

第三节、细胞分裂素（cytokinin, CTK）

1.发现:

THE CYTOKININS WERE DISCOVERED in the search for factors that stimulate plant cells to divide (i.e., undergo cytokinesis).

**1955, Skoog, 降解的鲱鱼精DNA (Herring Sperm DNA)
Breakdown Product of DNA**

**1956, 鉴定结构 6-呋喃氨基嘌呤, 6- furfurylaminopurine
激动素Kinetin**

1963, Letham, 玉米未成熟子粒中得到玉米素 Zeatin

1965, Skoog等建议命名为CTK (cytokinin, CK)

2.种类和化学结构

1) 腺嘌呤的衍生物

2) natural cytokinins

游离的细胞分裂素:

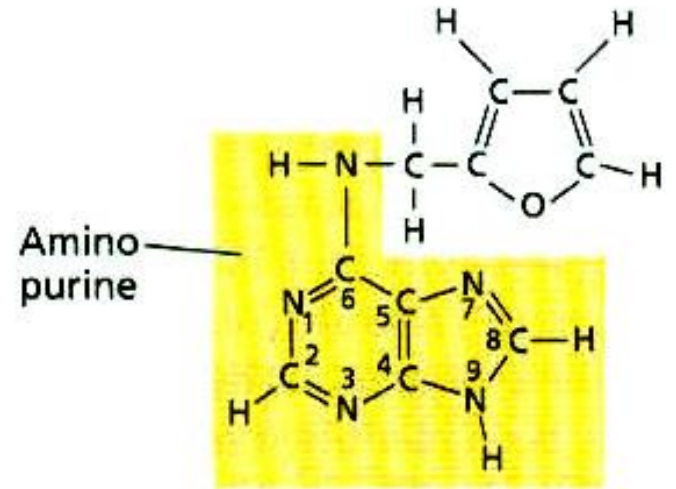
玉米素

玉米素核苷

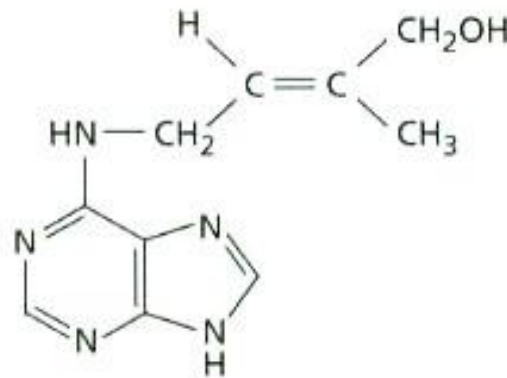
二氢玉米素

tRNA中的

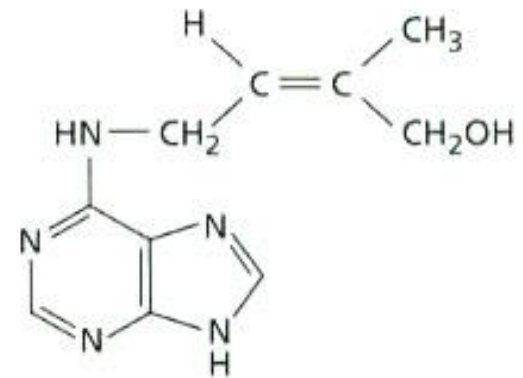
结合的;



Kinetin 激动素



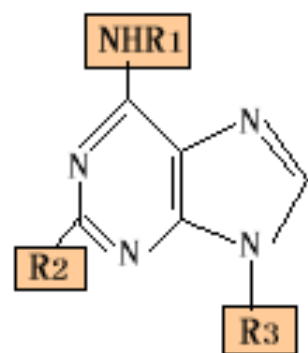
trans-Zeatin



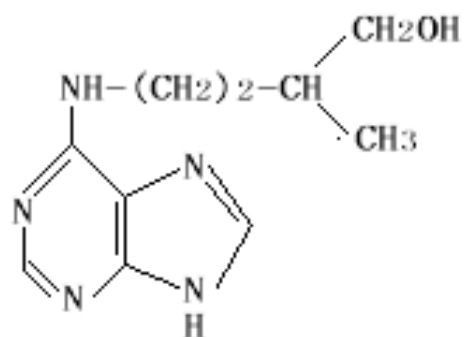
cis-Zeatin

6-(4-Hydroxy-3-methylbut-2-enylamino)purine

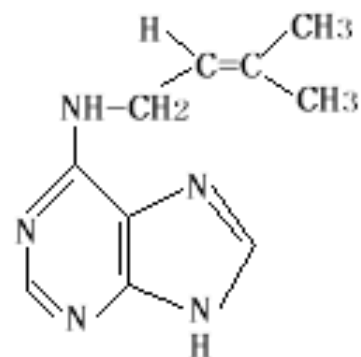
玉米素



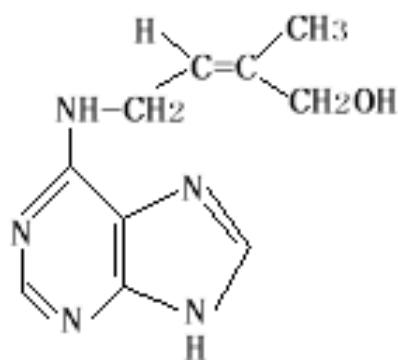
细胞分裂素通式



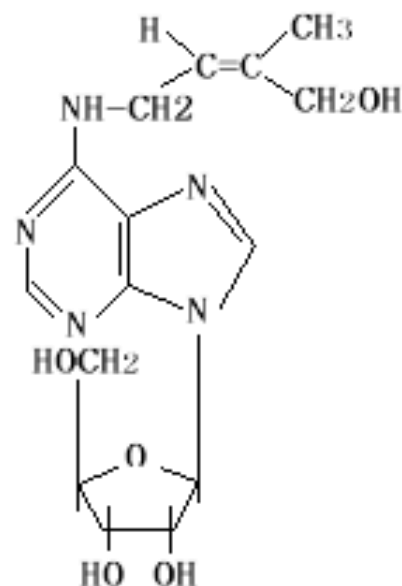
二氢玉米素Z



异戊烯基腺嘌呤 [9R] ipa



反式玉米素 [diH] Z

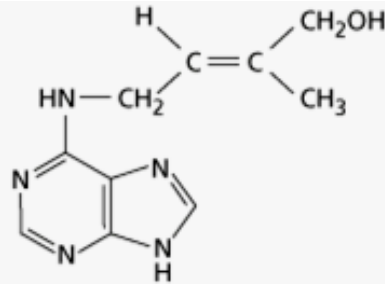


玉米素核苷 [9R] Z

Native plants cytokinins

More active

反式-玉米素

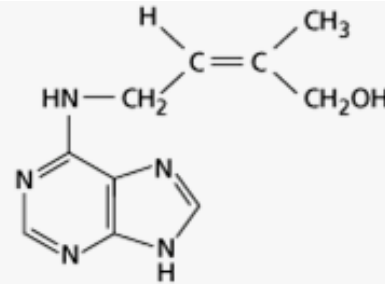


trans-Zeatin

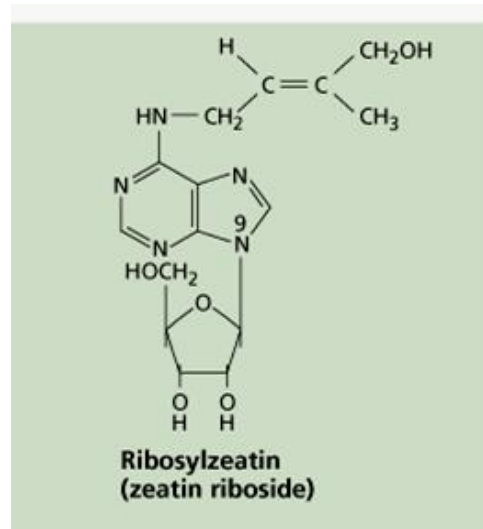
6-(4-Hydroxy-3-methylbut-2-enylamino)purine

