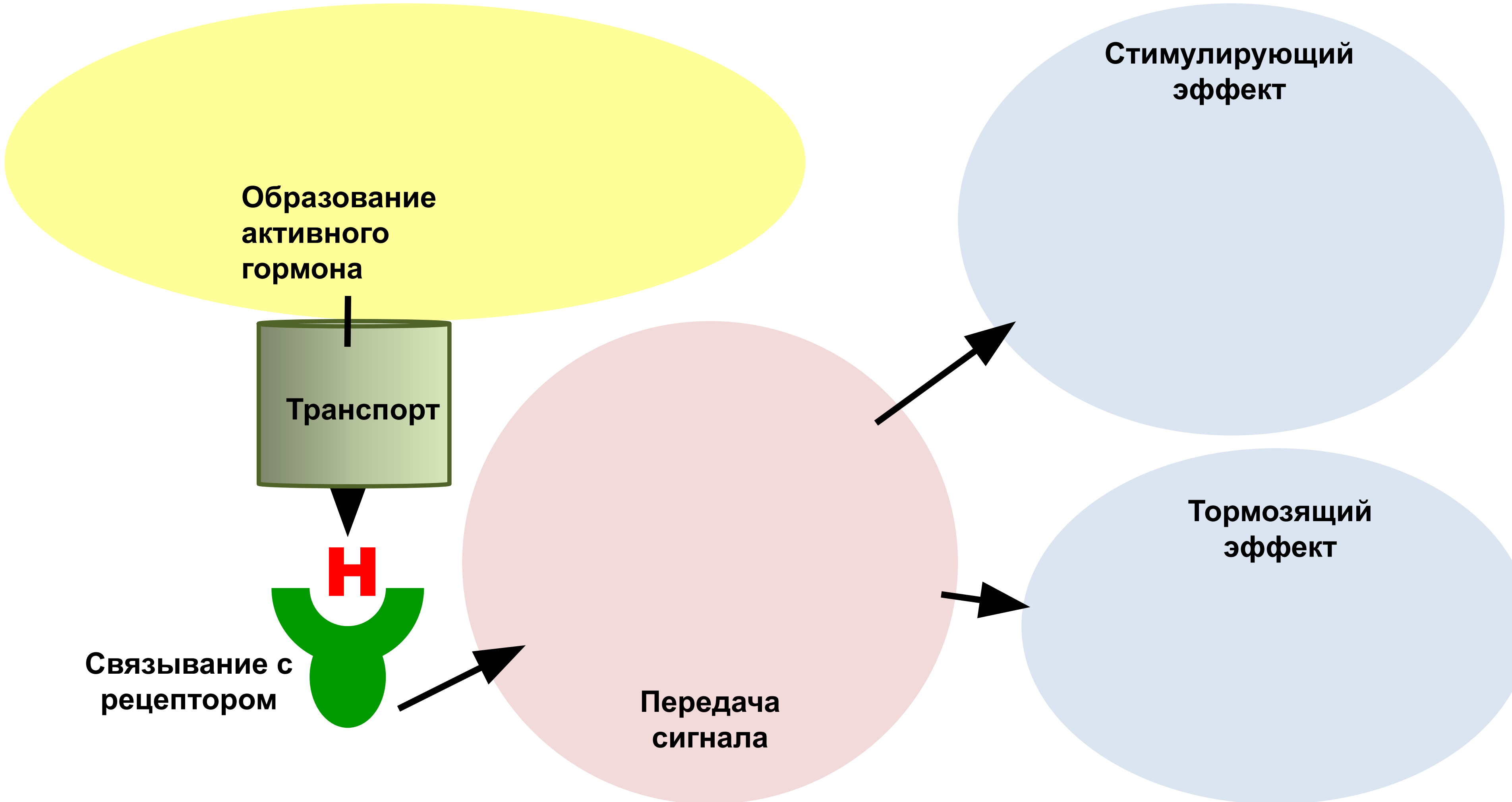
Брассиностероиды



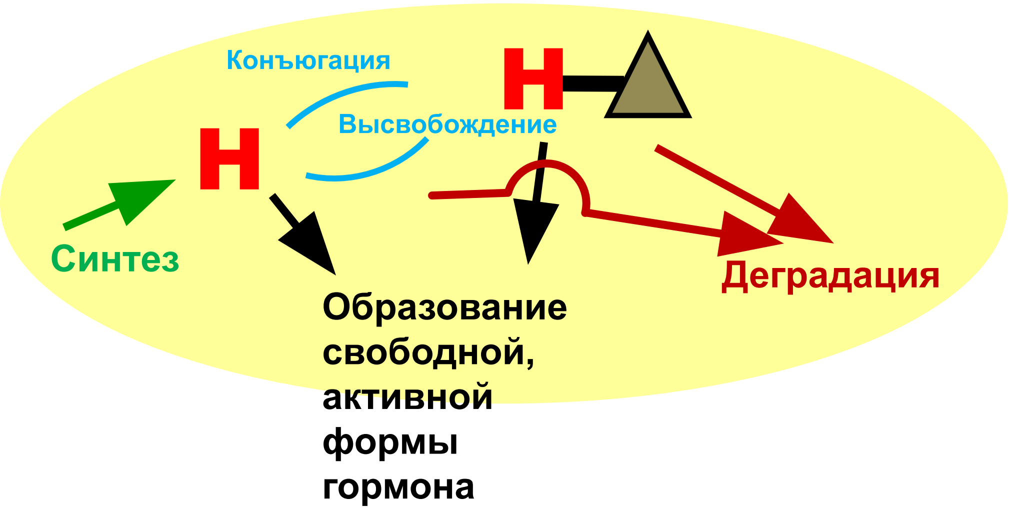
Wild type — Brassinosteroid biosynthesis mutants

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-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



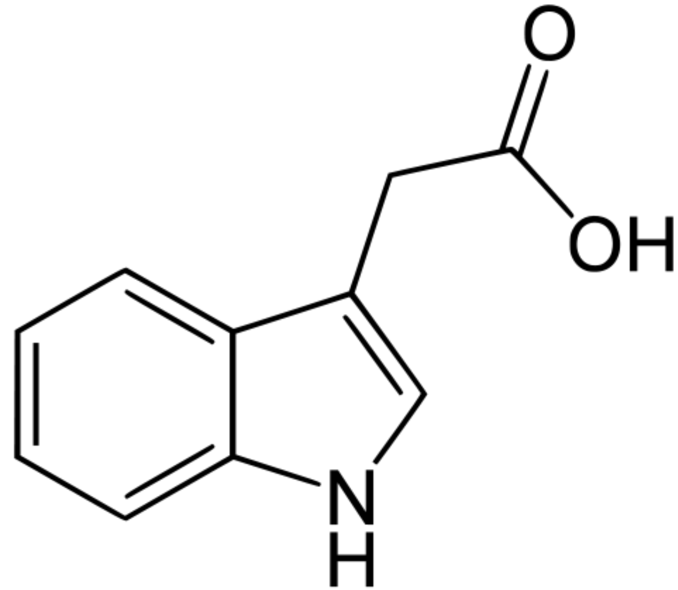
Синтез



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

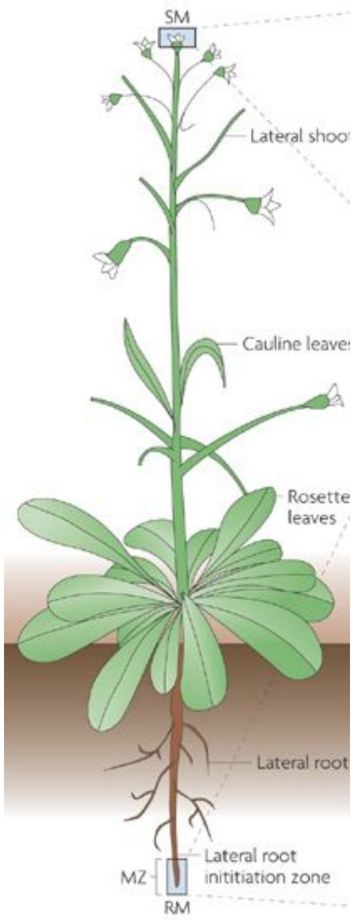
Инициация боковых органов в апикальной меристеме побега

Подавление ветвления побега

Развитие проводящей системы

Поддержка инициальных клеток апикальной меристемы корня

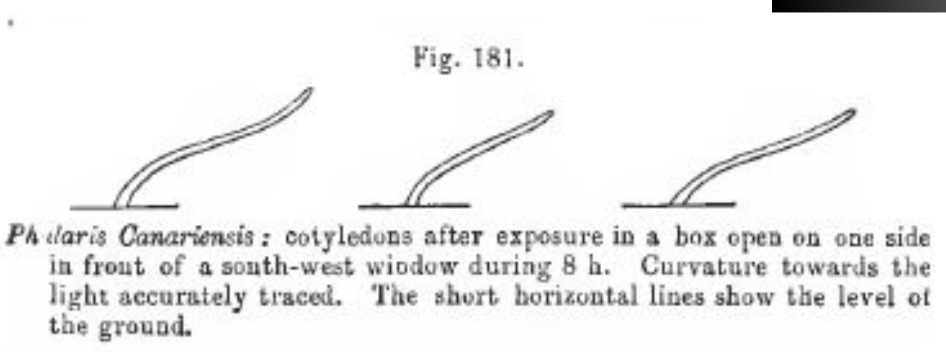
Поддержка ветвления корня

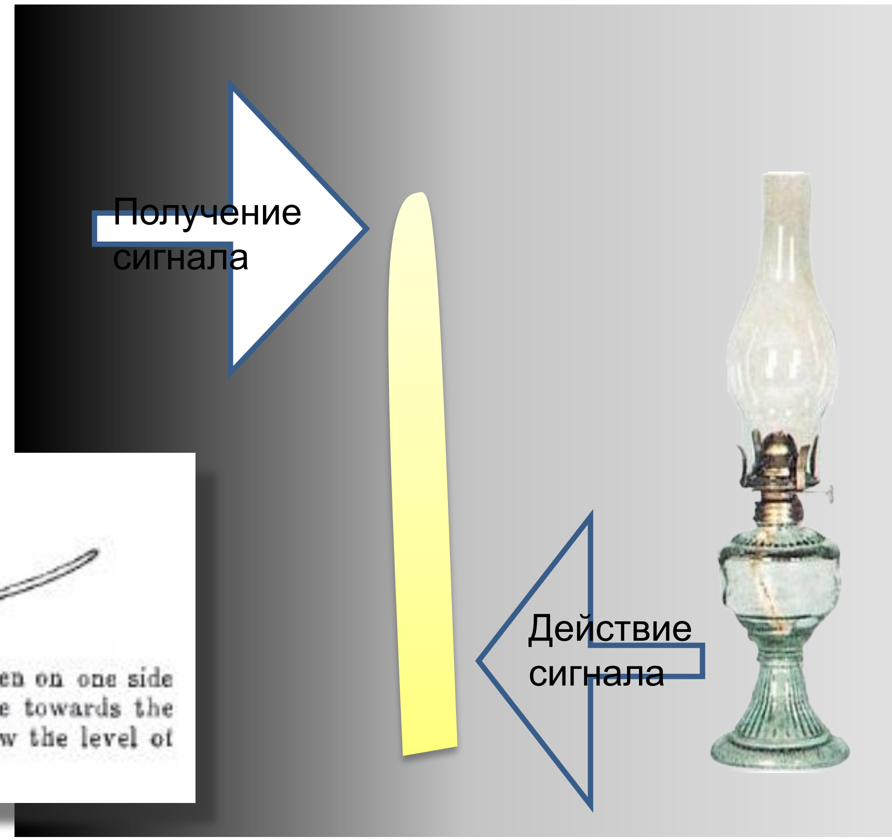


Wolters, H., and Jürgens, G. (2009). Survival of the flexible: Hormonal growth control and adaptation in plant development. Nat. Rev. Genet. 10: 305–317.

Ростовой контроль

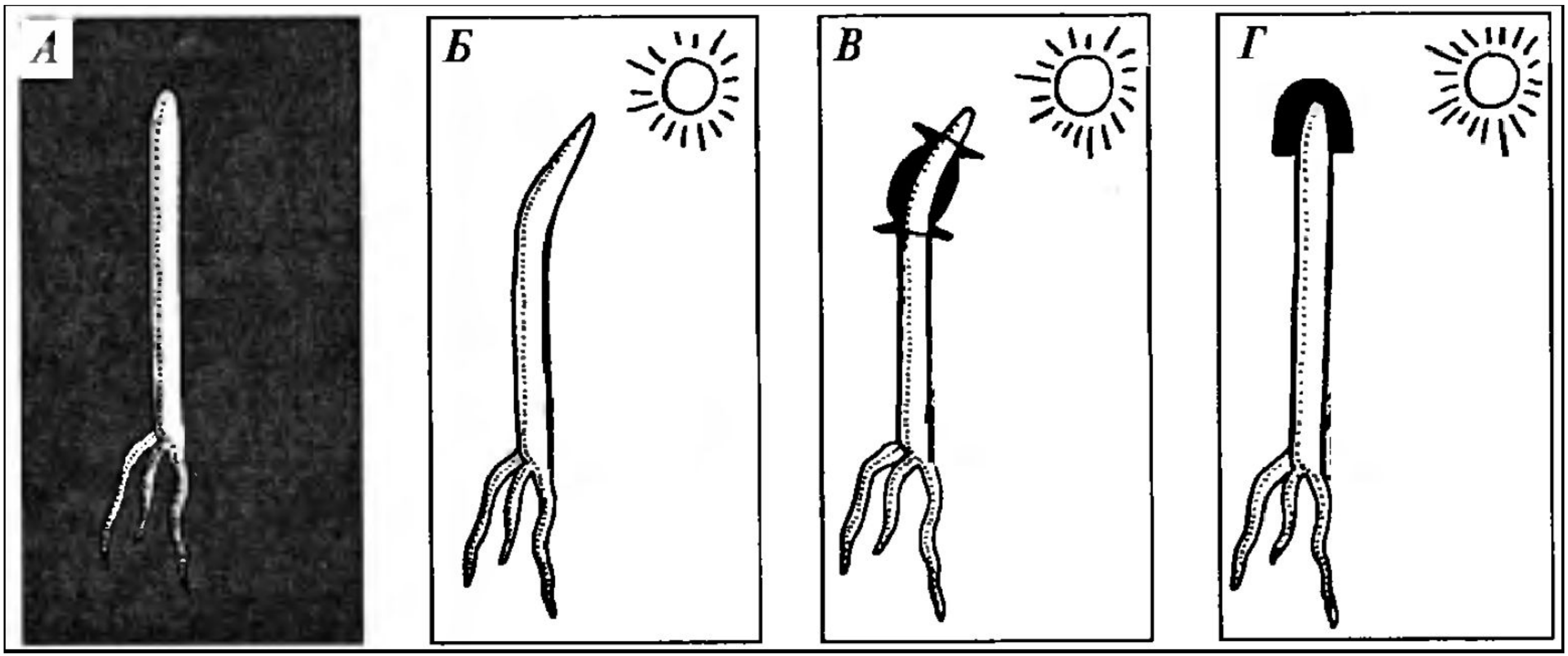
Опыт Ч. и Ф. Дарвинов



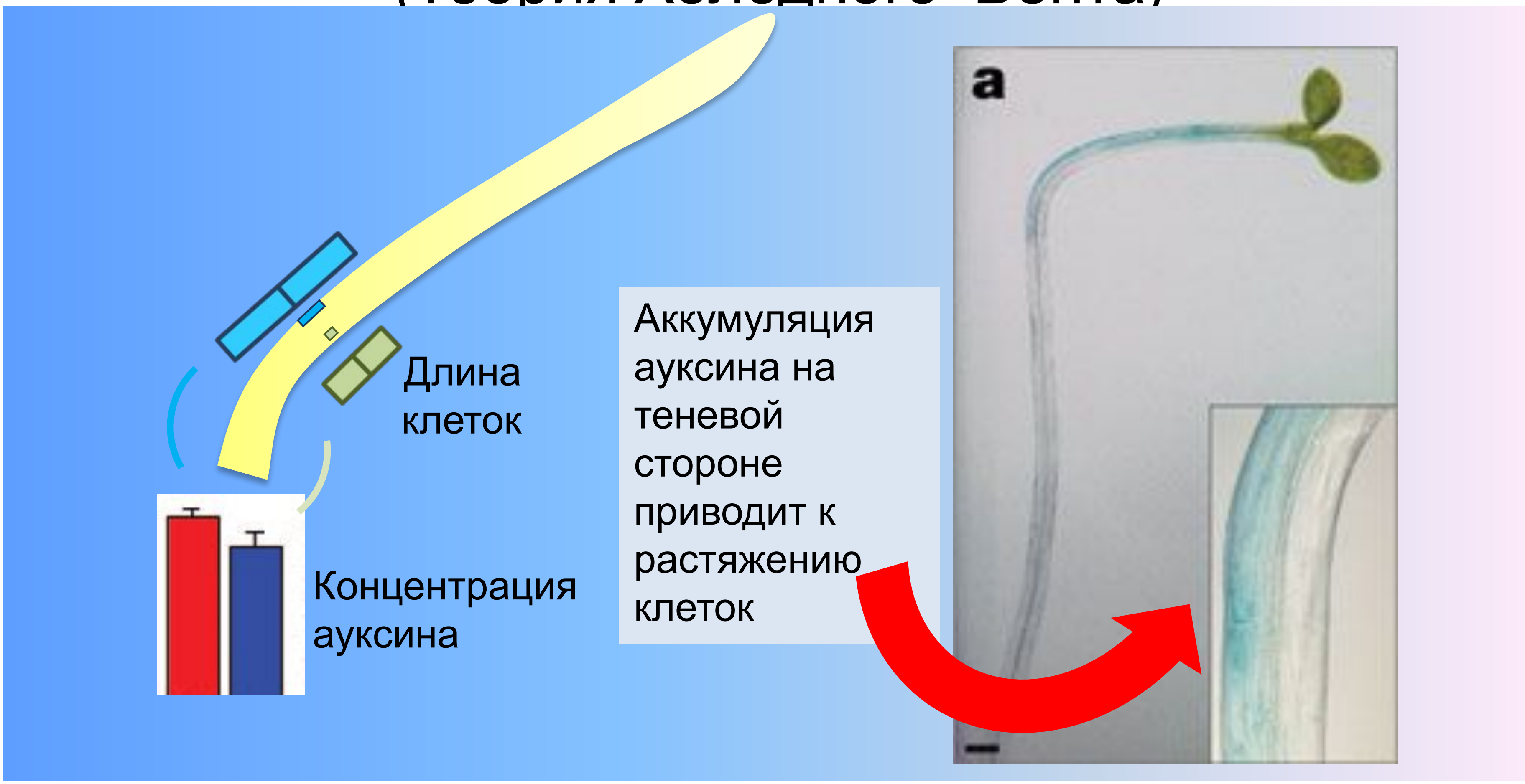


Coleoptile drawing from Darwin, C., and Darwin, F. (1881) The power of movement in plants. Available online.

