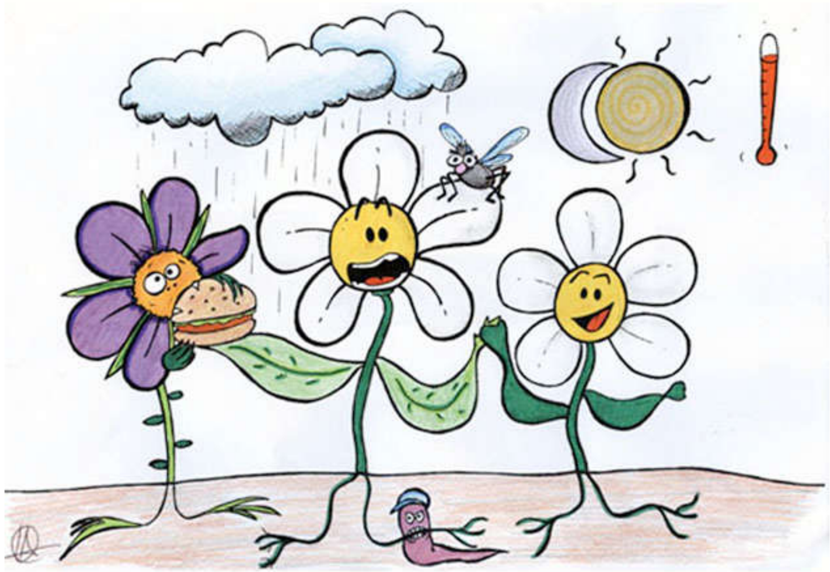
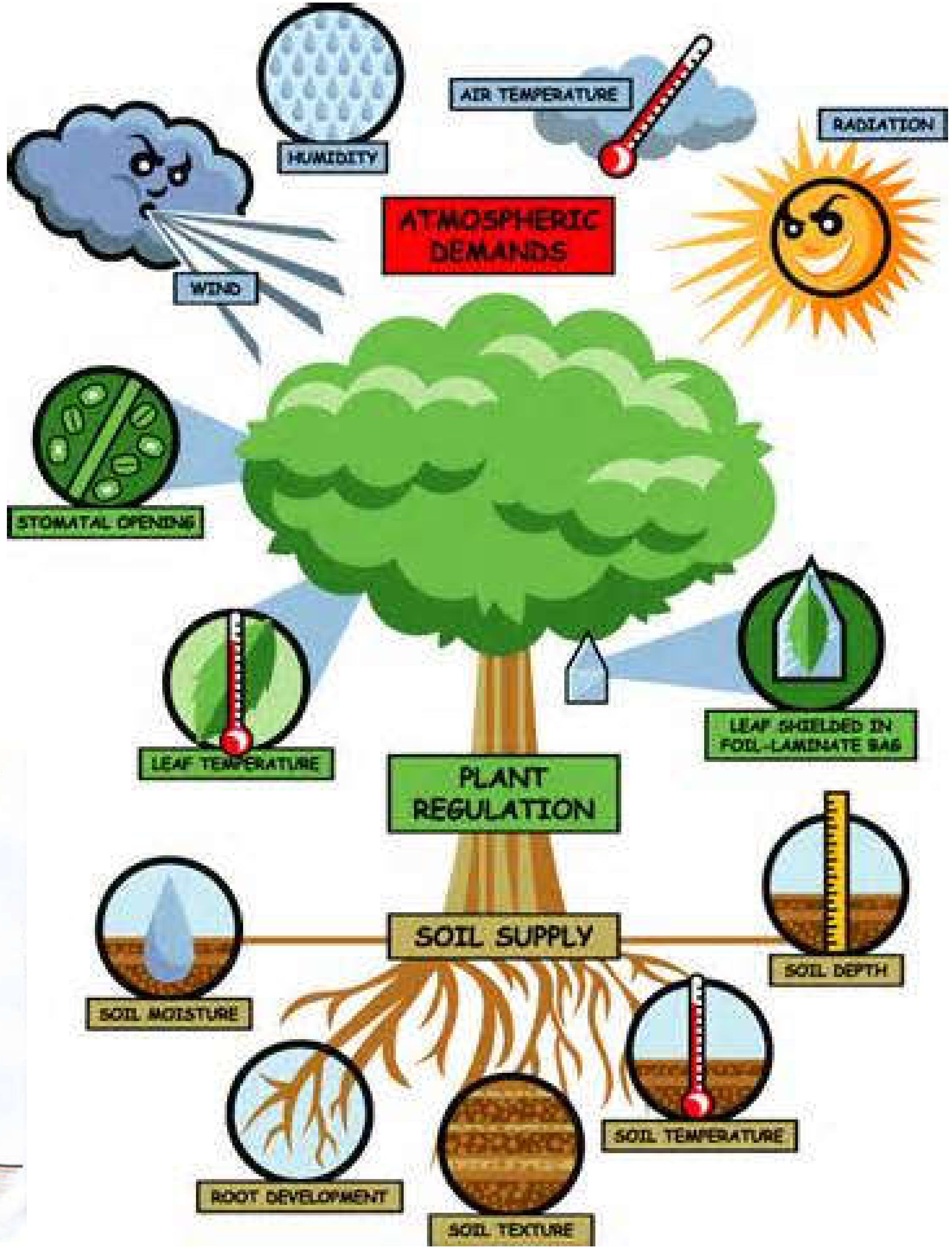
Chapter 45

Plant Responses to the Environment





Chapter 45 At a Glance

- 45.1 What Are Some Major Plant Hormones?
- 45.2 How Do Hormones Regulate Plant Life Cycles?
- 45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

45.1 What Are Some Major Plant Hormones?

Frits Went, 1903-1990

"........characterized by the property of serving as **chemical messengers**, by which the activity of certain organs is coordinated with that of others".

-*Frits Went and Kenneth Thimann, 1937*

Kenneth Thimann, 1904-1997

Phytohormones:

- signal molecules, chemicals
- a little amount of hormone is required
- act locally or in a long distance manner (**2 hints**)
- regulate cellular processes and plant development etc.

45.1 What Are Some Major Plant Hormones?

- Classical phytohormones

1. Auxins (植物生长激素)
2. Gibberellins (赤霉素)
3. Cytokinins (细胞分裂素)
4. Ethylene (乙烯)
5. Abscisic acid (脱落酸)
6. Florigen (成花素)

Phytohormones – old timers and newcomers

Some comes in groups!

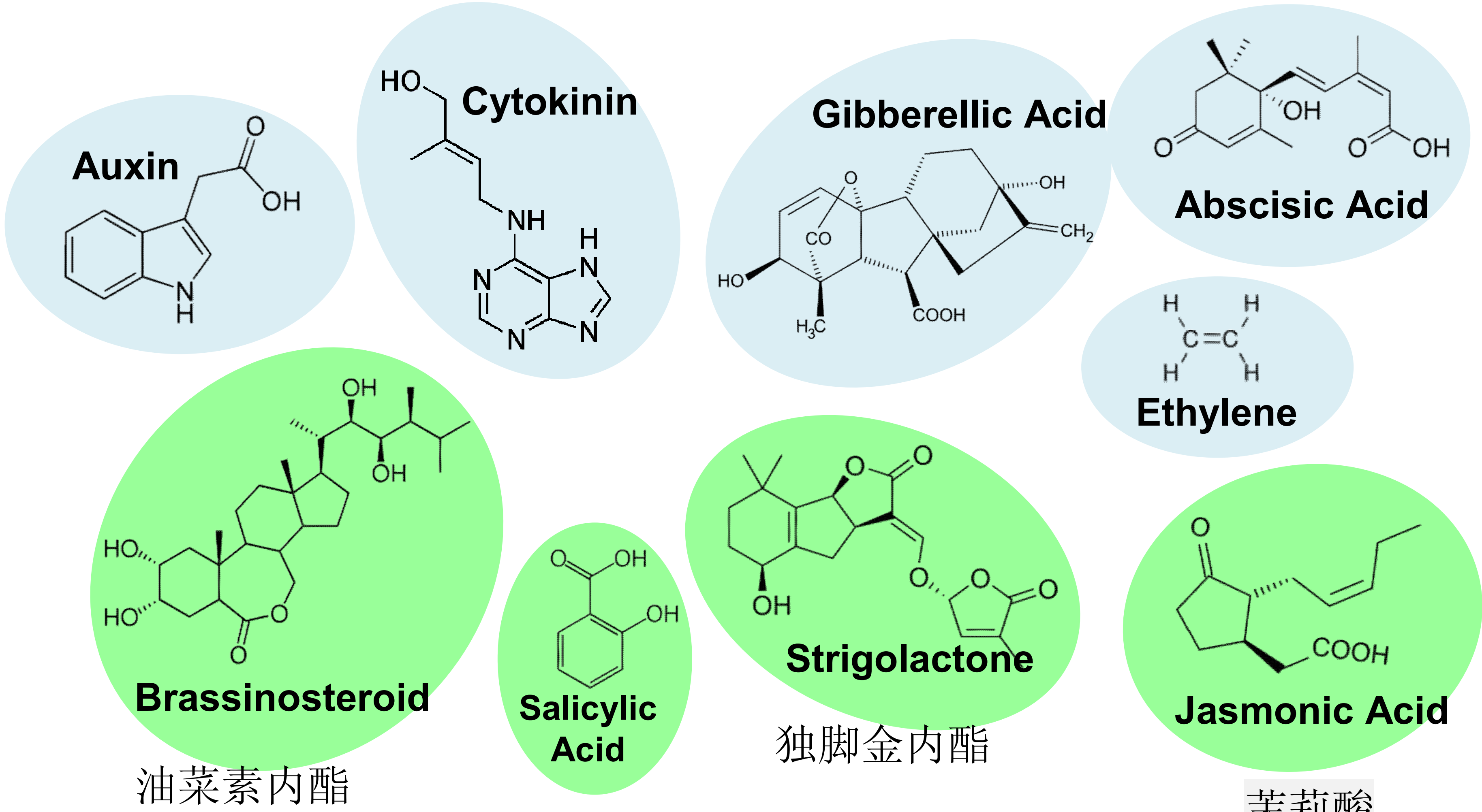


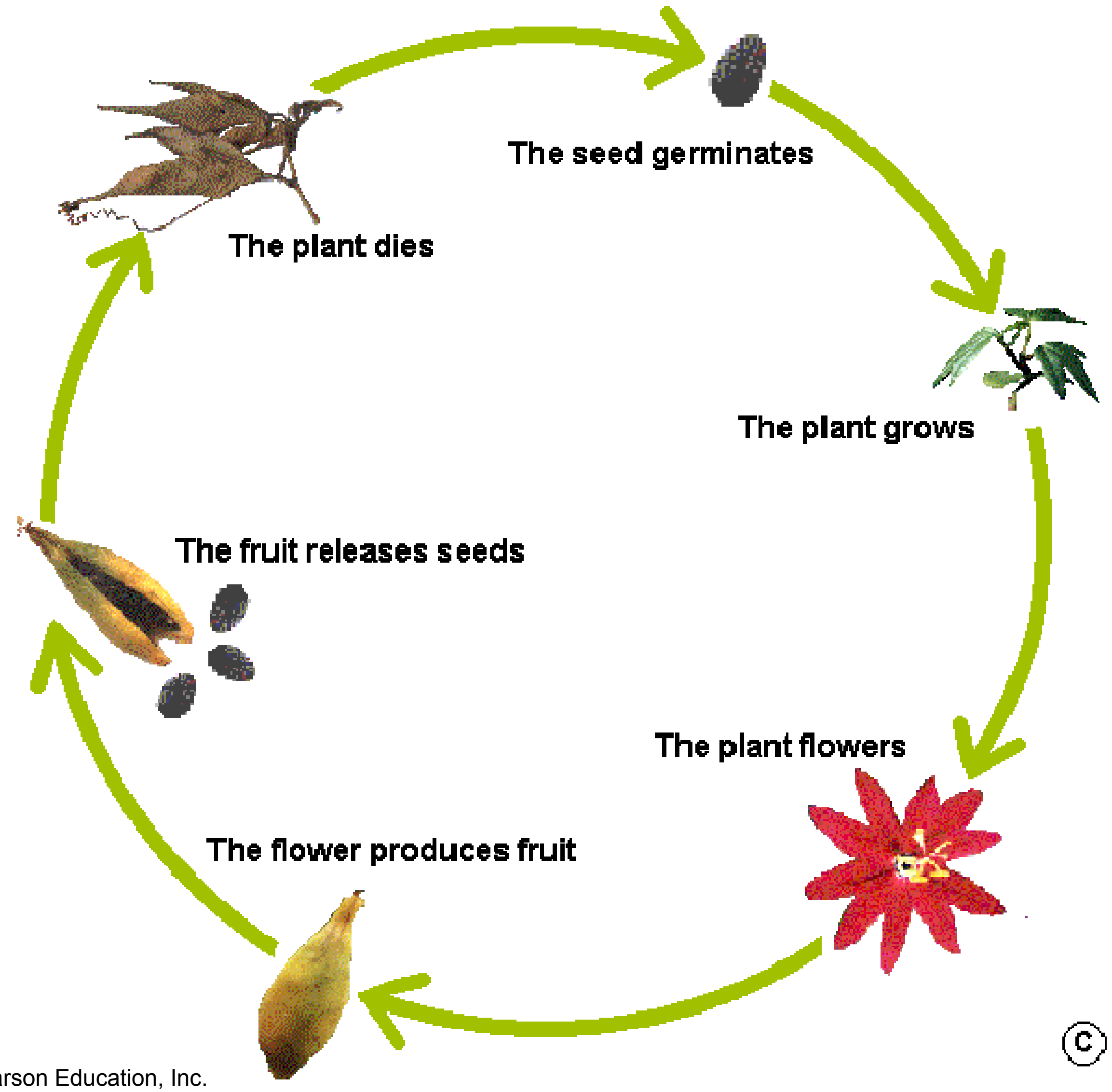
Table 45-1 Some Major Plant Hormones and Their Functions

TABLE 45-1 Some Major Plant Hormones and Their Functions

Hormone	Some Major Effects	Major Sites of Synthesis
Auxins	Promote cell elongation in shoots Inhibit growth of lateral buds (apical dominance) Promote root branching Control phototropism and gravitropism in shoots and roots Stimulate vascular tissue development Stimulate fruit development Delay senescence of leaves and fruit	Shoot apical meristem
Gibberellins	Stimulate stem elongation by promoting cell division and cell elongation Stimulate fruit development, and seed germination	Shoot apical meristem Plant embryos Young leaves
Cytokinins	Stimulate cell division throughout the plant Stimulate lateral bud sprouting Inhibit formation of branch roots Delay senescence of leaves and flowers	Root apical meristem
Ethylene	Promotes growth of shorter, thicker stems in response to mechanical disturbance Stimulates ripening in some fruits Promotes senescence in leaves Promotes leaf and fruit drop	Throughout the plant, particularly during stress and aging
Abscisic acid	Causes stomata to close Inhibits stem growth and stimulates root growth in response to drought Maintains dormancy in buds and seeds	Throughout the plant
Florigens	Stimulate flowering in response to day length	Mature leaves

Growth promoting: Auxin, Gibberellins (GA), Brassinosteroids (BR), cytokinins (CK)
Stress-related hormones: Salicylic acid (SA), Abscisic acid (ABA), Ethylene (ET), Jasmonic acid (JA)

45.2 How Do Hormones Regulate Plant Life Cycles?



45.2 How Do Hormones Regulate Plant Life Cycles?

- Each plant life cycle begins with a seed
  - Two hormones play major roles in seed germination

    1. Abscisic acid

       maintains seed dormancy

    2. Gibberellin

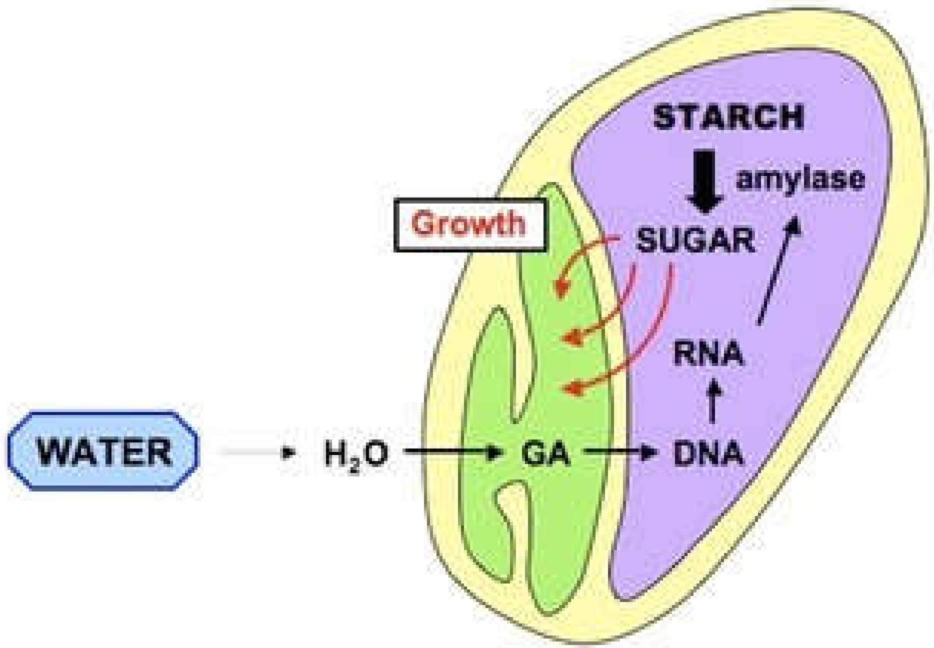
       stimulates seed germination

45.2 How Do Hormones Regulate Plant Life Cycles?

- Abscisic acid **maintains seed dormancy**
  - prolonged cold reduces the amount of abscisic acid within the seed
  - It requires a hard rain to wash the hormone away

45.2 How Do Hormones Regulate Plant Life Cycles?

- Gibberellin **stimulates** seed germination
  - Gibberellin **activates** genes that code for **enzymes** that break down the stored starch and reserves of the endosperm



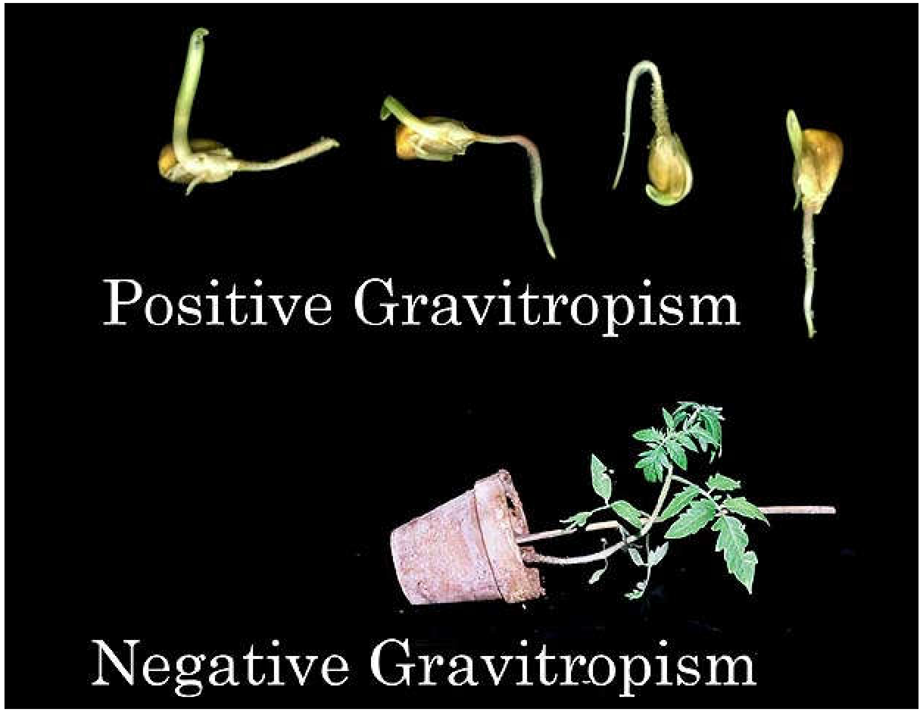
http://vce.bioninja.com.au/

45.2 How Do Hormones Regulate Plant Life Cycles?

- Auxin controls the **orientation** of the sprouting seedling
  - **tropisms (向性):** growth toward or away from stimuli
  - directional cues
    - **light**: phototropism (向光性)
    - **gravity**: gravitropism (向地性)
    - **Thigmotropism (向触性)**, a directional movement or change in growth in response to touch

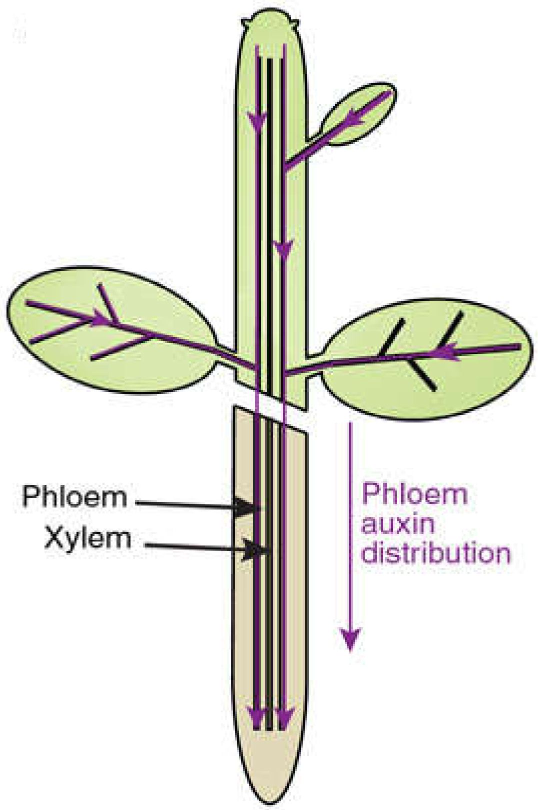
45.2 How Do Hormones Regulate Plant Life Cycles?

- Auxin stimulates shoot elongation **away from gravity and toward light**



Polar Auxin Transport (生长素的极性运输)

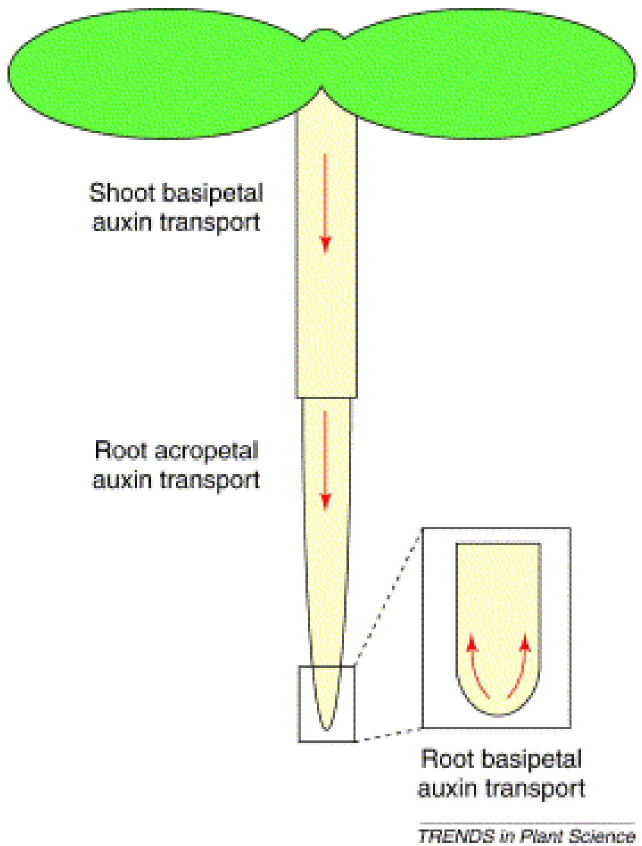
Auxin is synthesized in the **shoot and root apical meristem**



Auxin moves long distances through the **phloem.**

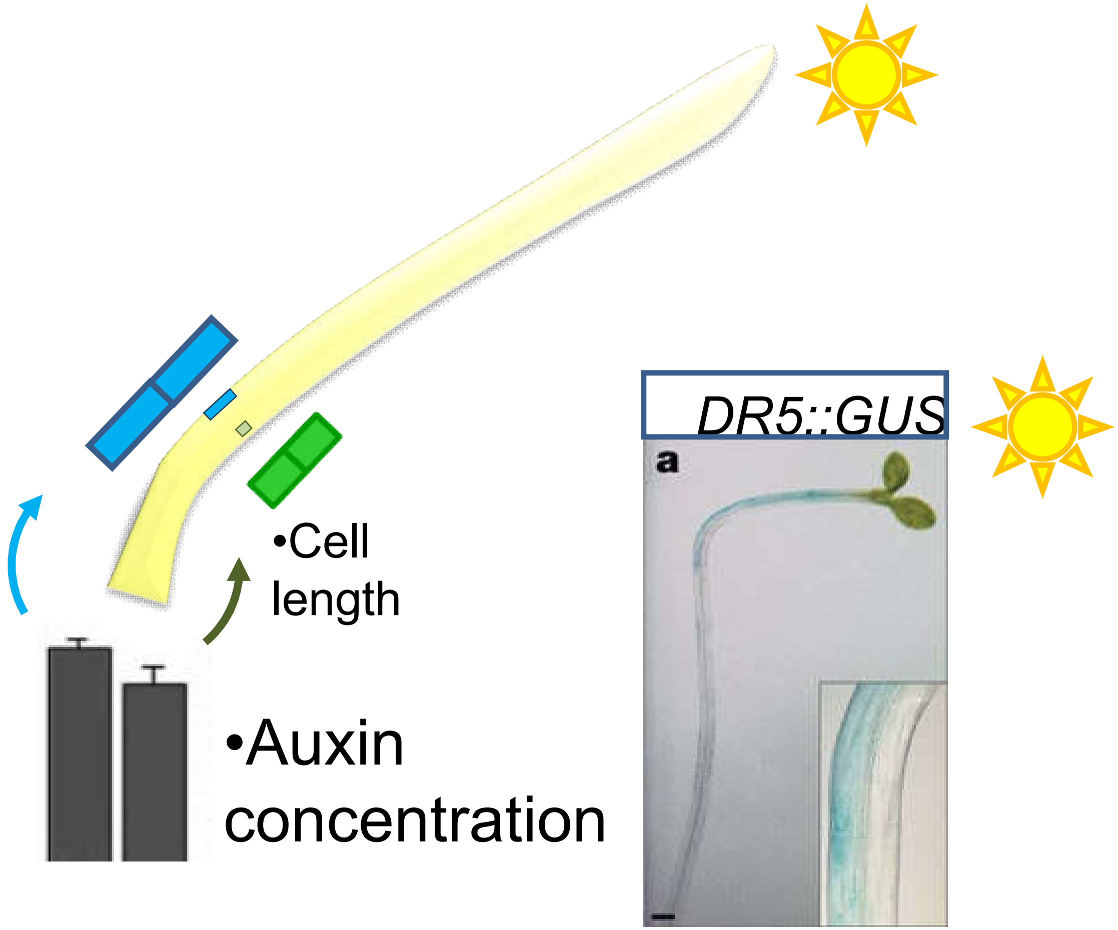
Auxin also moves via **auxin transport proteins**，**such as PINs**

Auxin normally moves from the tip of the shoot towards the tip of the root. At the root tip, auxin changes direction and moves short distances up the root again (basipetally).