Less active

顺式-玉米素

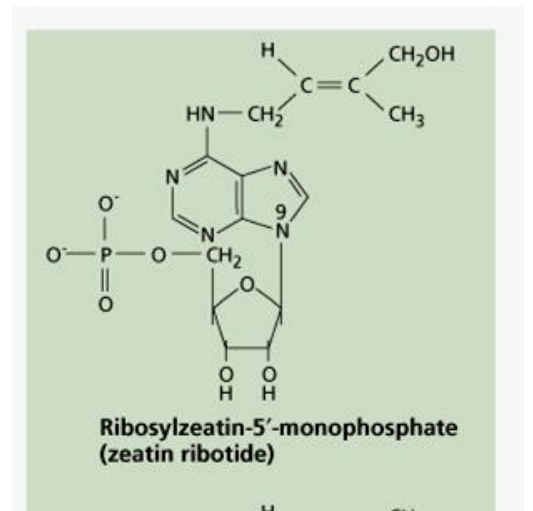


cis-Zeatin



Ribosylzeatin
(zeatin riboside)

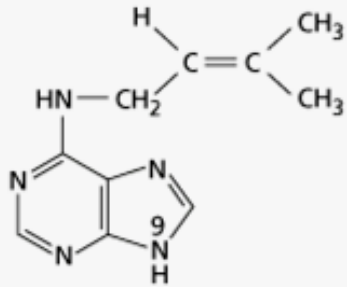
玉米素核苷
[9R]Z



Ribosylzeatin-5'-monophosphate
(zeatin ribotide)

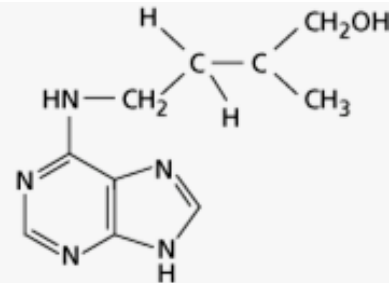
玉米素核苷-5'-磷酸
[9R-5'P]Z

Native plant cytokinins



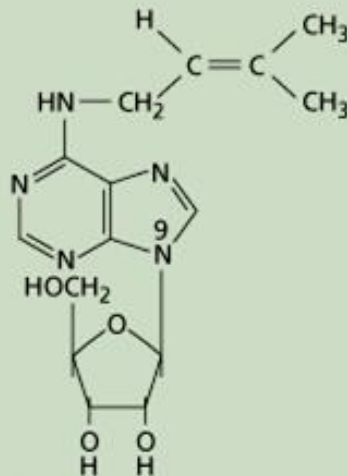
N⁶-(Δ²-Isopentenyl)-adenine
(i⁶Ade)

(iP异戊烯基腺嘌呤)



Dihydrozeatin

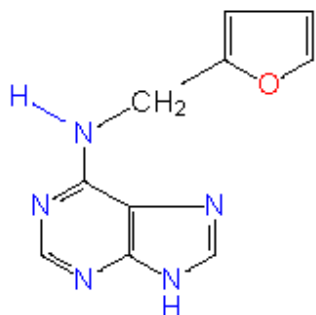
二氢玉米素
[diH]Z



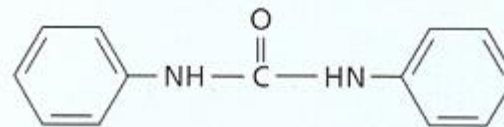
N⁶-(Δ²-Isopentenyl)-adenosine
(i⁶Ado)

([9R]iP异戊烯基腺苷)

Synthetic (人工合成) cytokinins

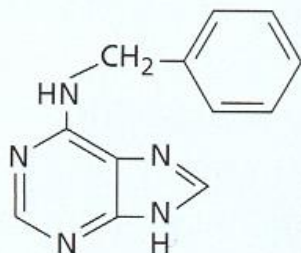


Kinetin (autoclaved DNA)
激动素 (高压灭菌后 DNA)



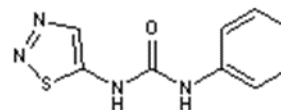
N,N'-Diphenylurea (nonamino
purine with weak activity)

(CPPU) 二苯脲



Benzyladenine
(benzylaminopurine)
(BA)

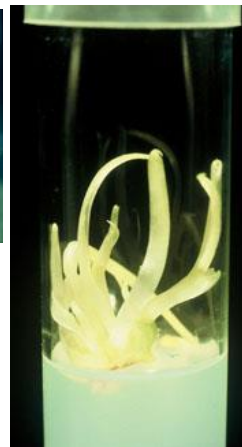
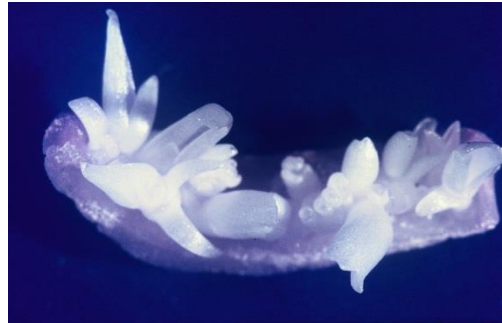
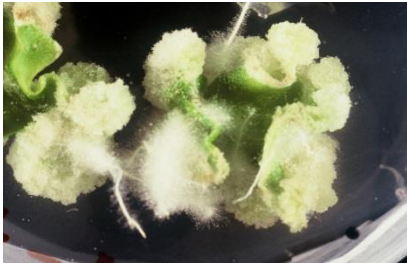
6-苄基腺嘌呤 (6-BA)



噻苯隆 Thidiazuron
TDZ

三、 Physiological role and application of CTK

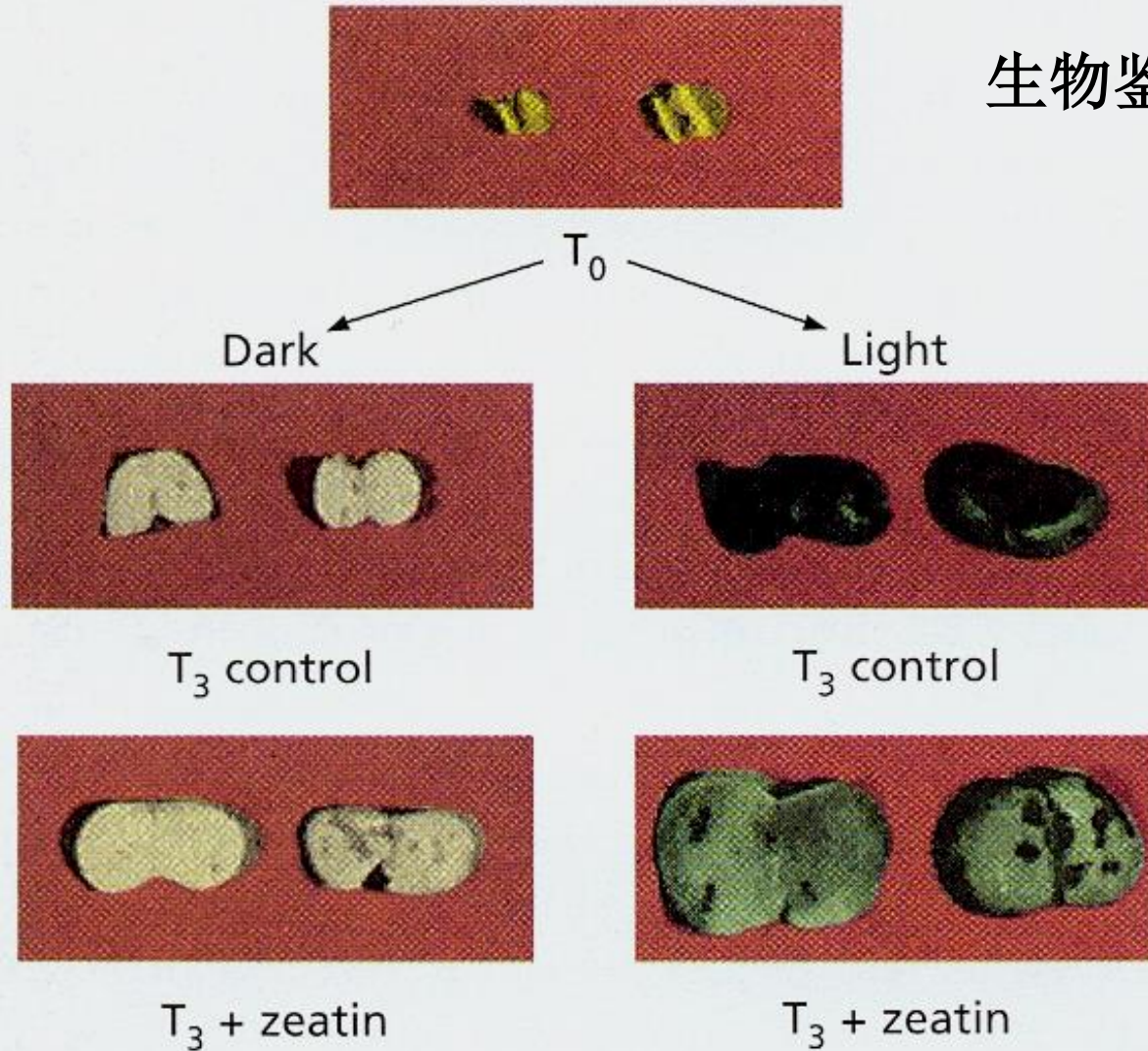
1、 Enhancing cell division and enlargement