Опыт Чарльза и Френсиса Дарвинов

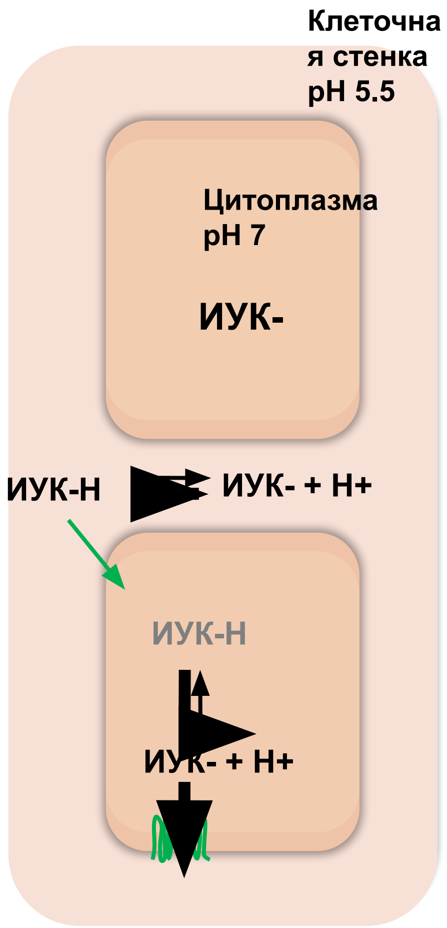


Неравномерный рост клеток – результат перемещения ауксина на затененную сторону (Теория Холодного- Вента)



Esmon, C.A. et al. (2006) A gradient of auxin and auxin-dependent transcription precedes tropic growth responses. Proc. Natl. Acad. Sci. USA 103: 236–241.
Friml, J., et al. (2002) Lateral relocation of auxin efflux regulator PIN3 mediates tropism in *Arabidopsis*. Nature 415: 806-809.

Полярный, базипетальный транспорт ауксина



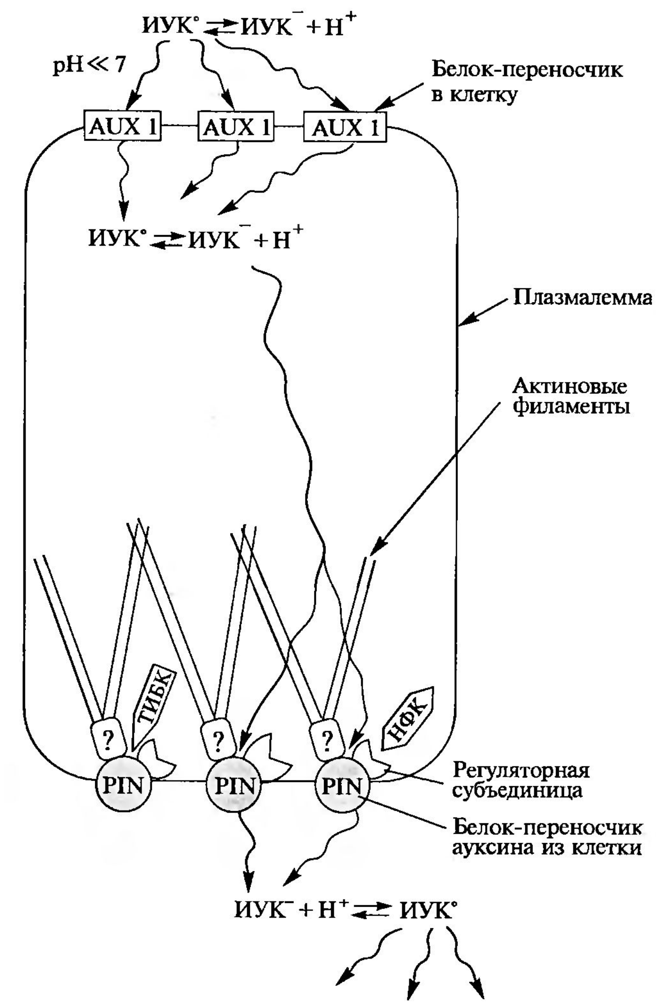
Ауксин - заряженный анион

(ИУК$^{-}$) 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 депротонизируется и активно выводится из клетки специфическим переносчиком

Redrawn from Robert, H.S., and Friml, J. (2009) Auxin and other signals on the move in plants. Nat. Chem. Biol. 5: 325-332.

Полярный транспорт ауксина

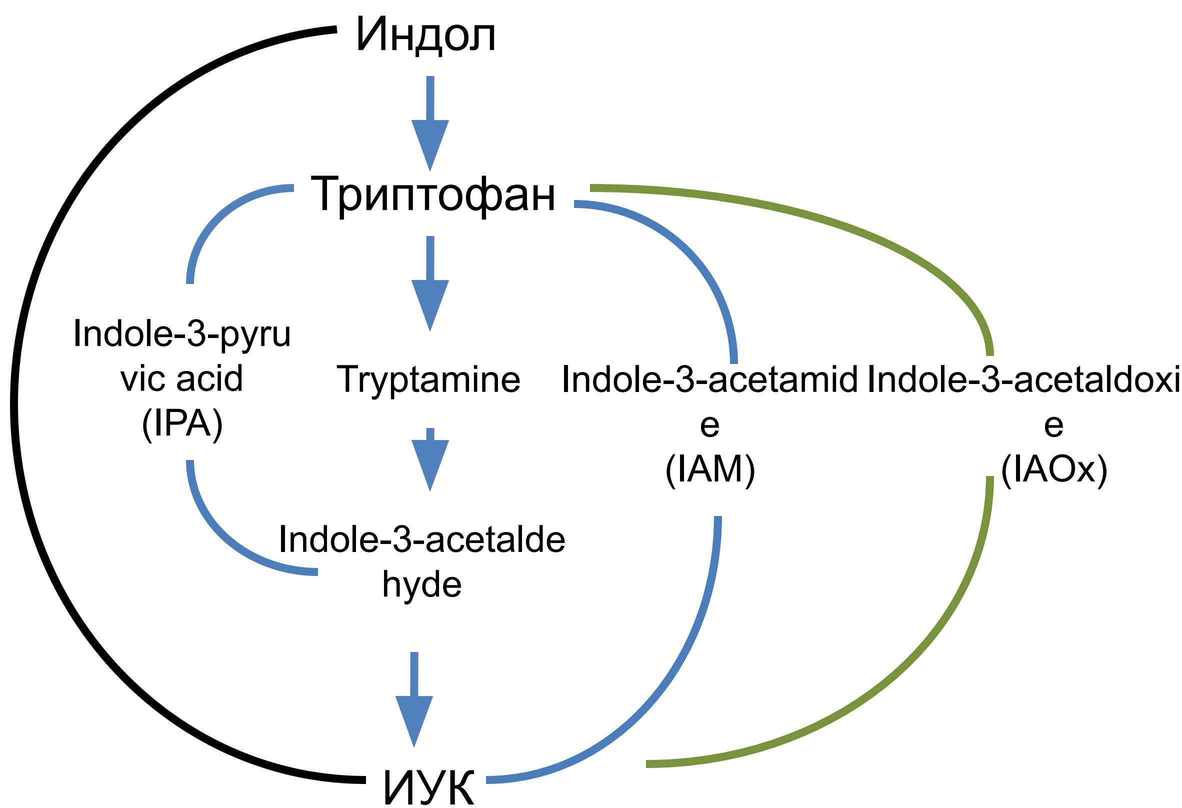


Транспорт ауксина сквозь клетки контролируется транспортными белками трех семейств, задающих направление транспорта молекулы.

Redrawn from Robert, H.S., and Friml, J. (2009) Auxin and other signals on the move in plants. Nat. Chem. Biol. 5: 325-332.

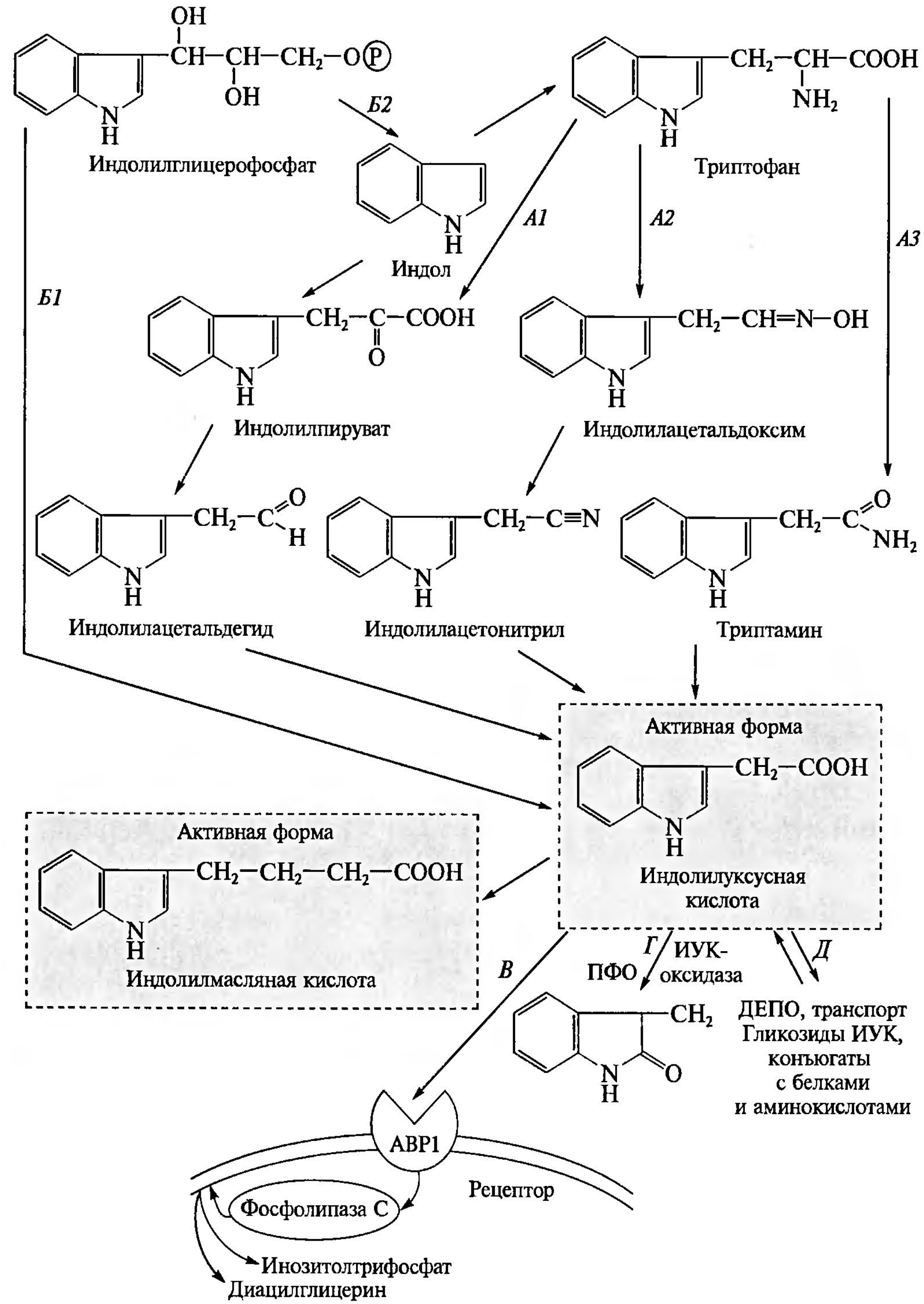
Биосинтез ауксина

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



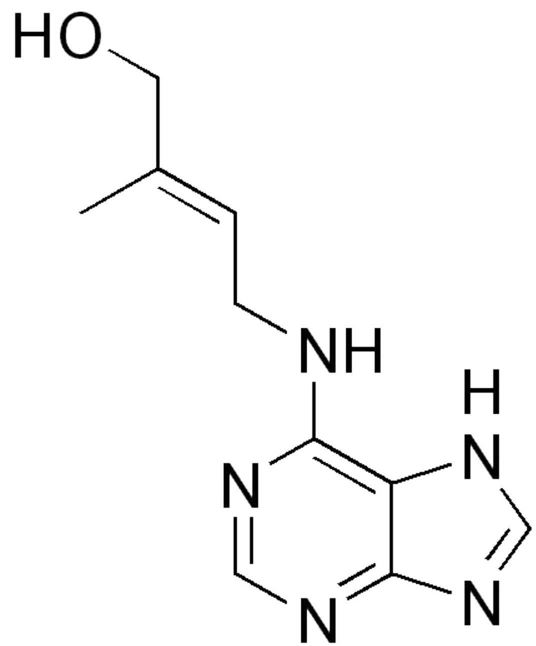
Adapted from Quittenden, L.J., Davies, N.W., Smith, J.A., Molesworth, P.P., Tivendale, N.D., and Ross, J.J. (2009). Auxin biosynthesis in pea: Characterization of the tryptamine pathway. Plant Physiol. 151: 1130-1138..

Синтез ауксина



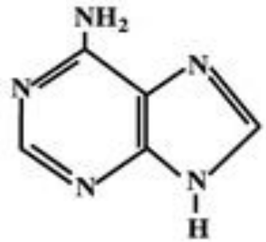
Цитокинин

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



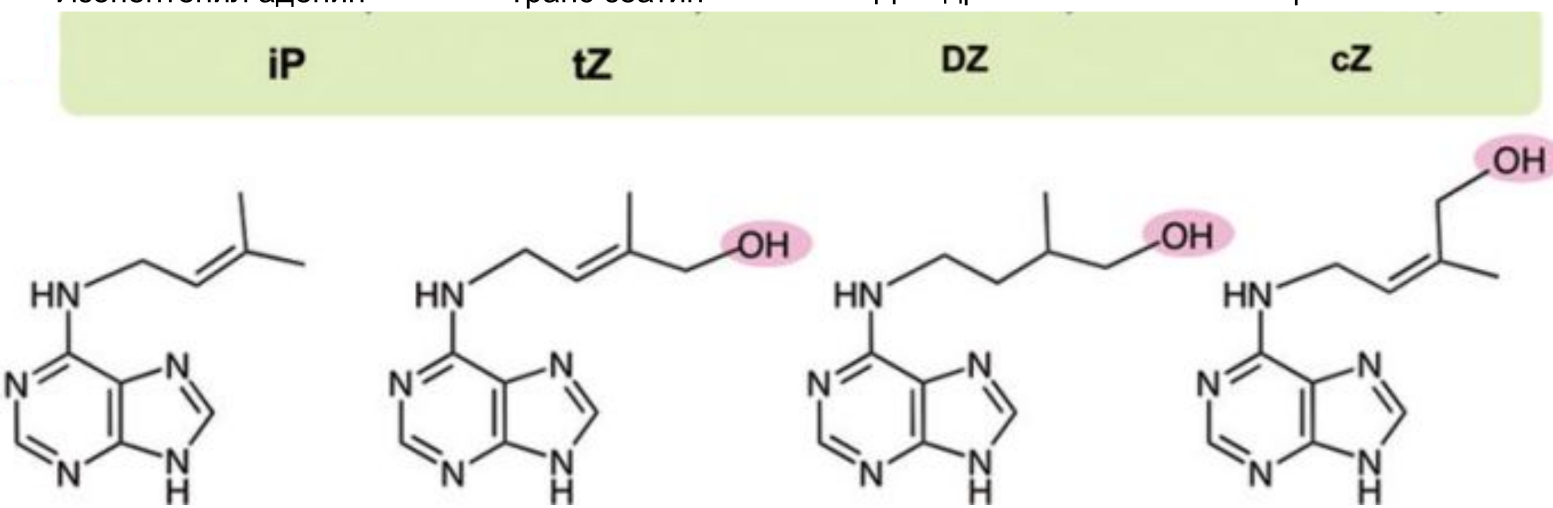
транс-зеатин

Цитокинины - семейство аденин-подобных соединений



adenine

Изопентенил аденин Транс-зеатин Дигидрозеатин Цис-зеатин



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

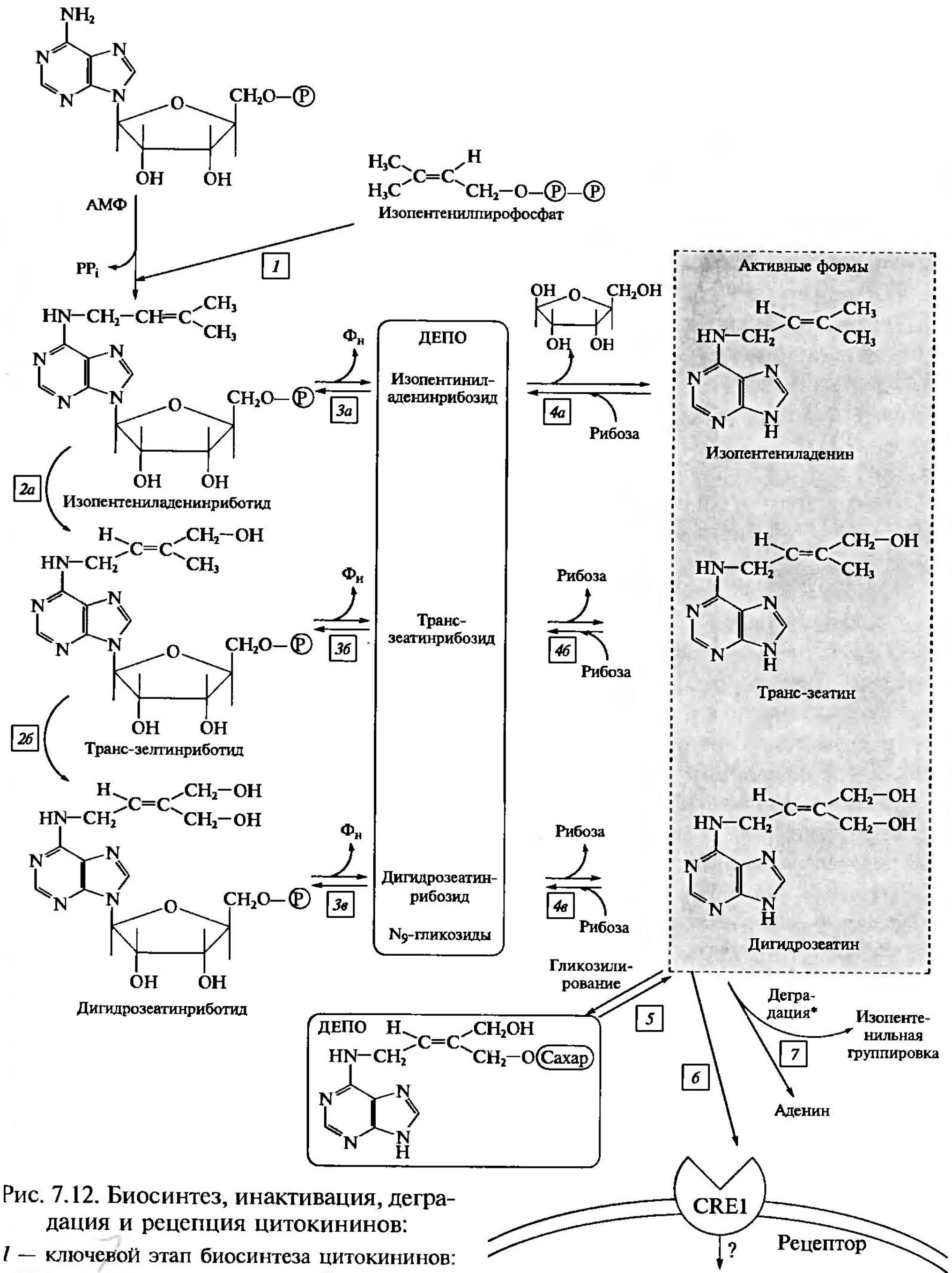


Рис. 7.12. Биосинтез, инактивация, деградация и рецепция цитокининов:

1 — ключевой этап биосинтеза цитокининов: присоединение изопентенильной группиров-

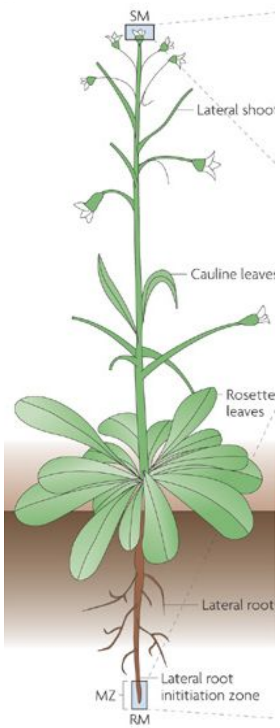
Цитокинины – антагонисты ауксина

Ауксин

Подавляет ветвление побега

ЦК

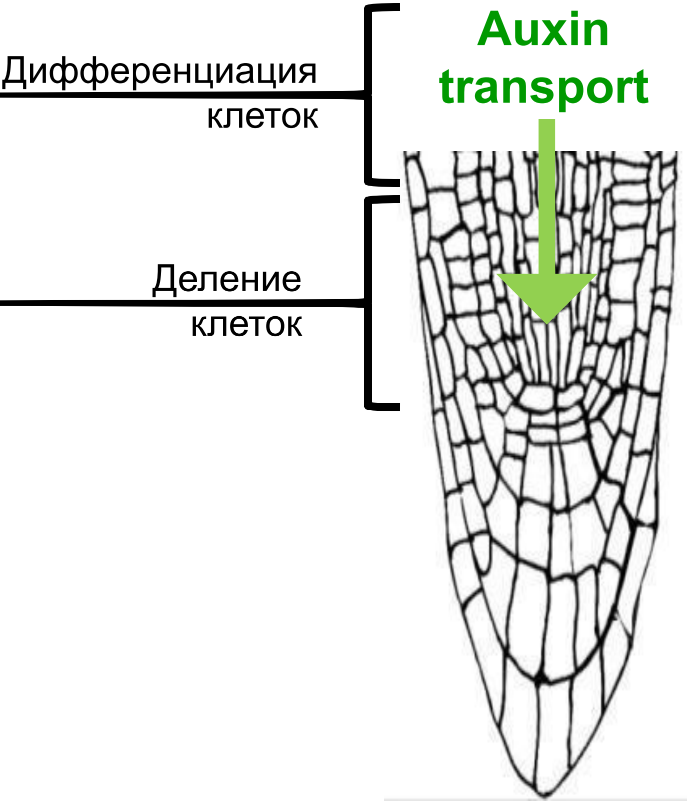
Стимулирует ветвление побега



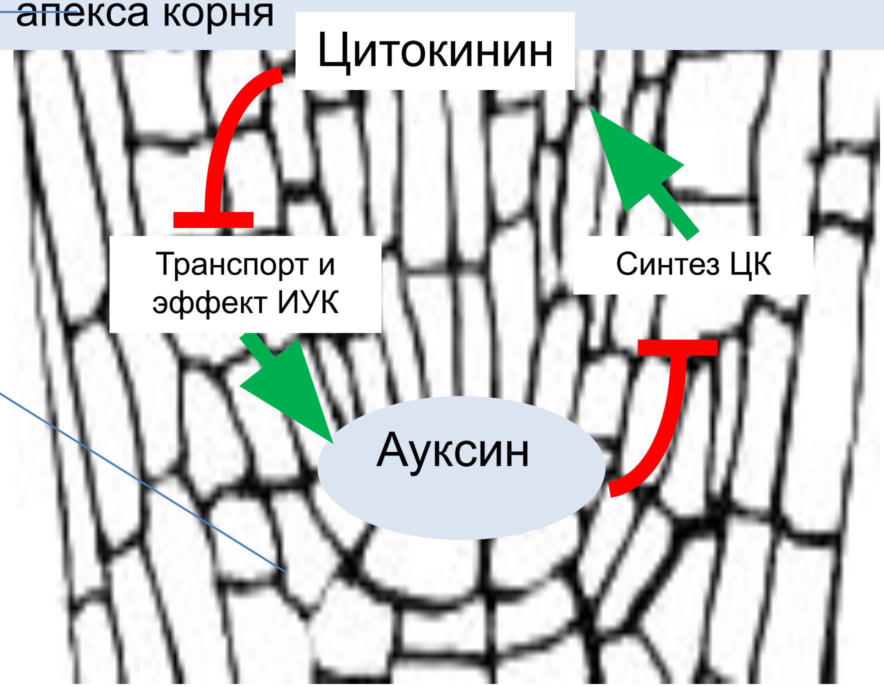
Поддерживает ветвление корней

Подавляет ветвление корней

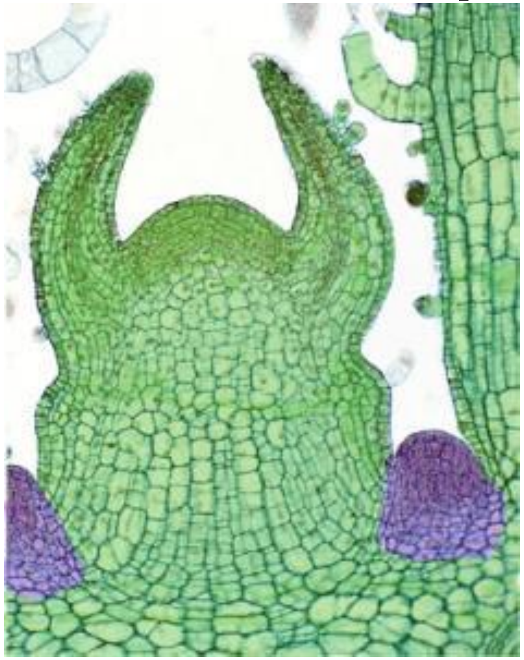
Ауксин и цитокинин взаиморегулируются в апексе побега



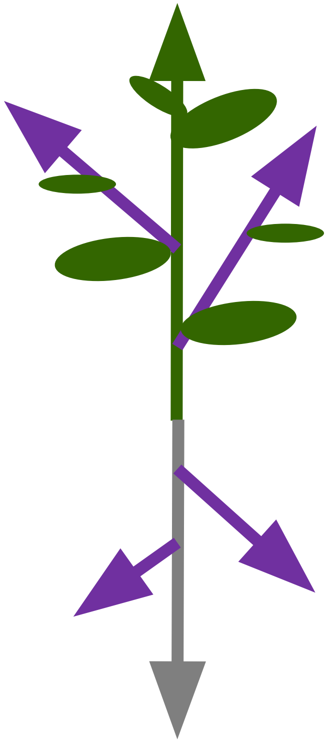
Путем взаимовлияния на синтез, транспорт и эффекты друг друга ИУК и ЦК устанавливают две взаимно исключающих модели координации активности клеток апекса корня



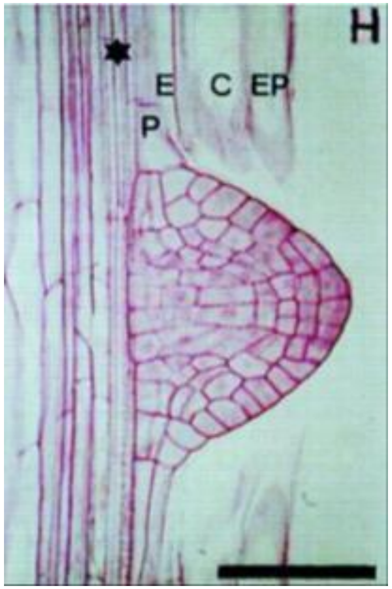
Ауксин, цитокинин и стриголактон контролируют ветвление



Ветвление побега стимулируется ЦК и подавляется ИУК и стриголактоном



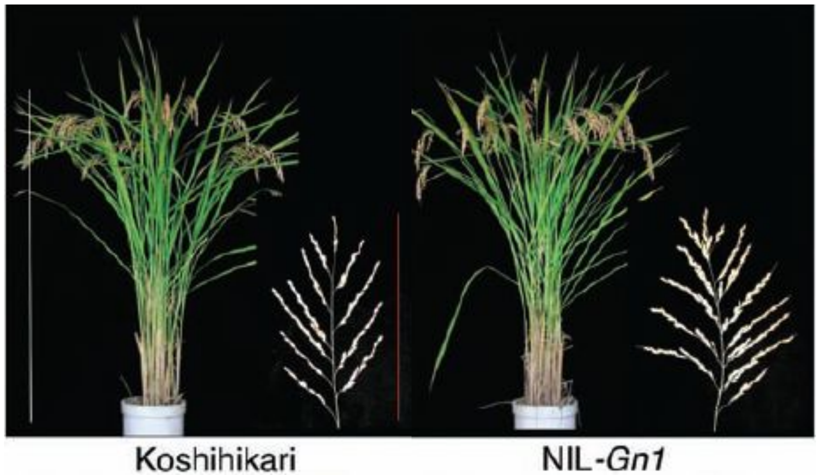
Рост боковых корней поддерживается ИУК и подавляется ЦК

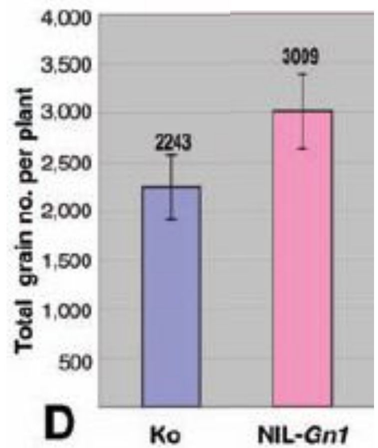


Ветвление контролирует все аспекты продуктивности растений от минерального питания до урожая зерна.

Coleus shoot image by Judy Jernstedt, BSA ; lateral root image from Casimiro, I., et al. (2001) Auxin transport promotes Arabidopsis lateral root initiation. Plant Cell 13: 843-852.

Cytokinins affect grain production and drought tolerance



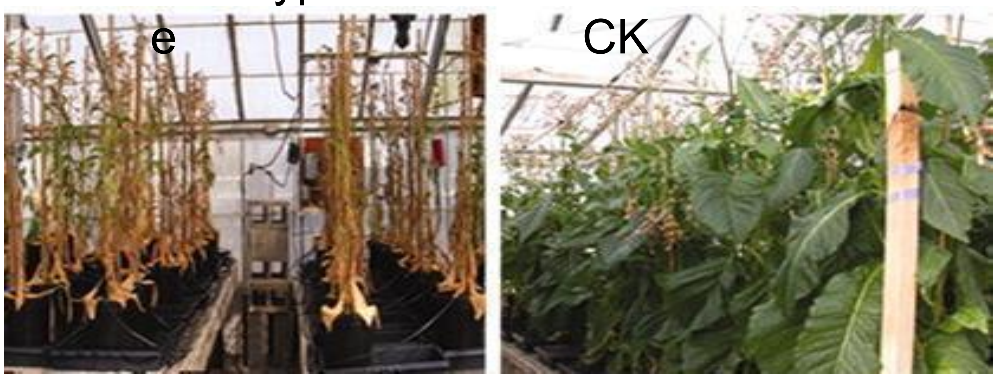


Rice plants that accumulate more CK can produce more grain per plant because of changes in inflorescence architecture.

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

Wild-type

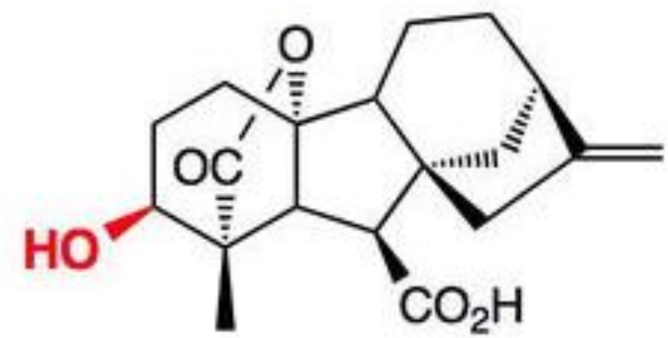
Elevated CK



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

Гиббереллин

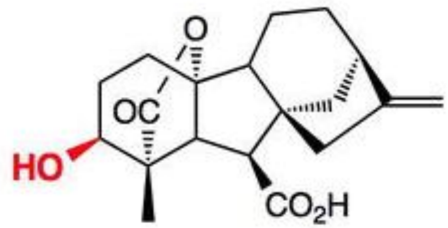
- Рост междоузлий
- Прорастание семян
- Цветение
- Определение пола у некоторых видов
- Стимуляция роста плодов



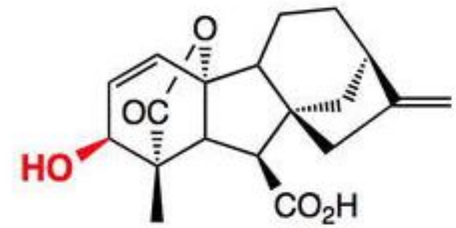
A Gibberellin (GA_4)

Гиббереллины – семейство веществ

GA_4 – главная активная форма GA у Arabidopsis

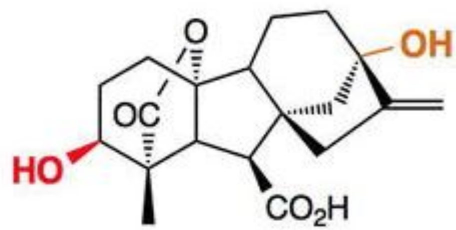


GA_4

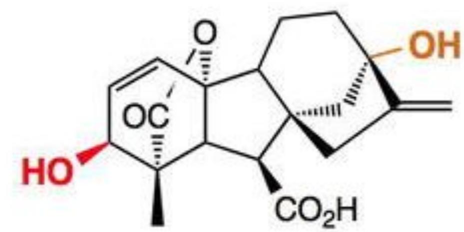


GA_7

Активны только некоторые формы ГК.



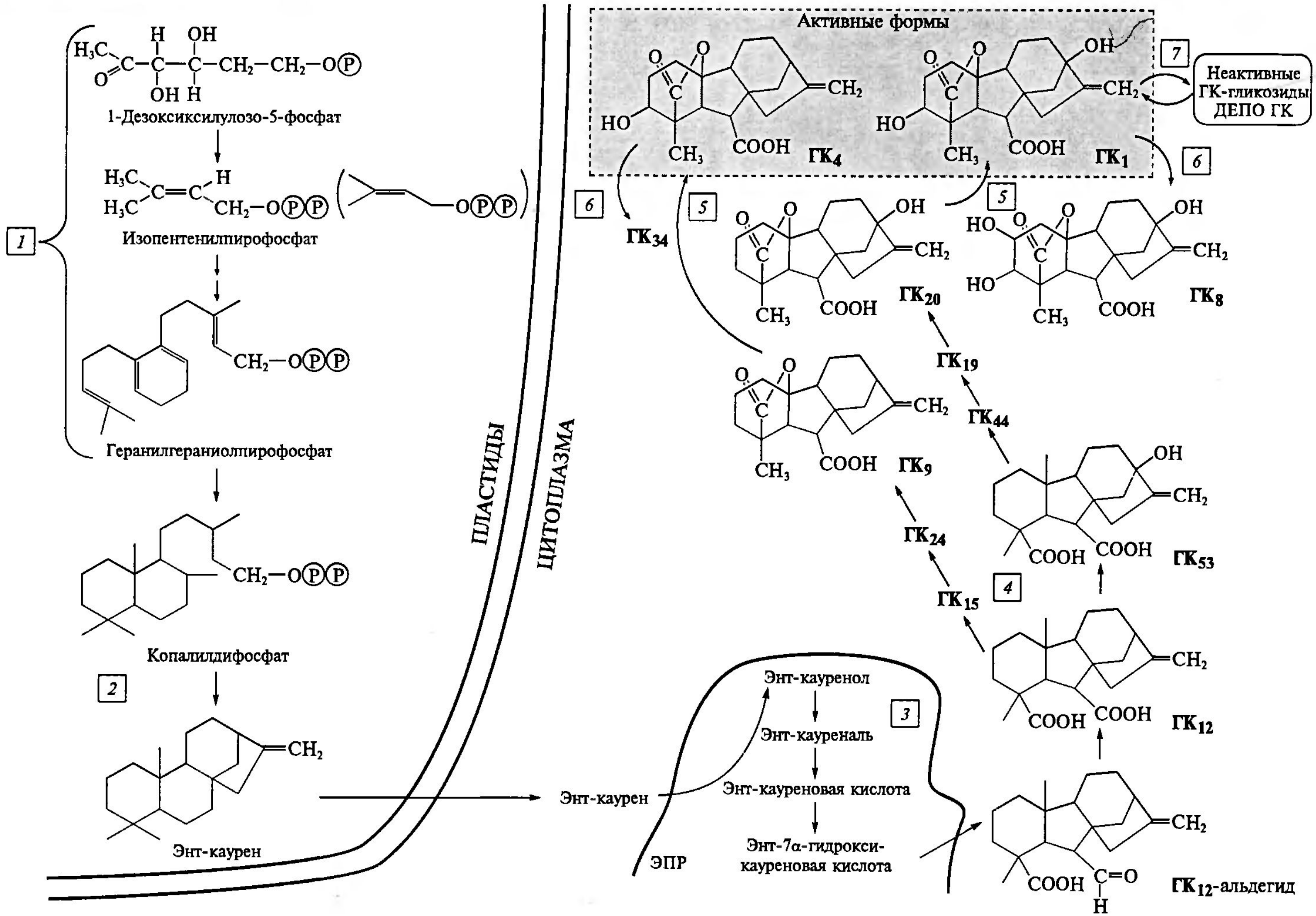
GA_1



GA_3

Sun T (2008) Gibberellin metabolism, perception and signaling pathways in *Arabidopsis*: September 24, 2008. The Arabidopsis Book. Rockville, MD: American Society of Plant Biologists. doi: 10.1199/tab.0103

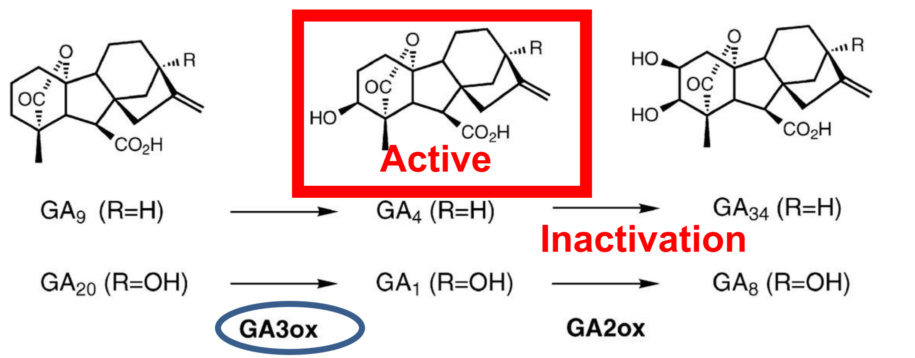
Синтез гиббереллина



Гиббереллин регулирует рост

Wild type — Gibberellin biosynthesis mutant *le*

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.