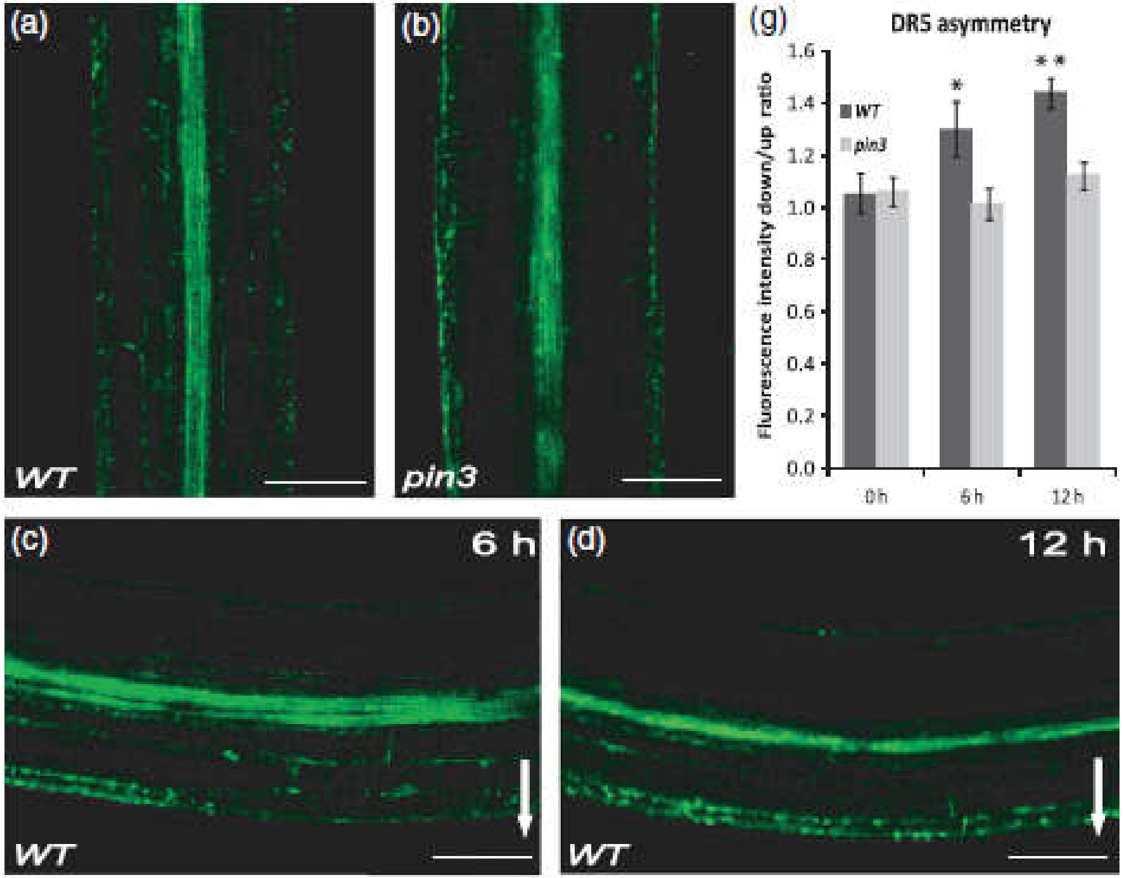
⑩Reprinted with permission from Macmillan Publishers, Ltd. Robert, H.S., and Friml, J. (2009) Auxin and other signals on the move in plants. Nat. Chem. Biol. 5: 325-332. Reprinted from Muday, G.K., and DeLong, A. (2001). Polar auxin transport: Controlling where and how much. Trends Plant Sci. **6:** 535–542, with permission from Elsevier.

Auxin controls phototropism



DR5::GUS, an auxin responsive reporter line

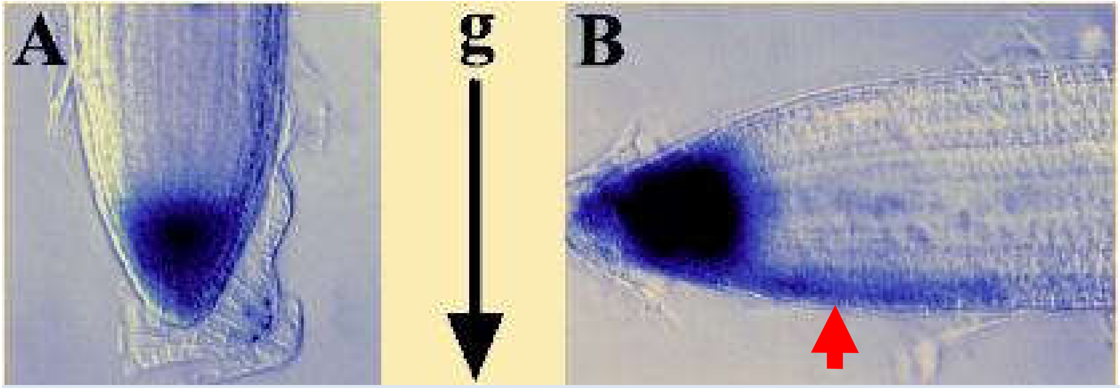
Auxin controls shoot gravitropism



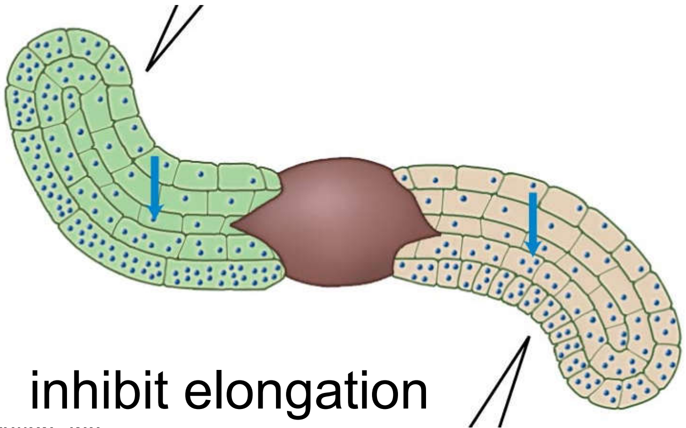
DR5::GFP

2011 *The Plant journal*

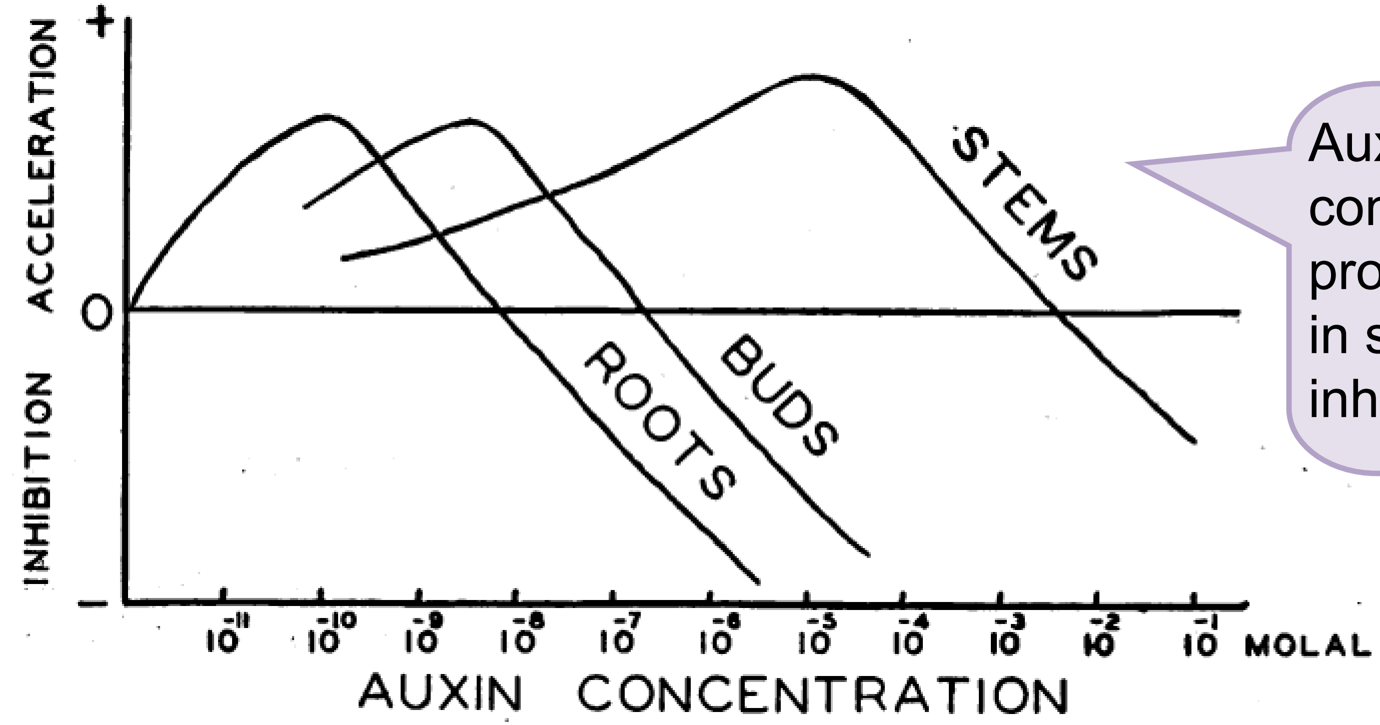
Auxin controls root gravitropism



DR5::GUS expression in vertically oriented root and root 6 hours after turning horizontal.



Different tissues were recognized to have different sensitivities to auxin

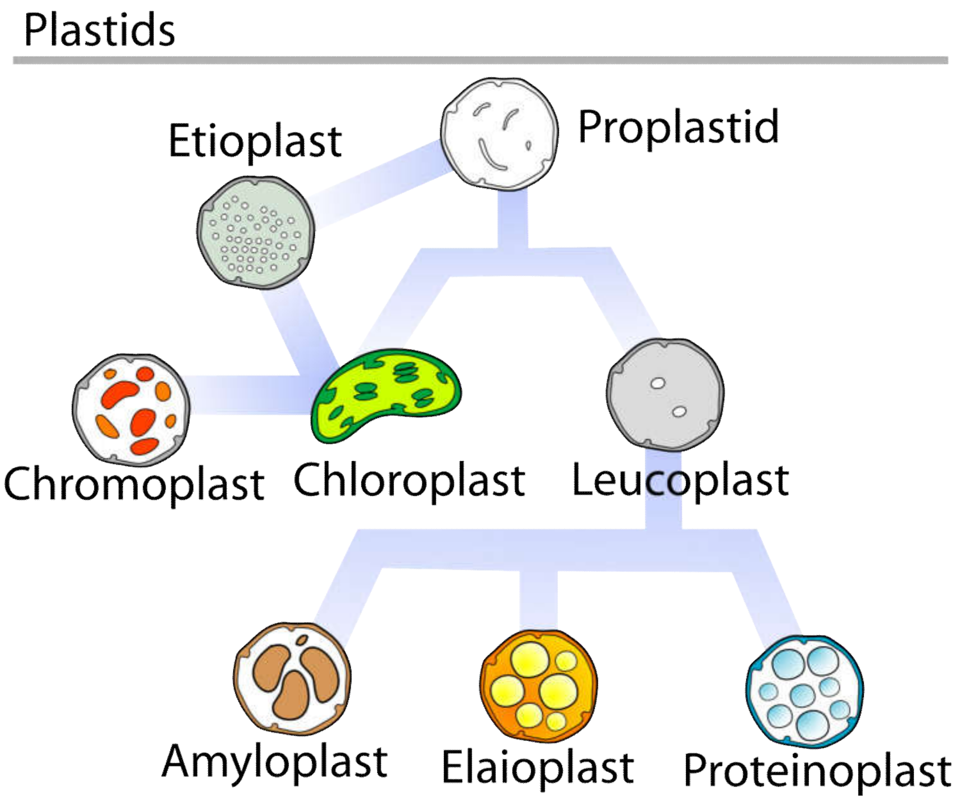


Auxin concentrations that promote elongation in stems can be inhibitory in roots.

•Thimann, K.V. (1938). Hormones and the analysis of growth. Plant Physiol. 13: 437-449.

45.2 How Do Hormones Regulate Plant Life Cycles?

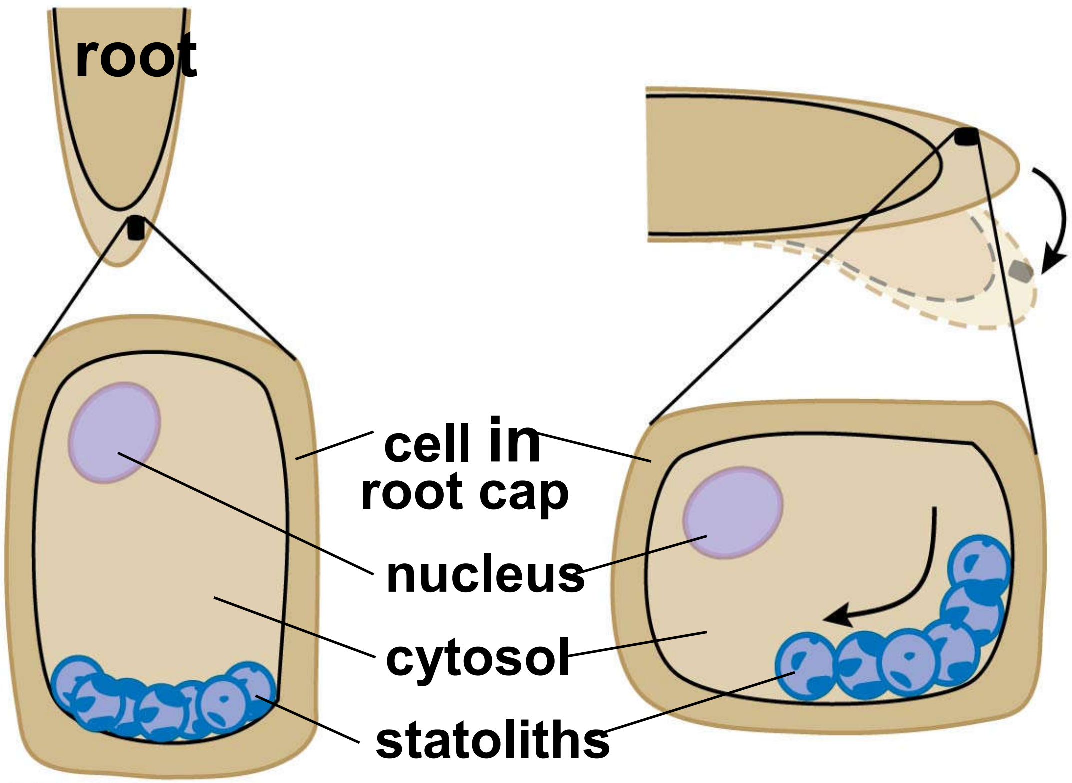
- How do plants sense gravity?
  - statoliths (平衡石): specialized **starch-filled plastids** (质体)

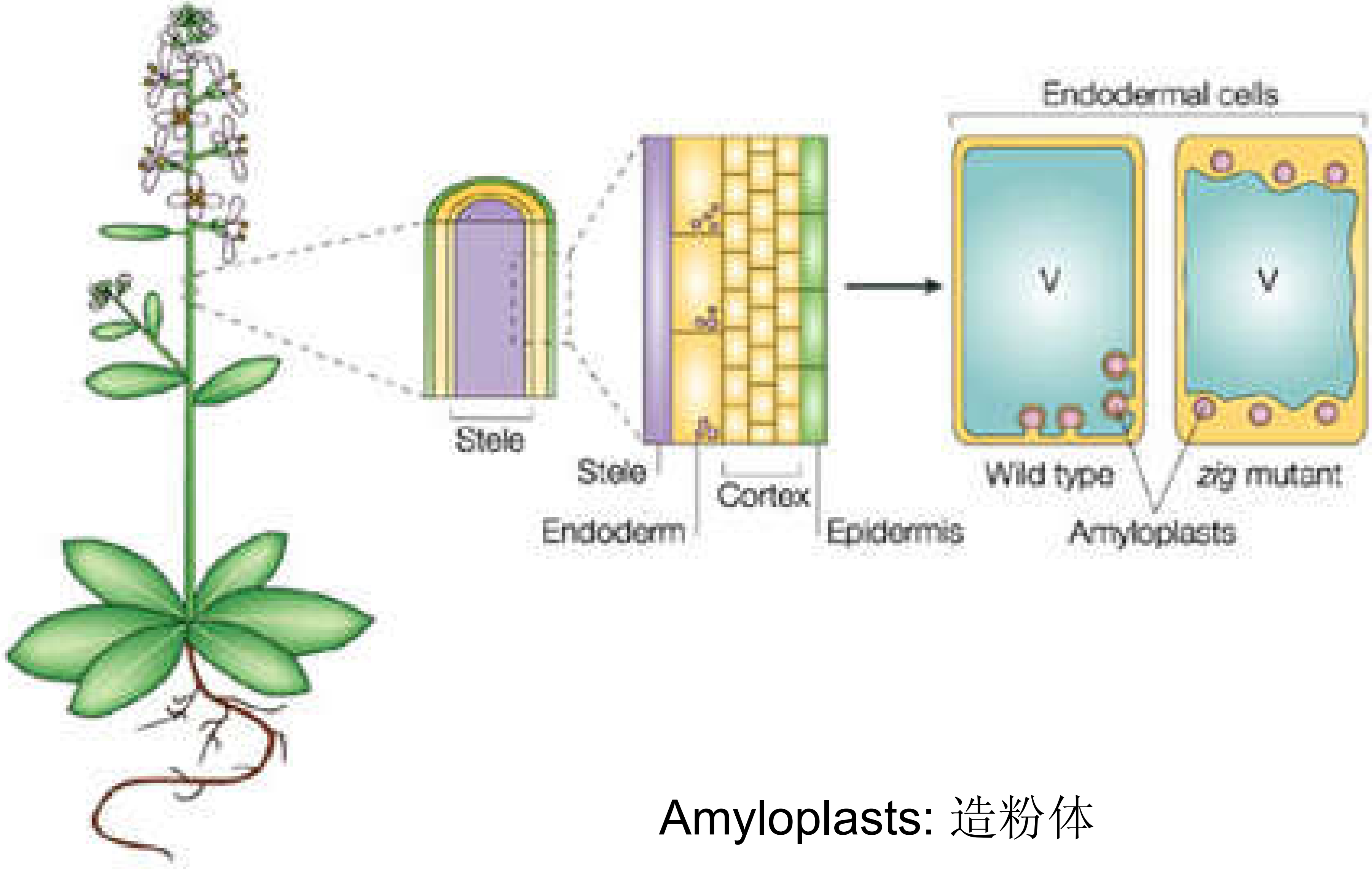


45.2 How Do Hormones Regulate Plant Life Cycles?

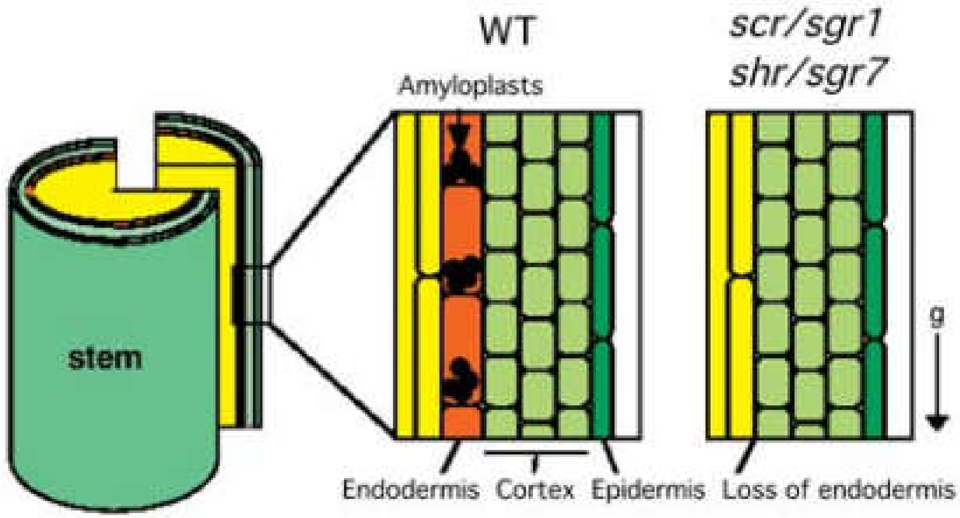
- How do plants sense gravity?
  - statoliths (平衡石): specialized **starch-filled plastids** (质体)
    - found in certain cells: endoderm of shoot and in **root cap** (根冠)

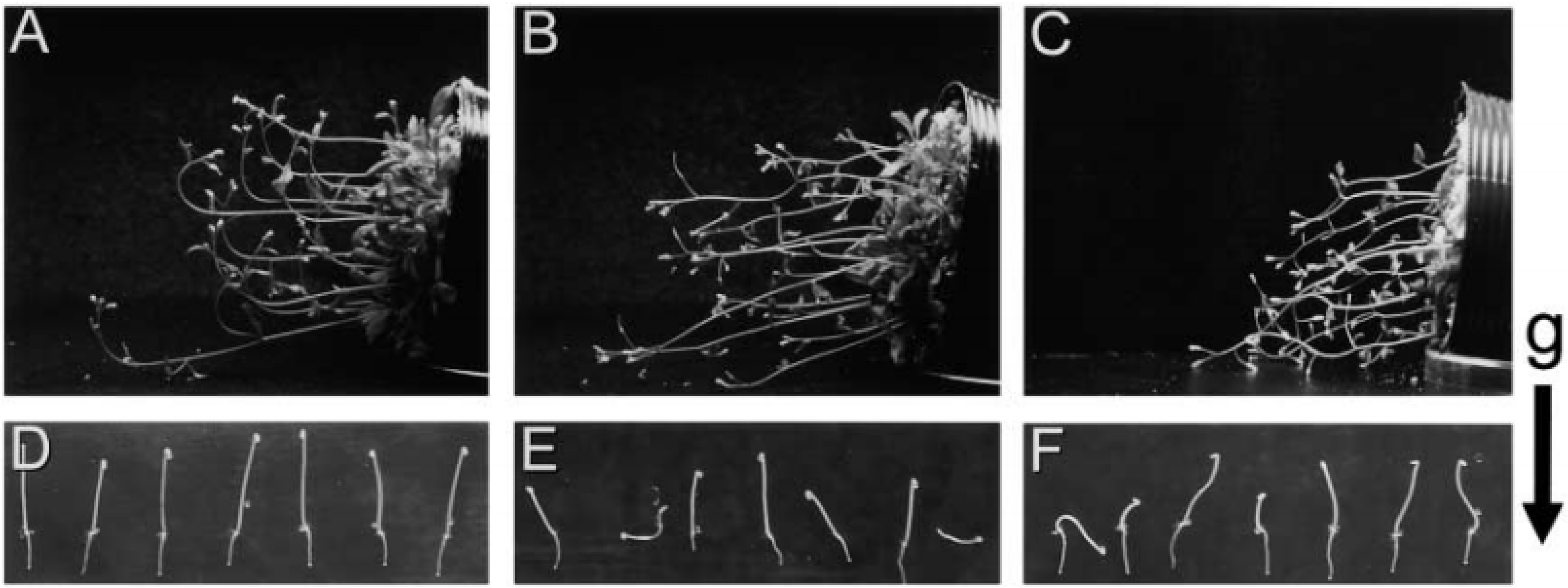
But, some mutant plants lacking statoliths still exhibit gravitropism





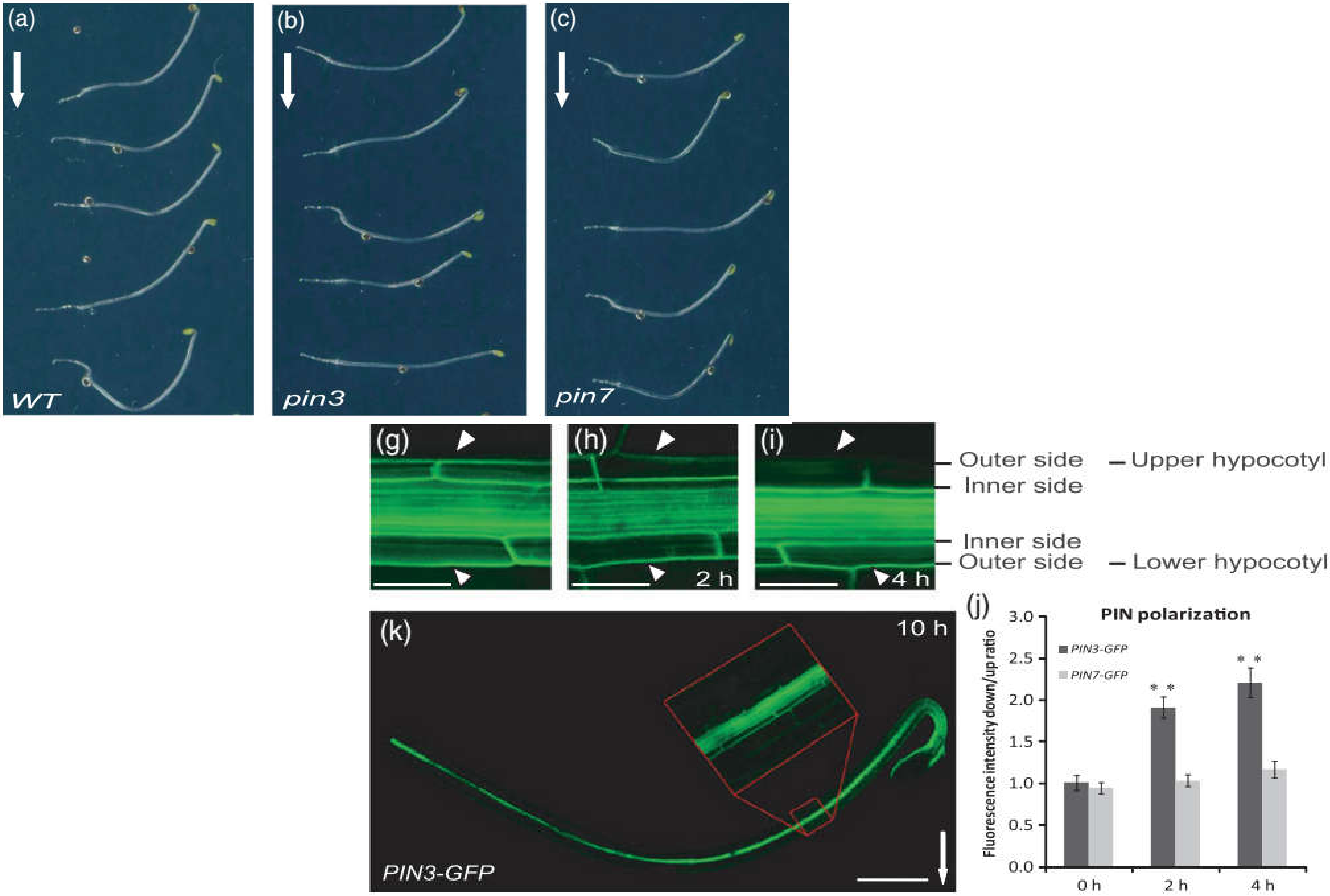
Amyloplasts: 造粉体





zig/sgr4

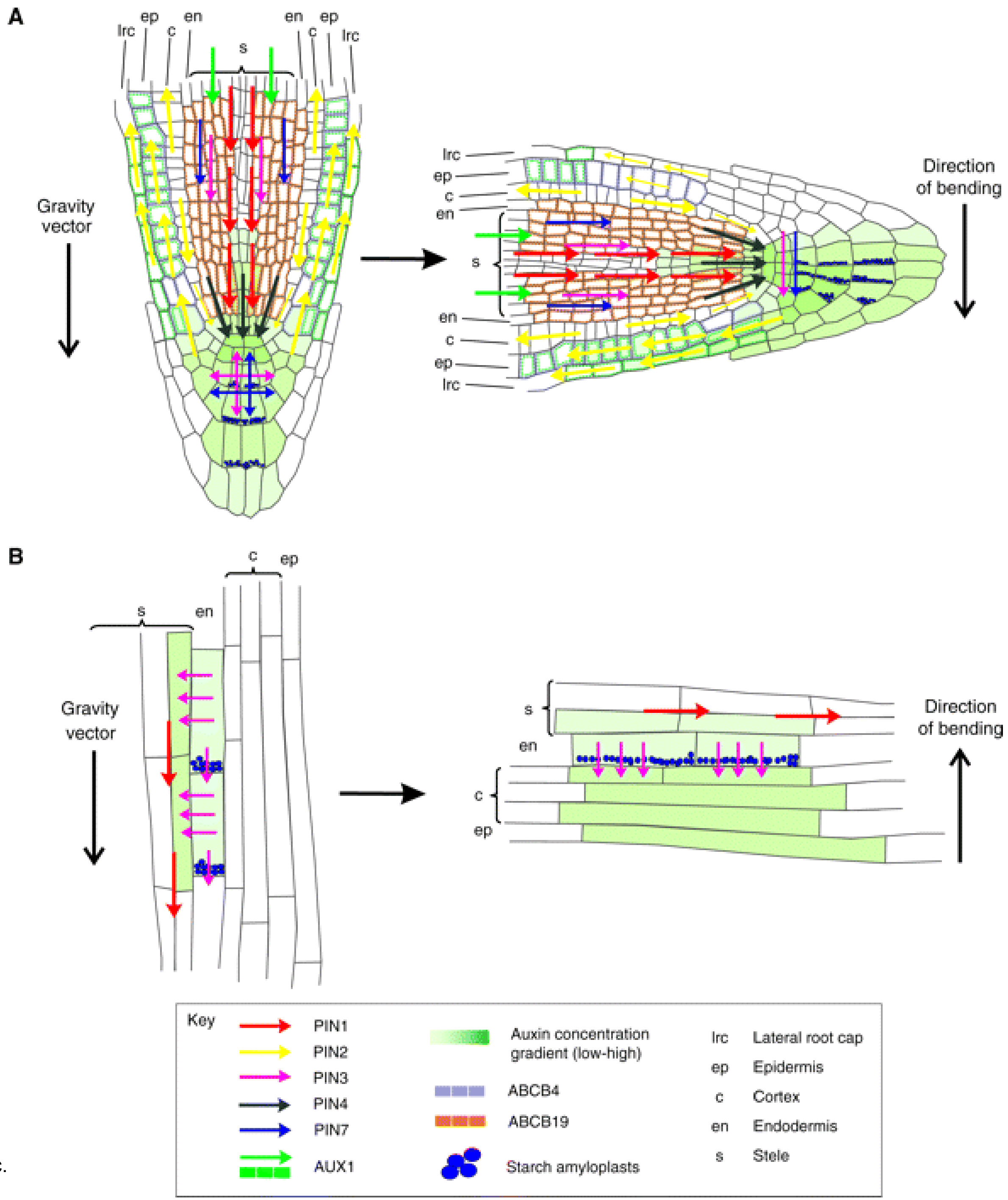
2002 Plant Cell Kato et.al.