植物组织培养

Promote expansion of dicot cotyledons (bioassay for cytokinins)

双子叶植物子叶的展开
生物鉴定方法



2、Inducing organ differentiation

愈伤组织产生根或芽，取决于CTK / IAA的比值。

CTK / IAA低，诱导root的分化；

比值居中，只生长不分化；

比值高，诱导shoot的分化。

Effects of auxin and cytokinin on differentiation

6 - B A M

10^{-5}

10^{-6}

10^{-7}

0

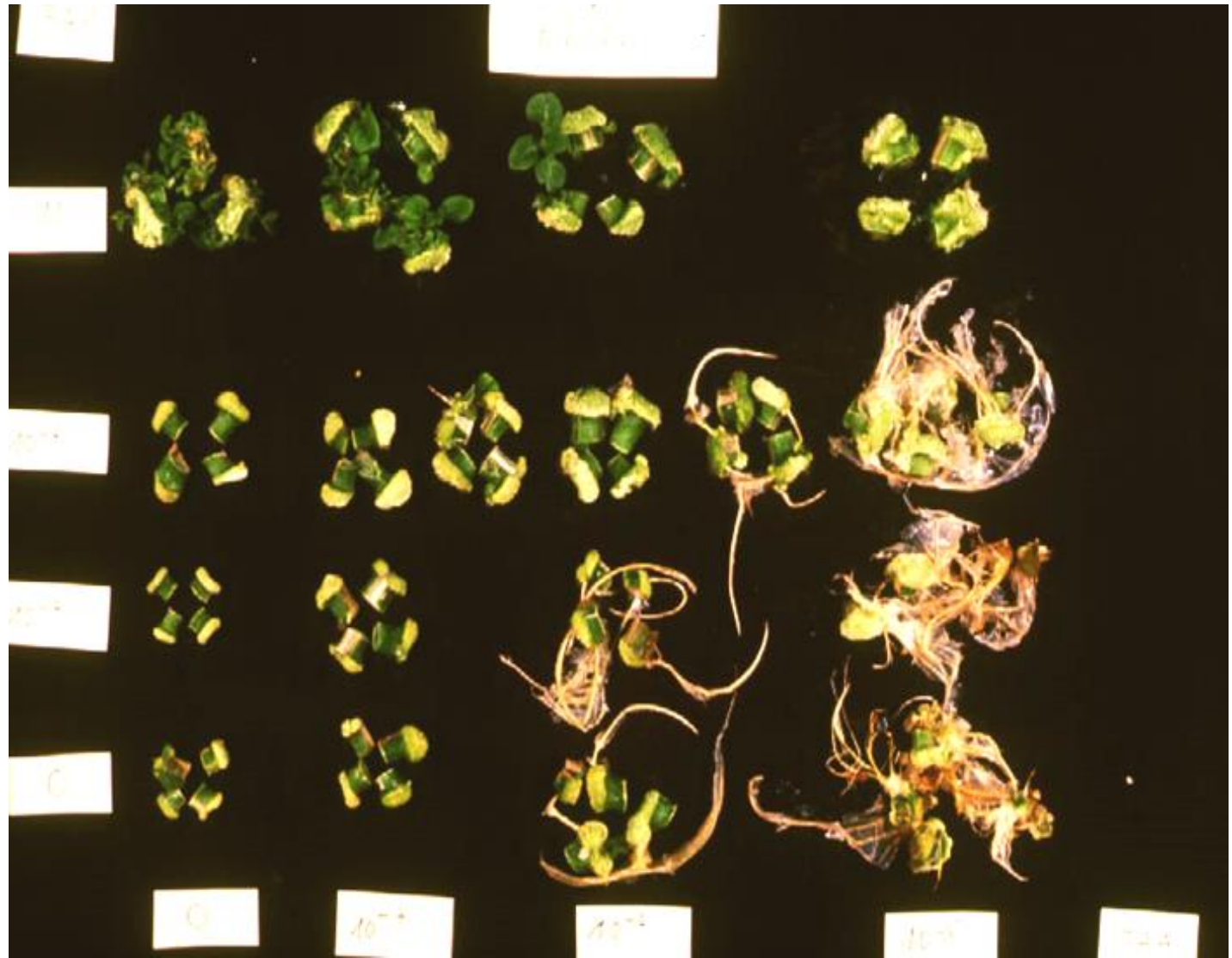
IAA (M)

0

10^{-7}

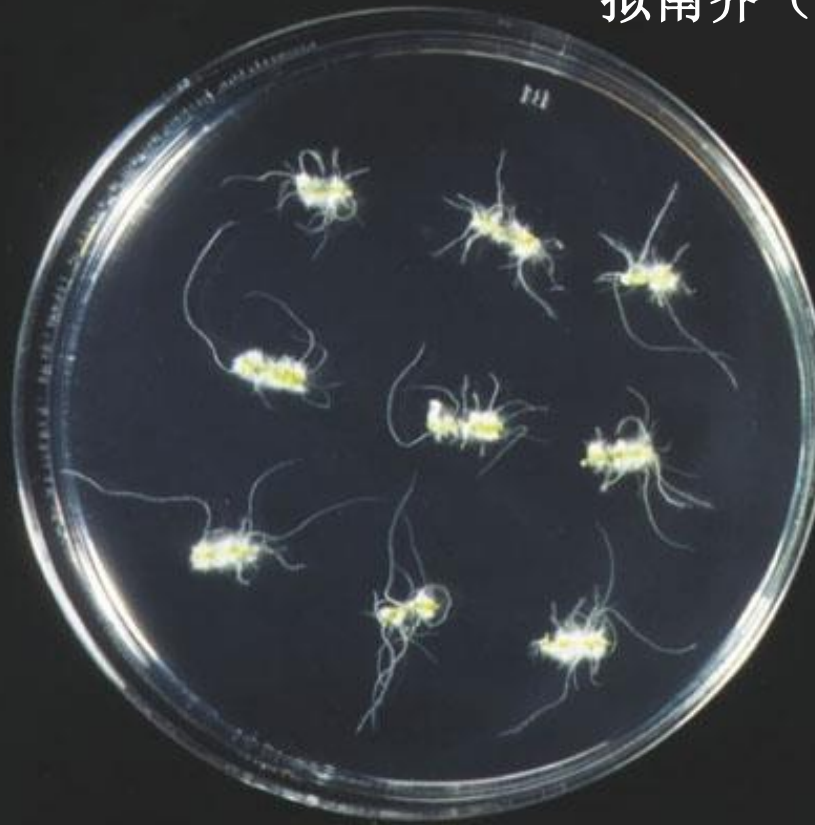
10^{-6}

10^{-5}

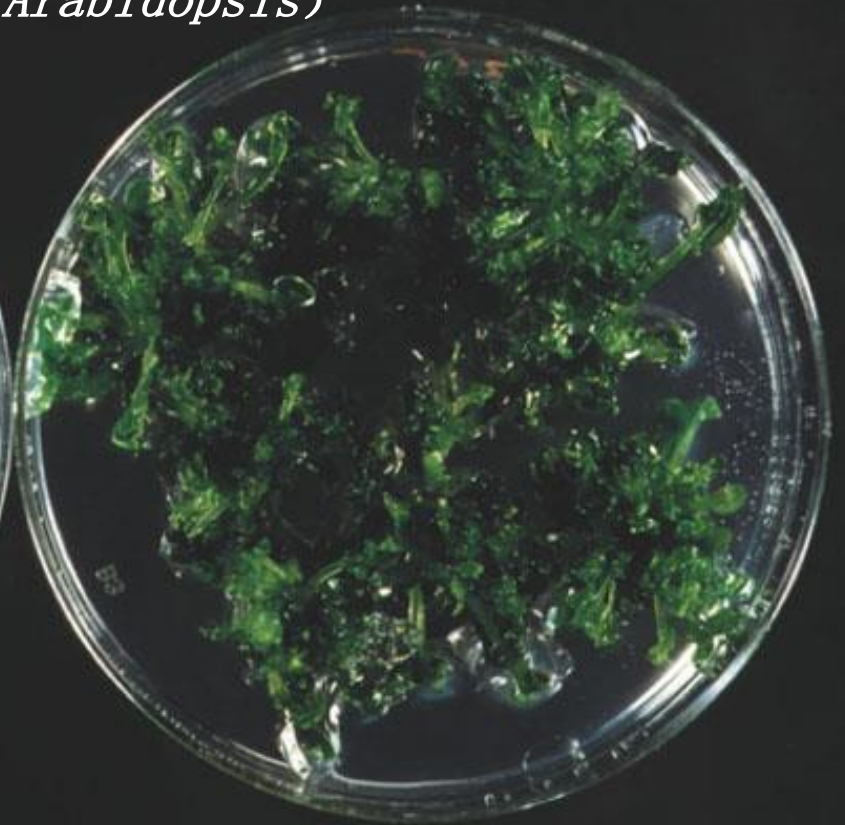


CTK促进侧芽的产生

拟南芥 (*Arabidopsis*)