Гены, контролирующие синтез ГК оказались важны для «зеленой и»

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

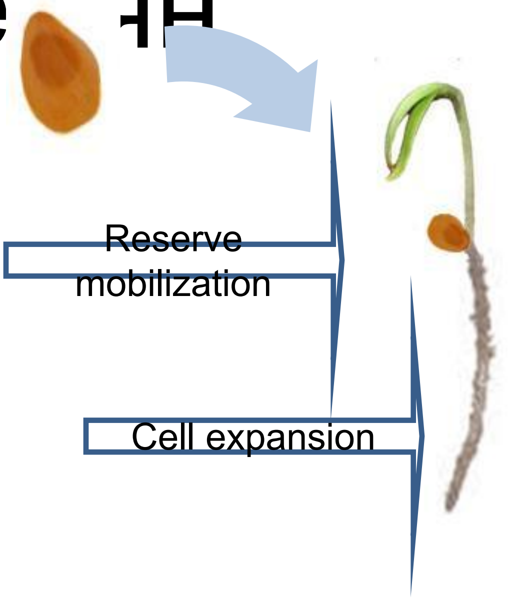
The semidwarf varieties put more energy into seed production than stem growth, and are sturdier and less likely to fall over.

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

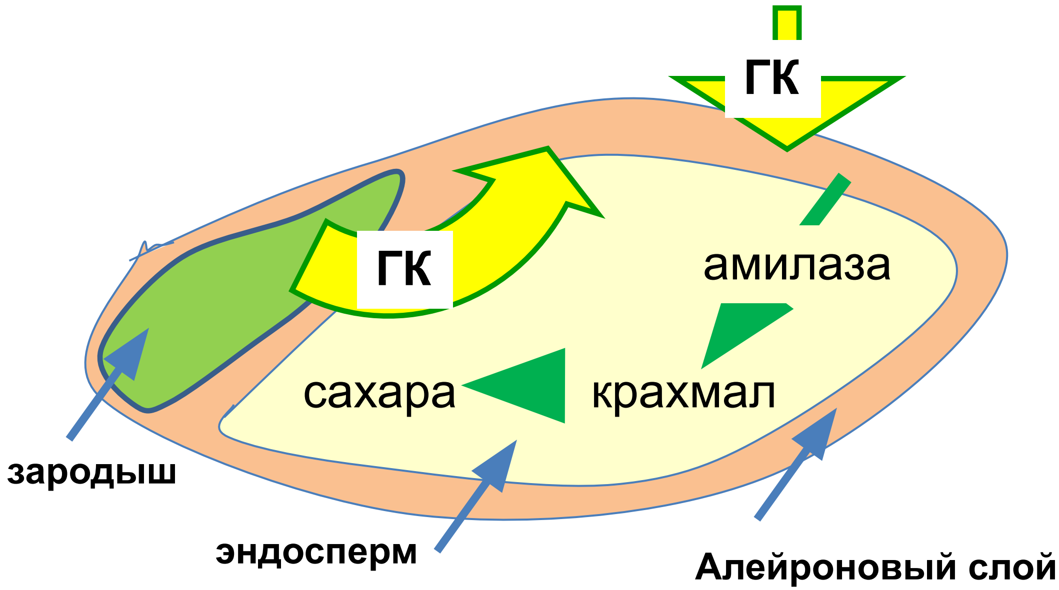
Photos courtesy of S. Harrison, LSU Ag centerPhotos courtesy of S. Harrison, LSU Ag center and The World Food Prize.

ГК важна для прорастания се ян

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



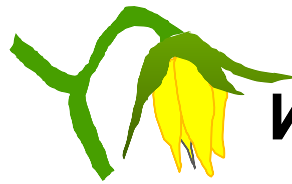
Стимуляция прорастания зерна



Images by Prof. Dr. Otto Wilhelm Thomé *Flora von Deutschland, Österreich und der Schweiz* 1885 and Chrisdesign.

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

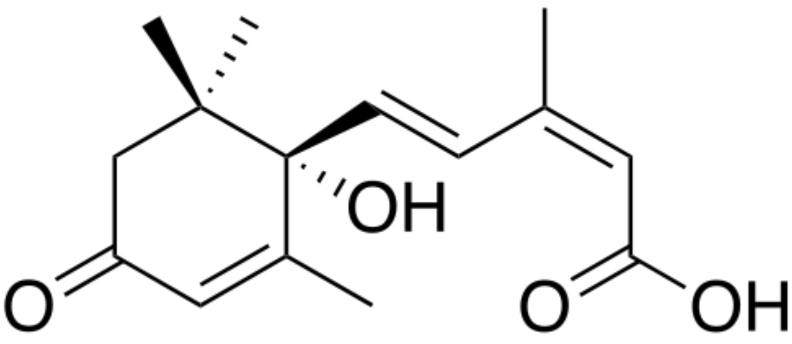
ГК

ИУК

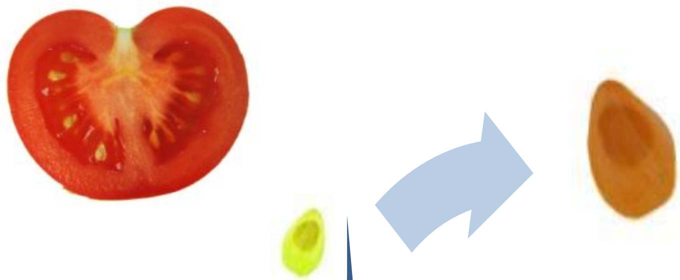
Photo credits: Grape flowers by Bruce Photo credits: Grape flowers by Bruce ReischPhoto credits: Grape flowers by Bruce Reisch; Strawberry flower by Shizhao

Абсцизовая кислота

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



ABA accumulates in maturing seeds



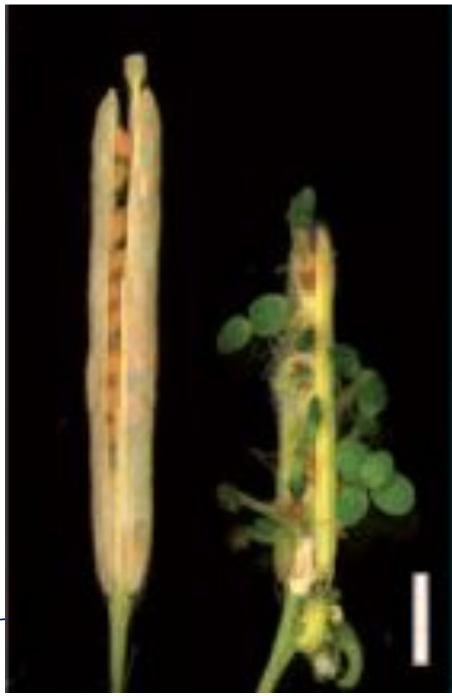
Embryonic patterning

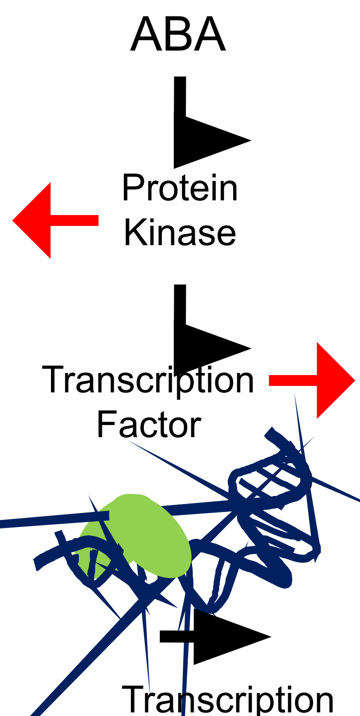
Reserve accumulation

Desiccation tolerance

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

ABA synthesis and signaling is required for seed dormancy





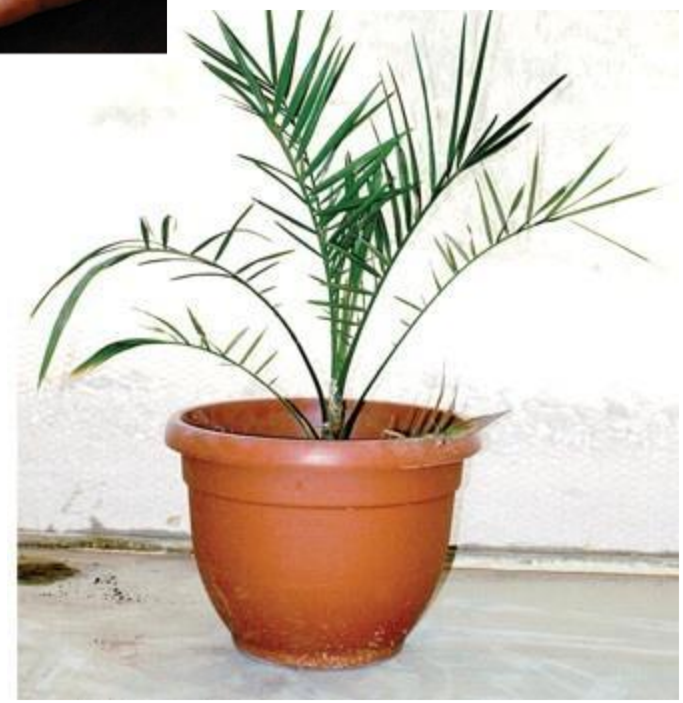
Loss of function of ABA signaling (protein kinase or transcription factor function) interferes with ABA-induced dormancy and causes precocious germination.

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: 1345–1363Nakashima, 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

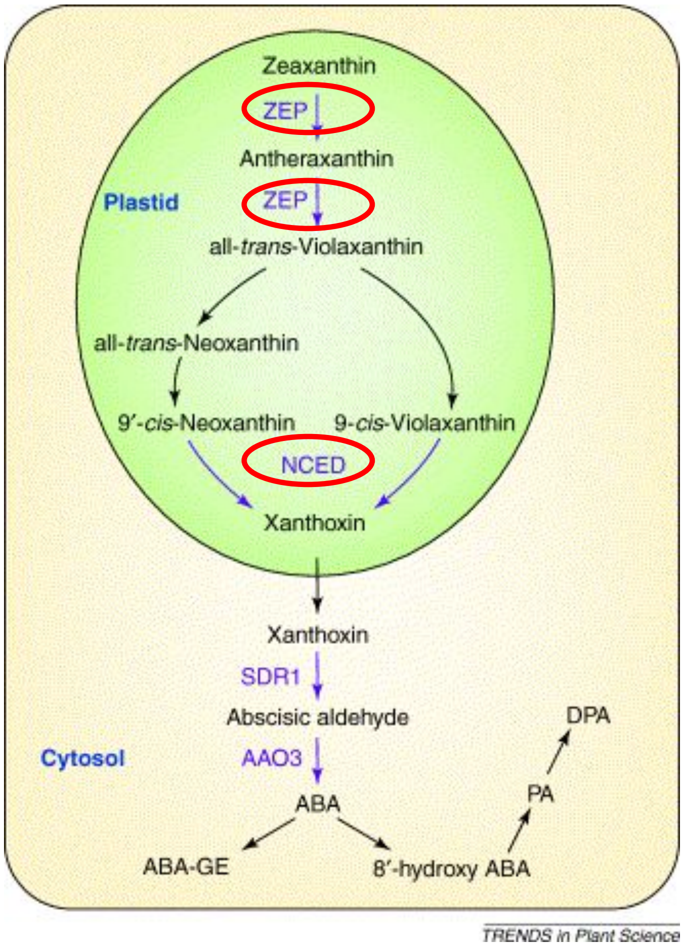
These date palm seeds are nearly 2000 years old, but still viable and capable of germination. Five
-hundred year old lotus seeds have also been successfully germinated. Having a thick seed coat may help these super seeds retain viability.

Date palm growing from 2000 year old seed.



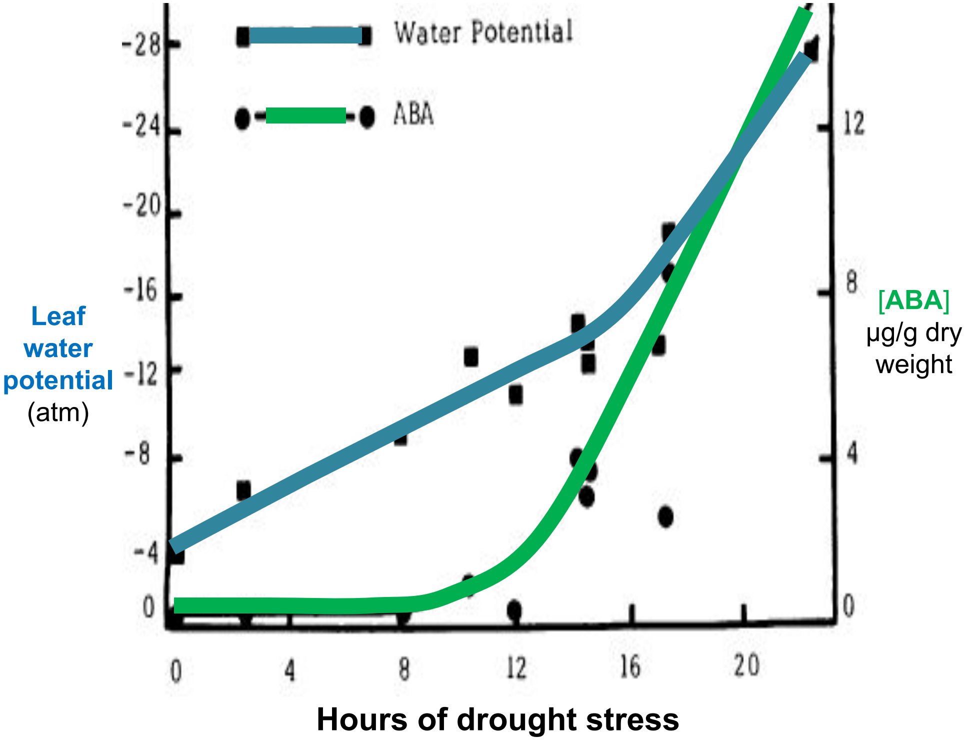
From Sallon, S., et al. (2008). Germination, genetics, and growth of an ancient date seed. Science 320: 1464From Sallon, S., et al. (2008). Germination, genetics, and growth of an ancient date seed. Science 320: 1464, with permission from AAAS Lotus picture by Peripitus

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.

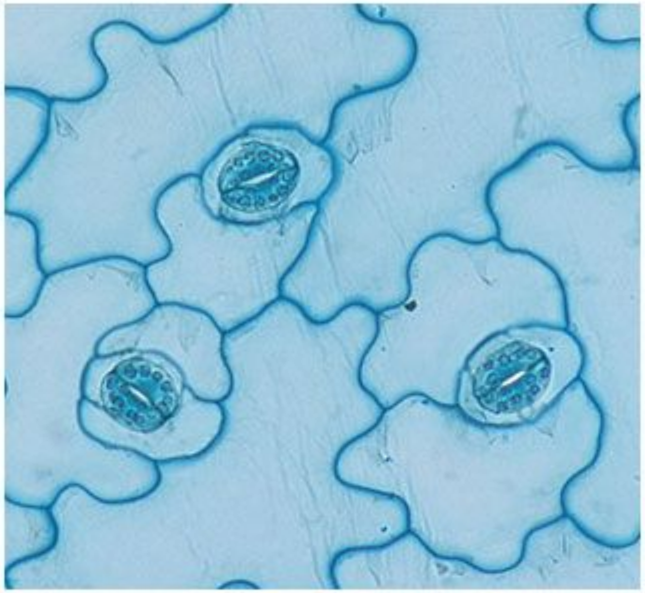
ABA synthesis is strongly induced in response to stress



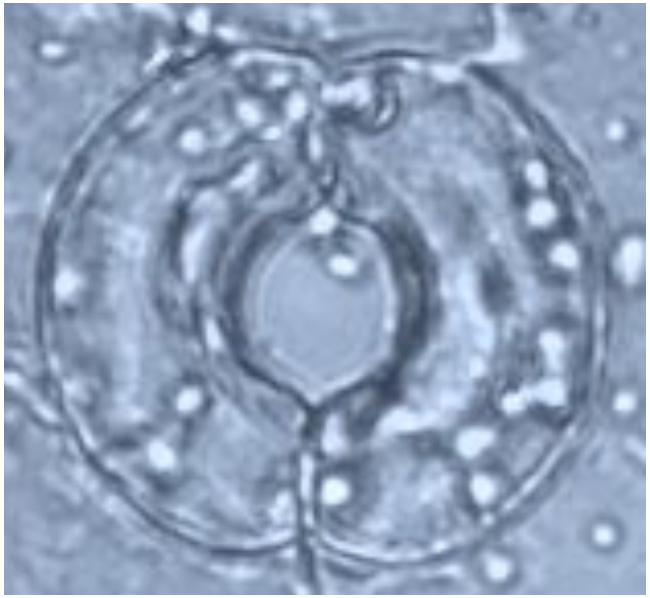
ABA levels rise during drought stress due in part to increased biosynthesis

R.L. Croissant, , Bugwood.org www.forestryimages.orgR.L. Croissant, , Bugwood.org www.forestryimages.org . Zabadel, T. J. (1974) A water potential threshold for the increase of abscisic acid in leaves. Plant Physiol. (1974) 53: 125-127.