2011 Plant Journal Rakusova

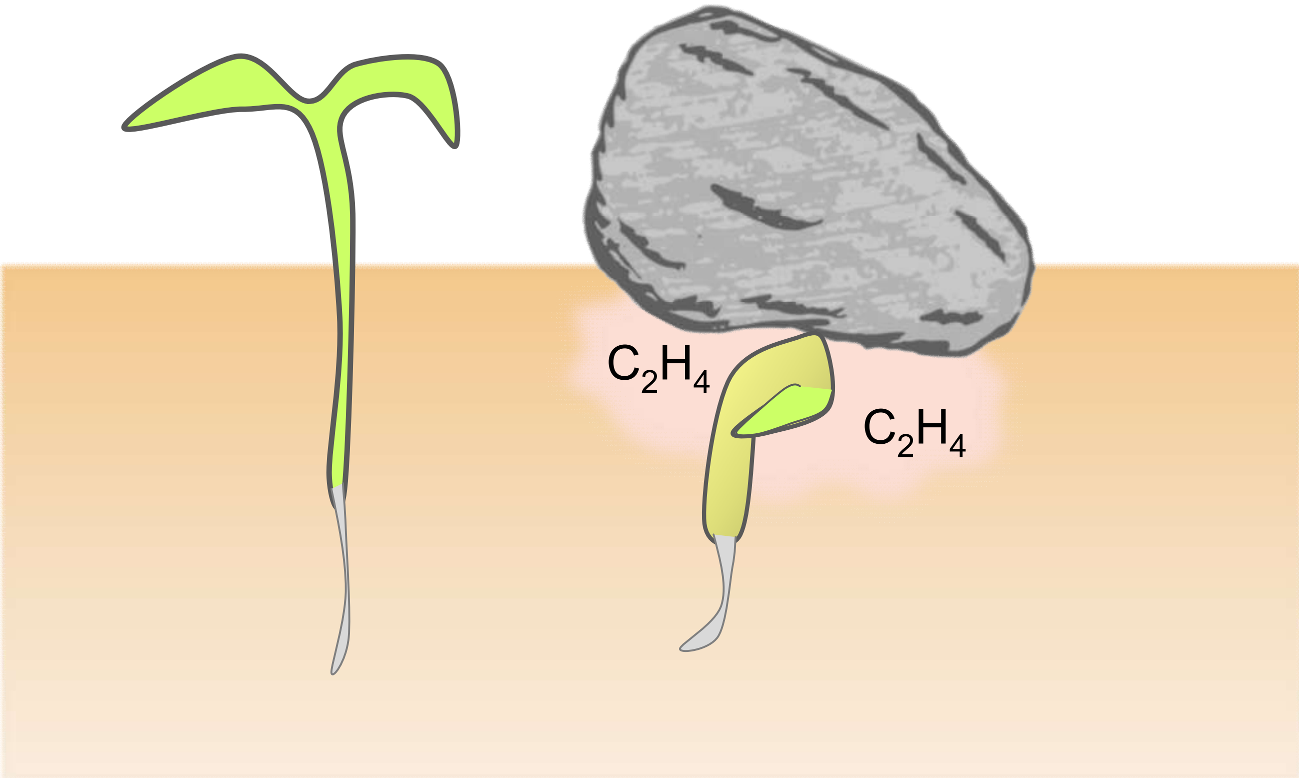
Root

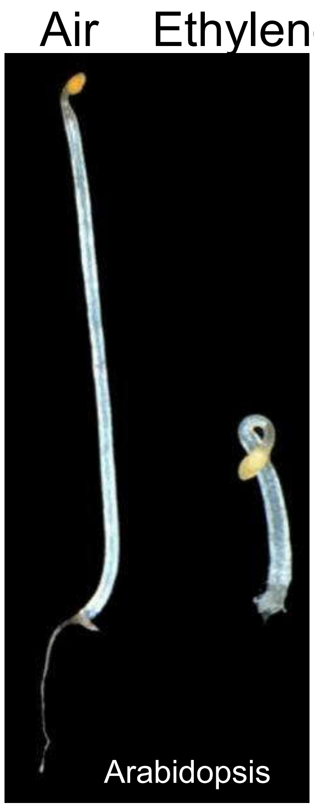
Shoot


A
lrc
ep
c
en
s
Gravity vector
Direction of bending
B
Gravity vector
Direction of bending
Key
PIN1
PIN2
PIN3
PIN4
PIN7
AUX1
Auxin concentration gradient (low-high)
ABCB4
ABCB19
Starch amyloplasts
lrc Lateral root cap
ep Epidermis
c Cortex
en Endodermis
s Stele

45.2 How Do Hormones Regulate Plant Life Cycles?

Ethylene induces the **triple response**:
- reduced elongation,
- hypocotyl swelling,
- apical hook exaggeration.





Gibberellins stimulate elongation and help determine the ultimate height of the plant

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

One of the most significant accomplishments of 20th century science was the development of semi-dwarf grain varieties which are deficient in GA synthesis or response.

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

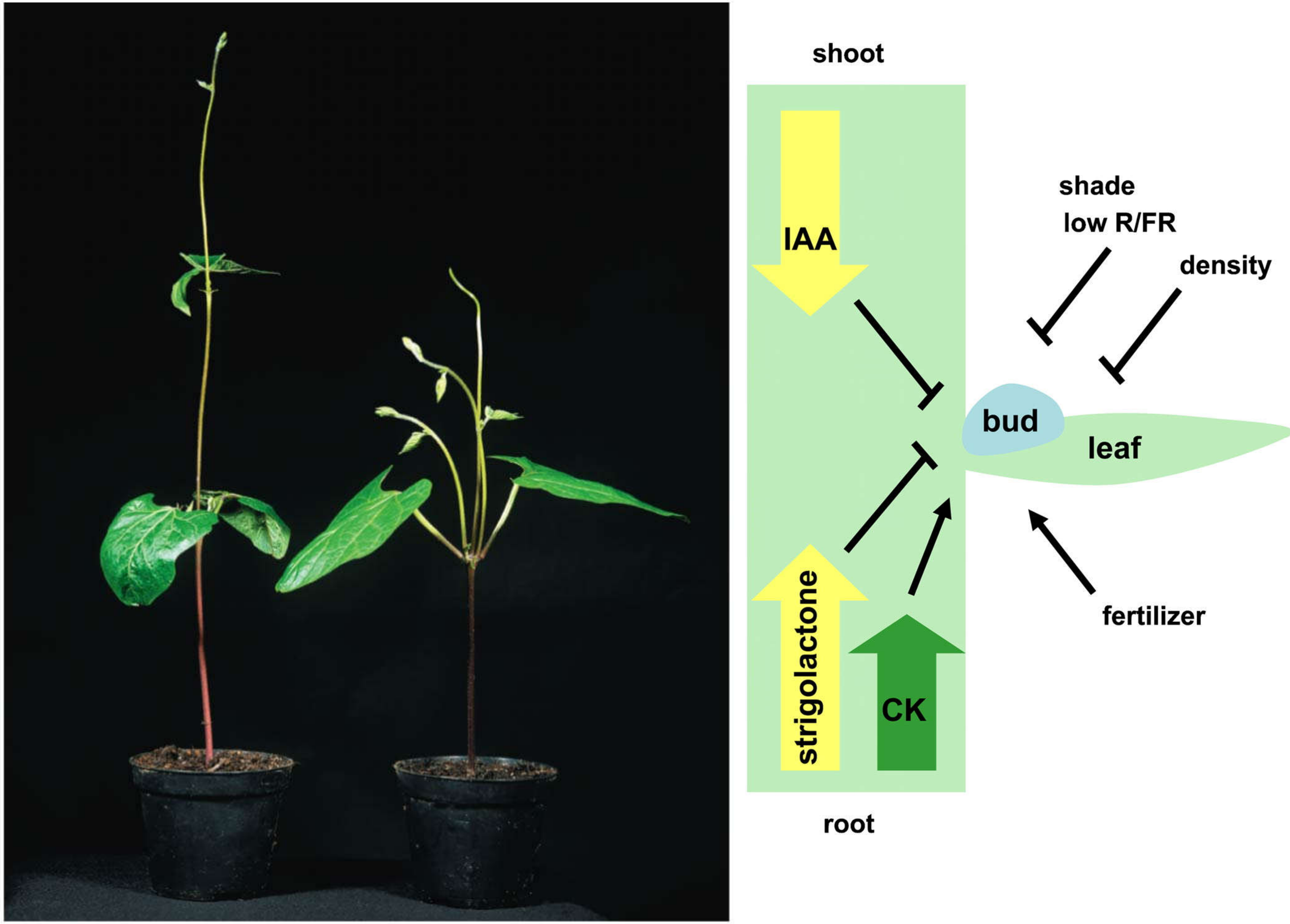
Some plants are treated with GA- synthesis inhibitors to maintain a shorter stature and prevent lodging (倒伏，tipping over).

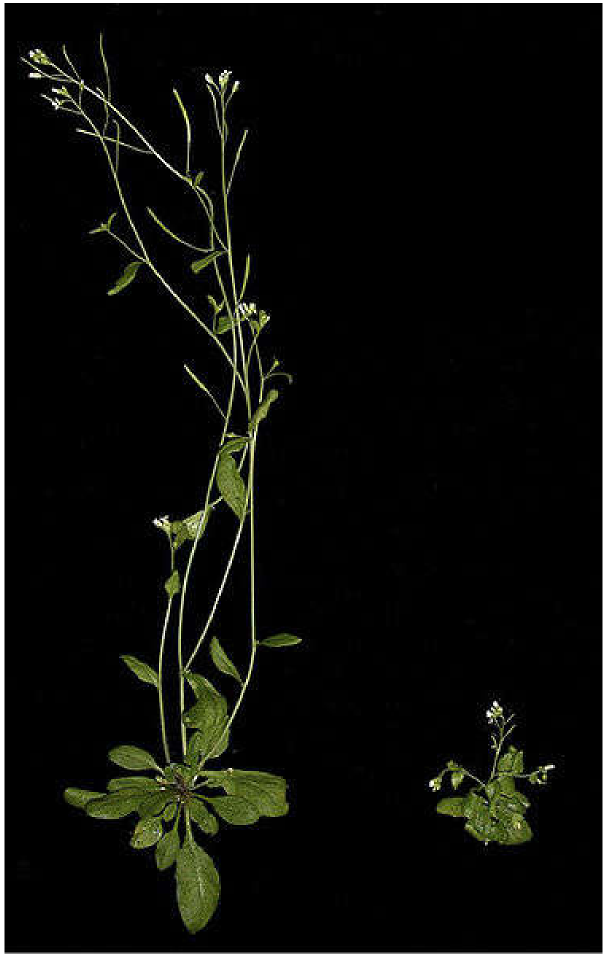
45.2 How Do Hormones Regulate Plant Life Cycles?

- Auxin and cytokinin control stem and root **branching**
  - The **size of the root and shoot systems of plants must be balanced**
  - Branching in **stems** is **inhibited by auxin and stimulated by cytokinin**
    - **apical dominance**

    Auxin produced in the shoot apical meristem travels down the stem and **inhibits lateral buds** from developing into branches

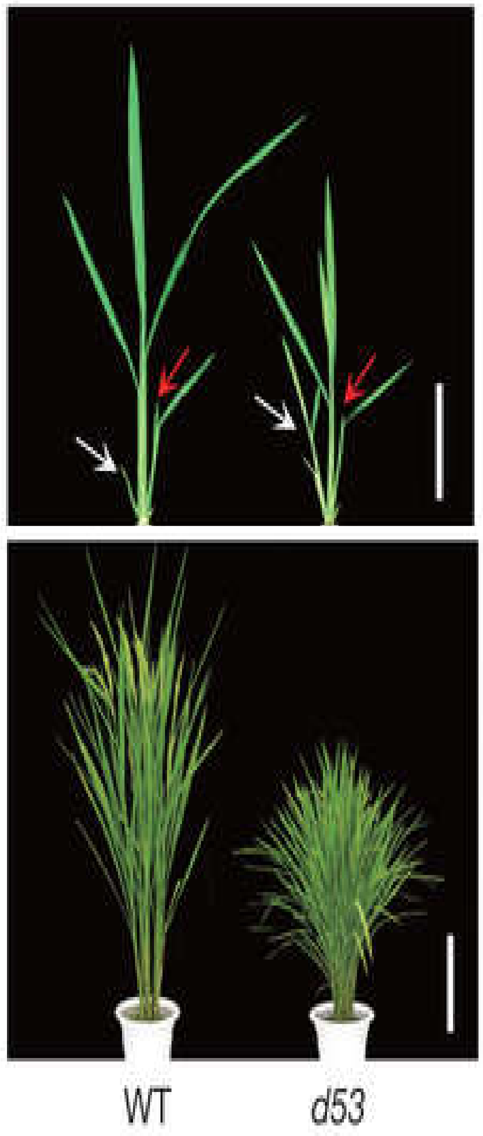
Figure 45-6 Apical dominance





Auxin mutant
(signaling)

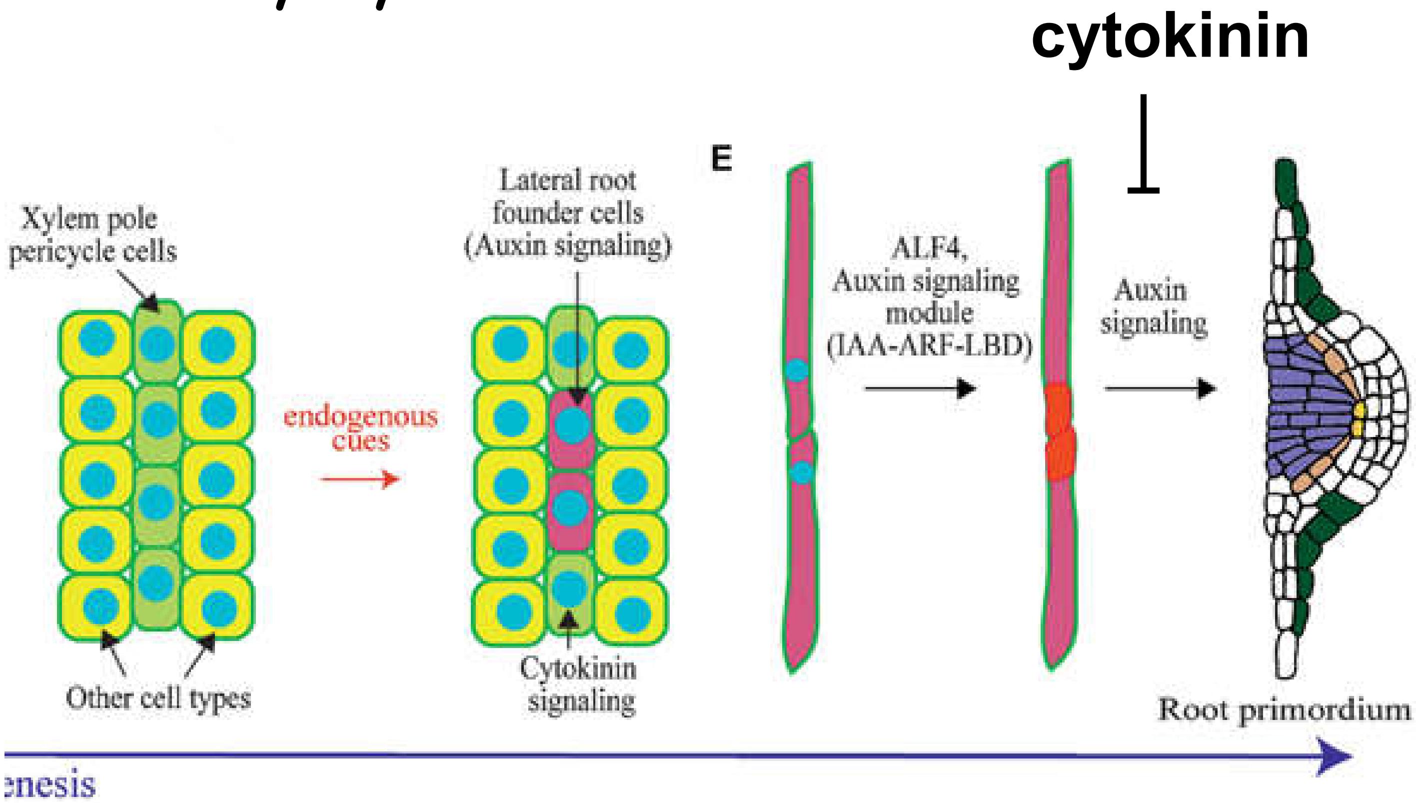
BR mutant
(signaling)



Stringolactone mutant
(signaling)

45.2 How Do Hormones Regulate Plant Life Cycles?

- **Branching in roots** is stimulated by auxin and inhibited by cytokinin

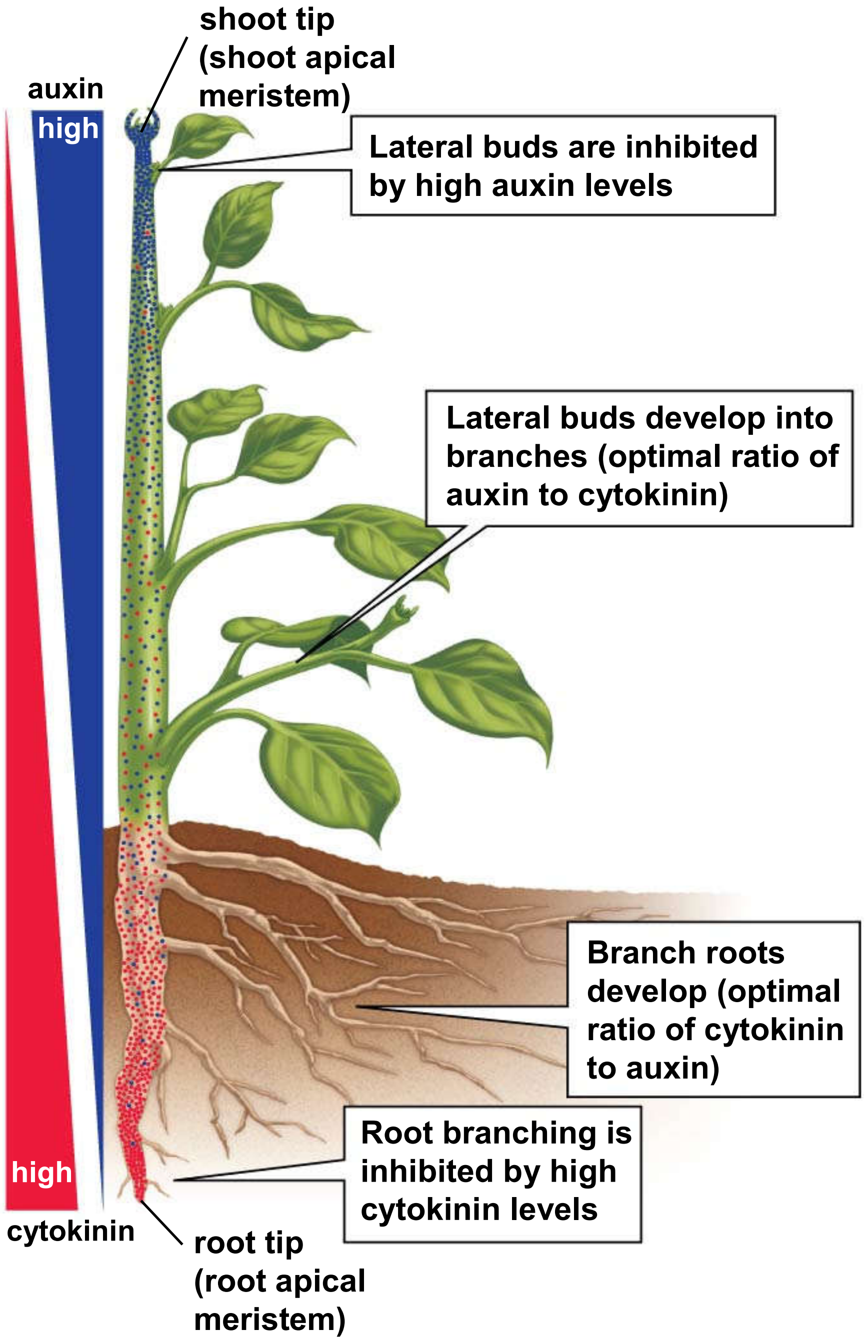


45.2 How Do Hormones Regulate Plant Life Cycles?

CK deficient

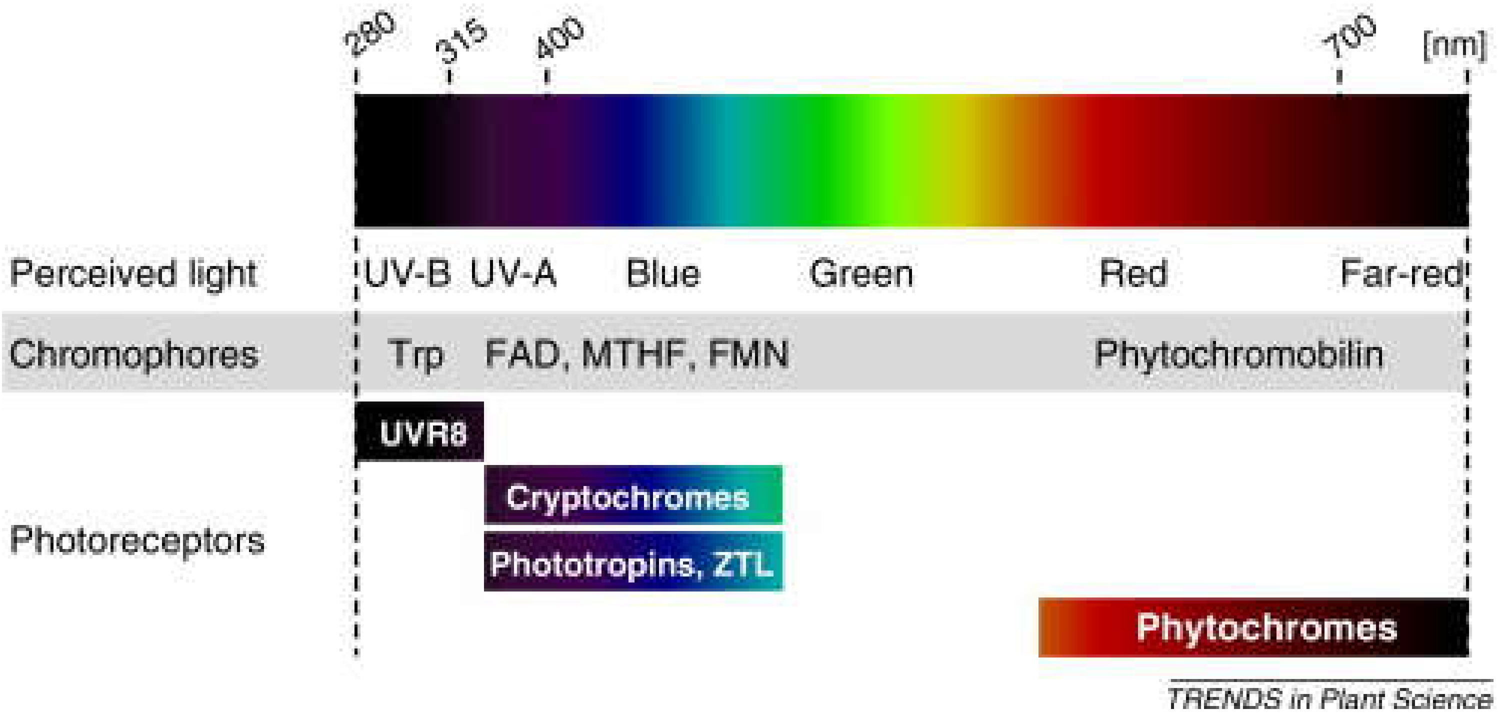
Auxin mutant
(transport)

Figure 45-7 The role of auxin and cytokinin in lateral bud sprouting



45.2 How Do Hormones Regulate Plant Life Cycles?

Photoreceptors (光受体)