IBA0.5 $\mu\text{g ml}^{-1}$



IBA0.5 $\mu\text{g ml}^{-1}$ +ZT2.0 $\mu\text{g ml}^{-1}$



3、延缓叶片衰老 Delays senescence of leaves

CTK使处理部分形成库 Promotes sink strength

氨基异丁酸

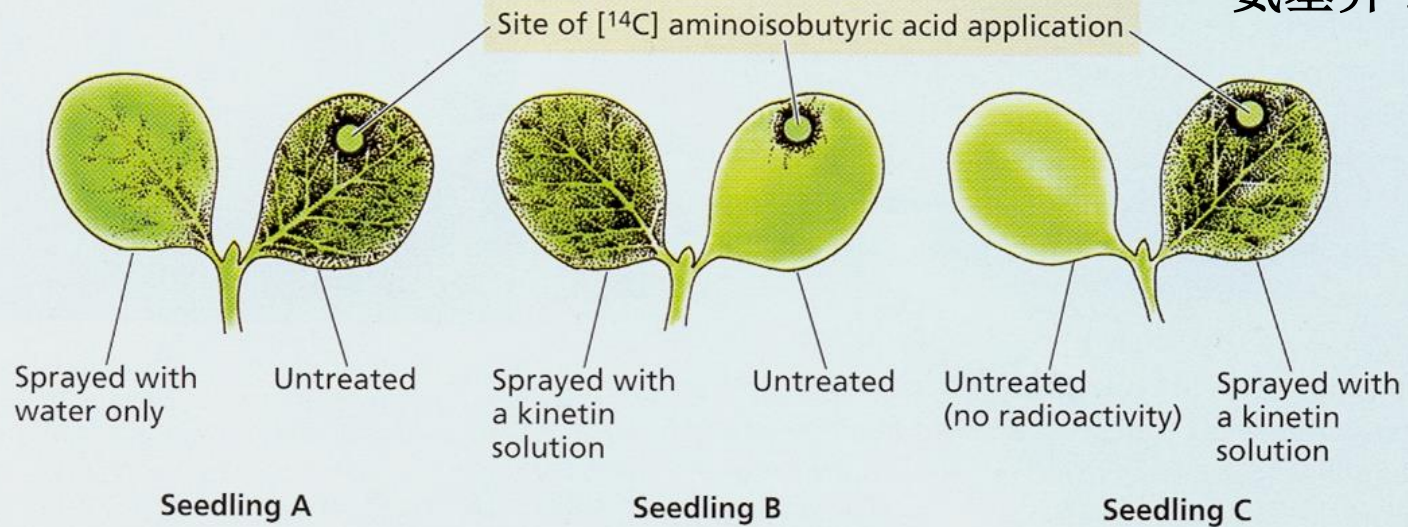


FIGURE 21.19 The effect of cytokinin on the movement of an amino acid in cucumber seedlings. A radioactively labeled amino acid that cannot be metabolized, such as

aminoisobutyric acid, was applied as a discrete spot on the right cotyledon of each of these seedlings. (Drawn from data obtained by K. Mothes.)



4、促进侧芽发育—消除顶端优势

De-dominance and enhancing lateral sprout

Promotes lateral bud formation (breaks apical dominance)

-CK



+CK

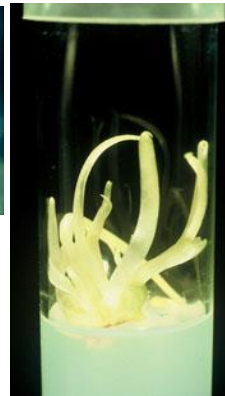
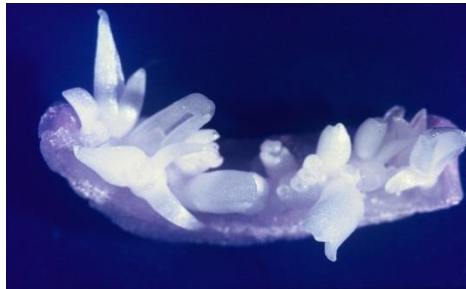


应用:

1. 组织培养

2. 延缓衰老 3. 果实膨大 (葡萄、草莓)