ABA regulates stomatal aperture by changing the volume of guard cels



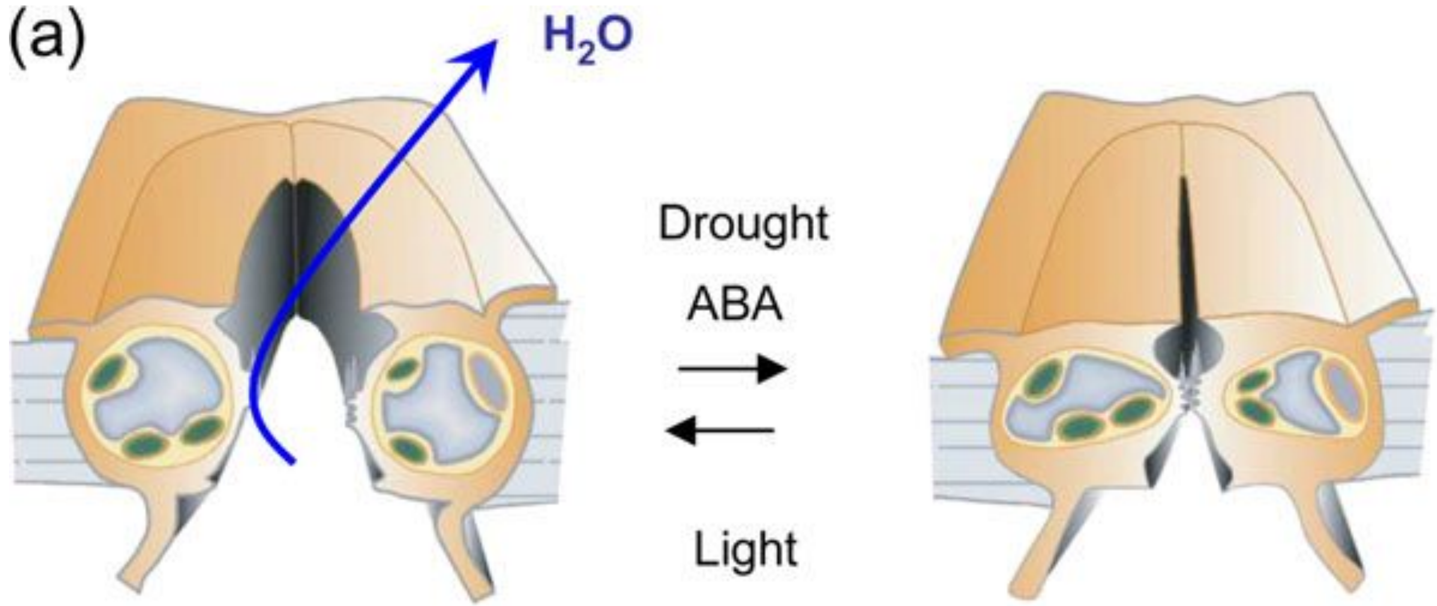
Pairs of guard cells surround the openings of plant pores called stomata.



Guard cells control the opening and closing of stomata to regulate gas exchange: a fine balance is required to allow CO_2 in for photosynthesis and prevent excessive water loss.

Guard cell image © John Adds, obtained through the SAPS Plant Science Image Database.

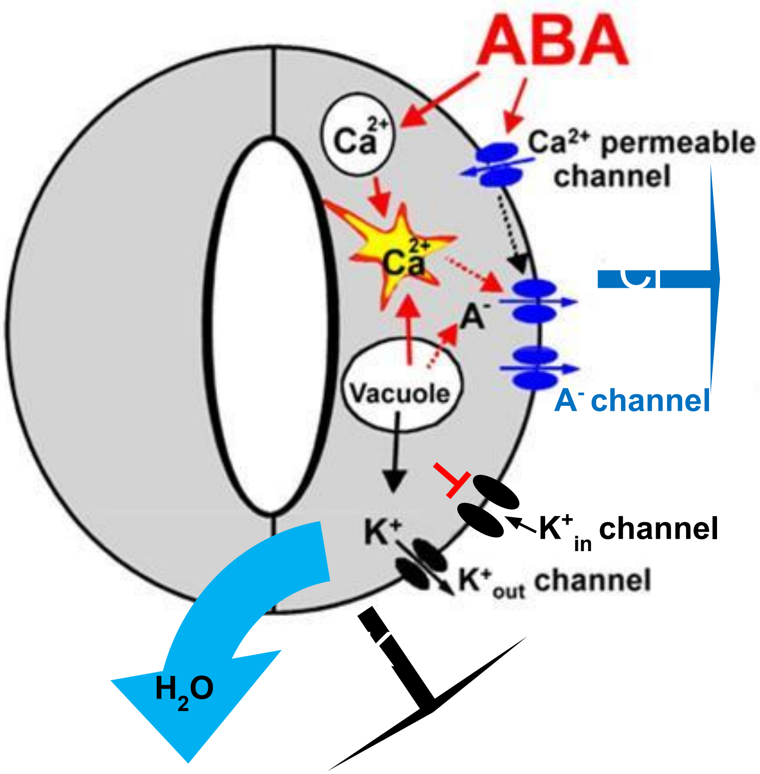
ABA controls stomatal aperture by changing the volume of guard cels



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.

Sirichandra, C., Wasilewska, A., Vlad, F., Valon, C., and Leung, J. (2009)The guard cell as a single-cell model towards understanding drought tolerance and abscisic acid action. Journal of Experimental Botany 2009 60: 1439-1463. © The Author [2009]. Published by Oxford University Press on behalf of the Society for Experimental Biology.

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



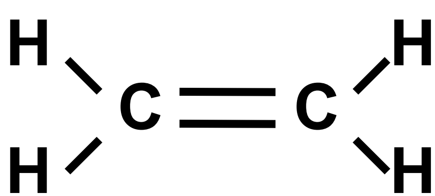
ABA triggers an increase in cytosolic calcium (Ca^{2+}), which activates anion channels (A^-) allowing Cl^- to leave the cell. ABA activates channels that move potassium out of the cell (K^+_{out}) and inhibits channels that move potassium into the cell (K^+_{in}). The net result is a large movement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

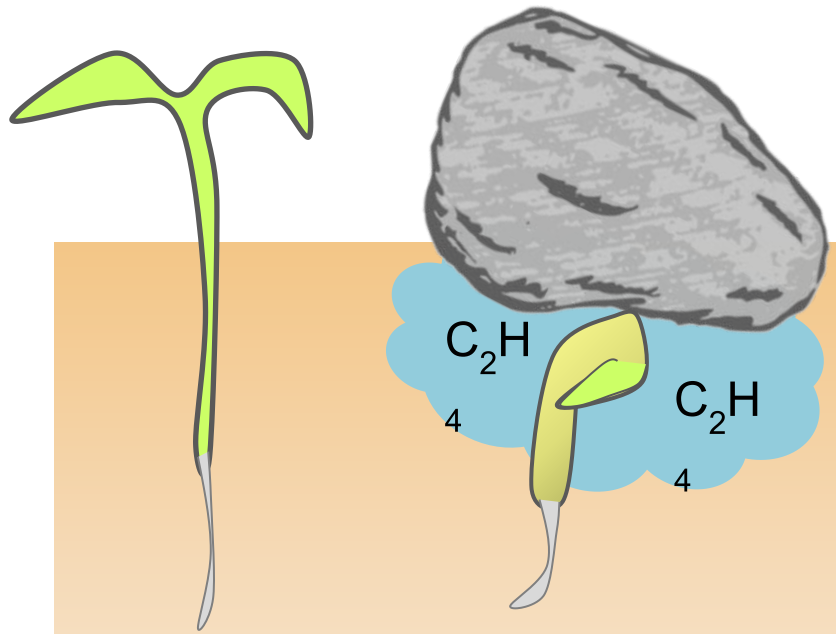
As ions leave the cell, so does water (by osmosis), causing the cells to lose volume and close over the pore.

Adapted from Kwak JM, Mäser P, Schroeder JI (2008) The clickable guard cell, version II: Interactive model of guard cell signal transduction mechanisms and pathways. The Arabidopsis Book, ASPB. doi: 10.1199/tab.0114.

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



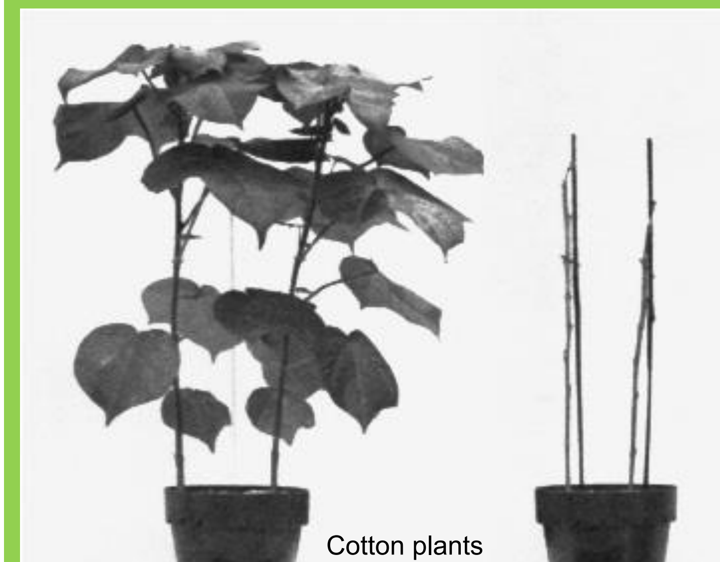


Ethylene induces the triple response:

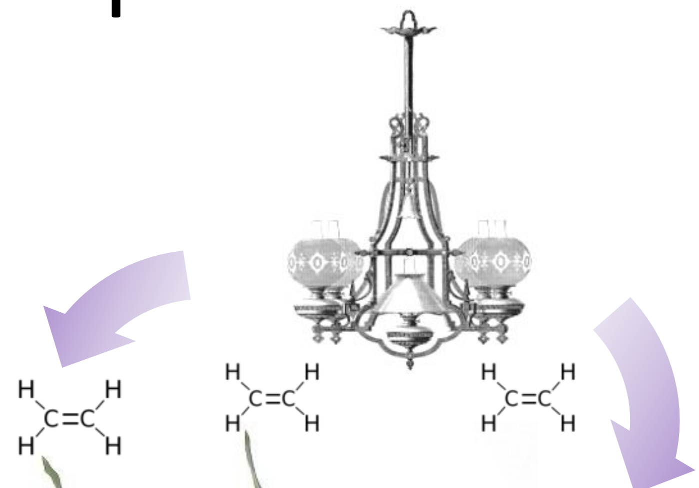
- reduced elongation,
- hypocotyl swelling,
- apical hook exaggeration.

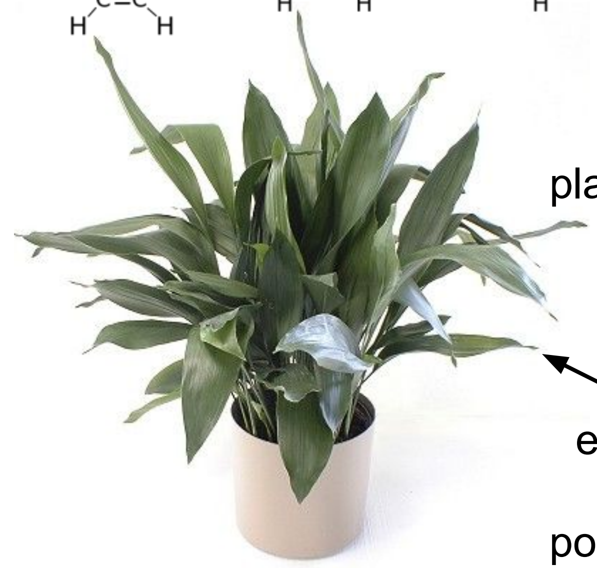
Ethylene promotes senescence of leaves and petals

Air (control)   7 days ethylene



Ethylene promotes leaf and petal senescence.





In gas-lit houses, plants were harmed by the ethylene produced from burning gas. **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

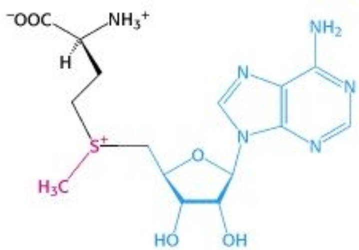
Limit production - high CO_2 or low O_2

Removal from the air -$KMnO_4$ reaction, zeolite absorption

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

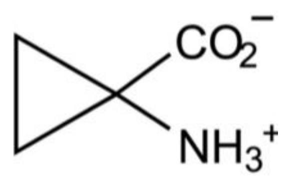
Reprinted from Serek, M., Woltering, E.J., Sisler, E.C., Frello, S., and Sriskandarajah, S. (2006) Controlling ethylene responses in flowers at the receptor level. Biotech. Adv. 24: 368-381 with permission from Elsevier.

Molecular genetic approaches can limit ethylene synthesis



S-adenosyl methionine

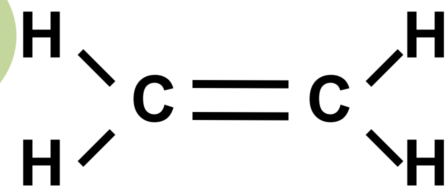
ACC synthase →



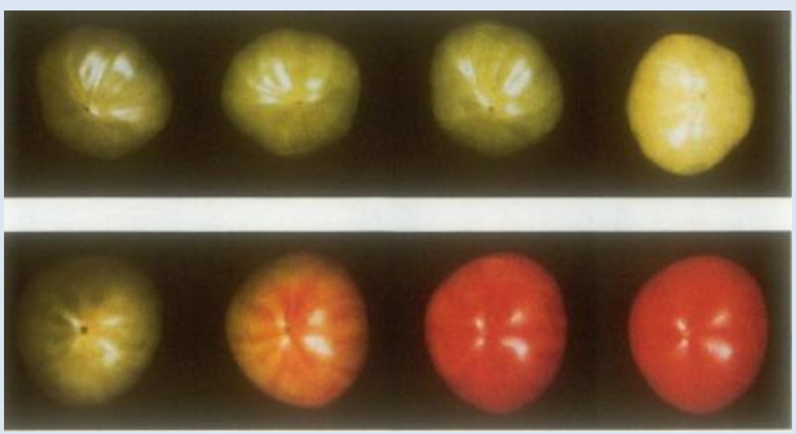
ACC

(1-aminocyclopropane-1-car boxylic acid)

ACC oxidase →



Ethylene



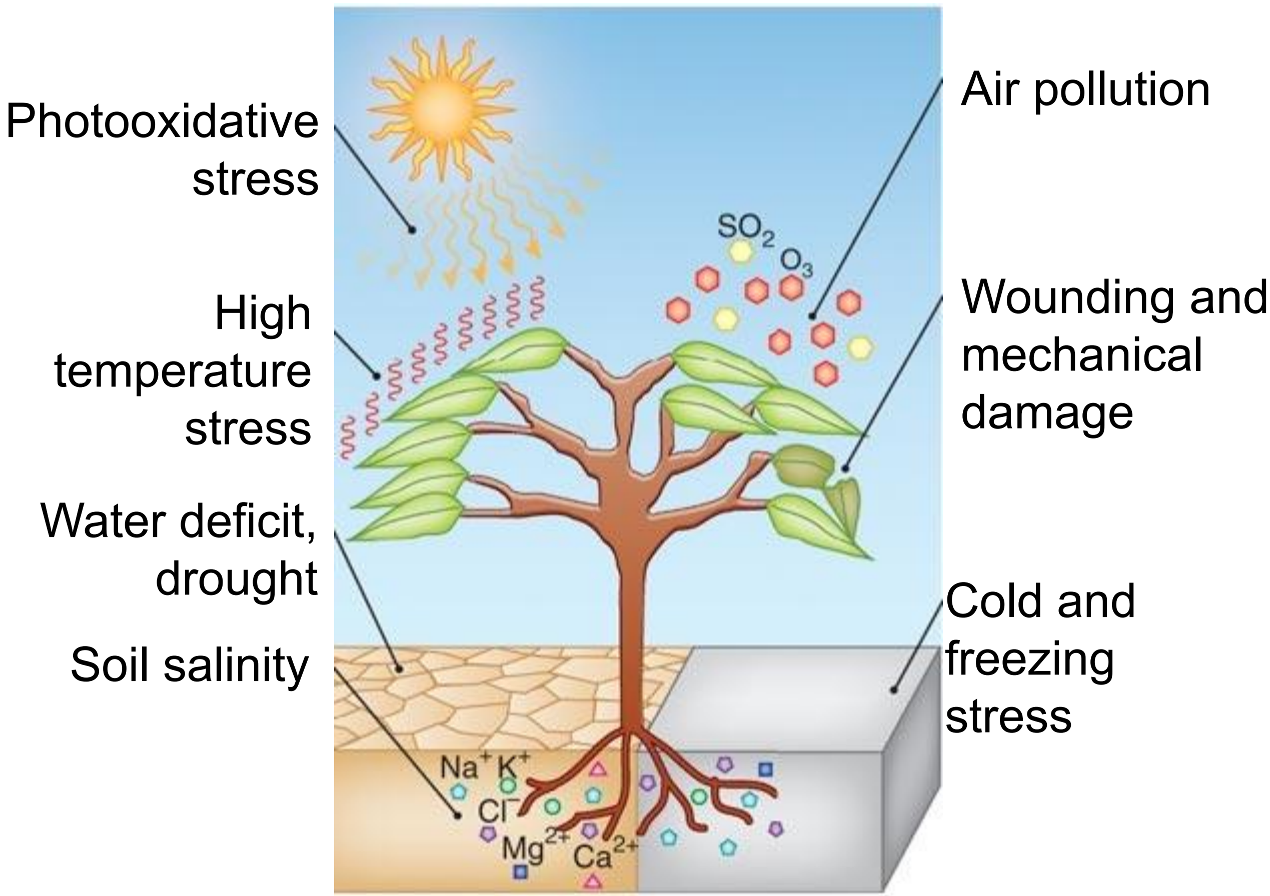
Antisense ACC synthase

Control

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

Theologis, A., Zarembinski, T.I., Oeller, P.W., Liang, X., and Abel, S. (1992) Modification of fruit ripening by suppressing gene expression. Plant Phys. 100: 549-551.

Hormonal responses to abiotic stress

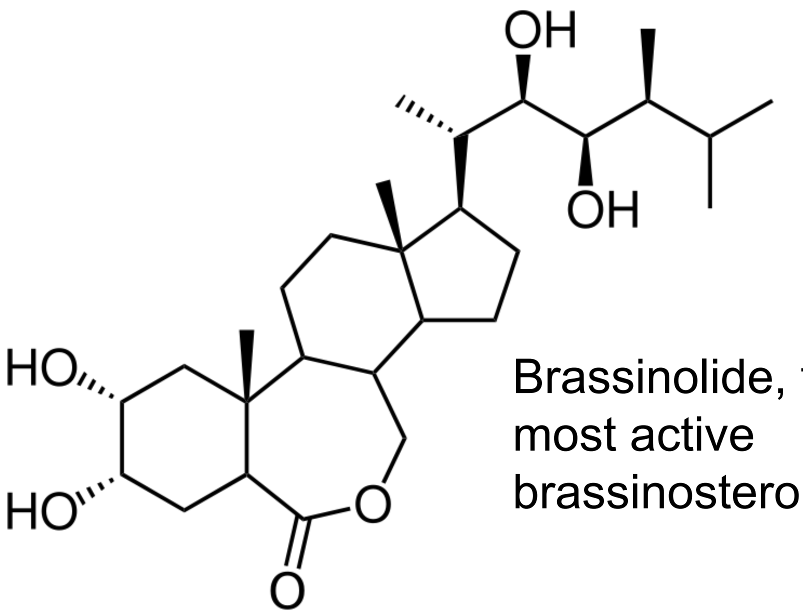


Plants' lives are very stressful.....