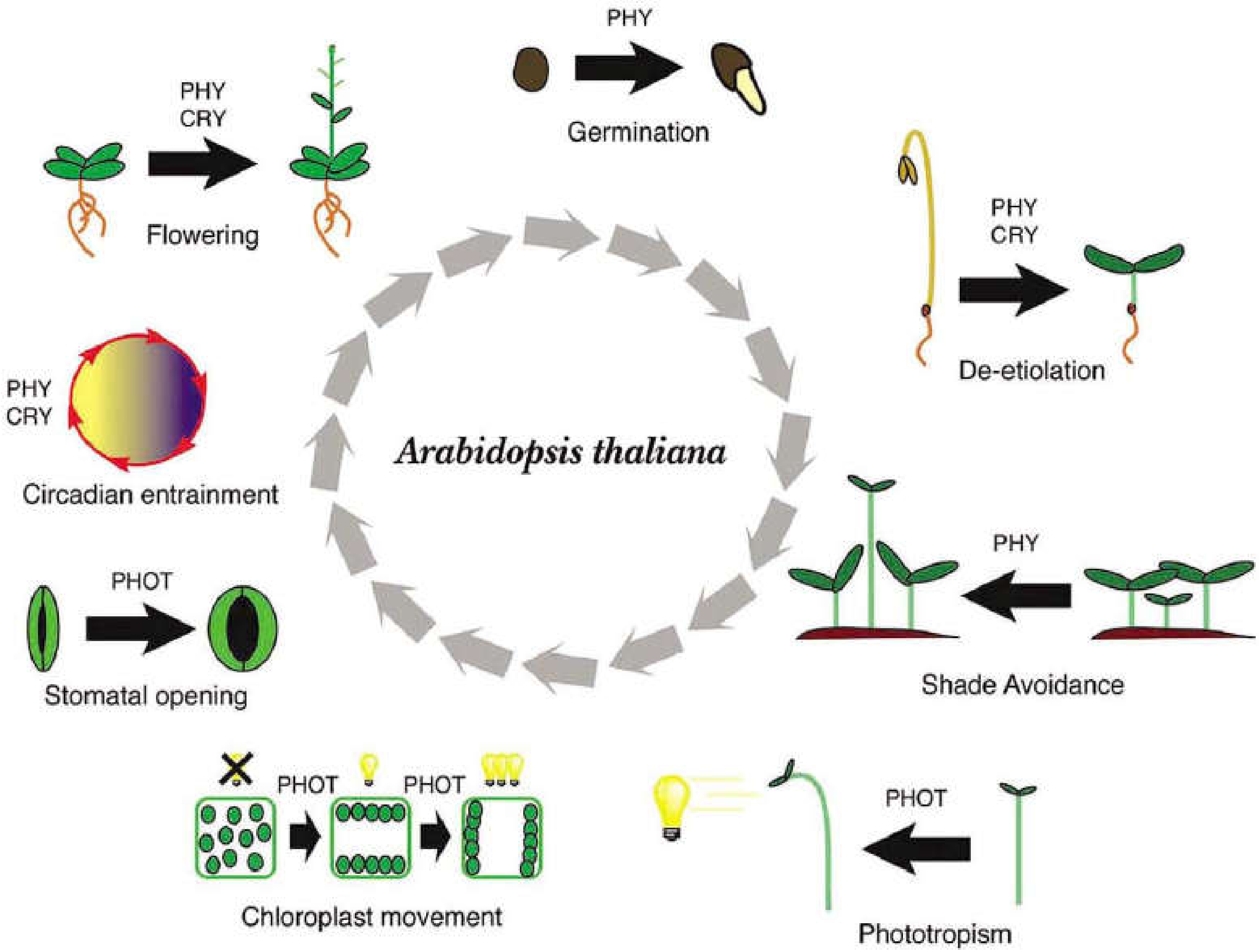
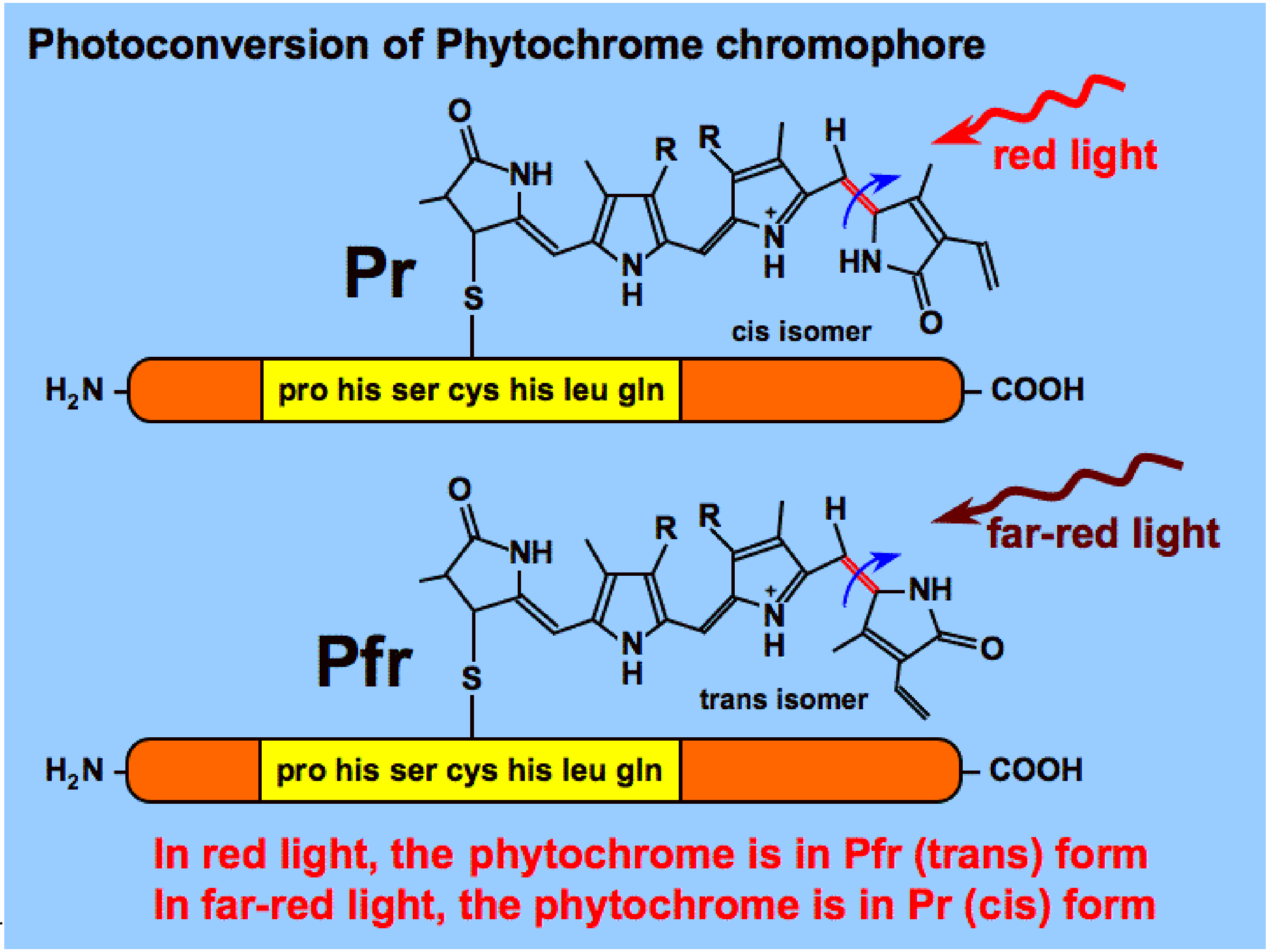


Fig. 2. Light-regulated development in the model plant species *Arabidopsis thaliana*. Light affects the development of *Arabidopsis* throughout its life cycle. Multiple aspects of development are regulated the photoreceptors phytochromes (PHY), crytochromes (CRY), or phototropins (PHOT) acting alone or in combination with each other.

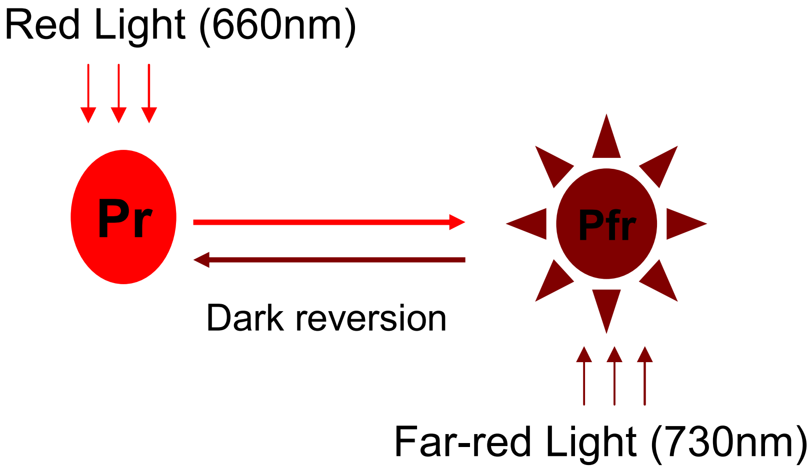
45.2 How Do Hormones Regulate Plant Life Cycles?

- phytochromes (光敏色素)



45.2 How Do Hormones Regulate Plant Life Cycles?

- phytochromes (光敏色素)
- P_r and P_{fr} form of phytochrome



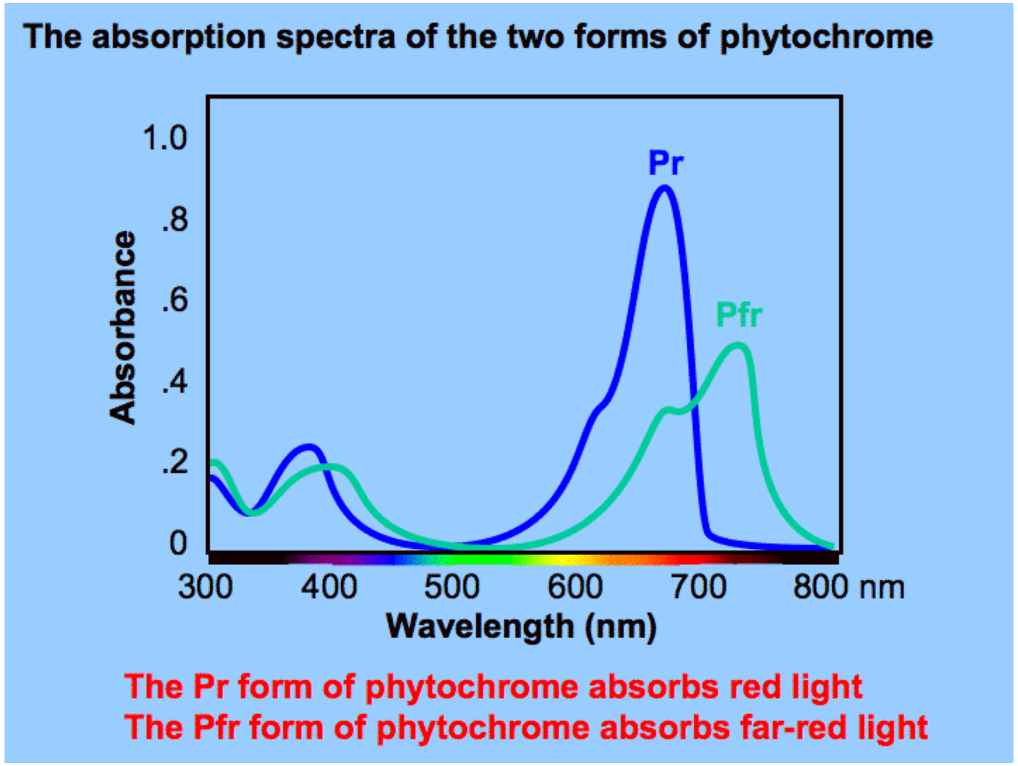
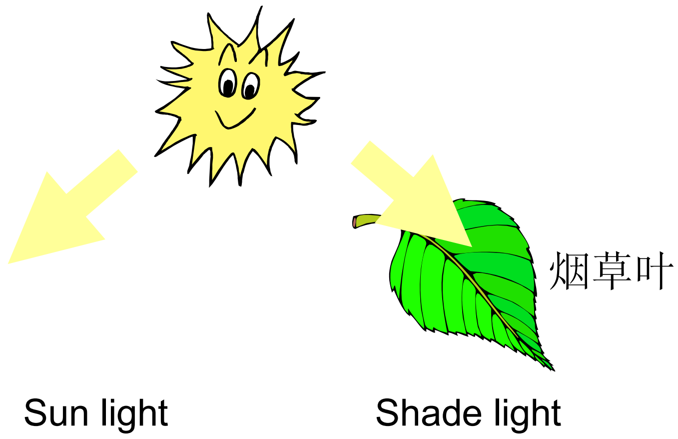


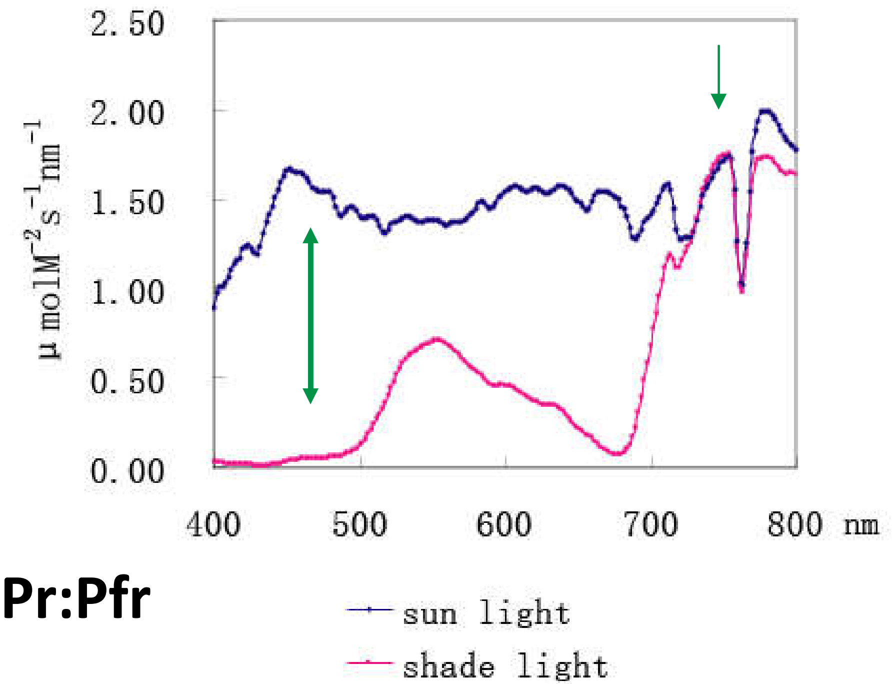
Table 45-2 Light and Phytochrome Activity

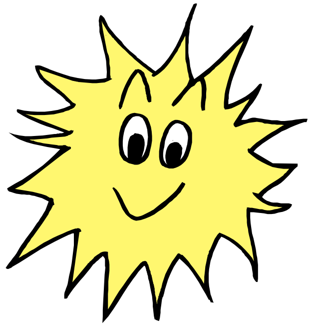
TABLE 45-2 Light and Phytochrome Activity

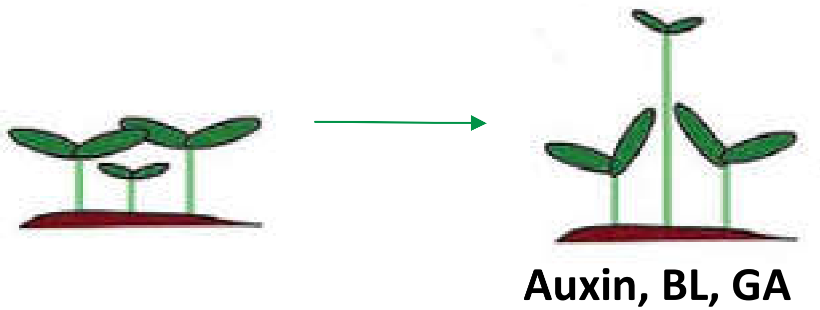
Light	Resulting Phytochrome	Activity
Red	P_{fr}	Active
Far-red	P_r	Inactive
White (sunlight)	$P_r + P_{fr}$	Active
Darkness	P_r	Inactive

植物的避荫反应









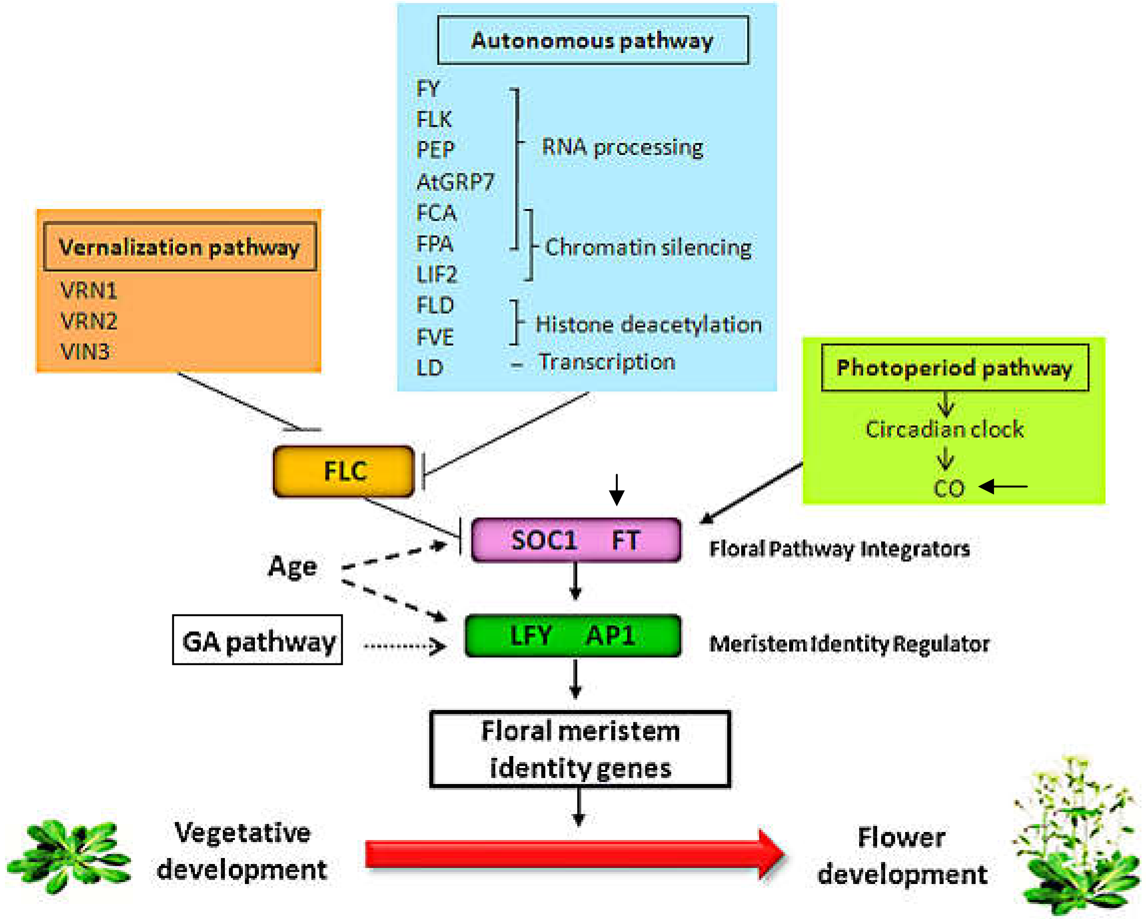
Pr:Pfr

避荫反应是当避荫植物处于其它植物的遮荫下或当检测到周围其它植物的存在时所诱导的一系列反应，其目的是通过快速长高，获得更充足的阳光和更有利的生存条件。

45.2 How Do Hormones Regulate Plant Life Cycles?

- Plants sense and respond to **light and darkness** (circadian clock,昼夜节律钟,生物钟)
  - controls flowering time and seed production
  - day-neutral plants (日中性植物,), flower independently of day length under favorable conditions
  - Long-day plants (长日照植物)
  - Short-day plants (短日照植物)

Flowering time control in Arabidopsis



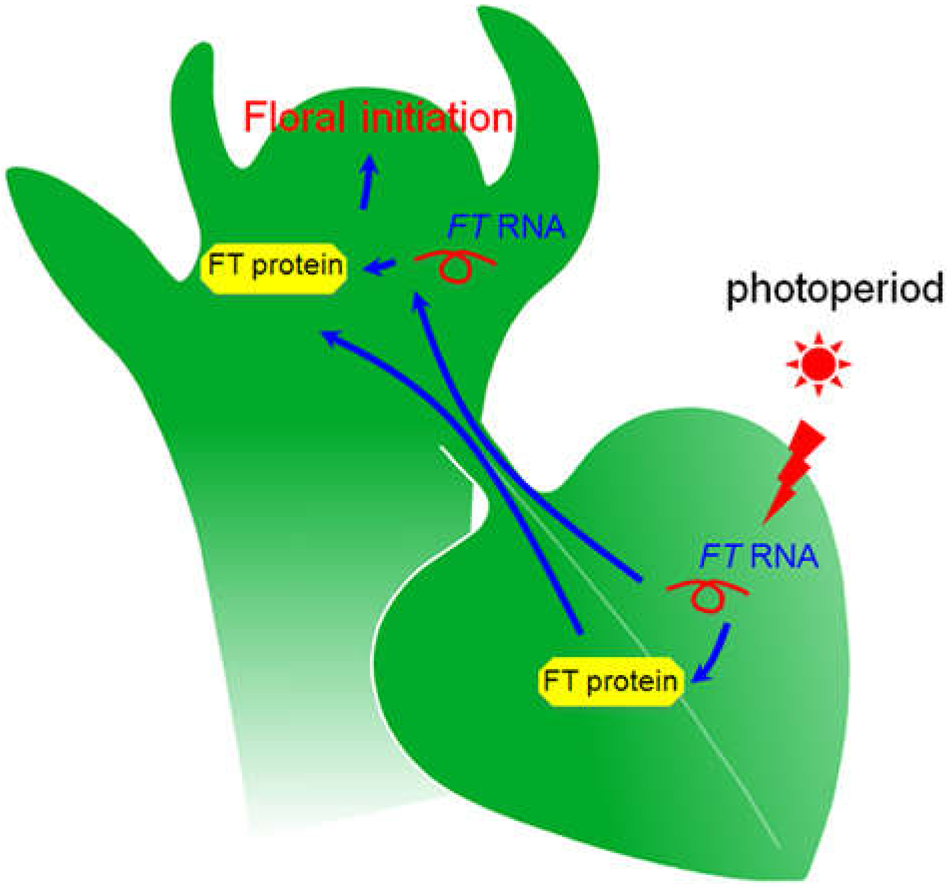
2014 Plant Science Yeap et. al.

45.2 How Do Hormones Regulate Plant Life Cycles?

- Florigen stimulates flowering in response to light cues

  - florigen: a hypothetical flowering-promoting substance (1930)

    - The florigen molecule was not identified until 2007



45.2 How Do Hormones Regulate Plant Life Cycles?

Circadian clock 生物钟

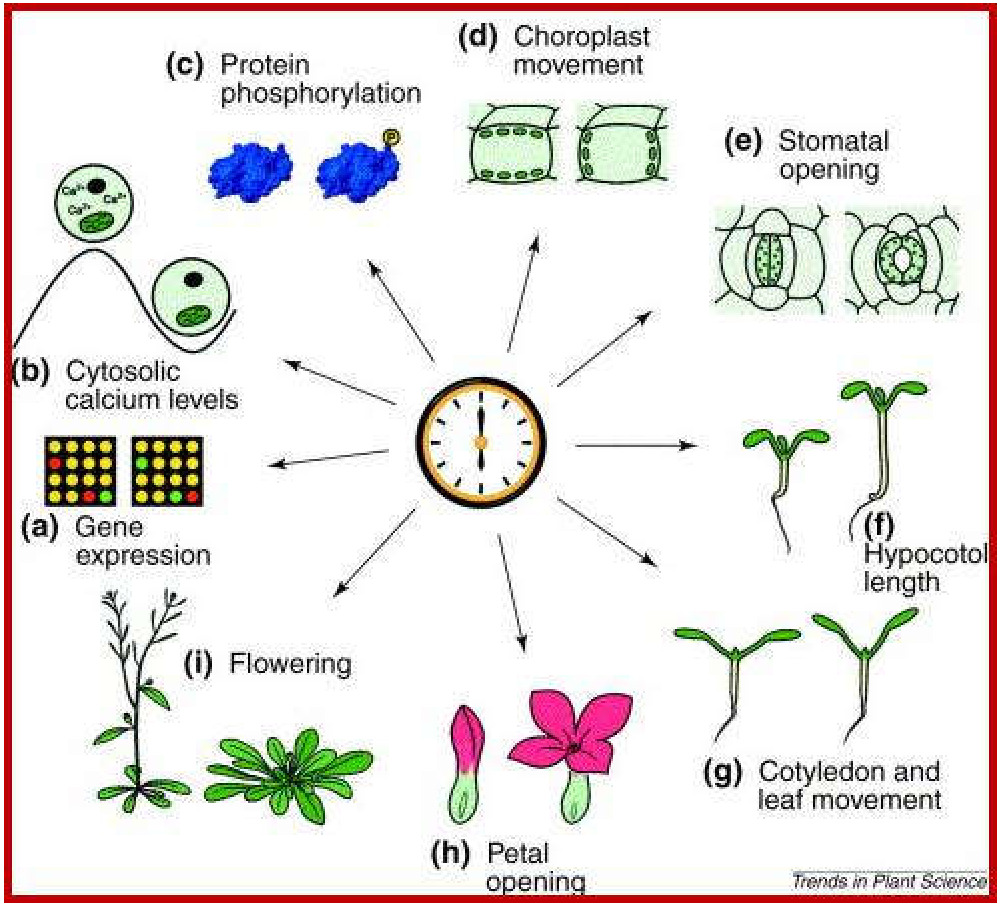
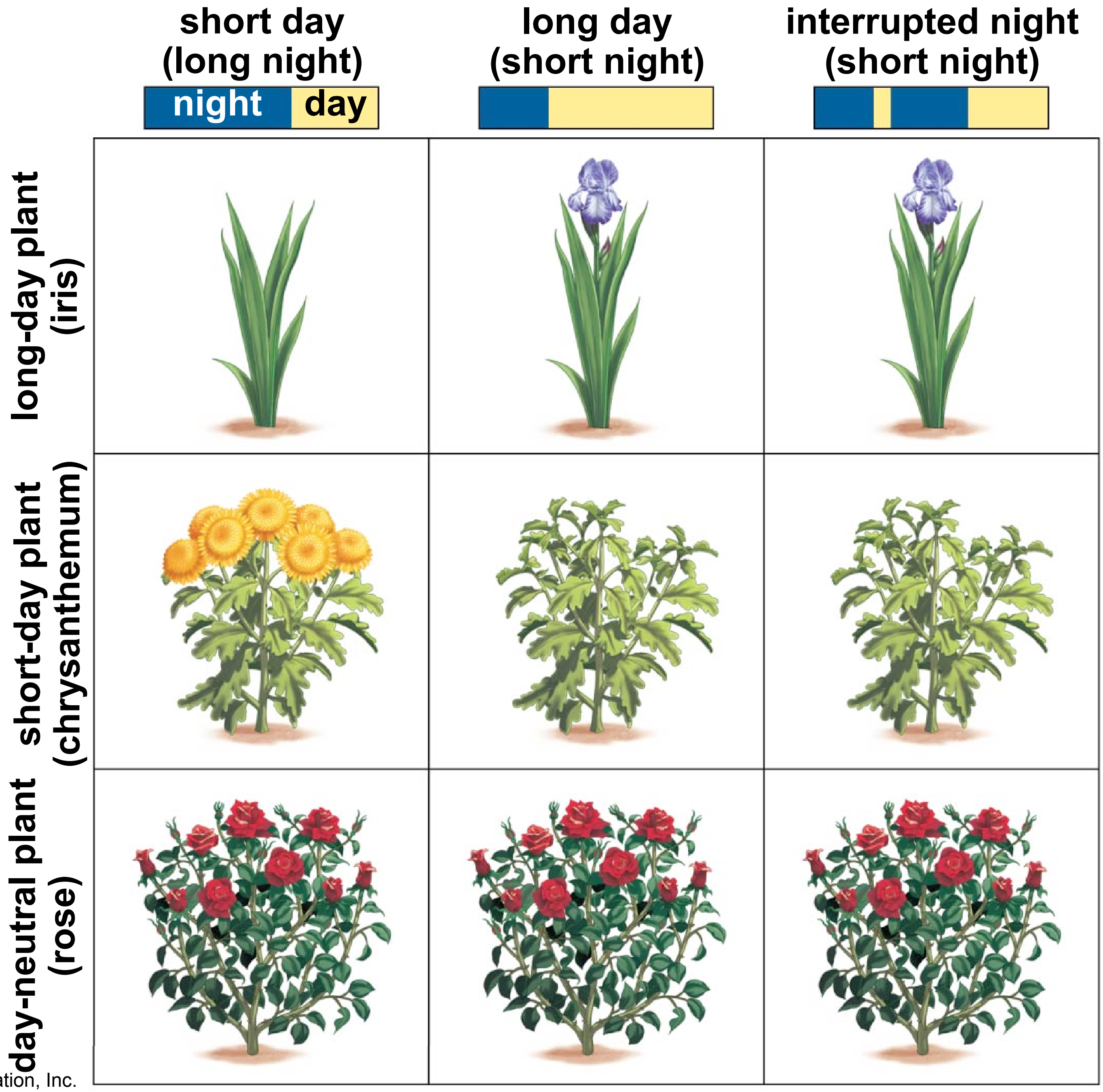
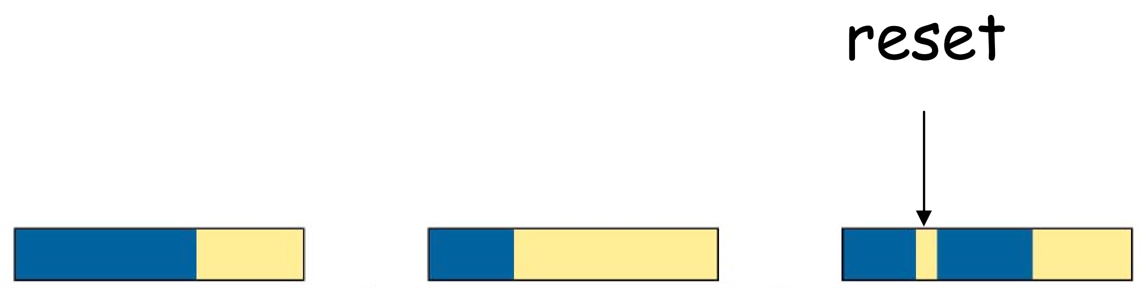


Figure 45-8 The effects of night length on flowering



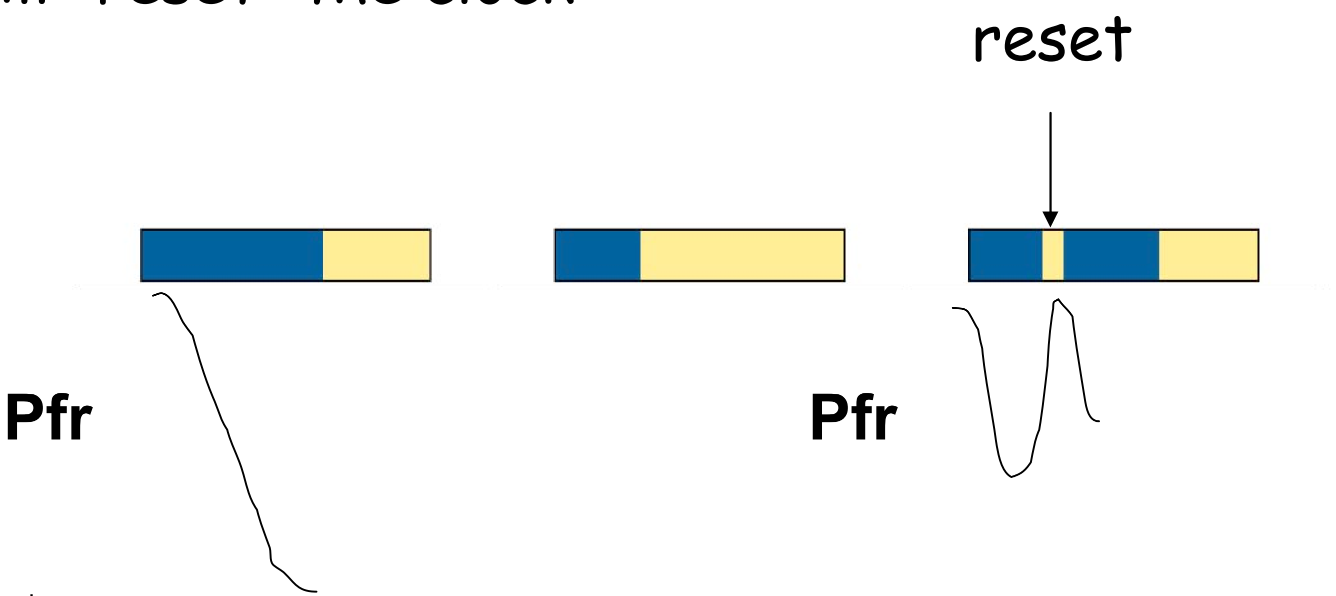
45.2 How Do Hormones Regulate Plant Life Cycles?