常用的人工合成药物为: **6-BA**, **CPPU**) 二苯脲



菜心叶片衰老调控 激素处理

对照

2 0 ppm 乙烯

2 mg/L 6-BA

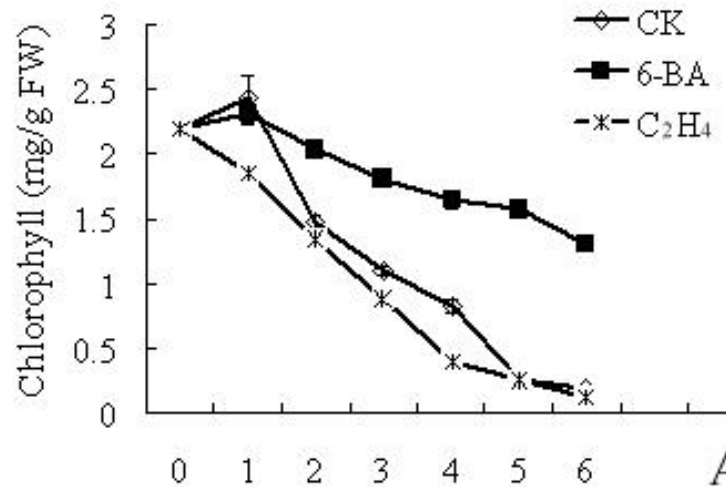
2天



4天



6天



叶绿素含量

四、分布和运输

分布：细菌、真菌、藻类植物和高等植物；
主要存在于进行细胞分裂的部位：茎尖、根尖、未成熟、萌发的种子等。

根部合成通过木质部运输（主要）在植物体内的运输无极性。

Cytokinins from the Root Are Transported to the Shoot via the Xylem

五、CTK_S的代谢及运输

(一) 生物合成

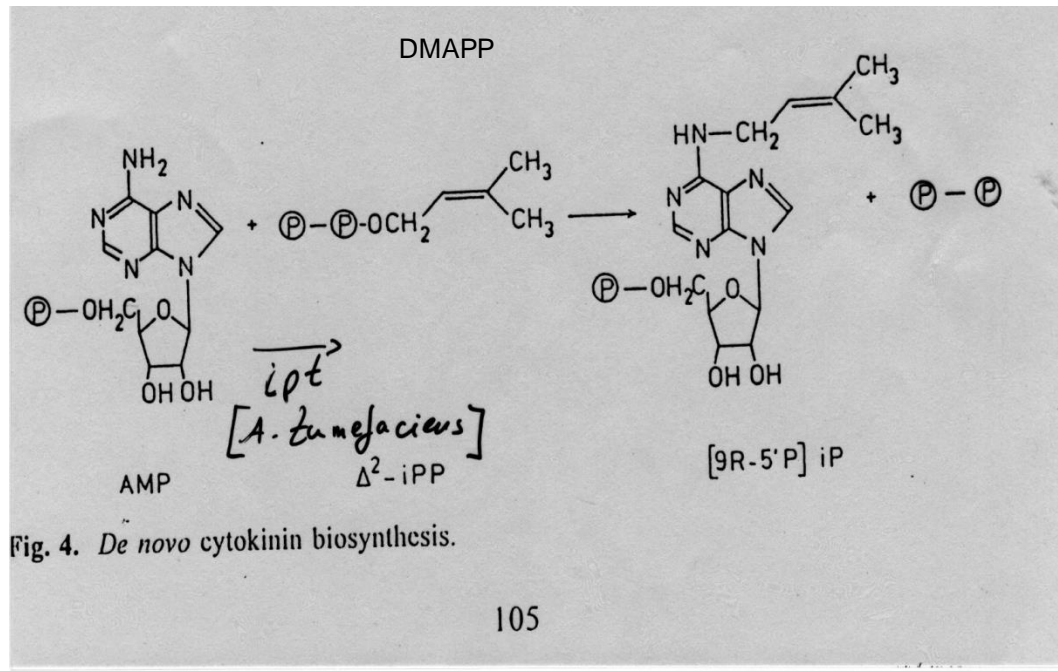
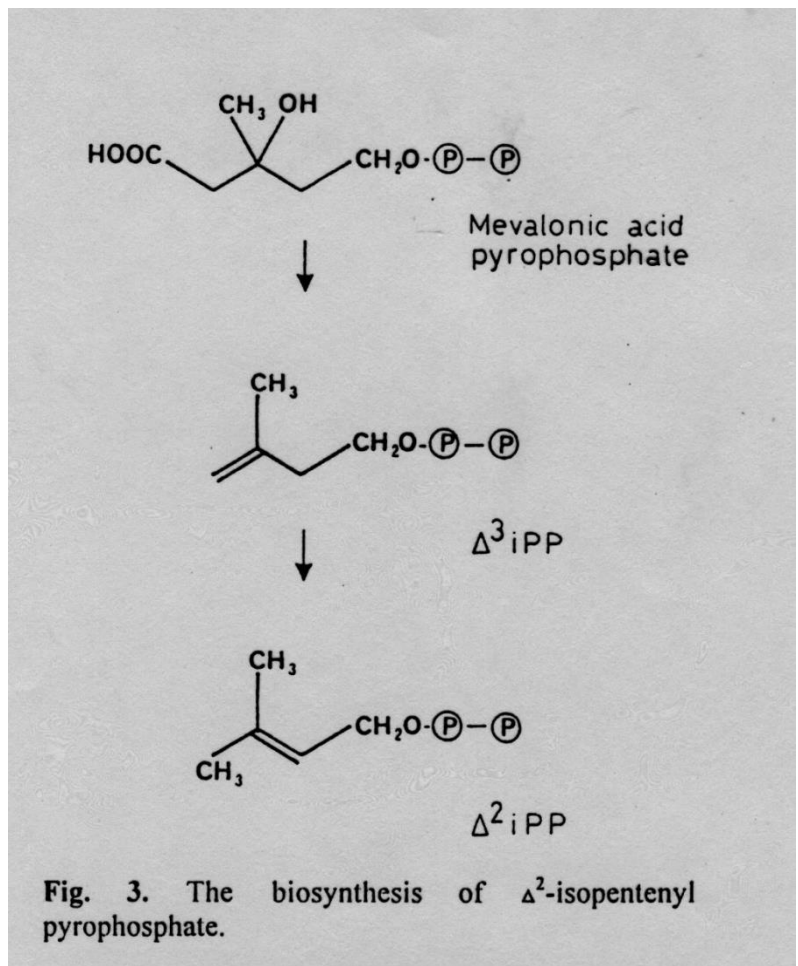
合成部位：根尖、生长中的种子和果实、茎尖。

合成途径：从头合成和tRNA水解

从头合成：前体：甲瓦龙酸/甲羟戊酸(mevalonic acid)

从头合成：前体：甲瓦龙酸

Cytokinin biosynthesis in bacteria



105

IPT酶 — isopentenyl transferase

isopentenyl diphosphate 异戊烯基焦磷酸(iPP) 异戊烯基转移酶

甲瓦龙酸



异戊烯基焦磷酸DMAPP



IPT

5'-ADP/ATP

异戊烯基腺苷-5'-磷酸盐 [9R]iP



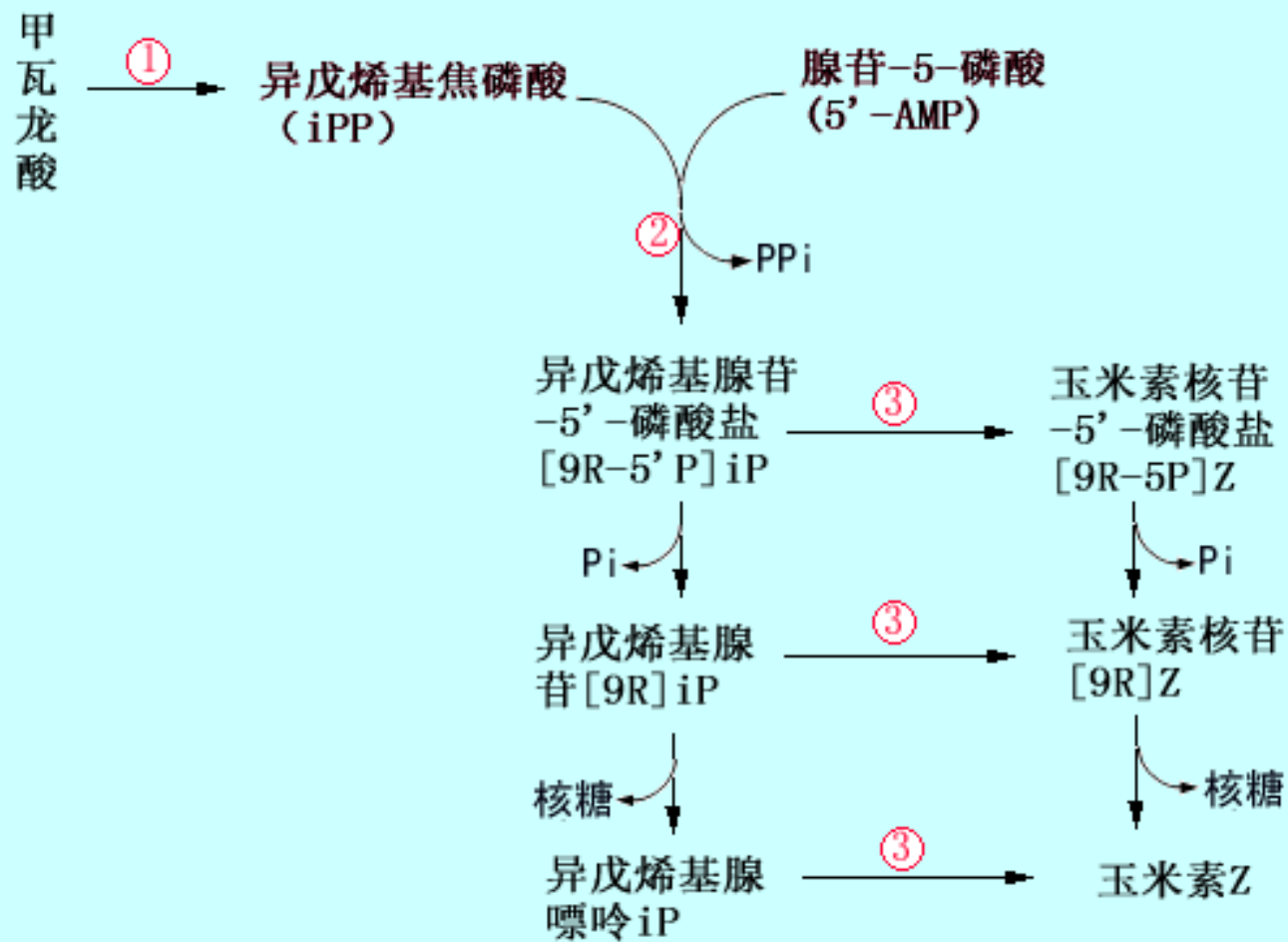
异戊烯基腺嘌呤 (iP)