ABA and ethylene help plants respond to stress.

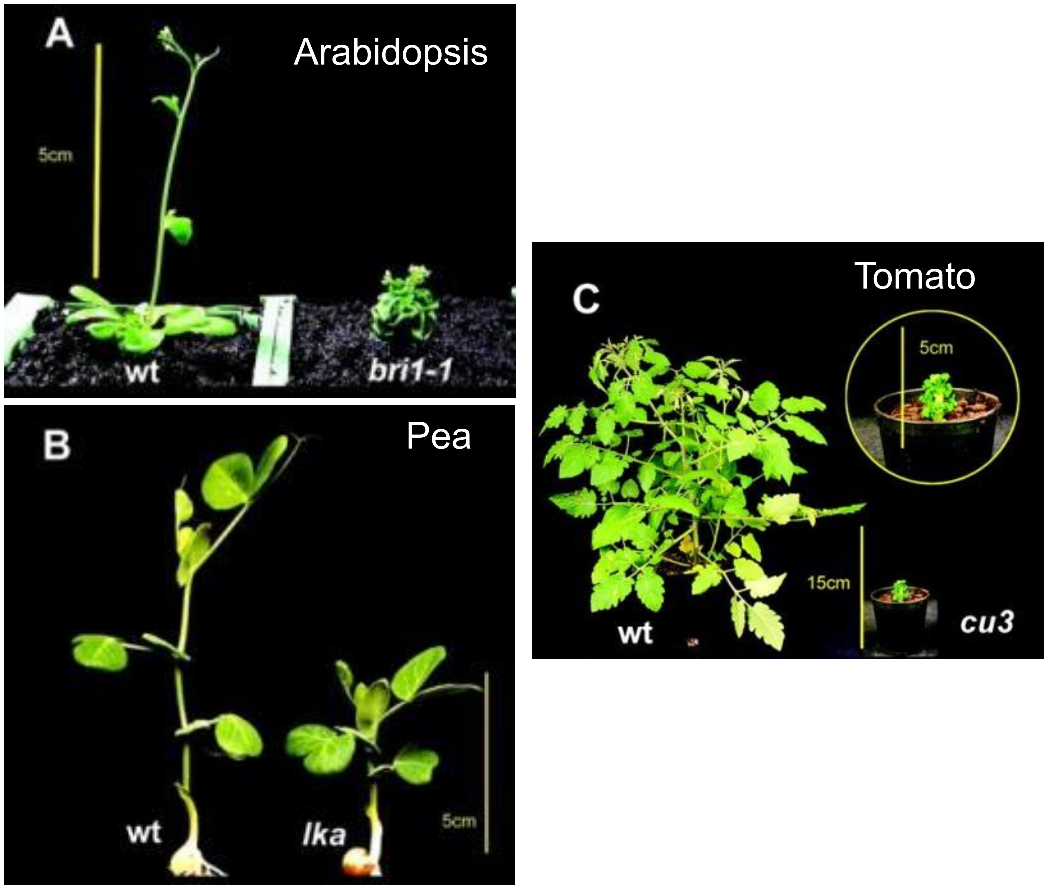
Brassinosteroids

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

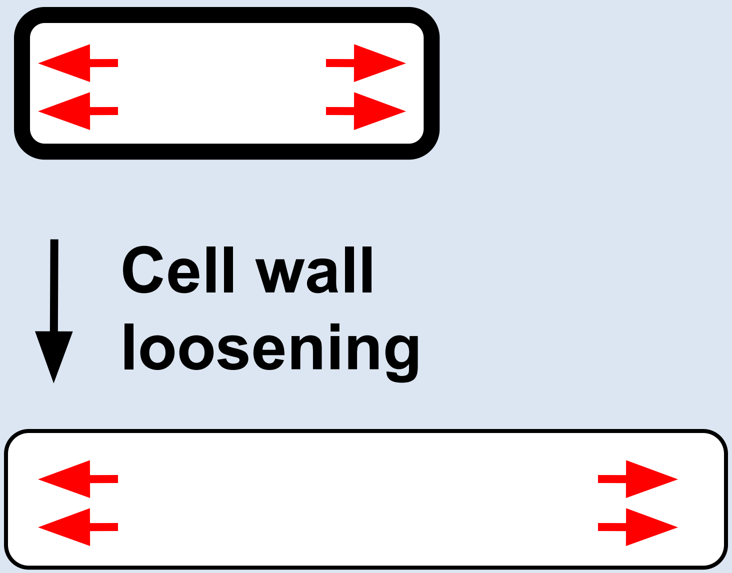


Brassinolide, the most active brassinosteroid

Brassinosteroid (BR) mutants are dwarfed



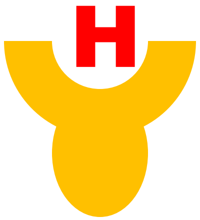
BRs promote cell elongation in part by loosening cell walls



Lowered resistance to internal turgor pressure; cell expansion

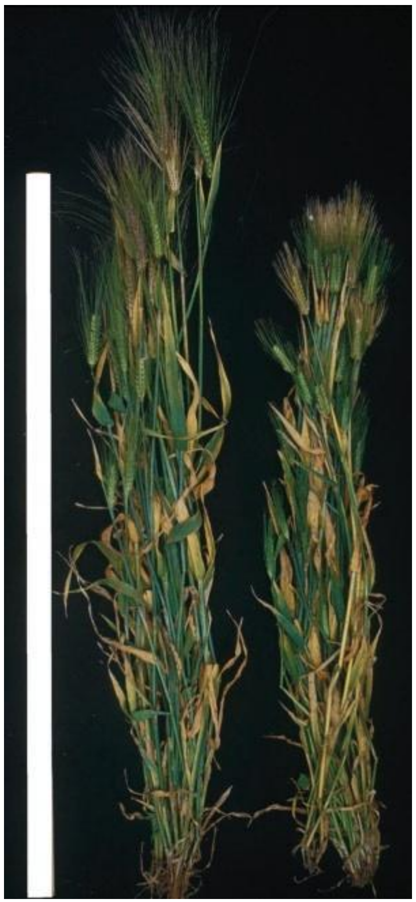
Bishop, G. J., and Koncz, C. Brassinosteroids and plant steroid hormone signaling. (2002) Plant Cell14: S97-S110.

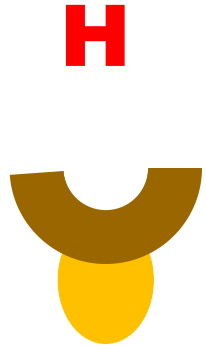
Reducing BR signaling produces dwarf barley



Wild-type

Cell elongation





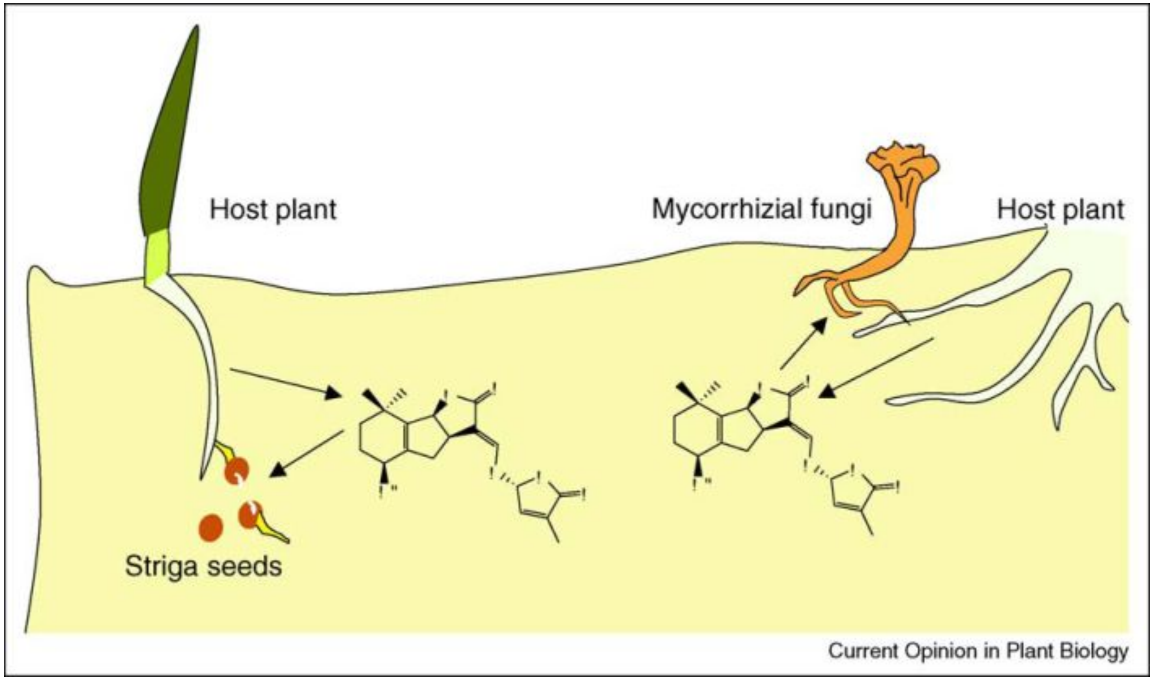
uzu

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.

Chono, M., et al., (2003) A semidwarf phenotype of barley uzu results from a nucleotide substitution in the gene encoding a putative brassinosteroid receptor Plant Physiology 133:1209-1219.

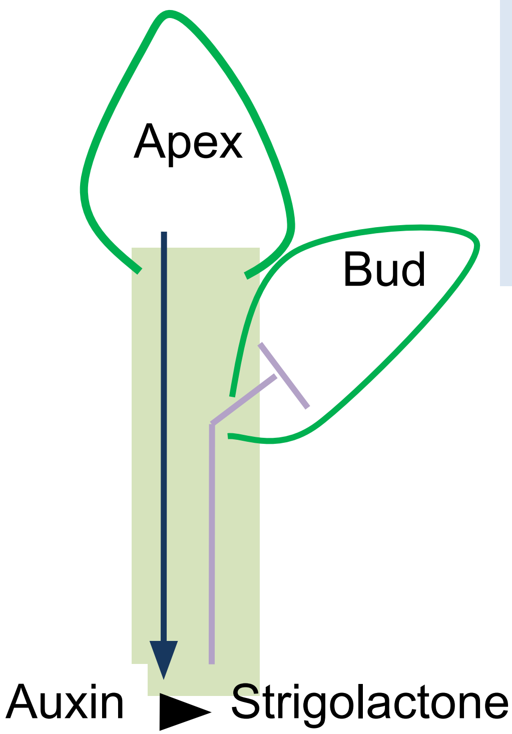
Strigolactones



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 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.

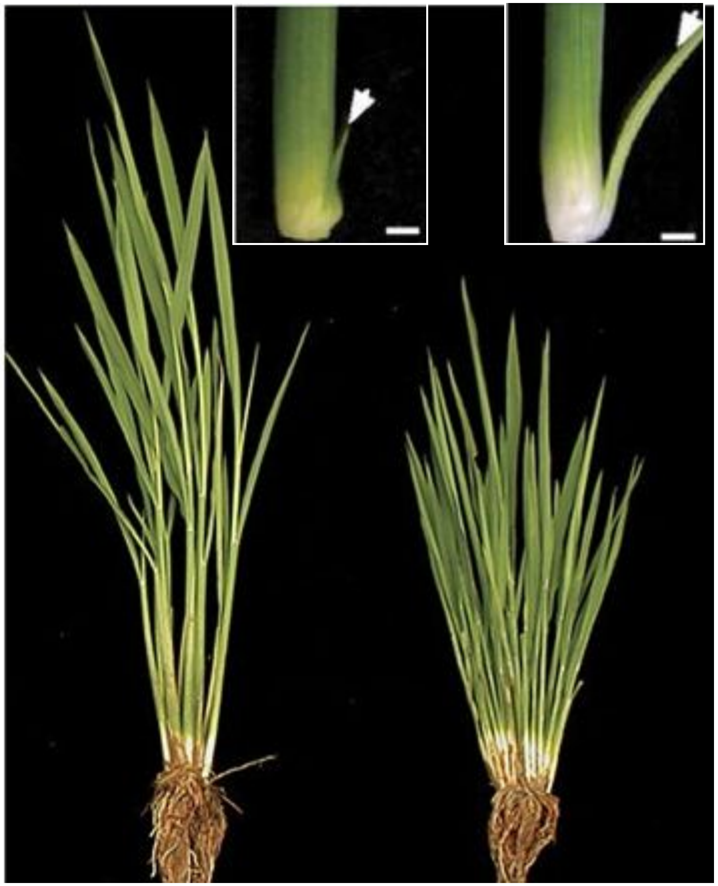
Strigolactones inhibit branch outgrowth



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.

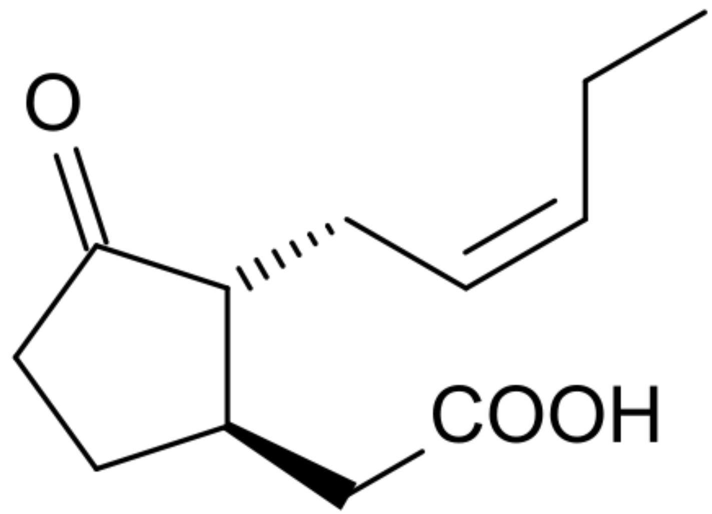
WT Mutant



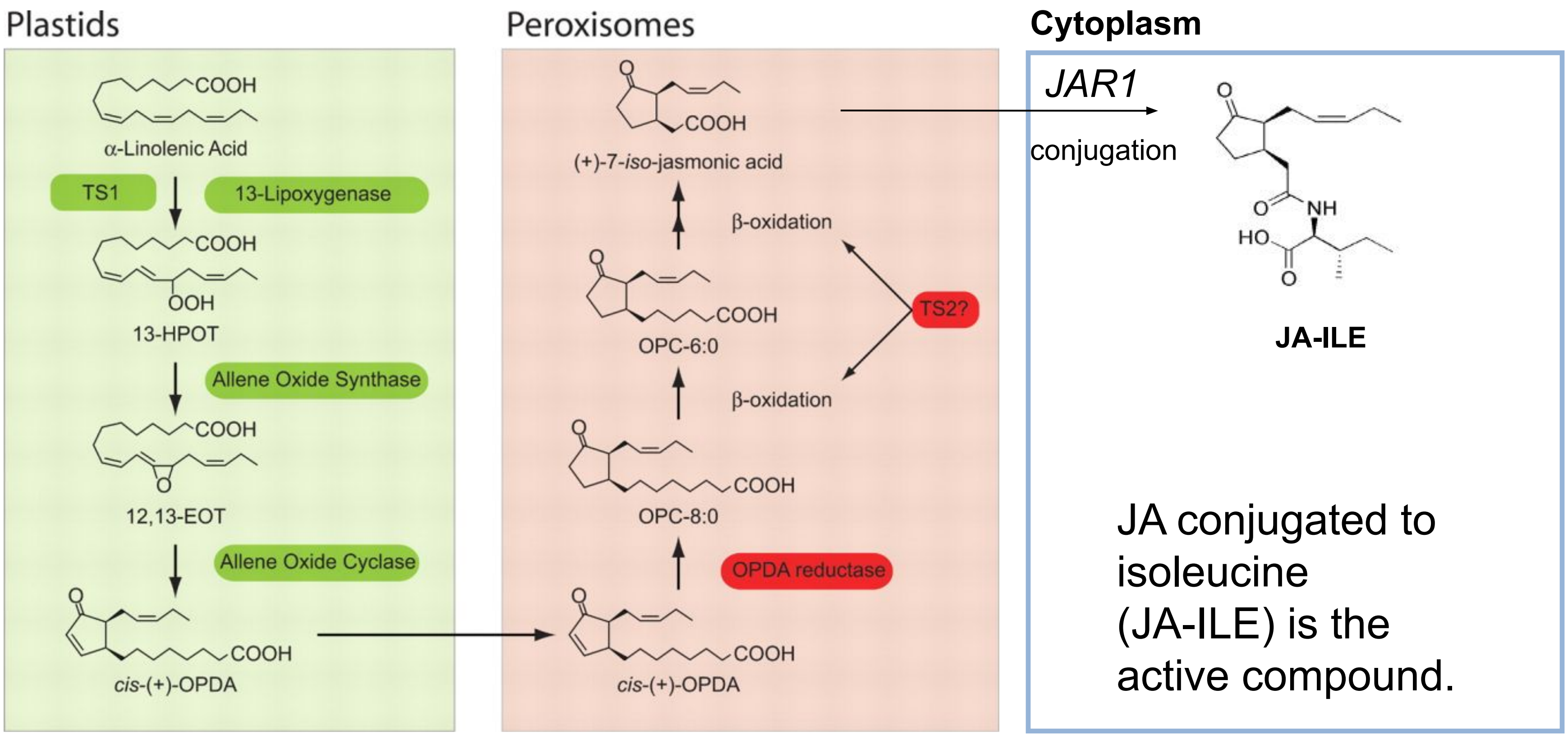
Lin, H., et al. (2009) DWARF27, an iron-containing protein required for the biosynthesis of strigolactones, regulates rice tiller bud outgrowth. Plant Cell 21: 1512-1525.