- Plants measure the duration of darkness using an internal **biological clock** that relies on complex biochemical reactions
  - If a plant in darkness is exposed to light of a certain wavelength, its **phytochrome** (光敏色素) molecules will "reset" the clock



45.2 How Do Hormones Regulate Plant Life Cycles?

- Plants measure the duration of darkness using an internal **biological clock** that relies on complex biochemical reactions
  - If a plant in darkness is exposed to light of a certain wavelength, its **phytochrome** (光敏色素) molecules will "reset" the clock



45.2 How Do Hormones Regulate Plant Life Cycles?

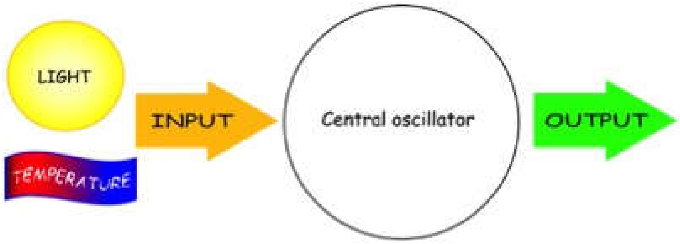
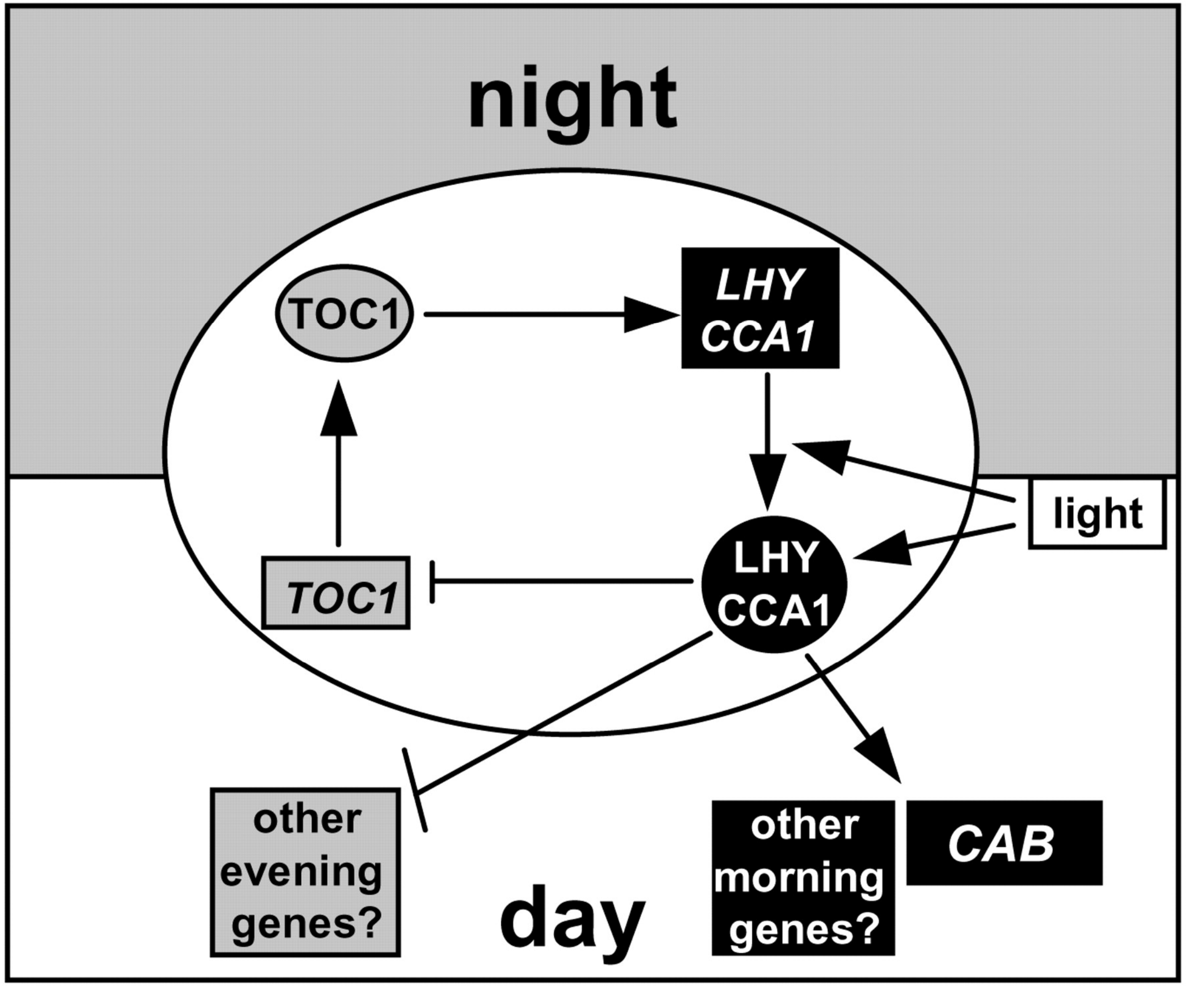


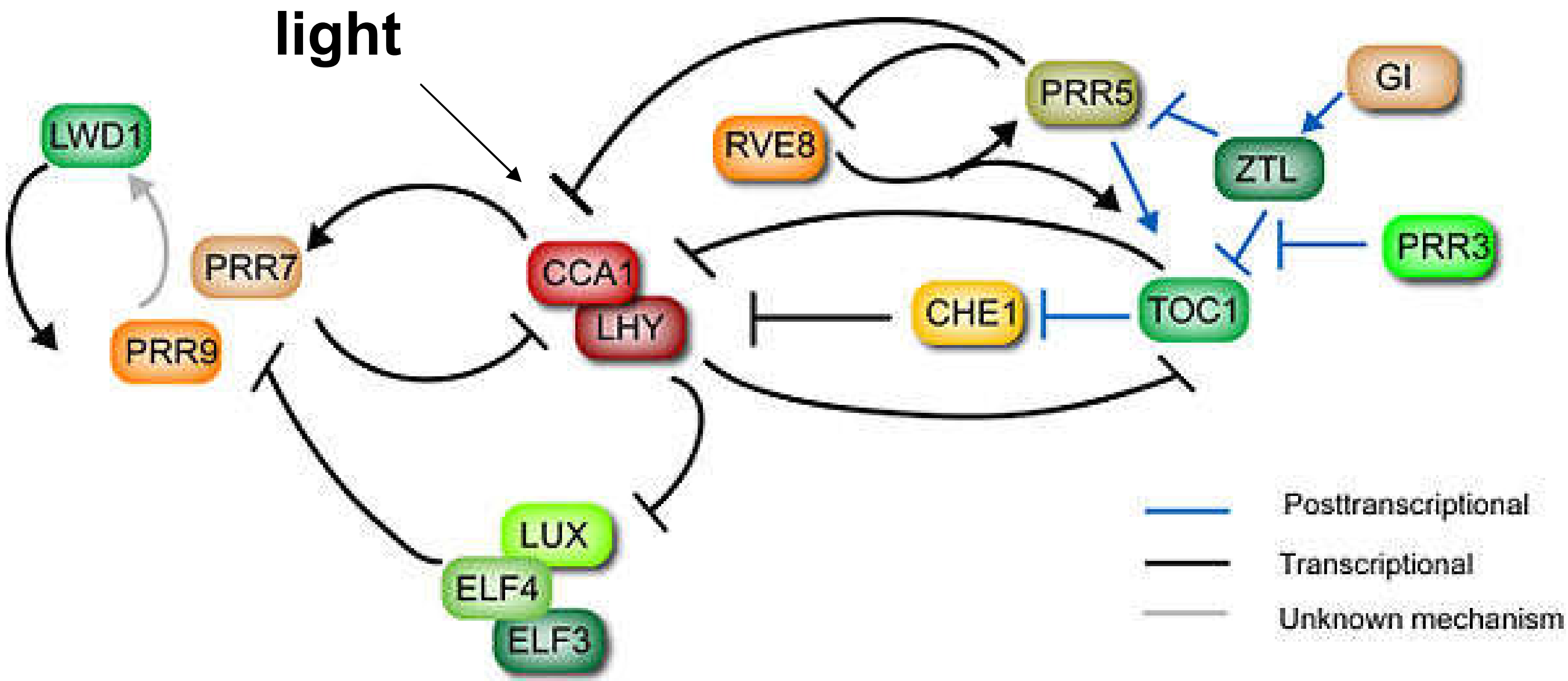
Figure1. Abstract view of a circadian system



Before 2012

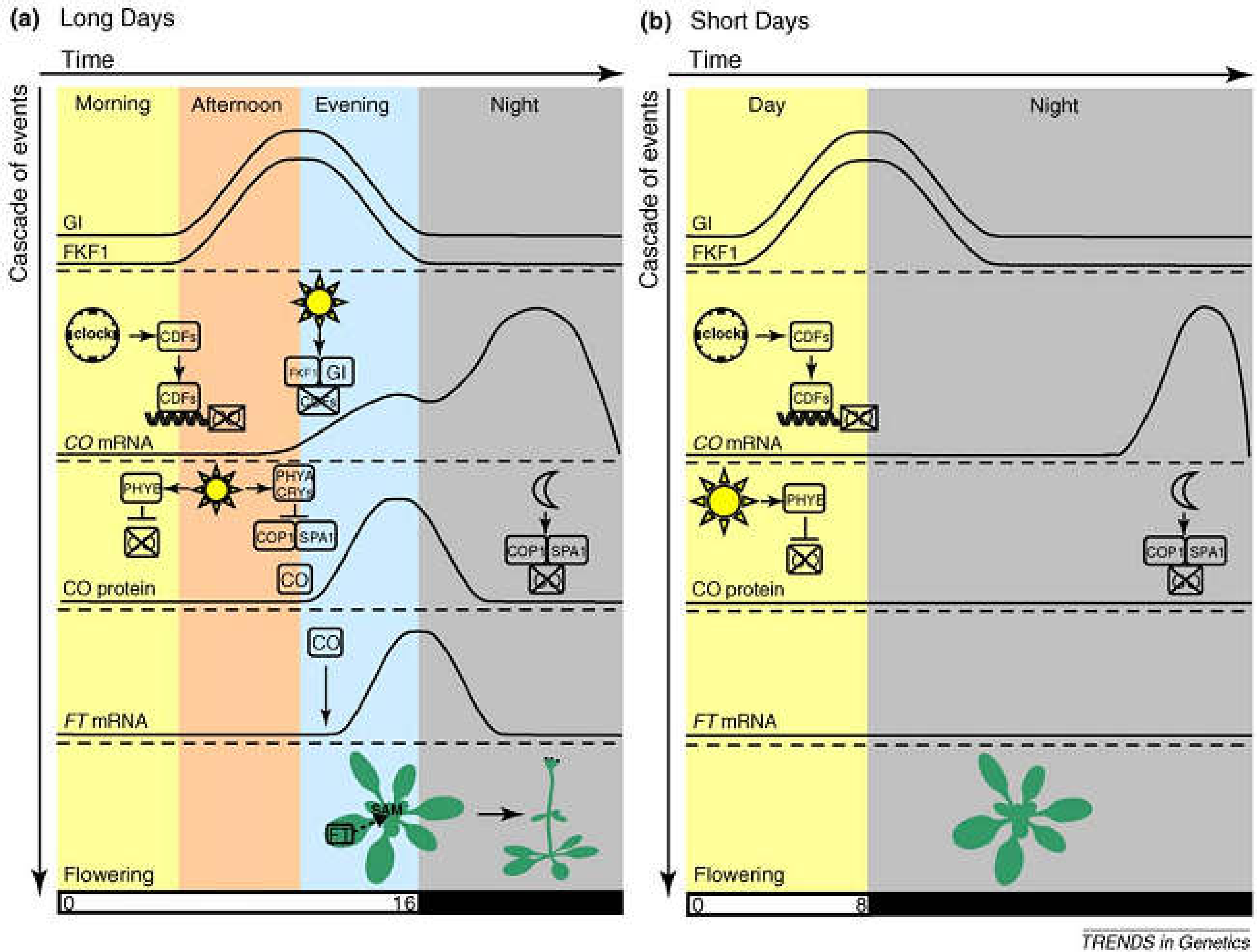
45.2 How Do Hormones Regulate Plant Life Cycles?

***Oscillator* 振荡器**

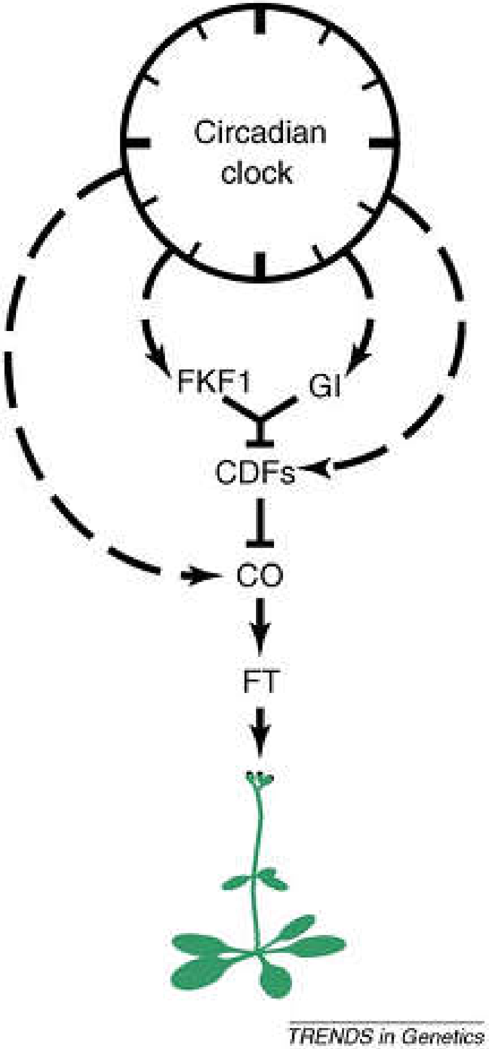


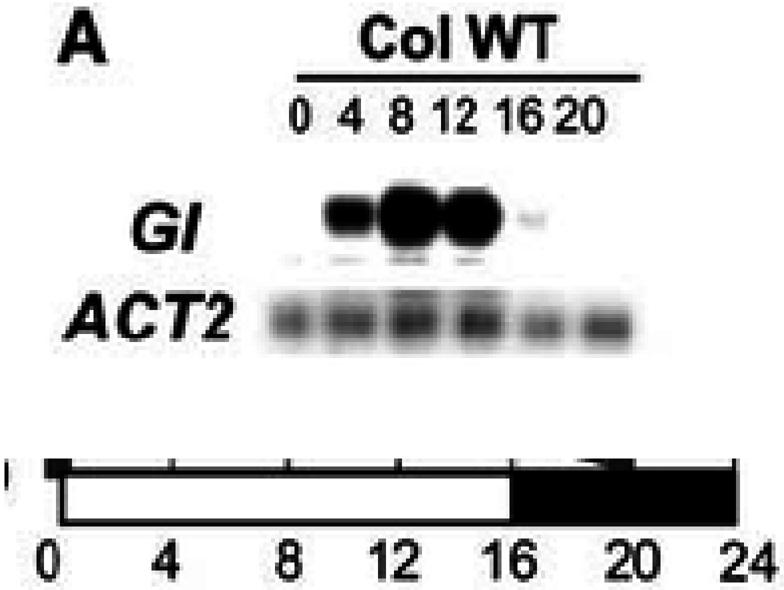
Current status of the Arabidopsis circadian clock (2014)

http://www.openwetware.org/wiki/Farre_Lab:Research



(a) Long Days
Time
Cascade of events
Morning
Afternoon
Evening
Night
GI
FKF1
clock
CDFs
CDFs
FKF1
GI
CDFs
CO mRNA
PHYB
PHYA
CRYs
COP1
SPA1
CO
COP1
SPA1
CO protein
CO
FT mRNA
SAM
FT
Flowering
0
16
(b) Short Days
Time
Cascade of events
Day
Night
GI
FKF1
clock
CDFs
CDFs
CO mRNA
PHYB
COP1
SPA1
CO protein
FT mRNA
Flowering
0
8
TRENDS in Genetics

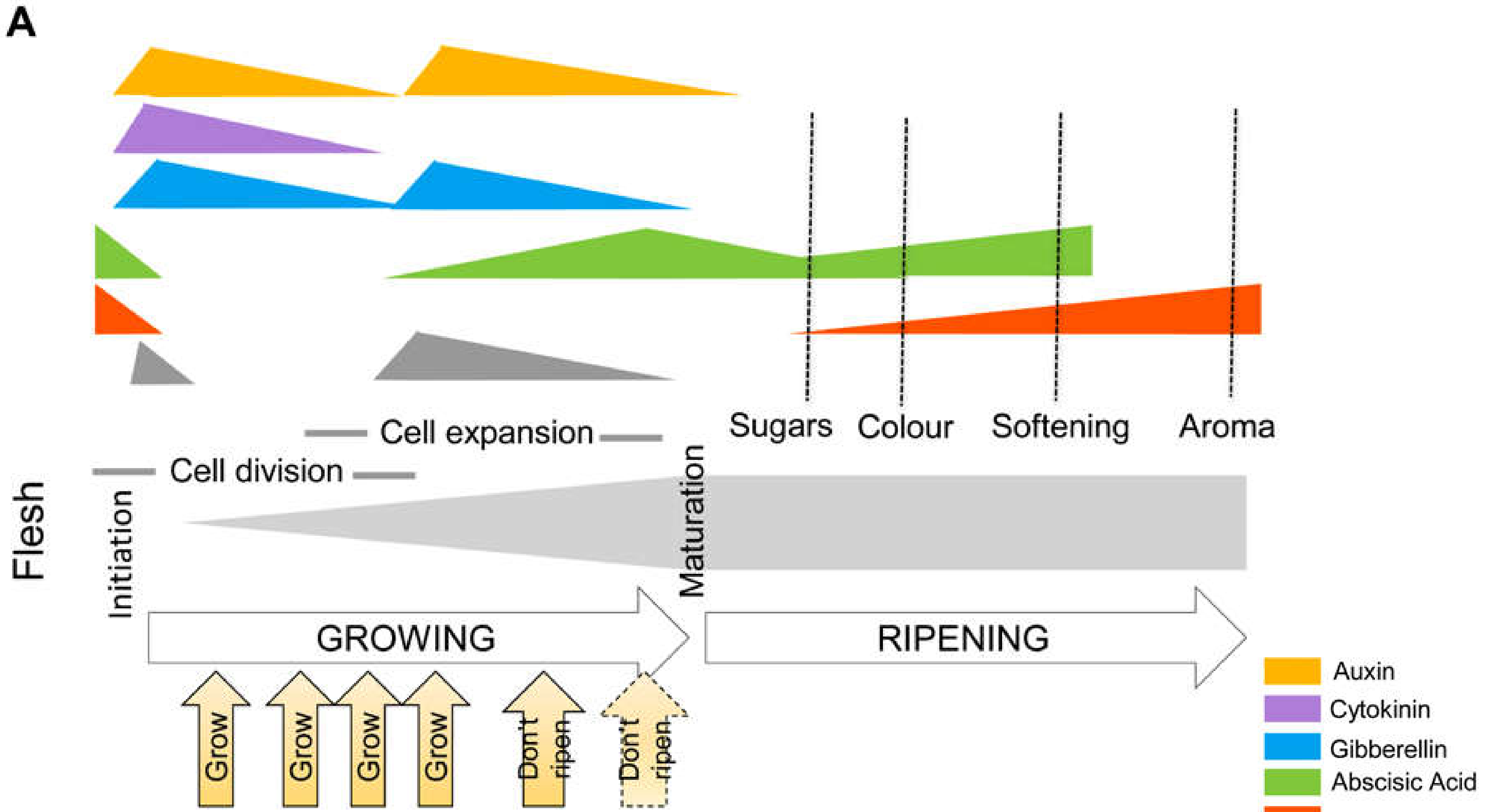

Circadian clock
FKF1
GI
CDFs
CO
FT
TRENDS in Genetics


A
Col WT
0 4 8 12 16 20
GI
ACT2
0 4 8 12 16 20 24

45.2 How Do Hormones Regulate Plant Life Cycles?

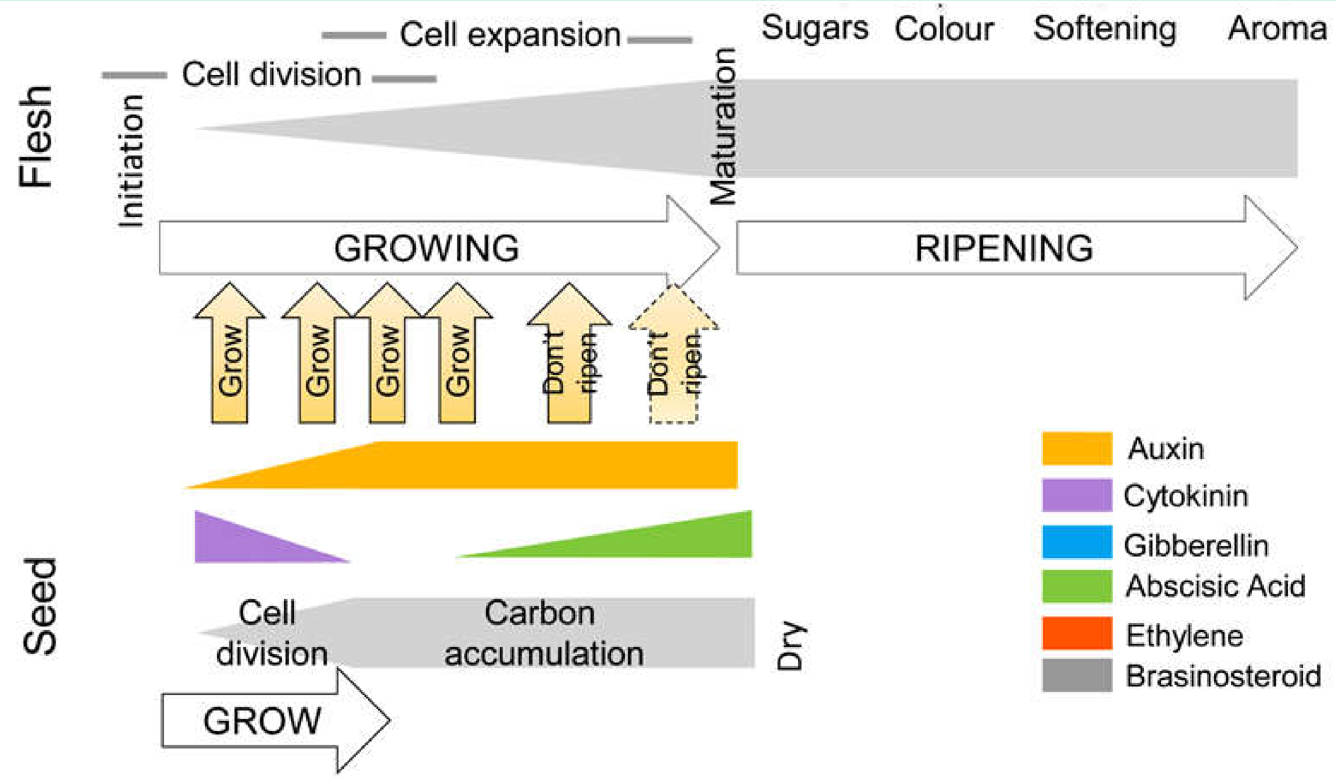
- Hormones coordinate the development and ripening of fruits and seeds
  - Seed maturation and fruit ripening are closely coordinated

45.2 How Do Hormones Regulate Plant Life Cycles?



McAtee et. al. 2013 *Frontiers in Plant Sciences*

45.2 How Do Hormones Regulate Plant Life Cycles?



The "seed control" hypothesis

the seeds communicate through hormones to the surrounding tissue(s) to promote fruit growth through firstly cell division and later on cell expansion

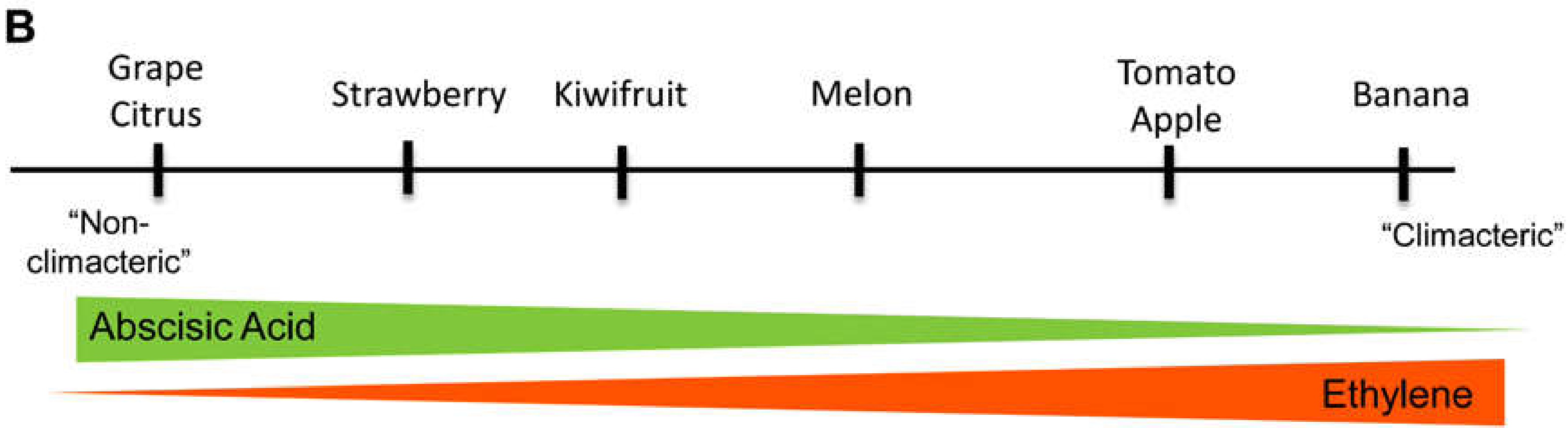
45.2 How Do Hormones Regulate Plant Life Cycles?