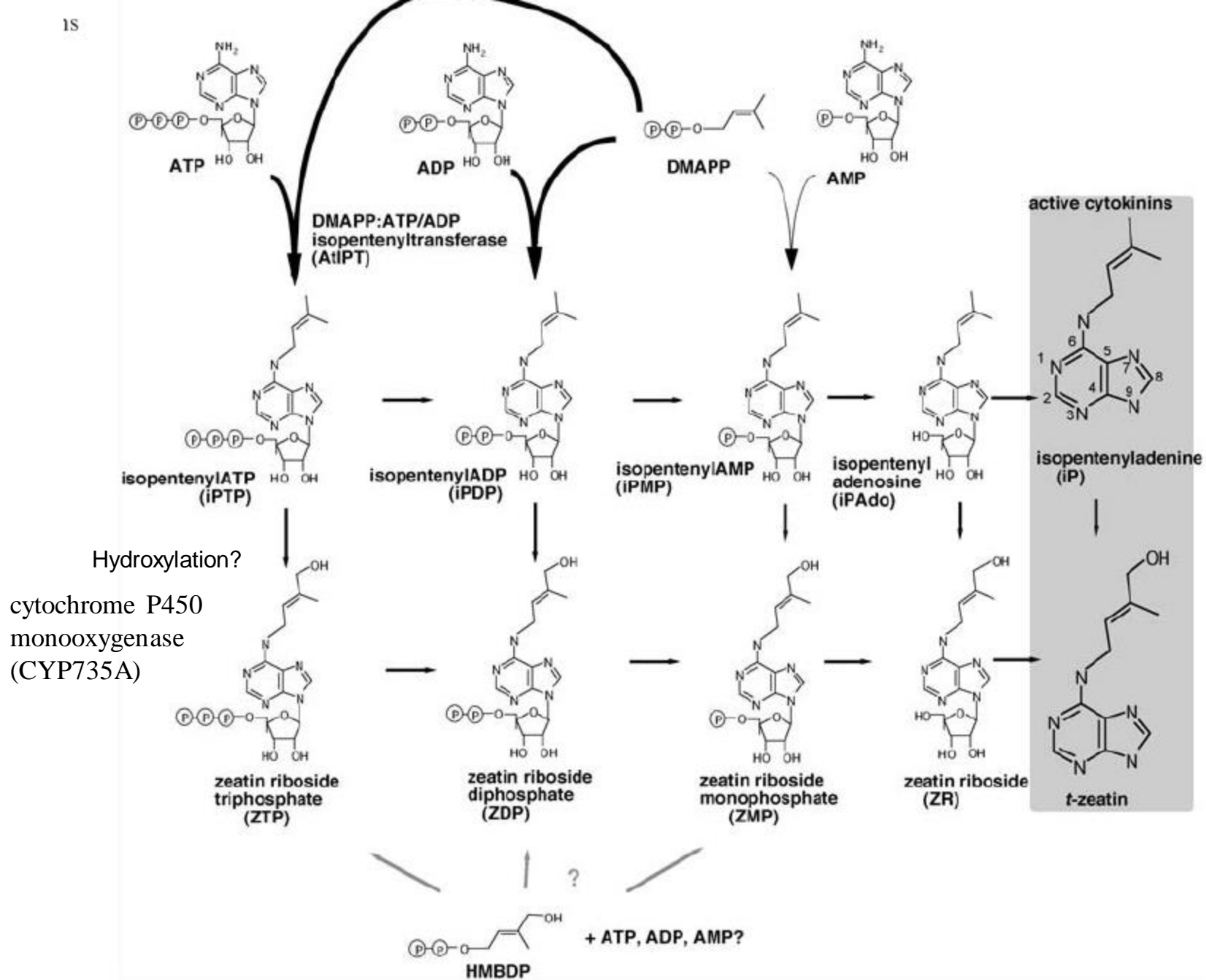


羟化酶
细胞色素P450氧化酶

玉米素(Z)