Jasmonates

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

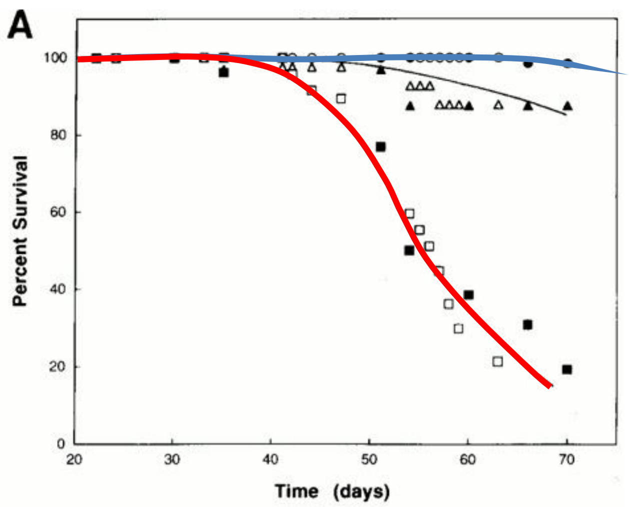


JA biosynthesis



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

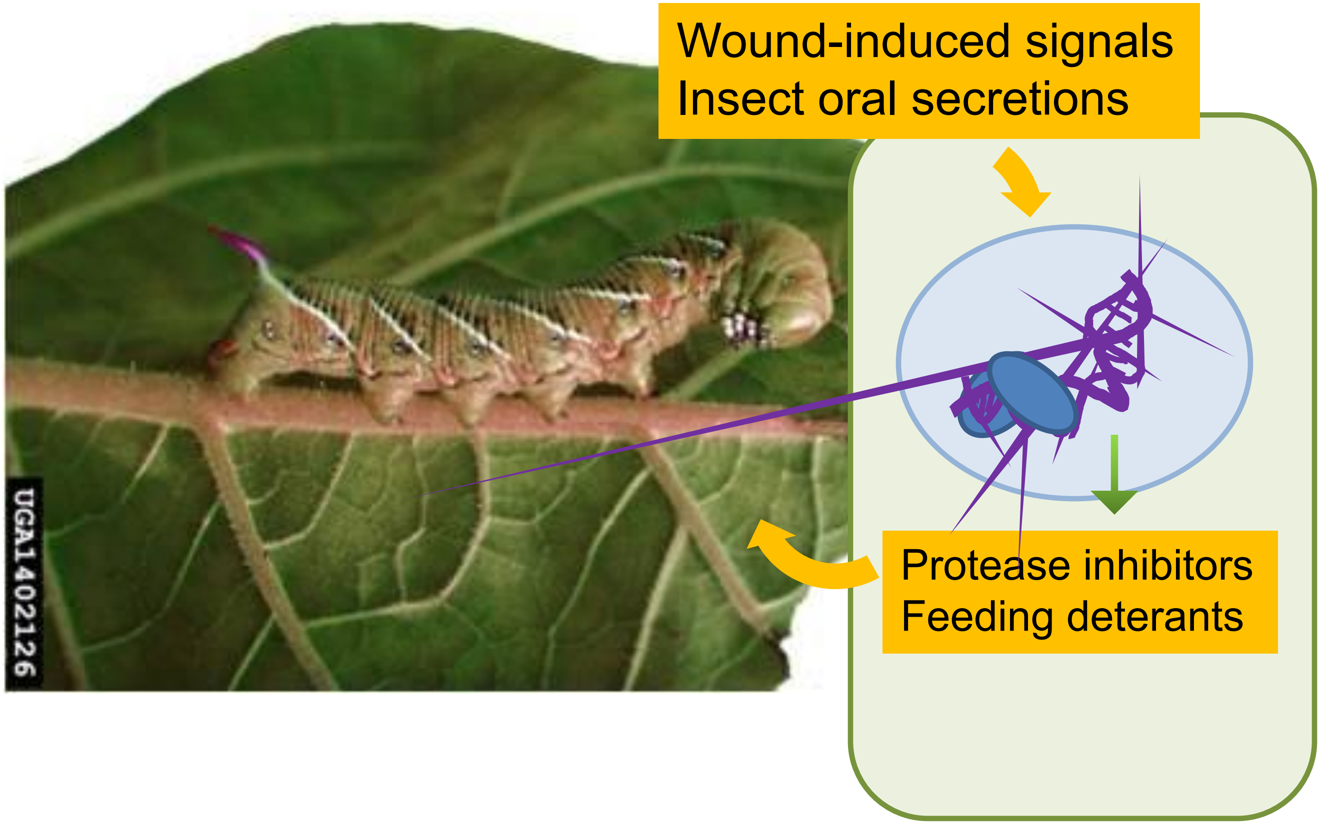


When exposed to hungry fly larvae, plants unable to produce JA have low rates of survival.

WT Mutant without JA

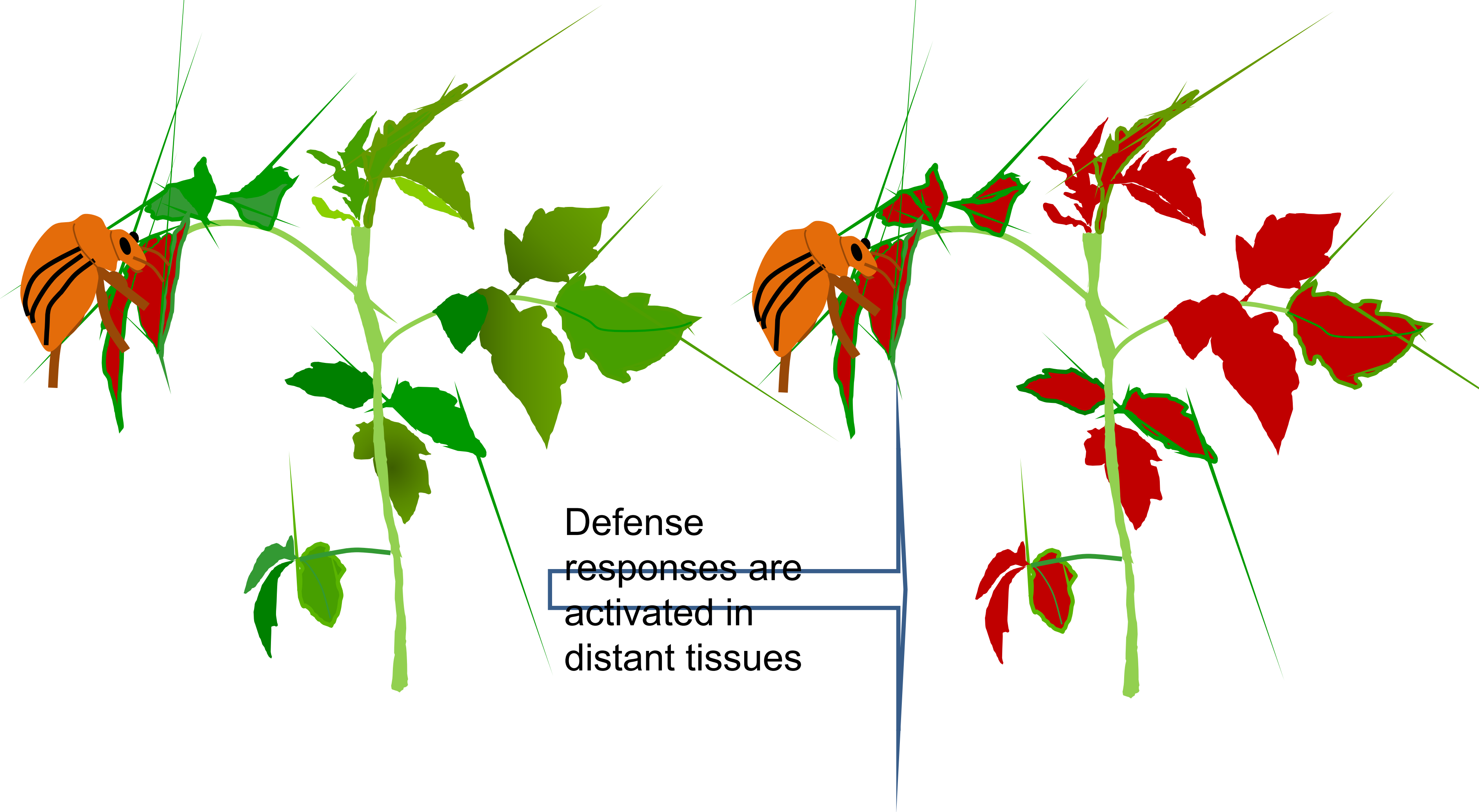
McConn, M., et al. (1997) Jasmonate is essential for insect defense in *Arabidopsis*. Proc. Natl. Acad. Sci. USA 94: 5473-5477.

Jasmonates induce the expression of anti-herbivory chemicals

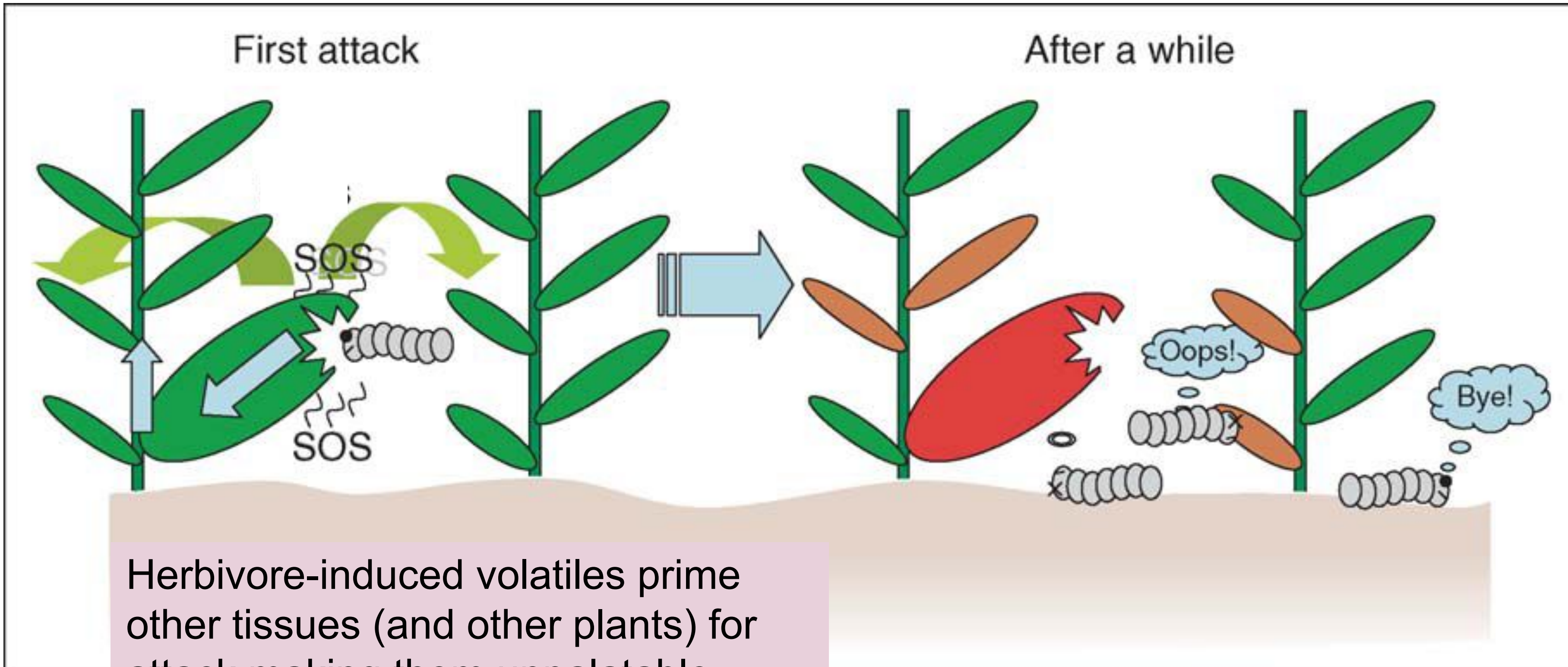


R.J. Reynolds Tobacco Company Slide SetR.J. Reynolds Tobacco Company Slide Set and R.J. Reynolds Tobacco Company, Bugworld.org

Jasmonates contribute to systemic defense responses



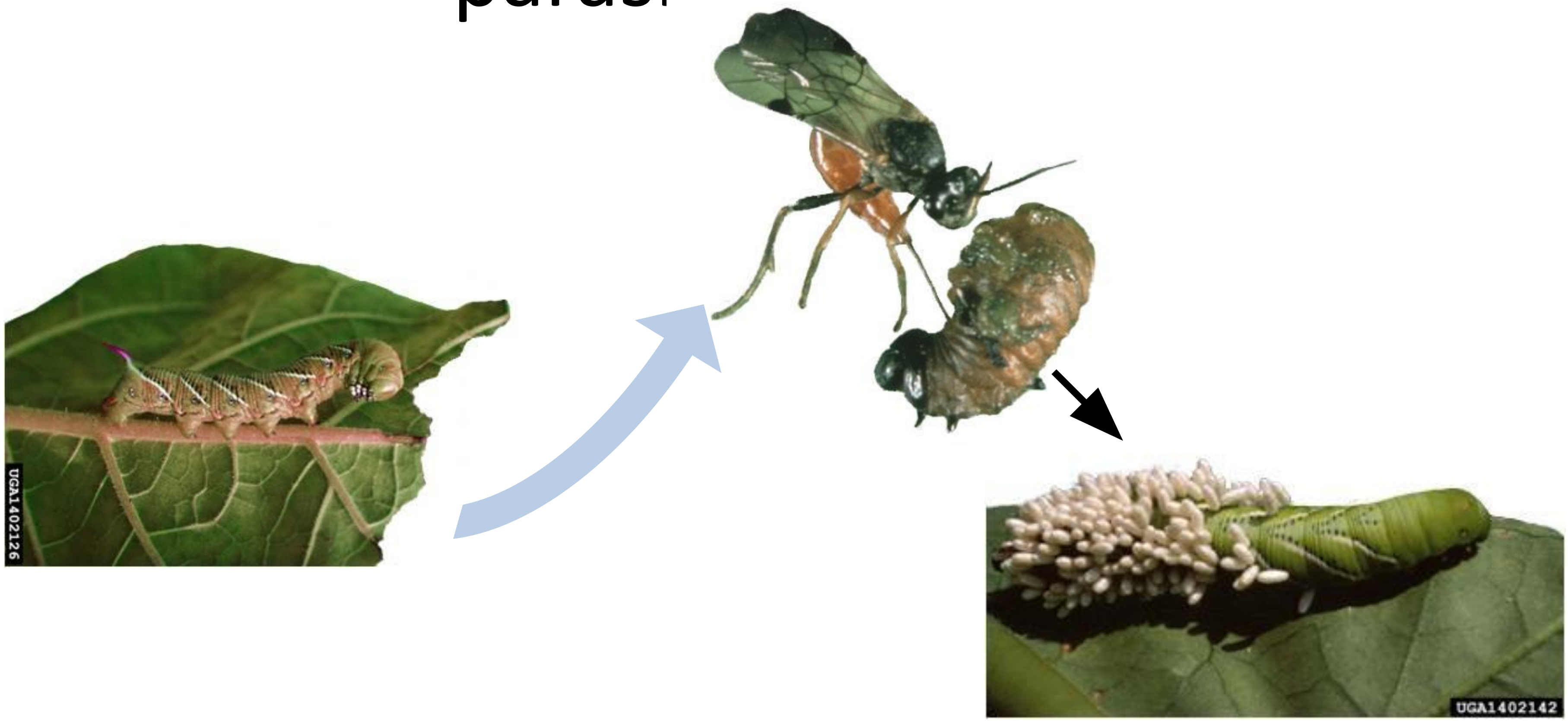
Jasomonates stimulate production of volatile signaling compounds



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

Reprinted from Matsui, K. (2006) Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. Curr. Opin. Plant Biol. 9: 274-280, with permission from Elsevier.

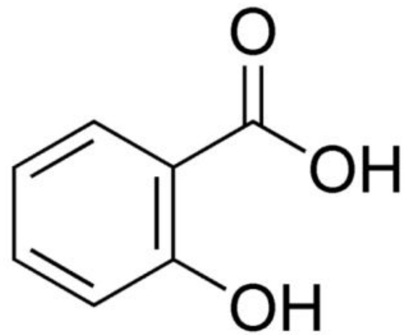
Herbivore-induced volatiles are recognized by carnivorous and parasitoid insects



[Tim Haye](#)Tim Haye, Universität Kiel, Germany Bugwood.org; [R.J. Reynolds Tobacco Company Slide Set](#)Tim Haye, Universität Kiel, Germany Bugwood.org; R.J. Reynolds Tobacco Company Slide Set and [R.J. Reynolds Tobacco Company](#), Bugworld.org

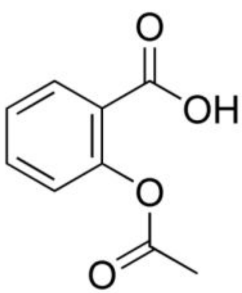
Salicylic Acid – plant hormone and painkiller

- 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.