+GA -GA

45.2 How Do Hormones Regulate Plant Life Cycles?

- Climacteric fruit (更年型果实；呼吸跃变型果实) vs. non-climacteric fruit

  Climacteric fruit are characterized by a ripening-associated increase in respiration and in ethylene production, the phytohormone ethylene being the major trigger and coordinator of the ripening process



45.2 How Do Hormones Regulate Plant Life Cycles?

- Senescence and dormancy prepare the plant for winter

In autumn, under the influence of **shortening days and falling temperatures**, plants undergo **senescence (衰老)**, a **genetically programmed** series of events that prepares the plant for winter

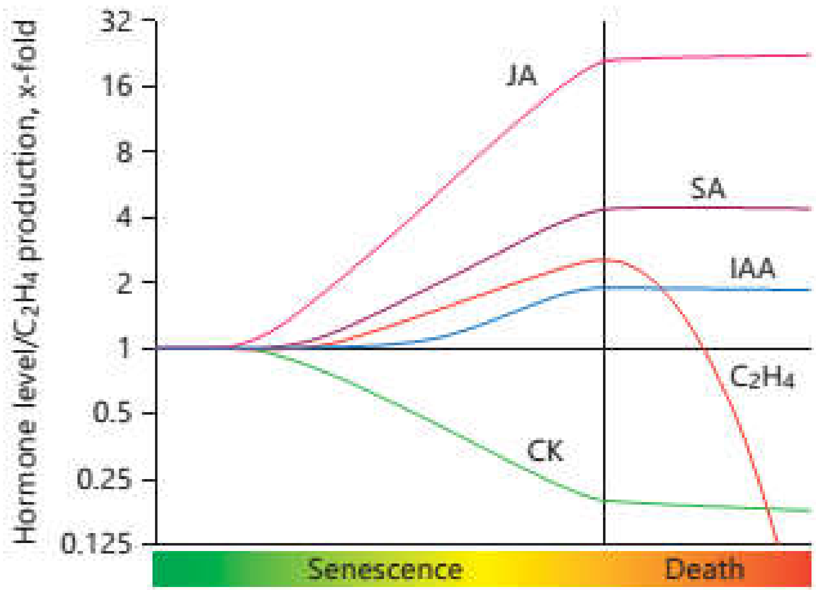
Khan et. al. 2014 *Gerontology*

45.2 How Do Hormones Regulate Plant Life Cycles?

During Leaf Senescence

- Starches and chlorophyll are broken down
- Dismantling of cellular organelles, degradation of protein, nucleic acid, lipid and remobilization of nutrients and nitrogen compounds
- Respiration is maintained and transcriptional machinery remains active
- Many hormones influence senescence

1. **Age-dependent, developmental senescence,**
2. **Stress-regulated senescence**

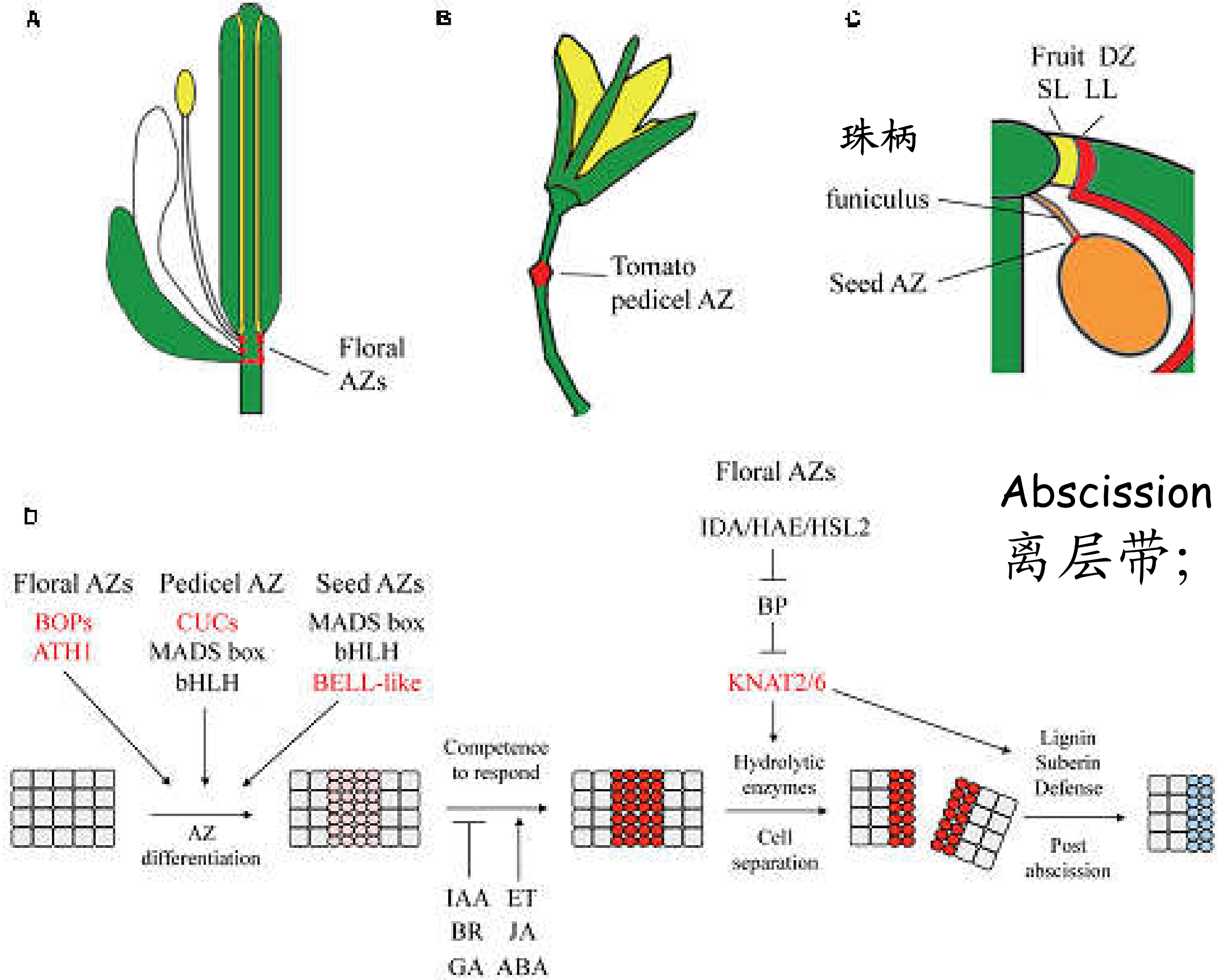


Khan et. al. 2014 *Gerontology*

45.2 How Do Hormones Regulate Plant Life Cycles?

- Senescence and dormancy prepare the plant for winter
  - In autumn, under the influence of **shortening days and falling temperatures**, plants undergo **senescence** (衰老), a **genetically programmed** series of events that prepares the plant for winter
- Abscission
  - The abscission layer is located where fruit or leaf stalks join the stem

45.2 How Do Hormones Regulate Plant Life Cycles?

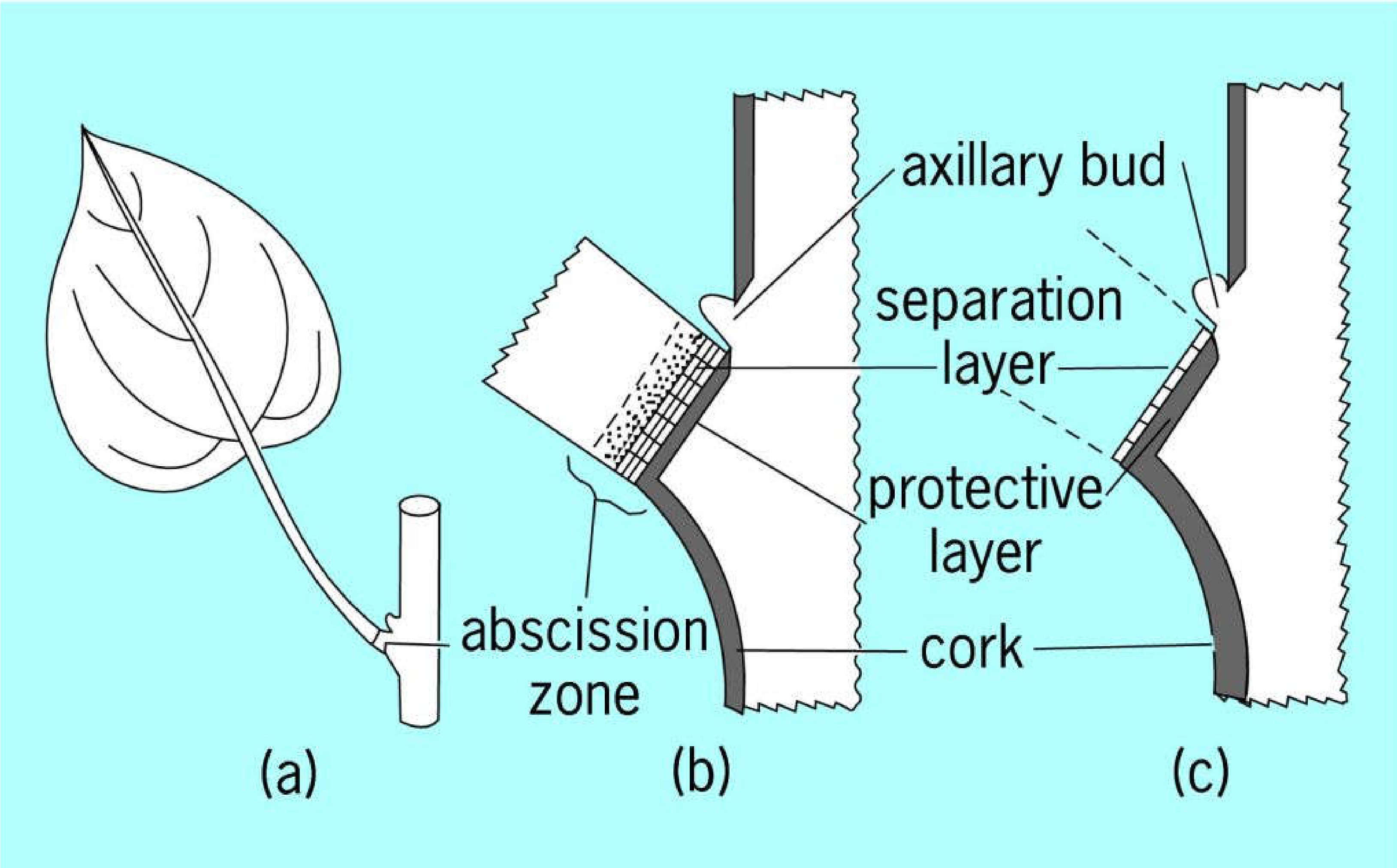


Abscission zones (AZs)
离层带；离层区

Suberin 软木脂

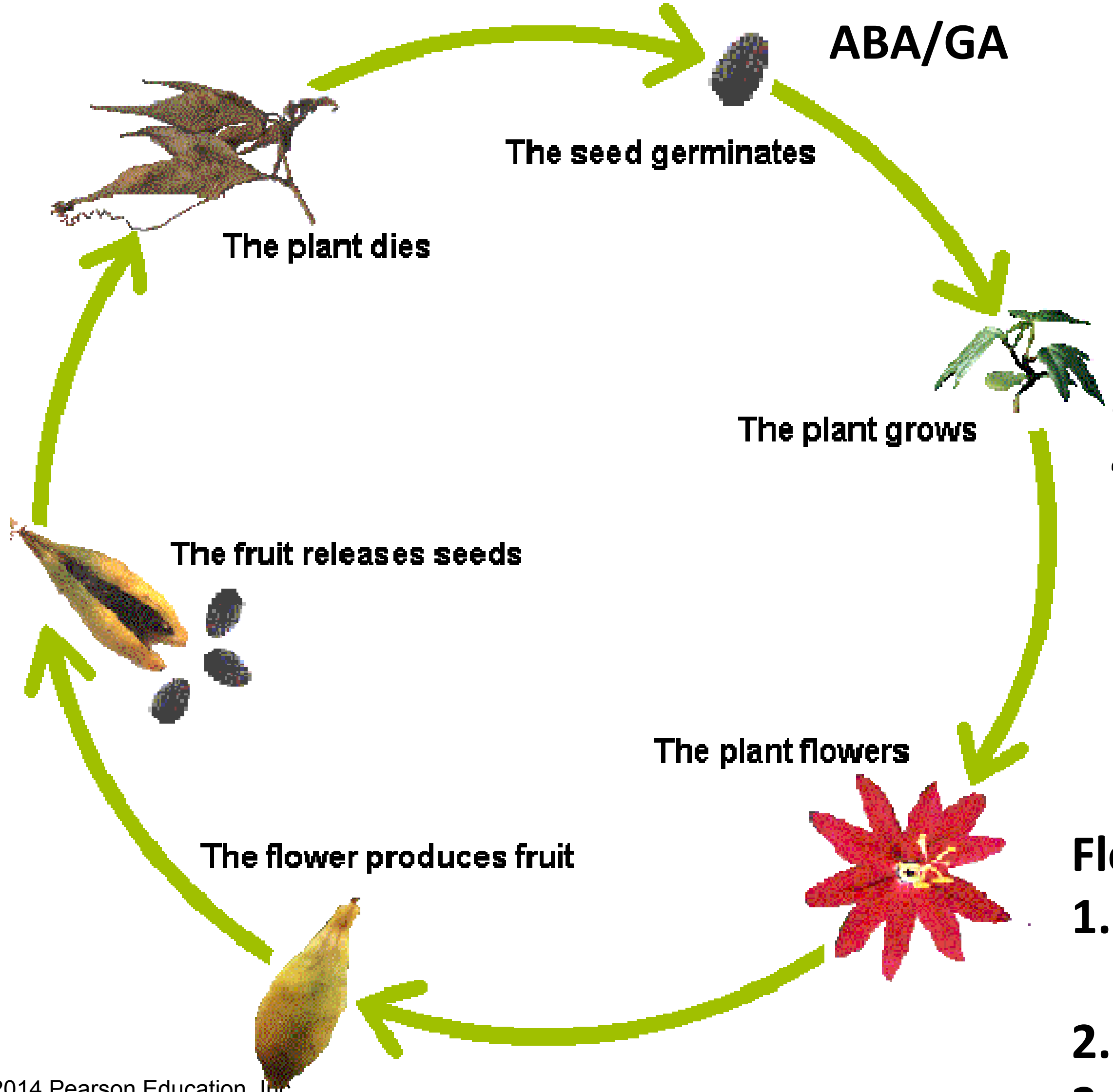
Hepworth et. al. 2015 *Frontiers in Plant Sciences*

45.2 How Do Hormones Regulate Plant Life Cycles?



http://encyclopedia2.thefreedictionary.com/abscission

Summary



ABA/GA

1. Gravitropism: Auxin
2. Triple response: ethylene
3. Elongation growth: GA
4. branching
   - Shoot: Cytokinin
   - Root: auxin
5. Influence from light
   - Phytochrome
   - Shade avoidance

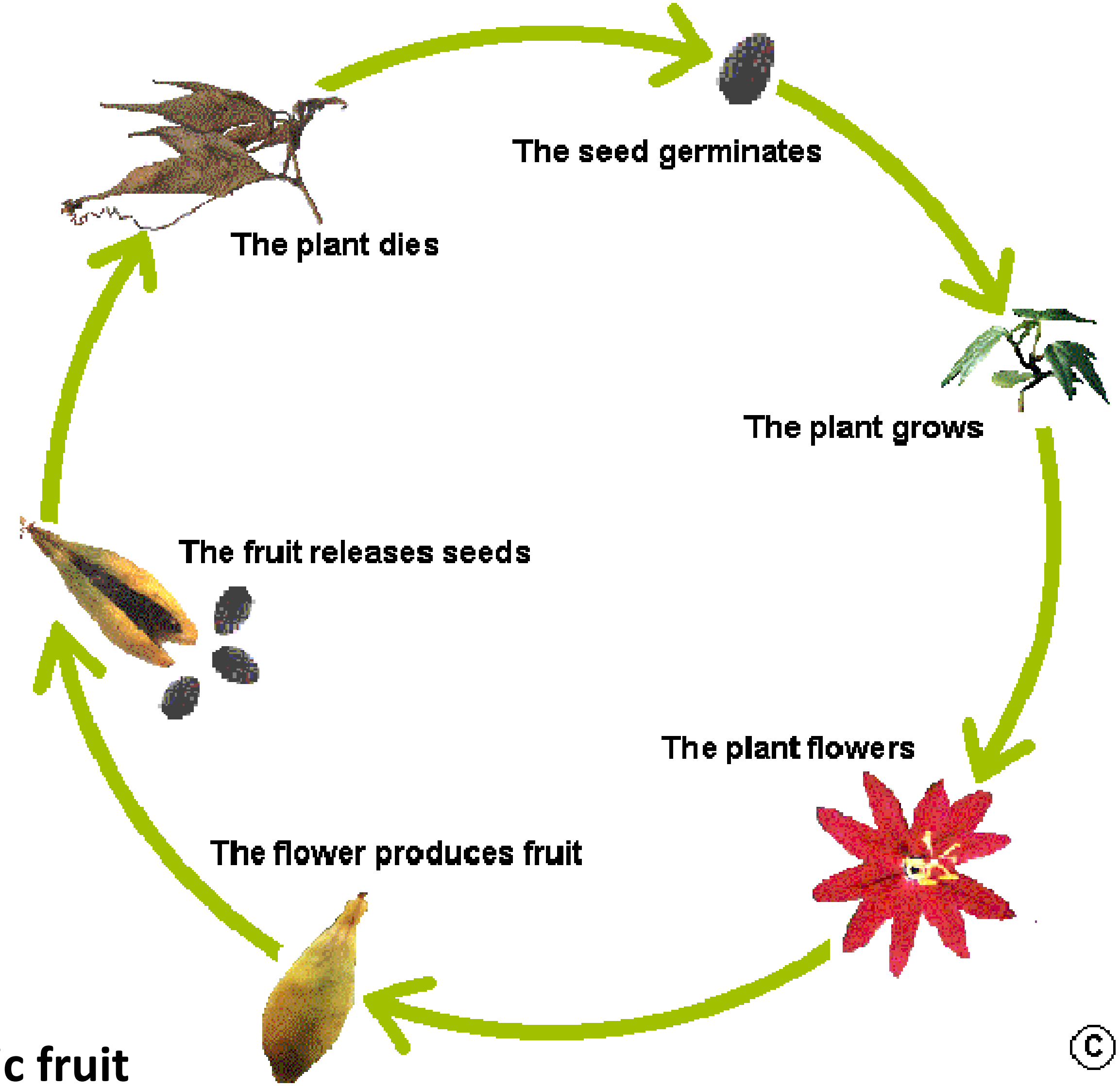
Flowering control

1. Four flowering time control pathways
2. Circadian clock:
3. Florigen

Summary

Senescence

- Leaf senescence
  - age-dependent
  - stress-dependent
- Abscission



Fruit growth: GA

Fruit ripening: ET/ABA

Climacteric / non-climacteric fruit

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

http://ww7.cienciaencanoa.com/legacy

Plant Defense– against microbial pathogens

Nonspecific defense mechanisms

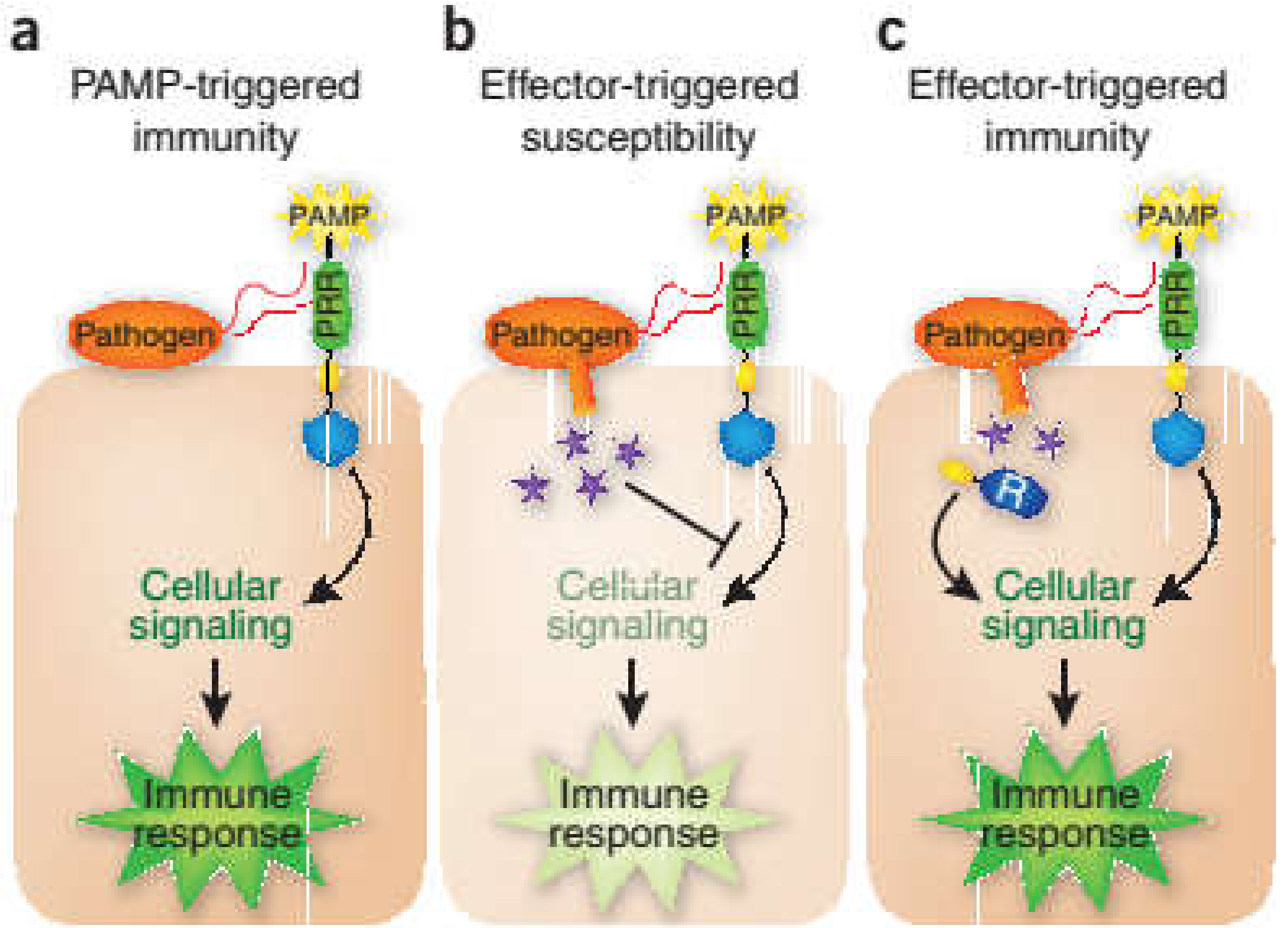
- Physical barrier
  - Waxy cuticle, cell wall, cell membrane
  - Callose (胼胝质), induced upon infections
- Chemical barrier
  - Saponin (皂素, glycosylated triterpenoids三萜)

Plant Defense– against microbial pathogens

Specific defense mechanisms

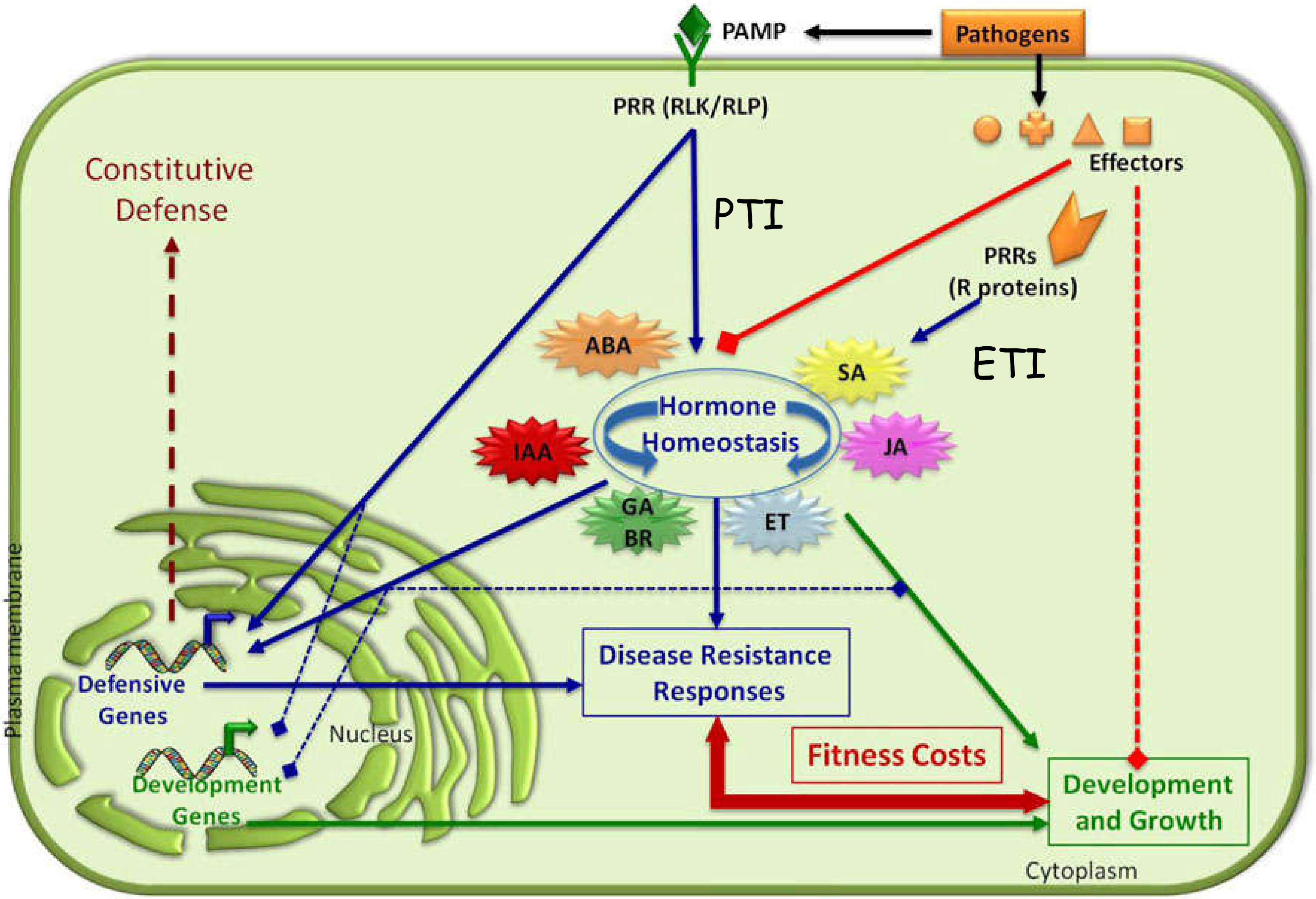
- PTI, PAMP triggered immunity
  - **PAMP/MAMP**: pathogen (病原体)/microbe-associated molecular patterns
  - Examples: flagellins and peptidoglycan (肽聚糖) (bacteria), chitin (fungi)
  - Recognized by pattern-recognition receptors (PRR) e.g. FLS2-flagellin
- ETI, effector triggered immunity
  - Plant evolved resistance proteins (R) that recognize the presence of some effectors (Avr) **directly or indirectly**, a mechanism so called **gene-for-gene interaction**
  - Effectors: molecules produced by pathogens, which modulate plant immunity and enable parasitic infection e.g. AvrPtoB—targets FLS2 for degradation
  - Example: R protein Prf **detects the presence of AvrPtoB**