IPT酶
isopentenyl transferase
甲戊烯基转移酶

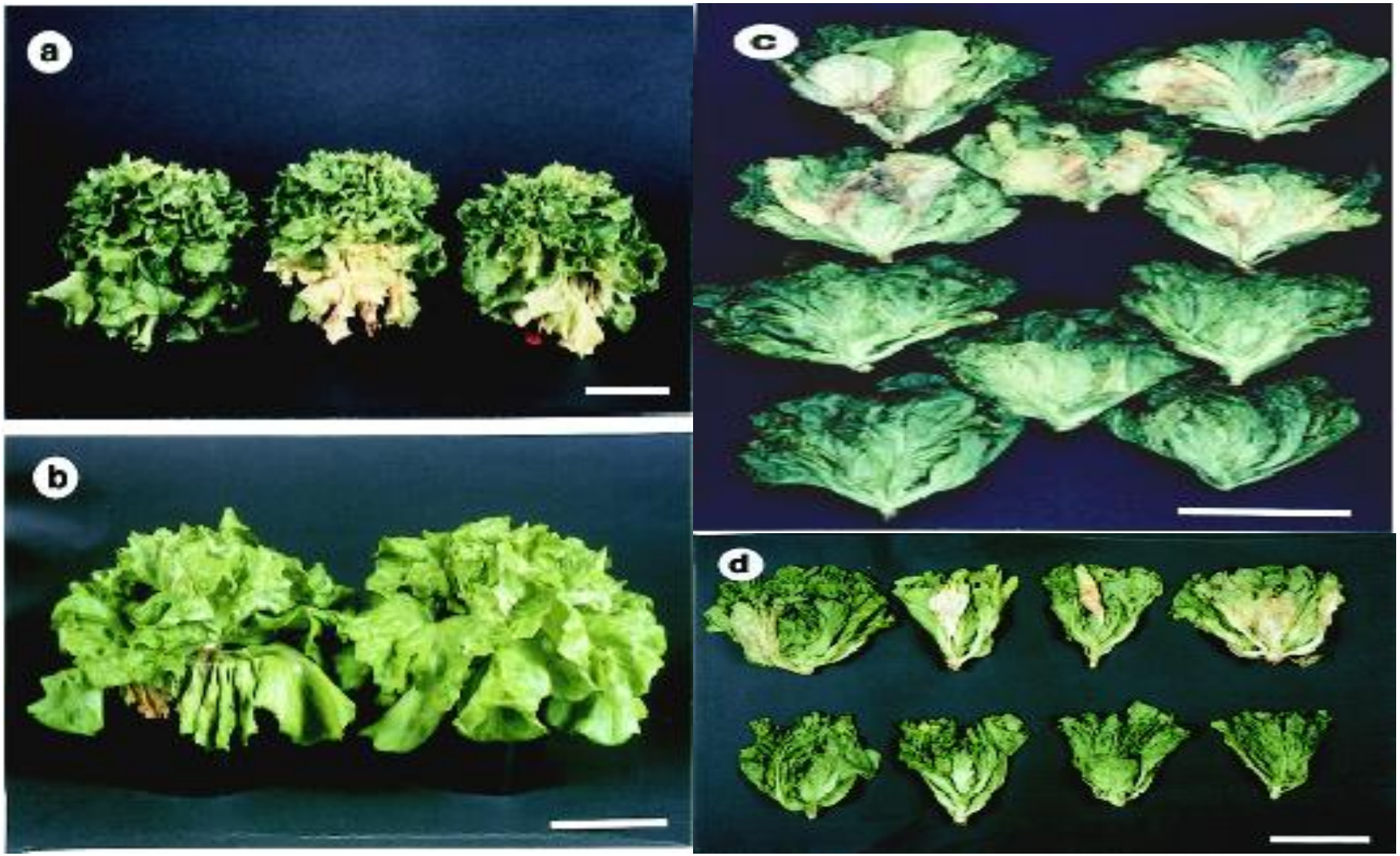


Plant expressing *ipt* gene remains green and photosynthetic

Age-matched control: advanced senescence, no photosynthesis

Molecular engineering work

Effects of P_{SAG12} -IPT gene expression on senescence



CTK_s的结合物、氧化和运输

Cytokinins Are Rapidly Metabolized

CTK_s的**结合物**有三类：与葡萄糖、氨基酸、核苷形成结合物。

CTK_s降解的主要方式是通过**细胞分裂素氧化酶cytokinin oxidase**氧化，释放出腺嘌呤。

在植物体内的**运输无极性**。根尖合成的由木质部导管运输到地上部分。

Cytokinin degradation modulates its effects

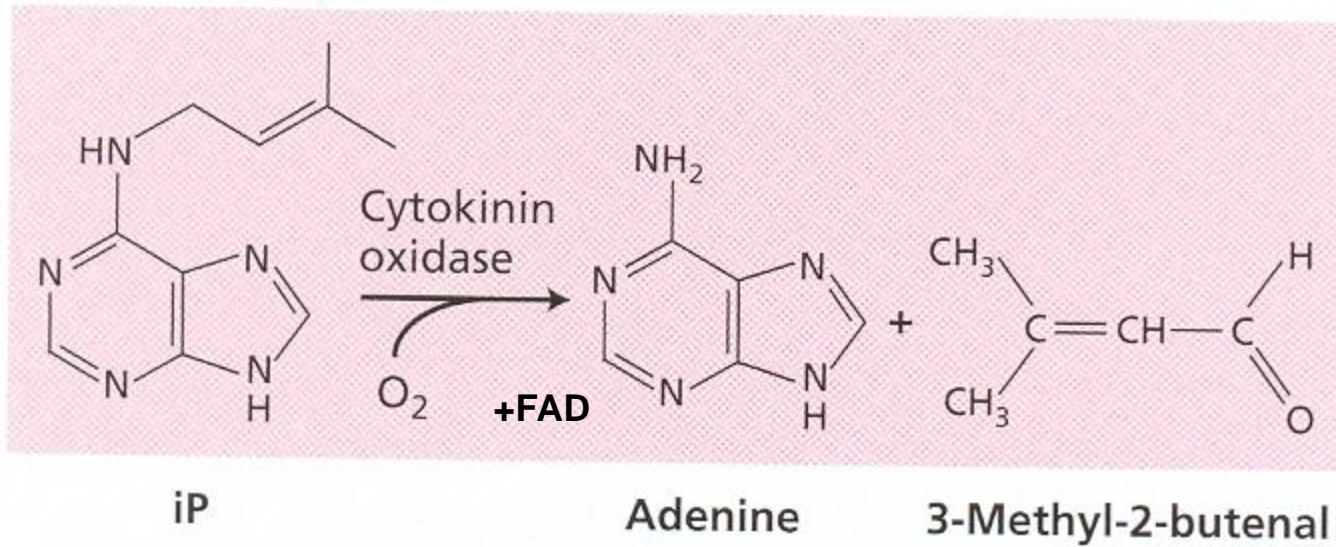


FIGURE 21.7 Cytokinin oxidase irreversibly degrades some cytokinins.

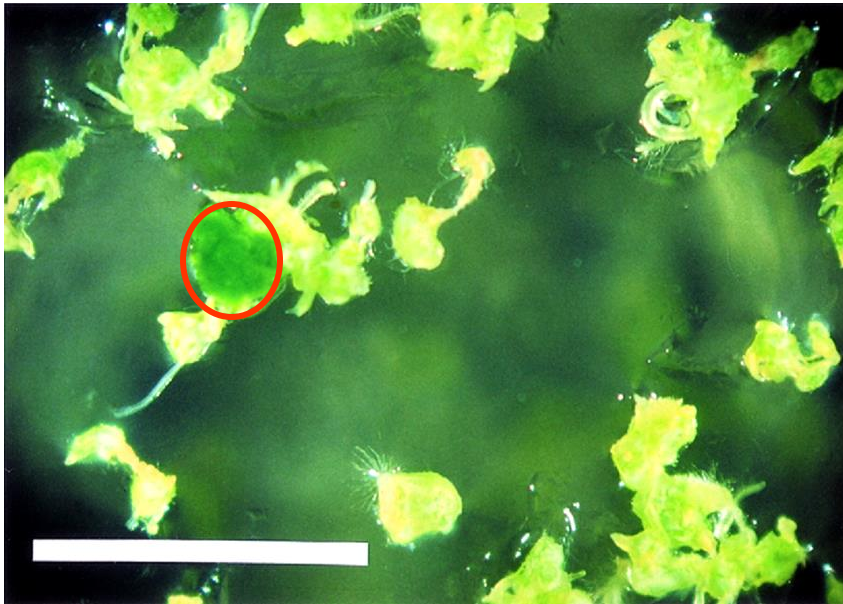
细胞分裂素氧化酶

六、CTK 的信号转导途径

(一) 受体

1. Search for cytokinin independent mutants (constitutive CK responsive)

Selection (50,000 seedlings): ability to develop callus and shoots in the absence of CK
5 isolates, termed CKI1-1 to CKI1-4 (cytokinin independent) (细胞分裂素独立1)



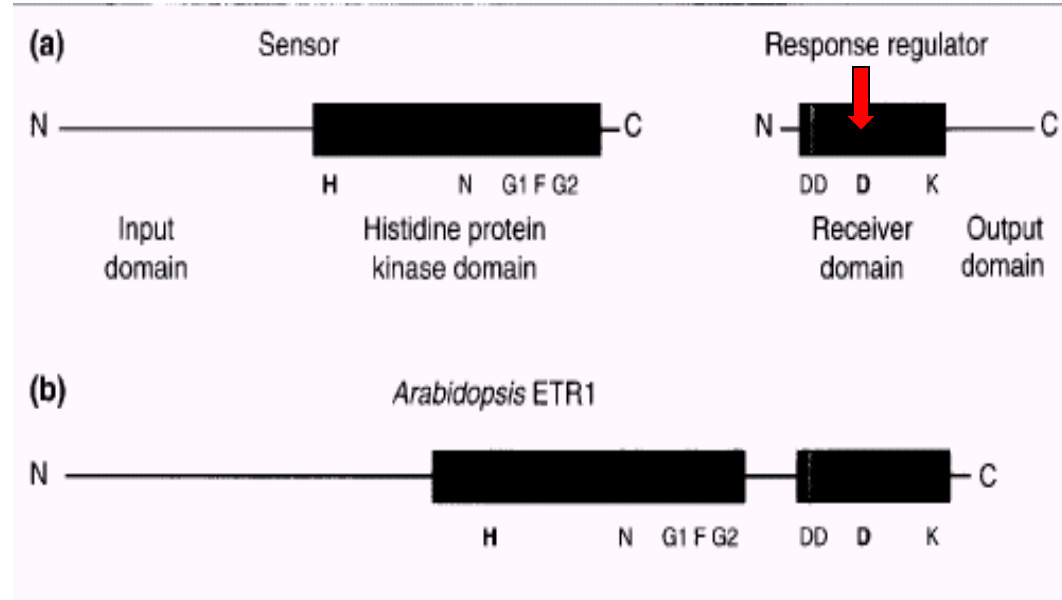
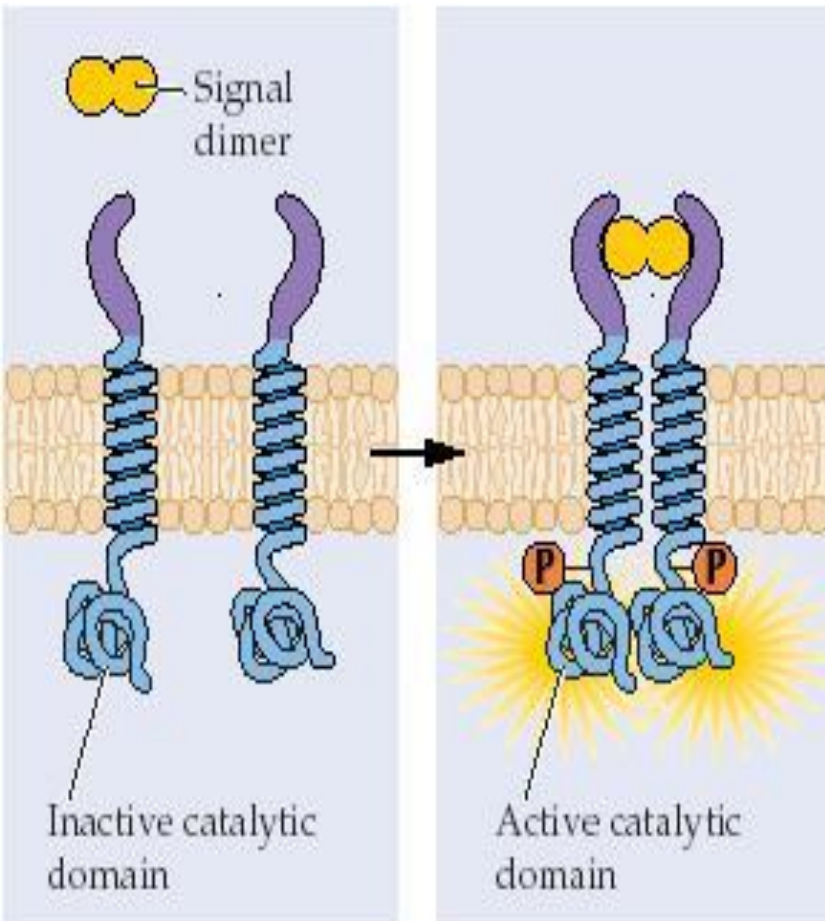
CKI1