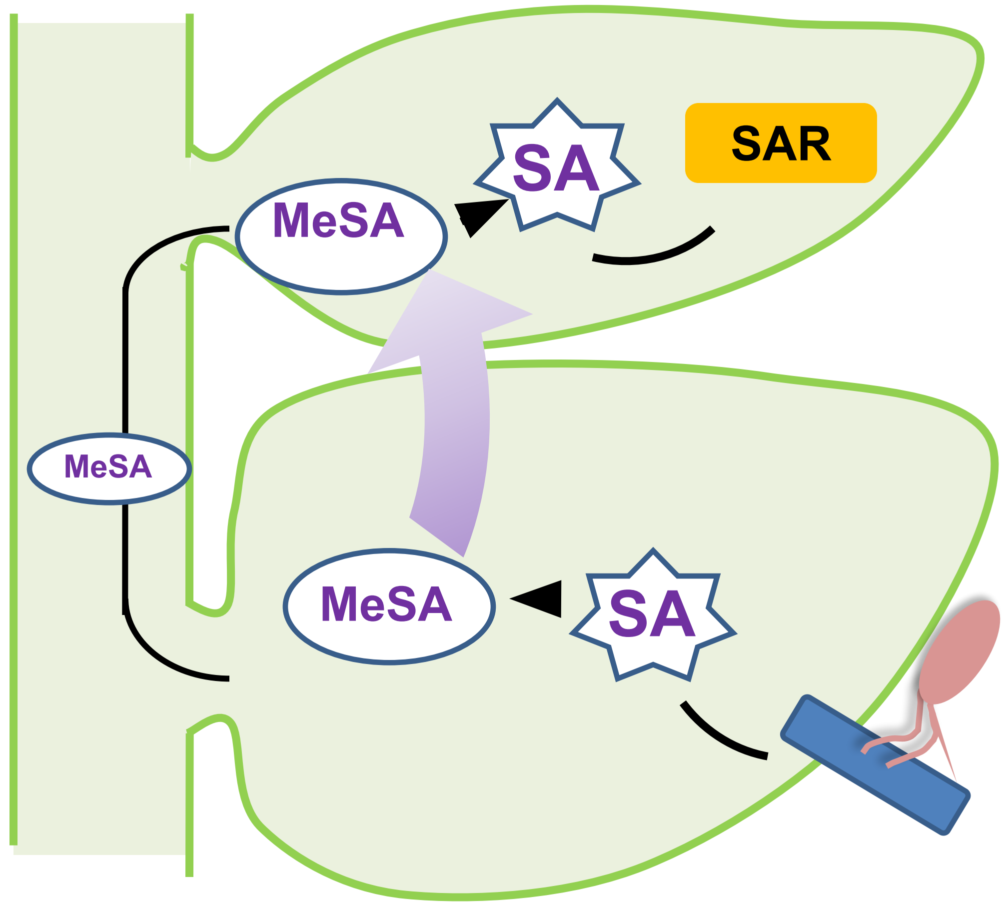
Acetylsalicylic Acid - aspirin

Photo credit: [Geaugagrrl]

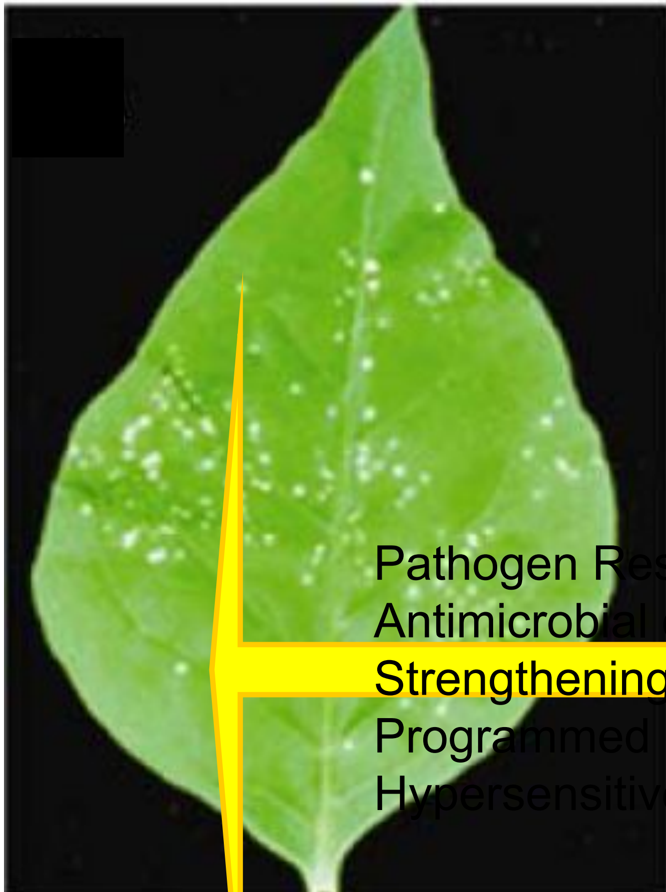
Salicylates contribute to systemic acquired resistance

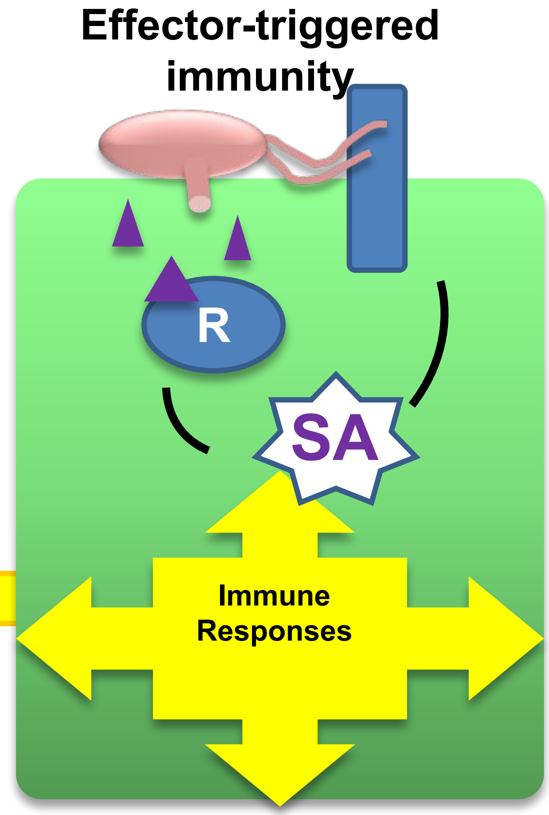
SA is necessary in systemic tissue for SAR, but the nature of the mobile signal(s) is still up in the air

It is likely that multiple signals contribute to SAR



The hypersensitive response involves cell death

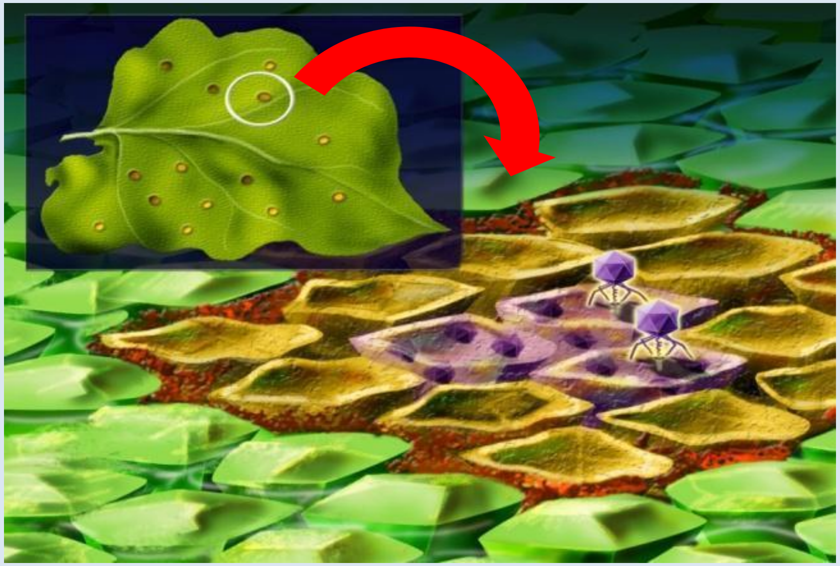




Pathogen Response (PR) genes
Antimicrobial compounds
Strengthening of plant cell walls
Programmed cell death
Hypersensitive response (HR)

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

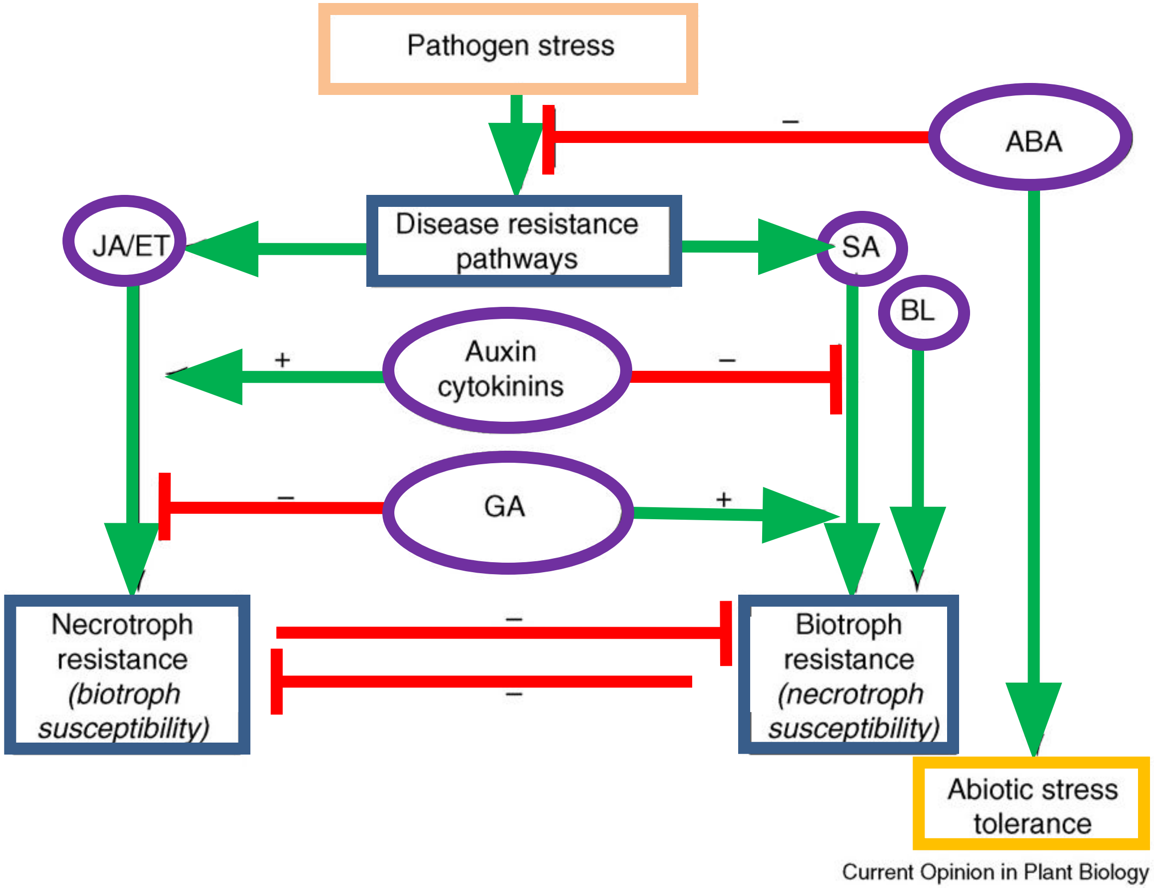


The HR kills the infected cells and cells surrounding them and prevents the pathogen from spreading.

Without a hypersensitive response, the pathogen can multiply.

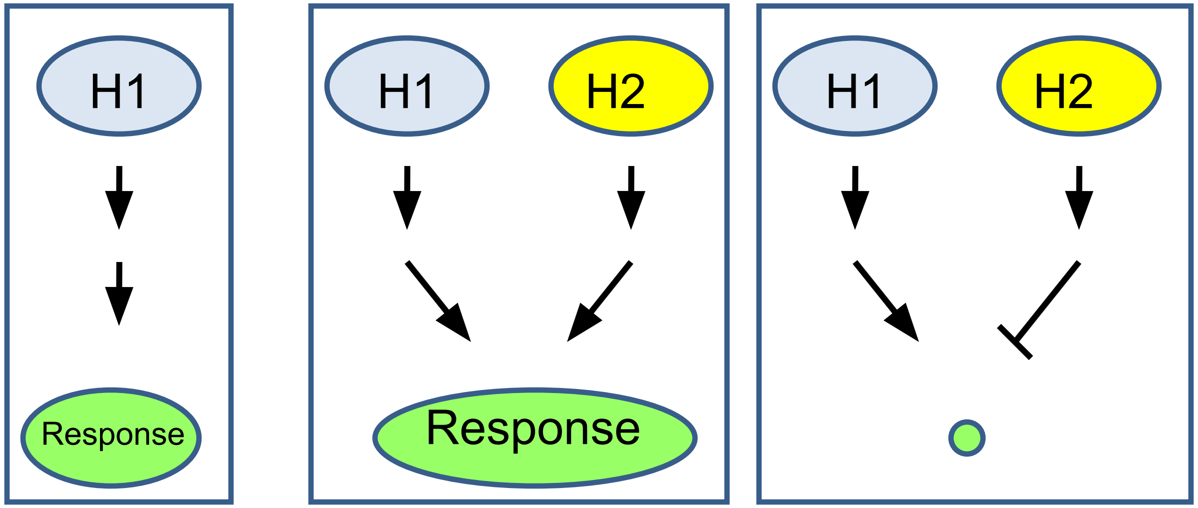
Drawing credit Credit: Nicolle Rager FullerDrawing credit Credit: Nicolle Rager Fuller, National Science Foundation; Photo reprinted by permission of Macmillan Publishers Ltd. Pruitt, R.E., Bowman, J.L., and Grossniklaus, U. (2003) Plant genetics: a decade of integration. Nat. Genet. 33: 294 – 304.

Other hormones affect defense response signaling



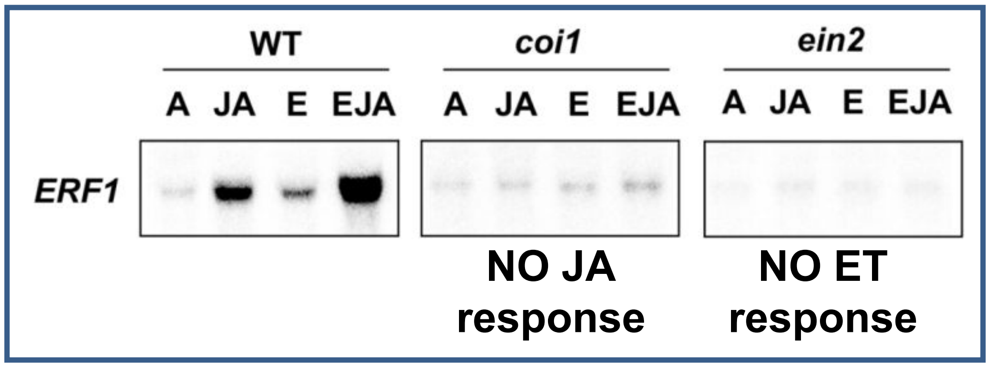
As part of their immune responses, plants modulate synthesis and response to other hormones. Some pathogens exploit the connections between growth hormones and pathogen-response hormones to their own advantage, by producing "phytohormones" or interfering with hormone signaling.

Crosstalk between hormone signaling pathways

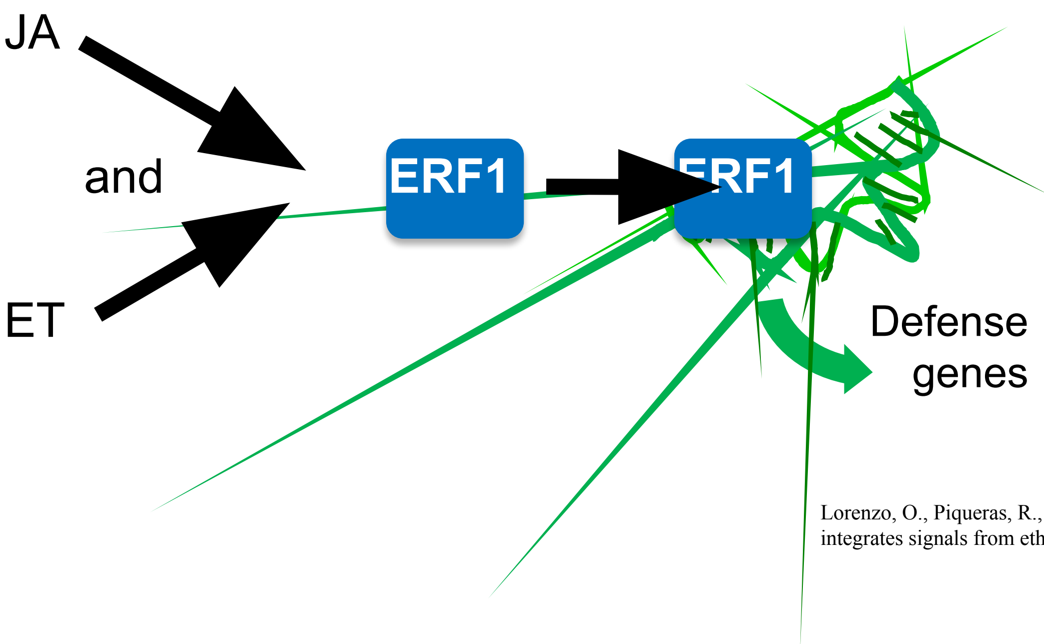


Crosstalk (or cross-regulation) occurs when two pathways are not independent. It can be positive and additive or synergistic, or negative.

Synergistic requirement for JA and ET signaling in defense response



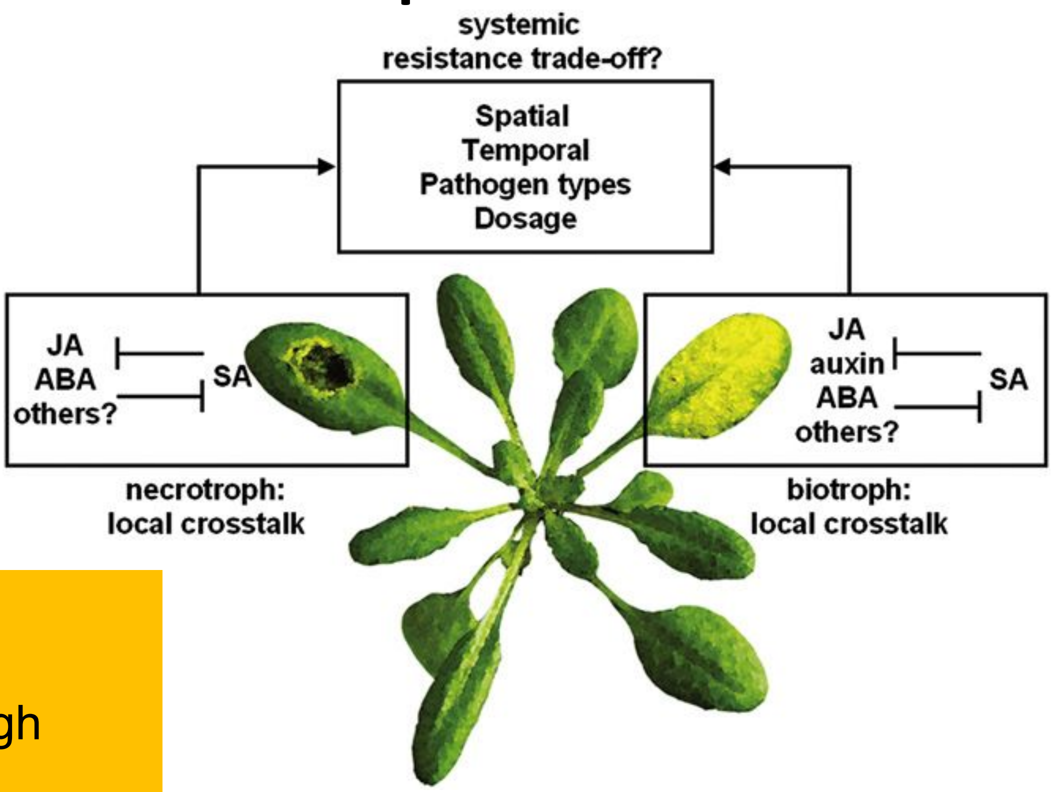
JA and ET signaling are both required for high-level expression of ERF1, a TF that induces defense gene expression



Lorenzo, O., Piqueras, R., Sánchez-Serrano, J.J., and Solano, R. (2003) ETHYLENE RESPONSE FACTOR1 integrates signals from ethylene and jasmonate pathways in plant defense. Plant Cell 15: 165-178.

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 Spoel, S.H., and Dong, X. (2008) Making sense of hormone crosstalk during plant immune responses. Cell Host Microbe 3: 348-351 with permission from Elsevier.