Plant Defense– against microbial pathogens



Pieterse et. al. 2009 *Natural Chemical Biology*

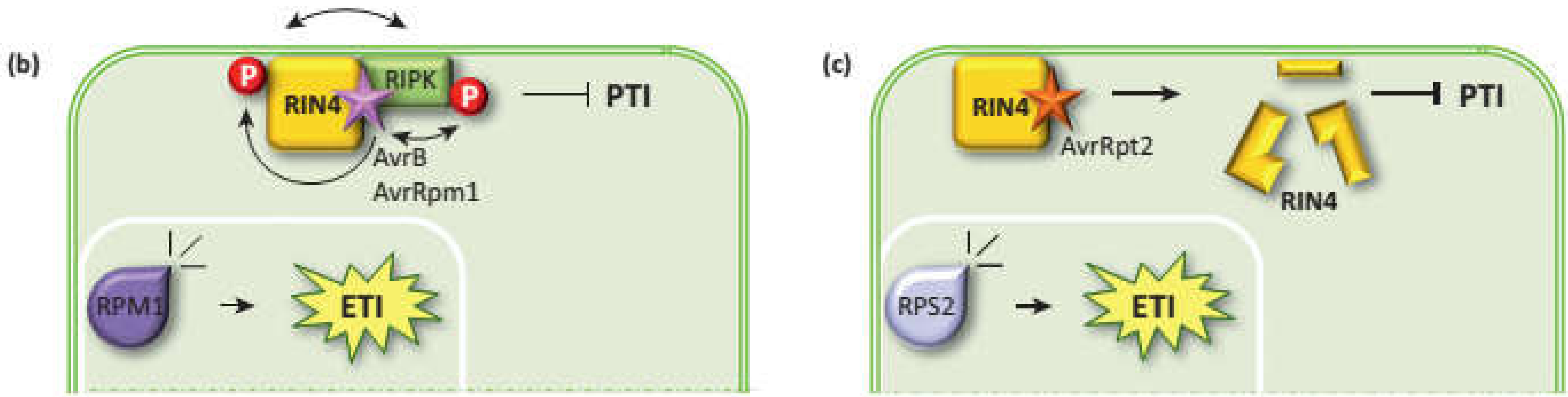
Plant Defense– against microbial pathogens



Denance et. al. 2013 *Frontiers in Plant Sciences*

Plant Defense– against microbial pathogens

Guard and guardee model



Guard: R protein;
Guardee: host proteins, targets of effectors

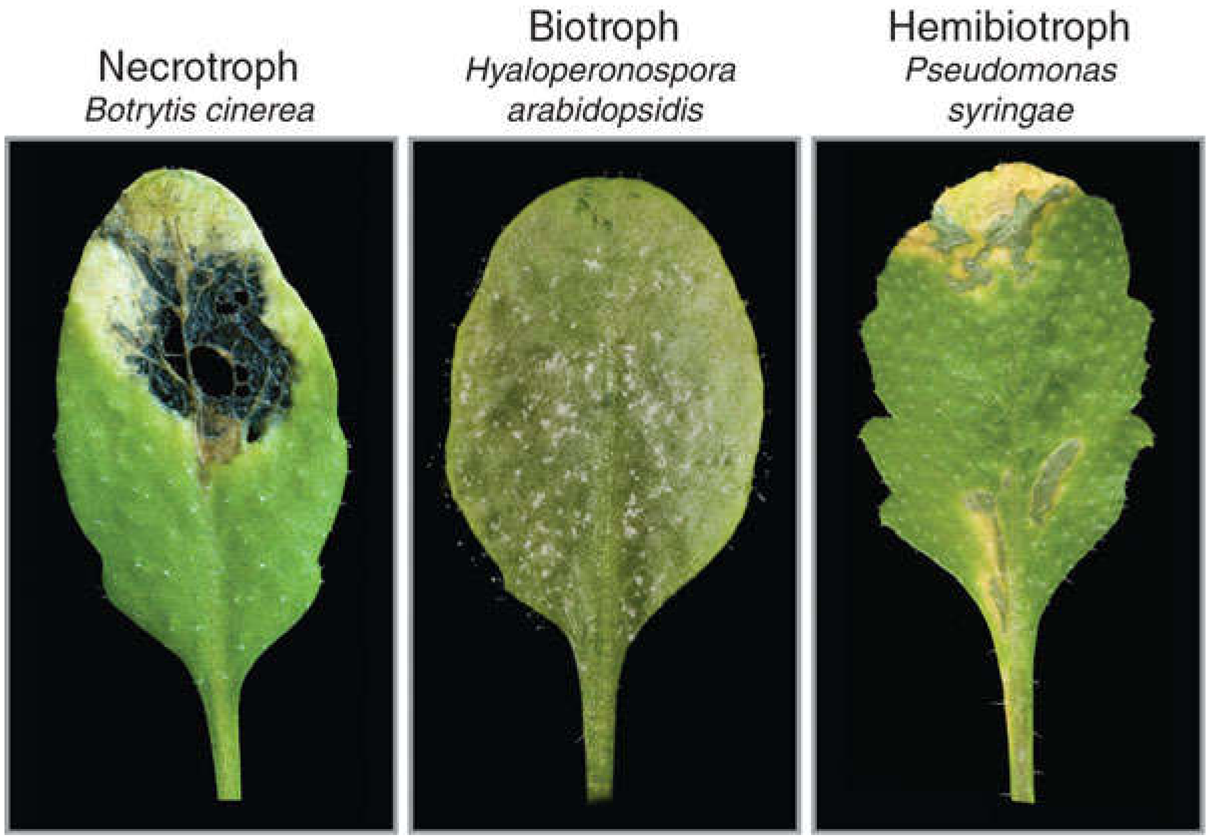
45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Local responses: occur **at the infection site**
- Acquired resistance **in uninfected tissues**
- Acquired resistance **in neighbouring plants**

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Local responses: occur **at the infection site**
  - Production of signal molecules and defense genes
  - Mediated by SA or JA/ET
  - In some cases, **hypersensitive cell death** (localized cell death) is induced to restrict pathogens
- Acquired resistance **in uninfected tissues**
- Acquired resistance **in neighbouring plants**

Biotrophic and necrotrophic pathogens

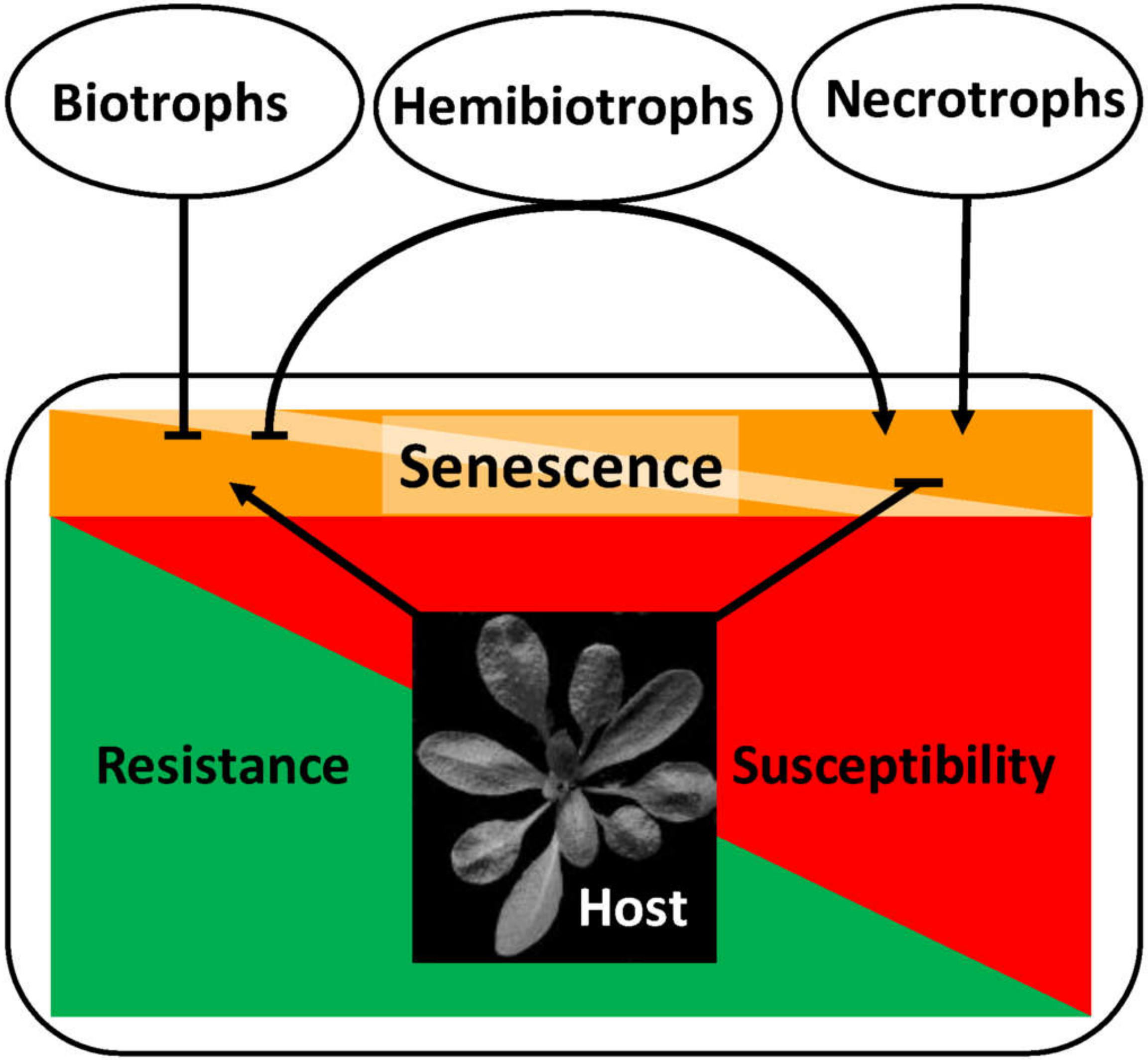


Biotrophs（活体营养型） feed on living host tissue

necrotrophs（死体营养型）cause die-off and feed on the remains

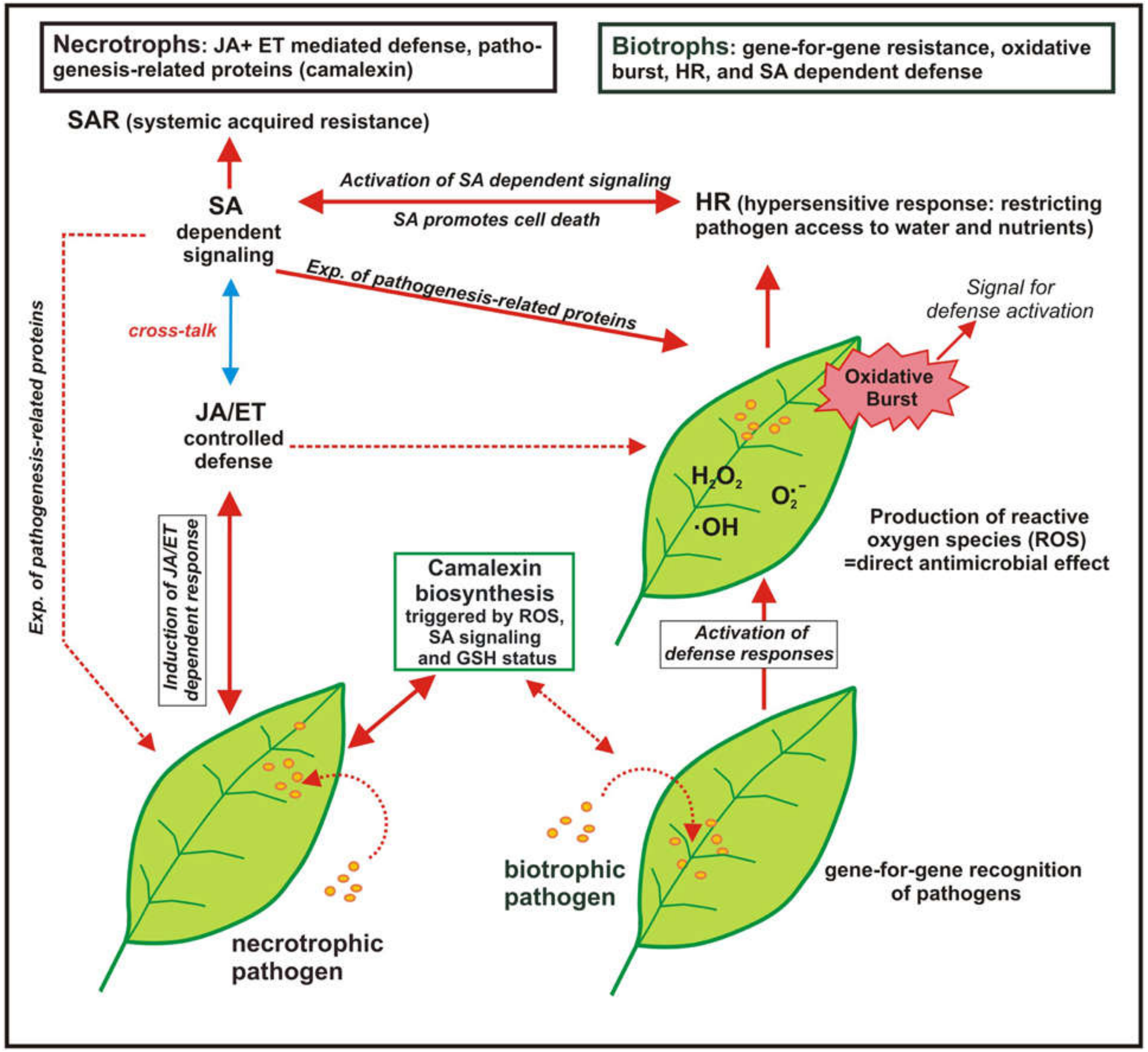
Pieterse et. al. 2009 ***Natural Chemical Biology***

Biotrophic and necrotrophic pathogens



Haffner et. al. **2015** *Plants*

Biotrophic and necrotrophic pathogens



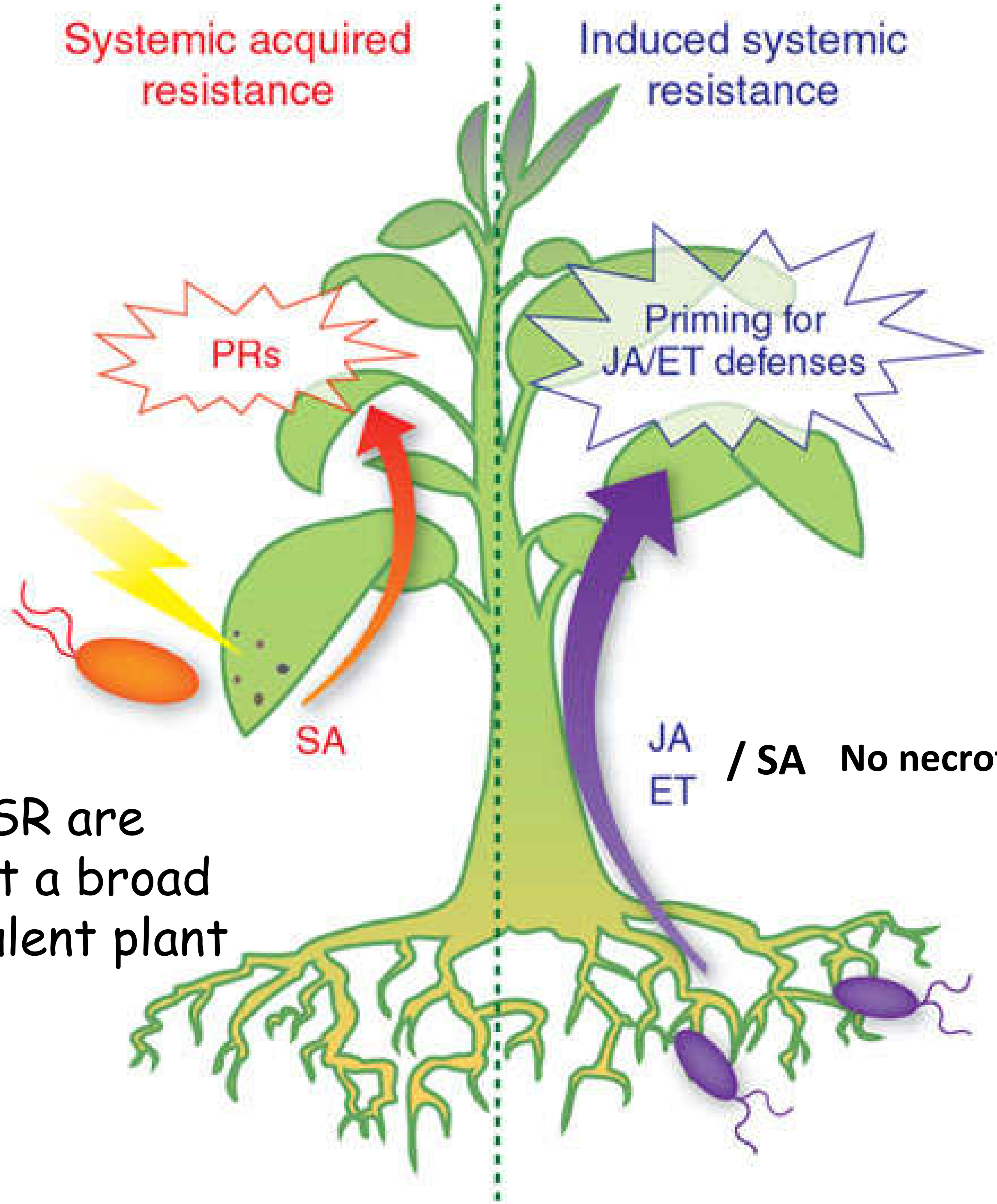
Avr-R interaction

Bloem et. al. **2015** *Frontiers in Plant Science*

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Local responses: occur **at the infection site**
  - Production of signal molecules and defense genes
  - In some cases, hypersensitive cell death (localized cell death) is induced to restrict pathogens
  - Mediated by SA or JA/ET
- Acquired resistance **in uninfected tissues**
  - SAR: Systemic acquired resistance (is typically activated in healthy systemic tissues of locally infected plants)
  - ISR: Induced systemic resistance (typically activated upon colonization of plant roots by beneficial microorganisms)
- Acquired resistance **in neighbouring plants**

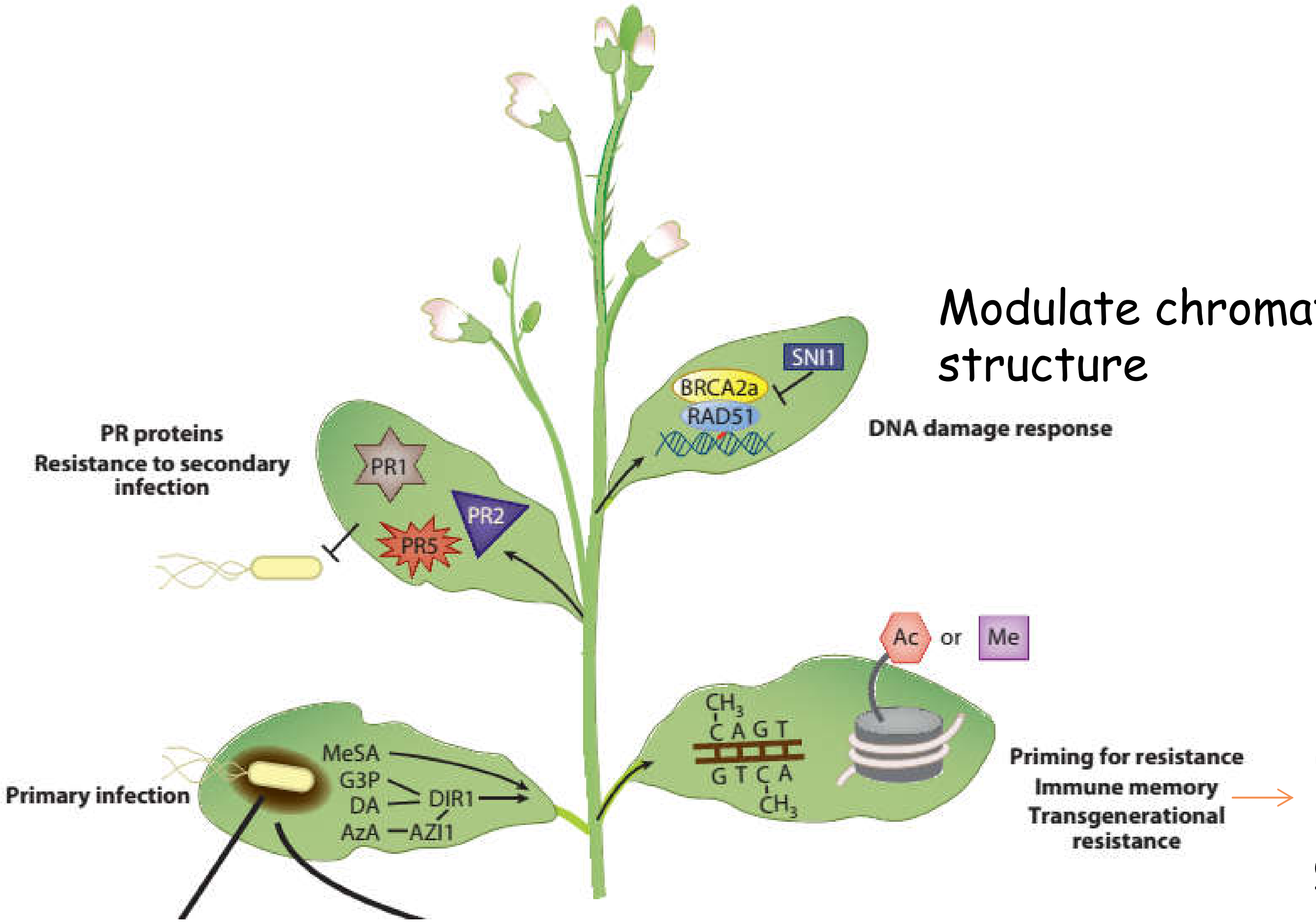
Necrotic lesion
Especialy during
hypersensitive cell death



/ SA No necrotic lesion

Both SAR and ISR are effective against a broad spectrum of virulent plant pathogens.

Acquired resistance responses

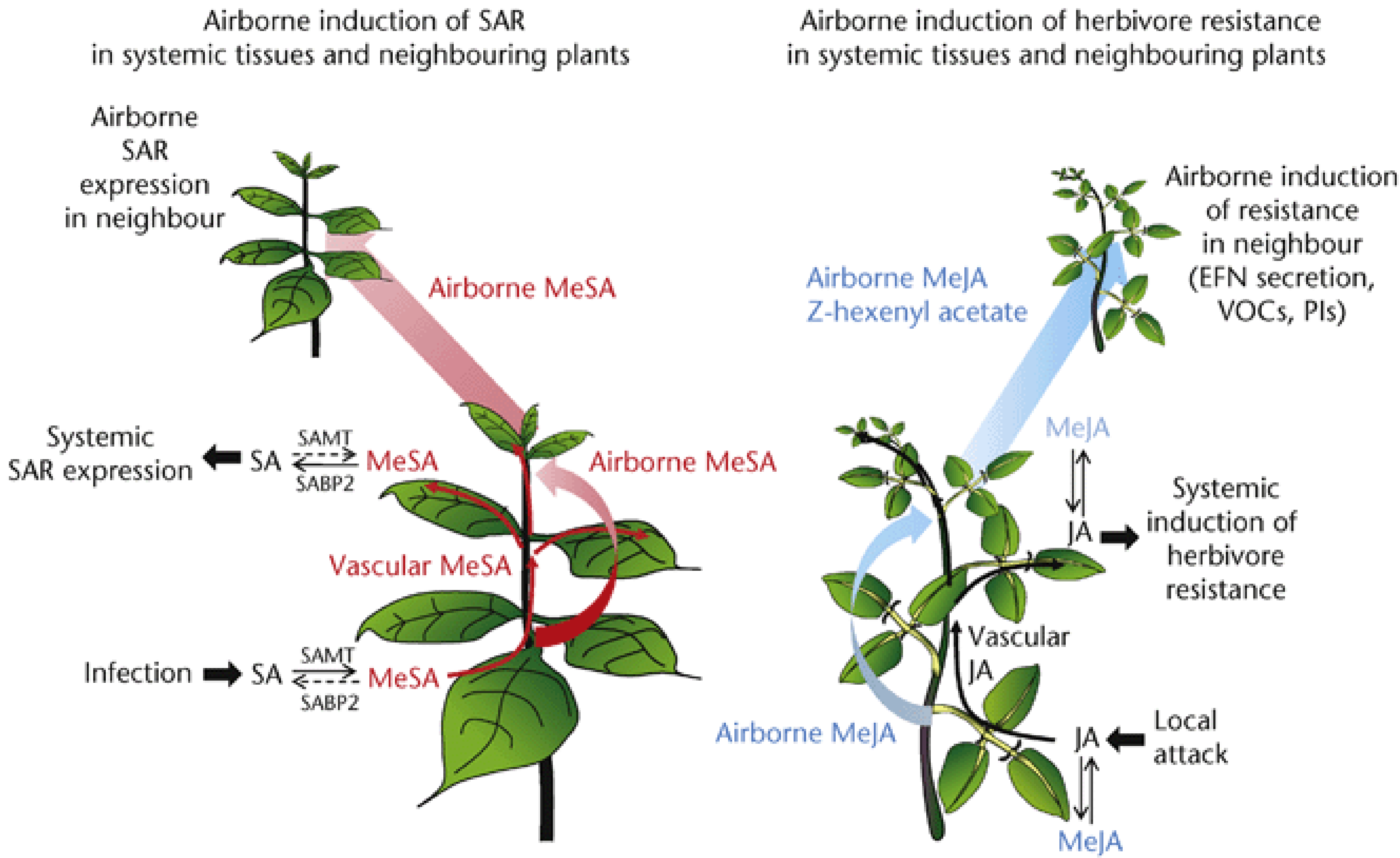


Modulate chromatin structure

Pass on to next generation

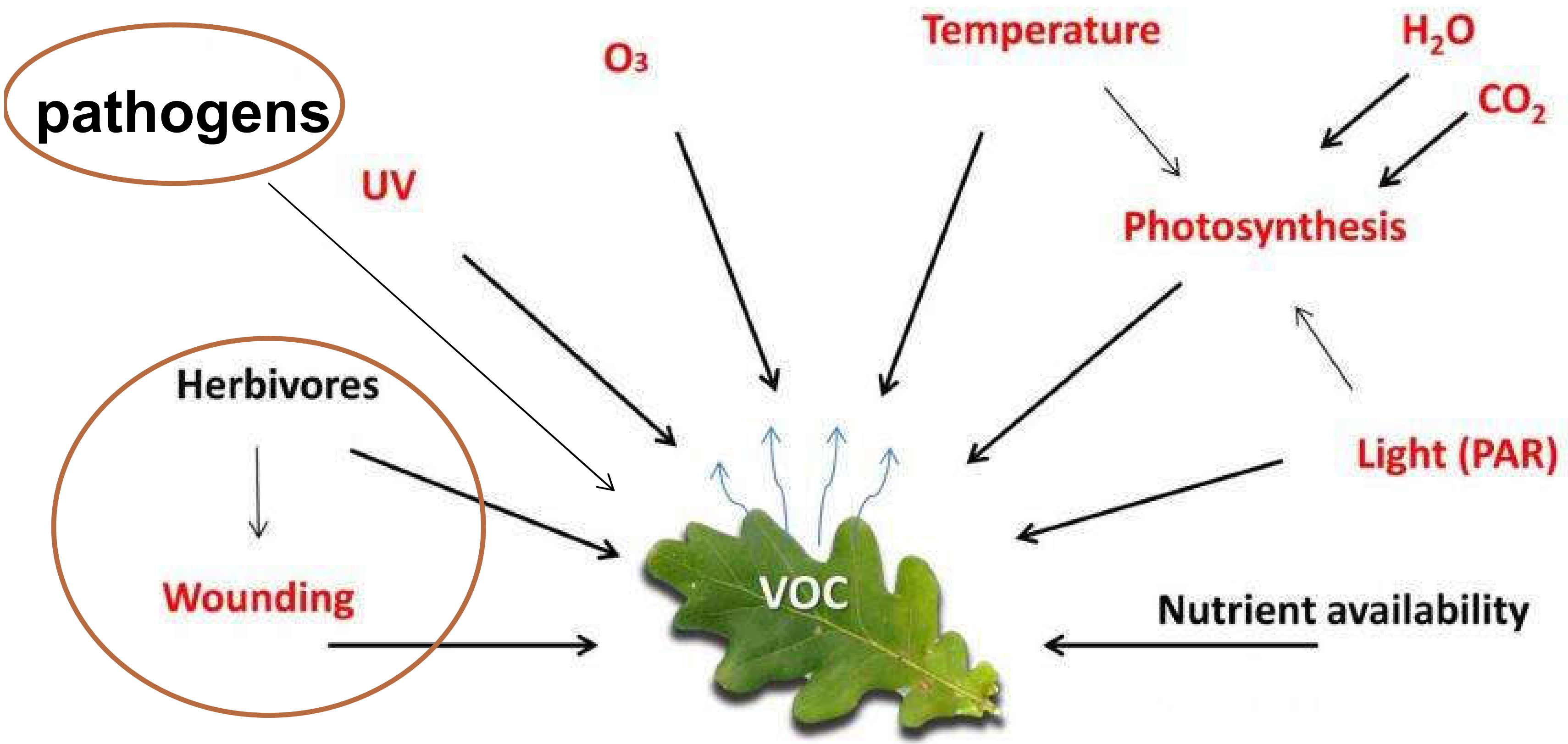
45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Local responses: occur **at the infection site**
  - Production of signal molecules and defense genes
  - In some cases, hypersensitive cell death (localized cell death) is induced to restrict pathogens
  - Mediated by SA or JA/ET
- Acquired resistance **in uninfected tissues**
  - SAR: Systemic acquired resistance (is typically activated in healthy systemic tissues of locally infected plants)
  - ISR: Induced systemic resistance (typically activated upon colonization of plant roots by beneficial microorganisms)
- Acquired resistance **in neighbouring plants**
  - Can occur between plants of the same / different species