二员组分系统介导的跨膜信号转换

组氨酸蛋白激酶 (HPK)

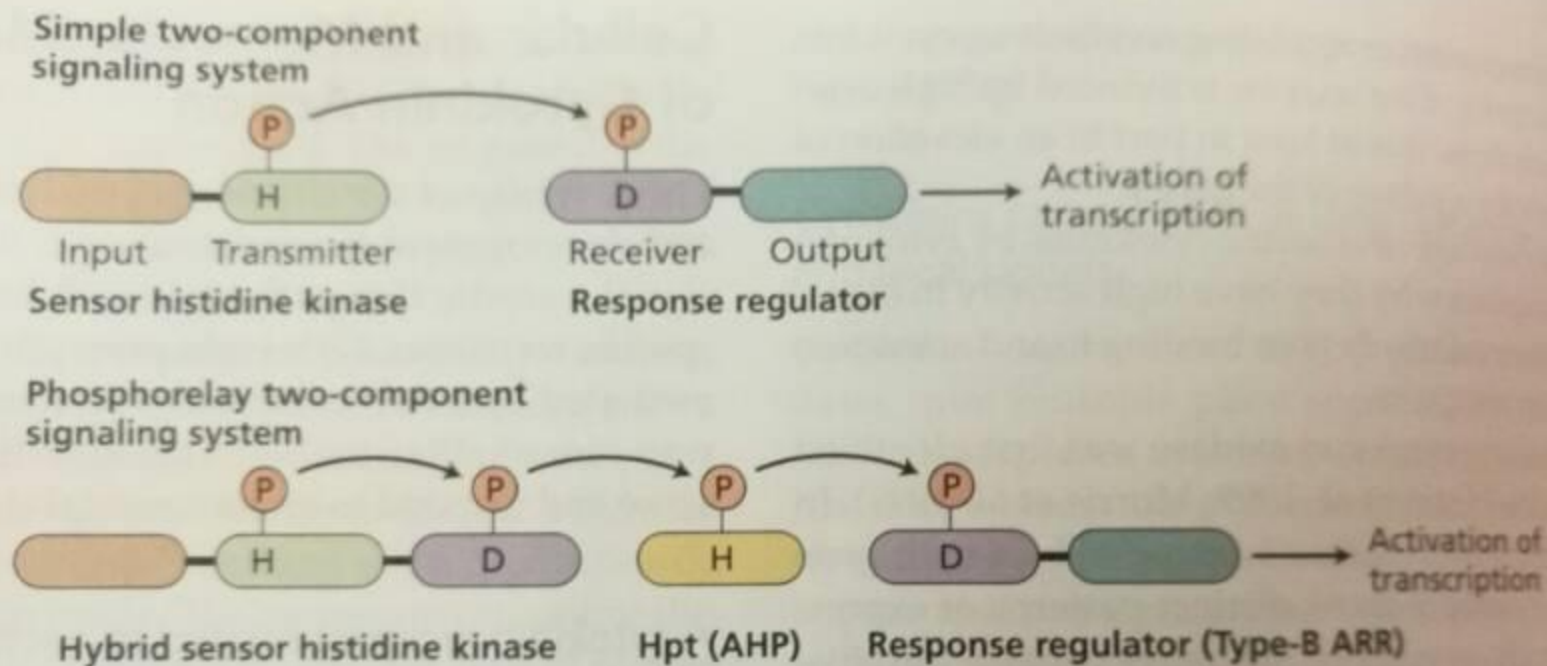
反应调节蛋白

(response-regulator protein RR)



细胞分裂素受体 *CRE1* (*cytokinin receptor 1*)

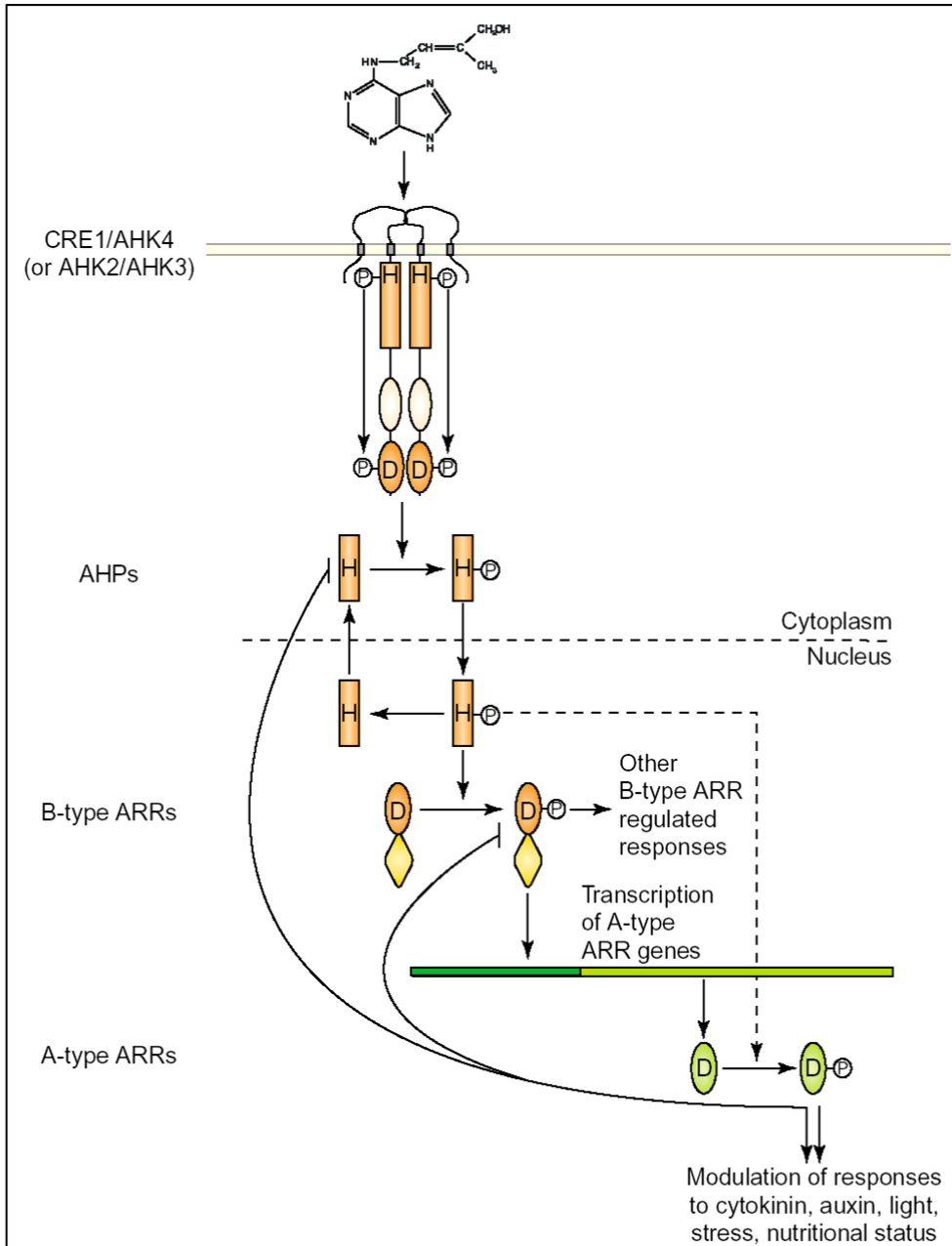
CKI1 (*cytokinin independent 1*)



1.6 Simple versus phosphorelay types of two-component signaling systems. (A) In simple two-component systems, the input domain is the site where the signal is sensed. This domain regulates the activity of the histidine kinase domain, which when activated autophosphorylates a conserved histidine residue. The phosphate is then transferred to an aspartate residue located within the receiver domain of a response

regulator. Phosphorylation of this aspartate regulates the activity of the output domain of the response regulator, which in many cases is a transcription factor. (B) In the phosphorelay-type two-component signaling system, an extra set of phosphotransfers is mediated by a histidine phosphotransfer protein (Hpt) called AHPs in Arabidopsis. The Arabidopsis response regulators are called ARRs. H, histidine; D, aspartate.

CK signal transduction pathway



Cytokinin Signaling in *Arabidopsis*