Airborne induction of SAR
in systemic tissues and neighbouring plants
Airborne
SAR
expression
in neighbour
Airborne MeSA
Systemic
SAR expression
SA
SAMT
SABP2
MeSA
Airborne MeSA
Vascular MeSA
Infection
SA
SAMT
SABP2
MeSA
Airborne induction of herbivore resistance
in systemic tissues and neighbouring plants
Airborne induction
of resistance
in neighbour
(EFN secretion,
VOCs, PIs)
Airborne MeJA
Z-hexenyl acetate
MeJA
JA
Systemic
induction of
herbivore
resistance
Vascular
JA
Airborne MeJA
JA
Local
attack
MeJA

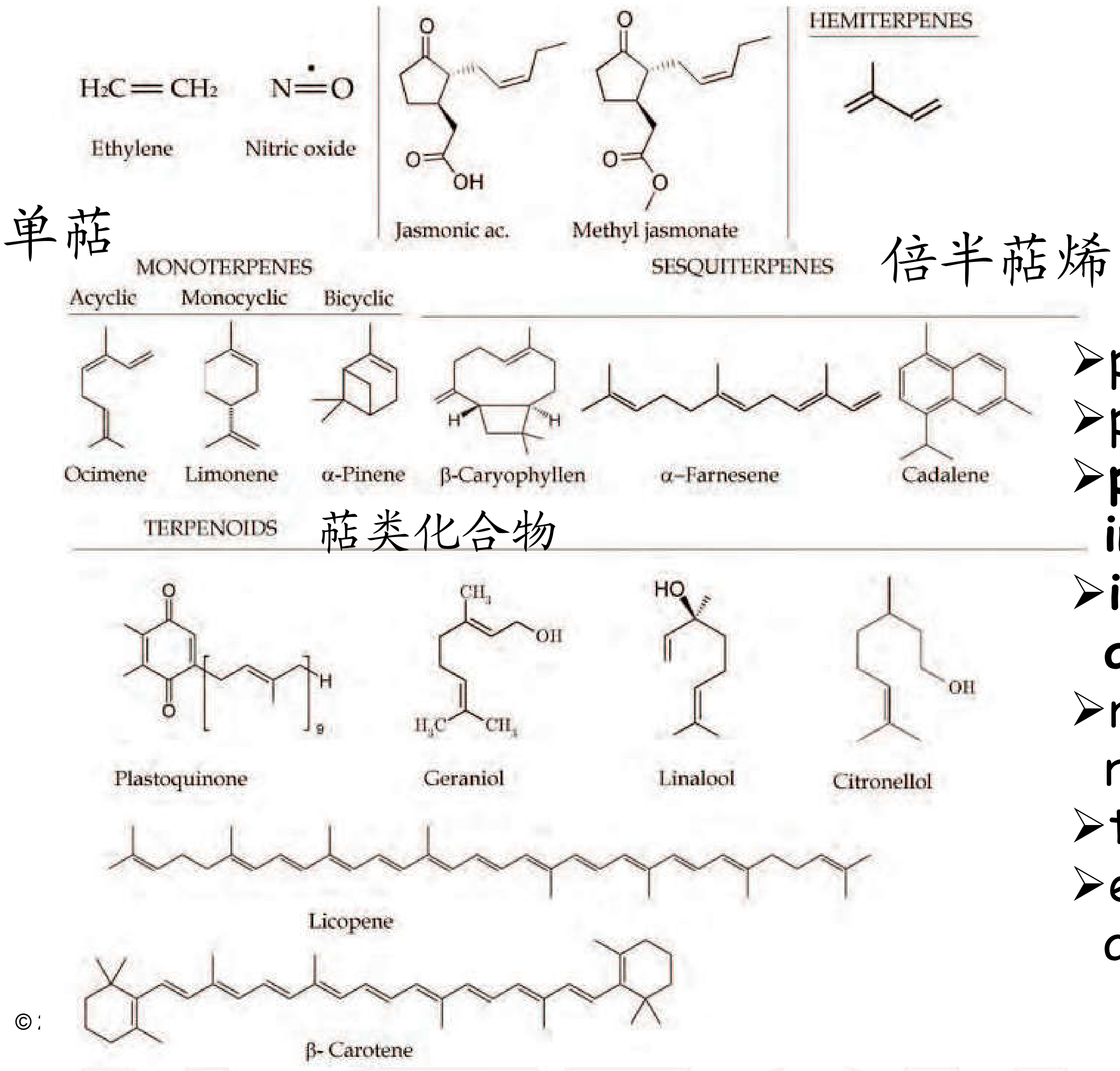
VOC: volatile organic compounds



Impact of abiotic and biotic factors on plant VOC emission. The factors in red are affected by any plant enclosure.

Materie et. al. **2015** *Bioone*

VOC: volatile organic compounds



- pollinator attraction,
- plant-plant communication,
- **plant-pathogen interactions,**
- **indirect plant defense against insects**
- reactive oxygen species removal,
- thermo-tolerance
- environmental stress adaptation.

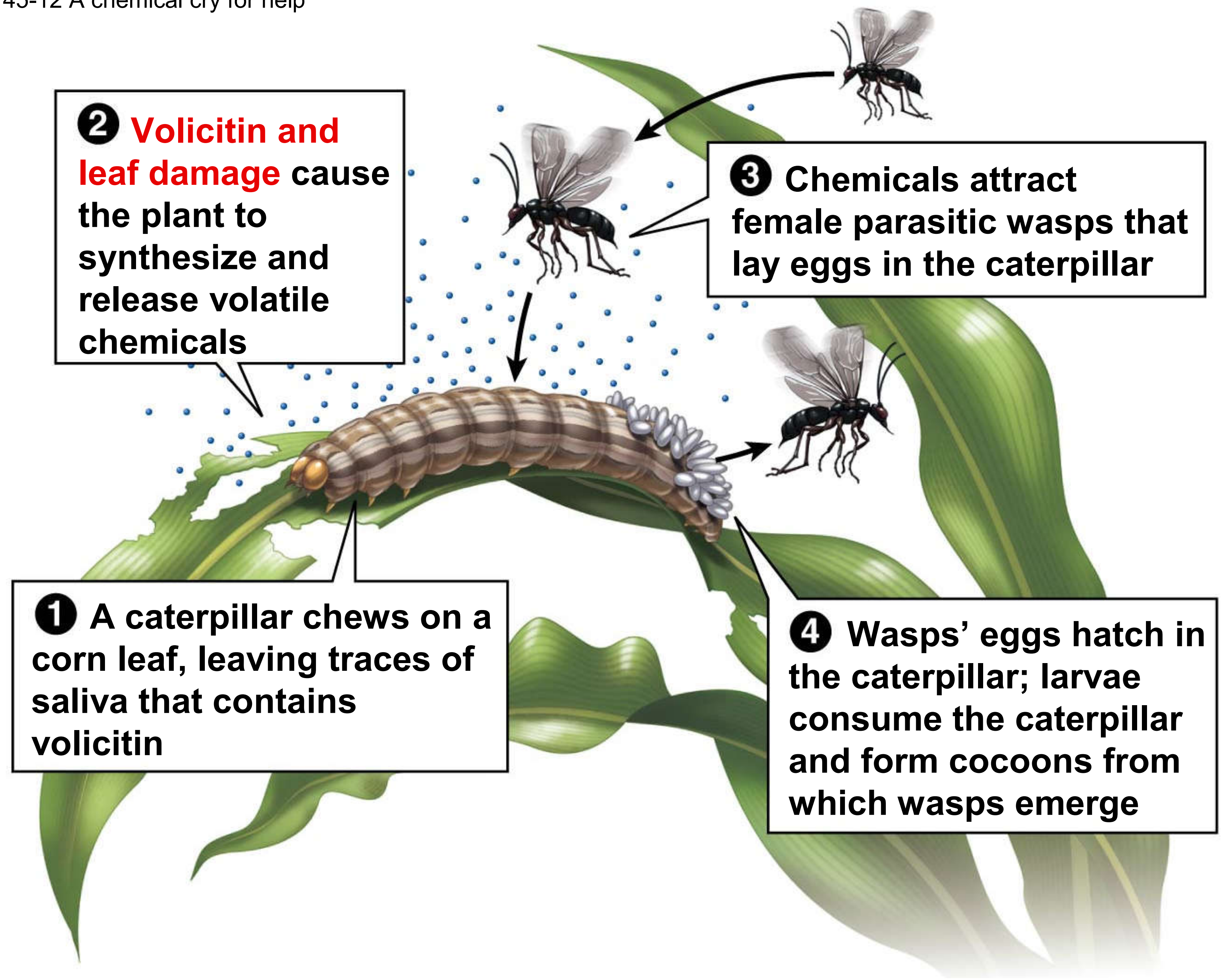
VOCs in Plant defense

- Induce defense response in neighbouring plants
  - By infected plants
  - By wounded plants
  - BUT, some insects can sense these VOCs to localize target plants
  - Some plants change components of VOCs after insect attack
    - Wild tobacco plants munched on by hornworms (hawk moth caterpillars 天蛾的幼虫) release different chemicals at different times

VOCs in Plant defense

- Induce defense response in neighbouring plants
- summon insect "bodyguards" when being attacked

Figure 45-12 A chemical cry for help



VOCs in Plant defense

- Induce defense response
- summon insect "bodyguards" when being attacked
  - lima bean (利马豆) plants that are attacked by spider mites (六点黄蜘蛛) release a chemical that attracts a carnivorous mite that preys on the spider mite

Plant Defense– against insects

- Plant senses
  - Wounding
  - Chemicals in saliva
- Plant respond by
  - produce signaling molecules, e.g. JA, ET, VOCs
  - stimulates responses that make the plant **more distasteful, more difficult to eat, or more toxic**
    - **nicotine (** 尼古丁, 烟碱**)**, a poison used commercially as an insecticide
    - Radish plants attacked by caterpillars produce a **bitter-tasting chemical** and grow **more spiny hairs** on their leaves

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Sensitive plants react to touch

(a) Before the leaves are touched

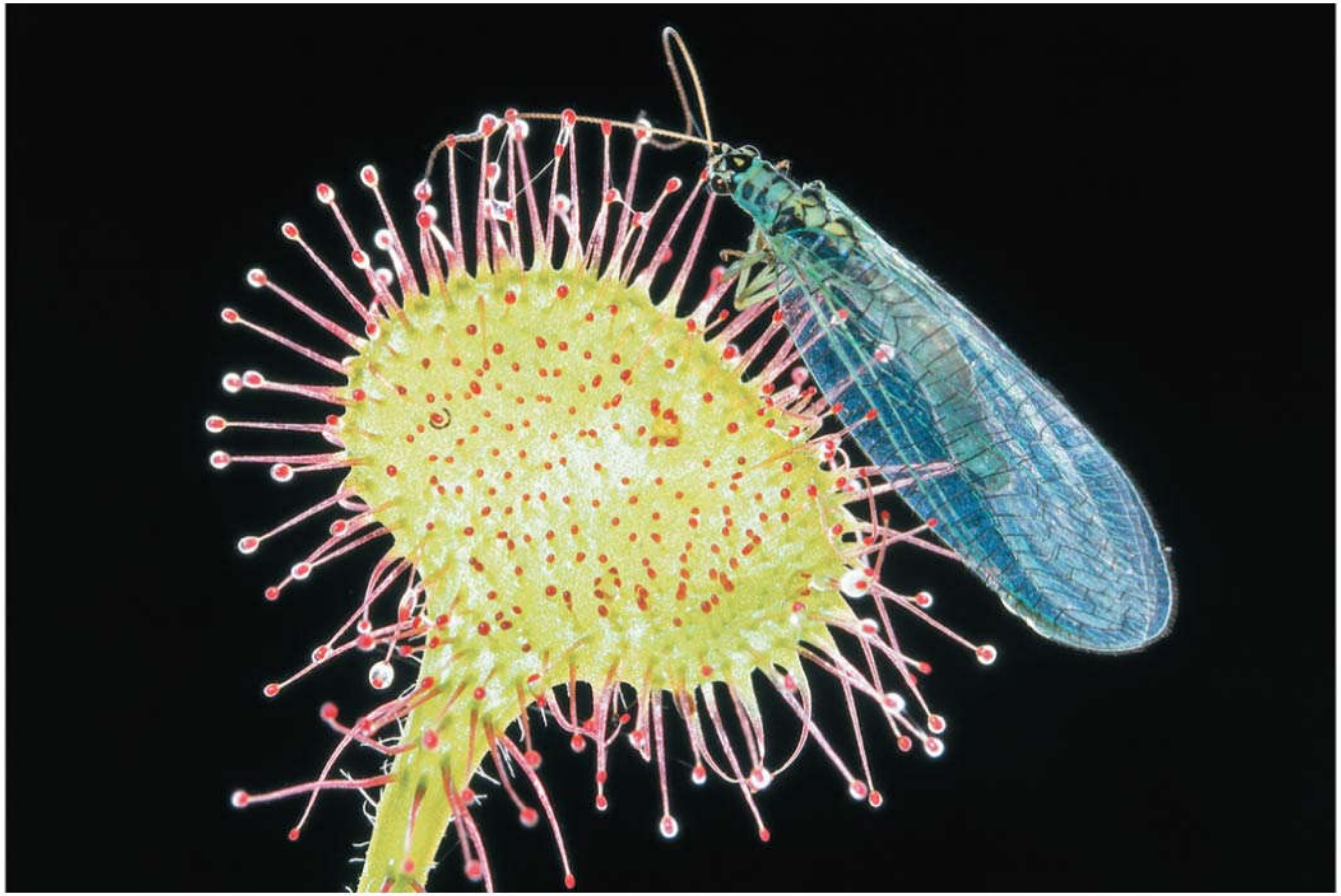
(b) After the leaves are touched

thigmotropism (向触性),

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

- Carnivorous sundews (毛毡苔) and bladderworts (狸藻类植物) respond rapidly to prey
  - Some plants have evolved ingenious prey-catching behavior

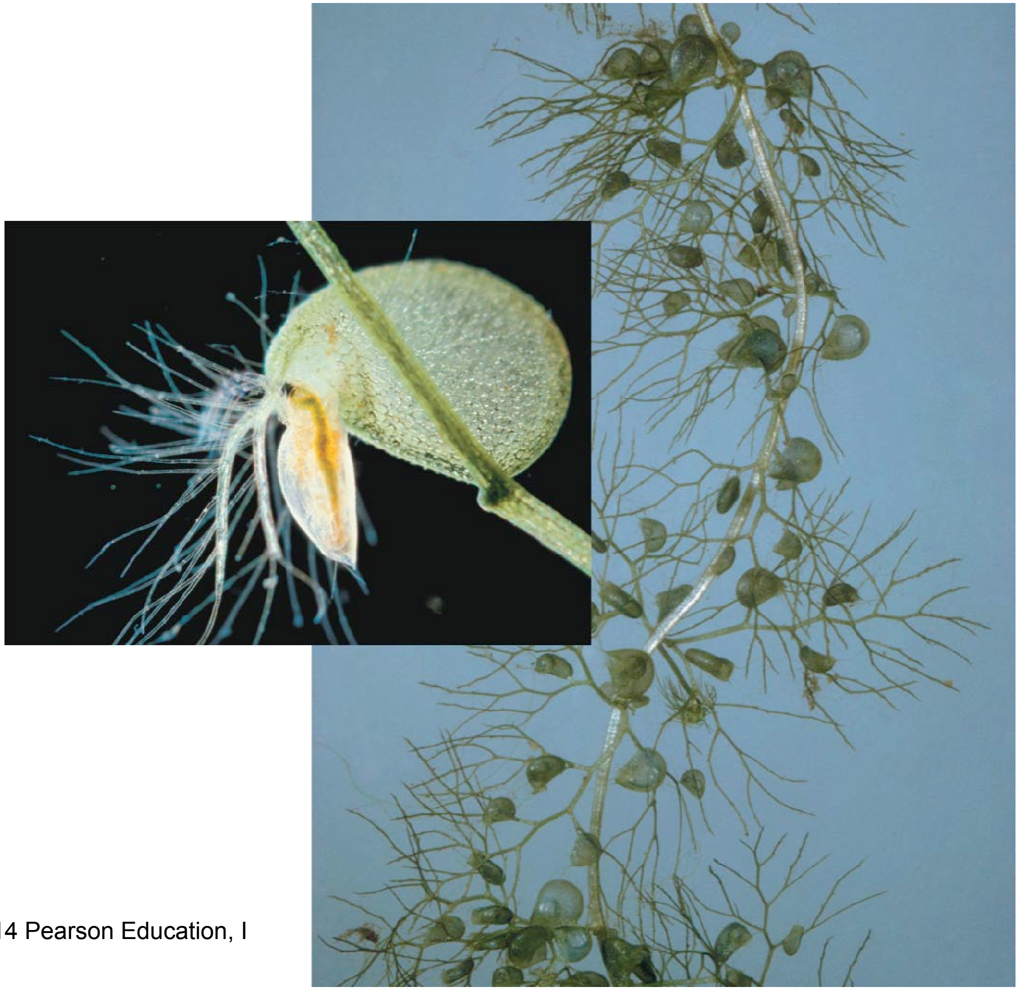
Figure 45-14 A sundew with its insect prey

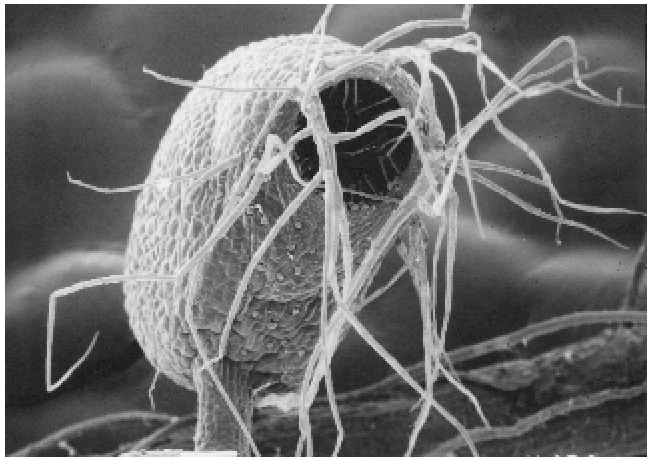


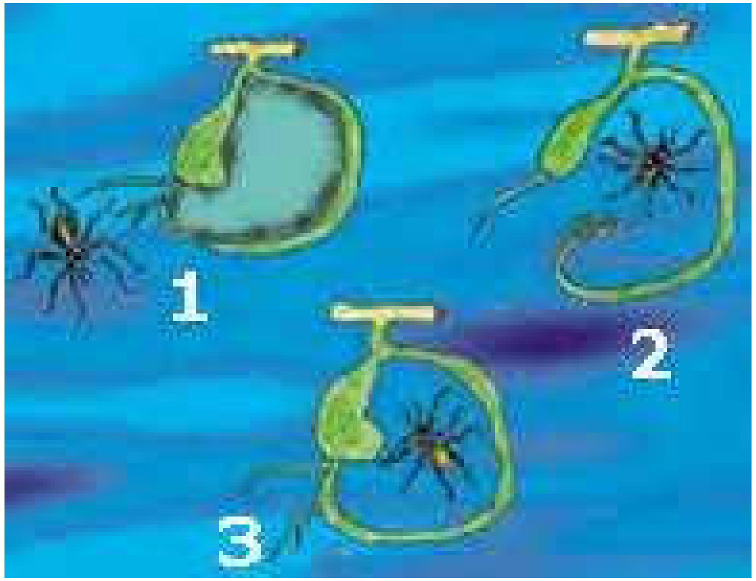
Sundew leaves

45.3 How Do Plants Communicate, Defend Themselves, and Capture Prey?

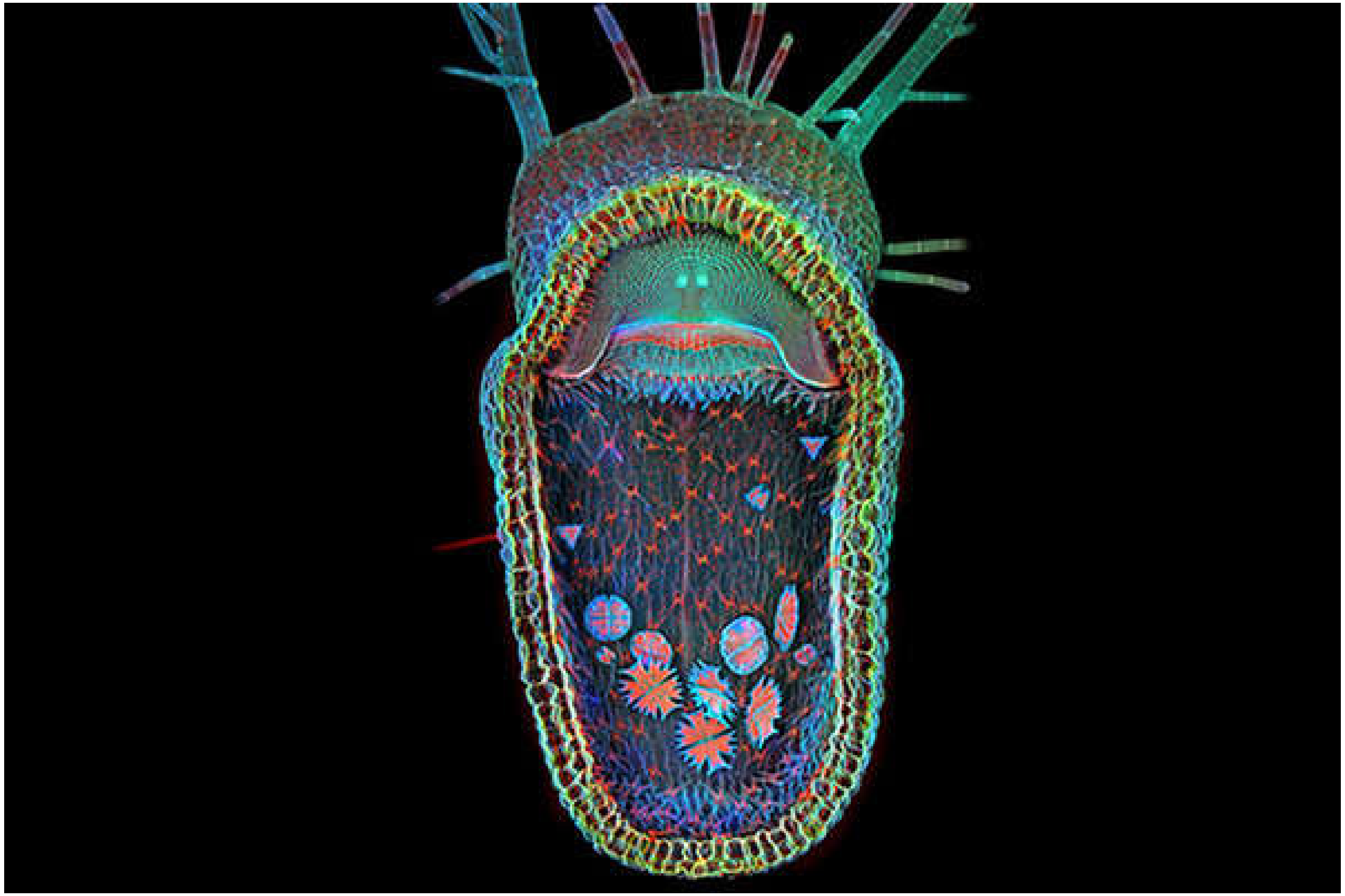
- The world's speediest plant is the predatory aquatic bladderwort (狸藻类植物)







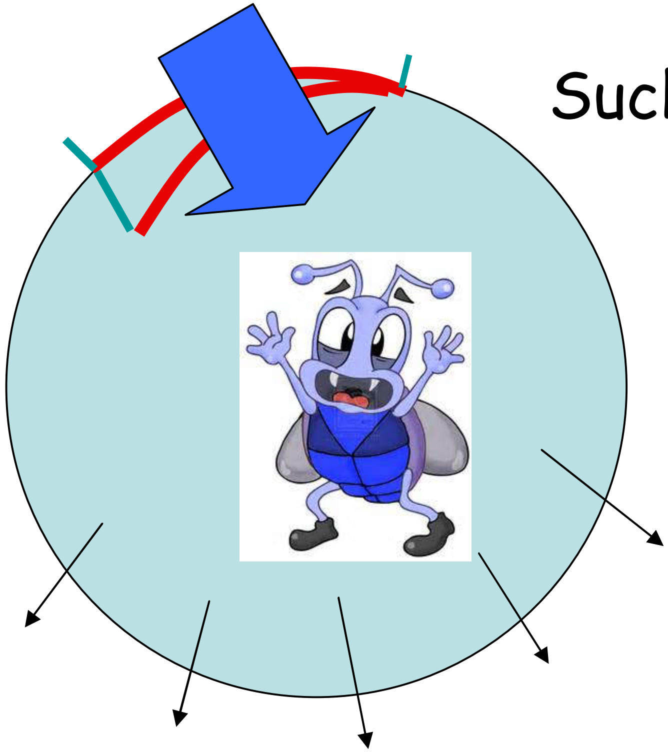
The bladder's trapdoor opens inwards, sucking in the prey in around one thousandth of a second



The gaping "mouth" of an aquatic killer that sucks in prey just a millisecond after the victims trigger its teensy hairs has been captured in a spellbinding image that has snagged first prize in a micro-photo competition.

http://www.csmonitor.com/Science/2013/1216/Gaping-jaws-of-carnivorous-plant-win-microphotography-prize

Sealed by sticky secretions



Suck in water and prey

Ions being transported out

Water leaves the bladder by osmosis

Summary

Defense against micribial pathogens

Nonspecific defense mechanisms

- Physical barrier
- Chemical barrier

Specific defense

- PTI, PAMP triggered immunity
- ETI, effector triggered immunity

Defense at different sites

- Local responses: occur **at the infection site: biotrophic/ necrotrophic**
- Acquired resistance **in uninfected tissues: SAR, ISR**
- Acquired resistance **in neighbouring plants: VOC**

Defense against insects

- sense
- Defense mechanism

Capture prey

The end of the Plant section!