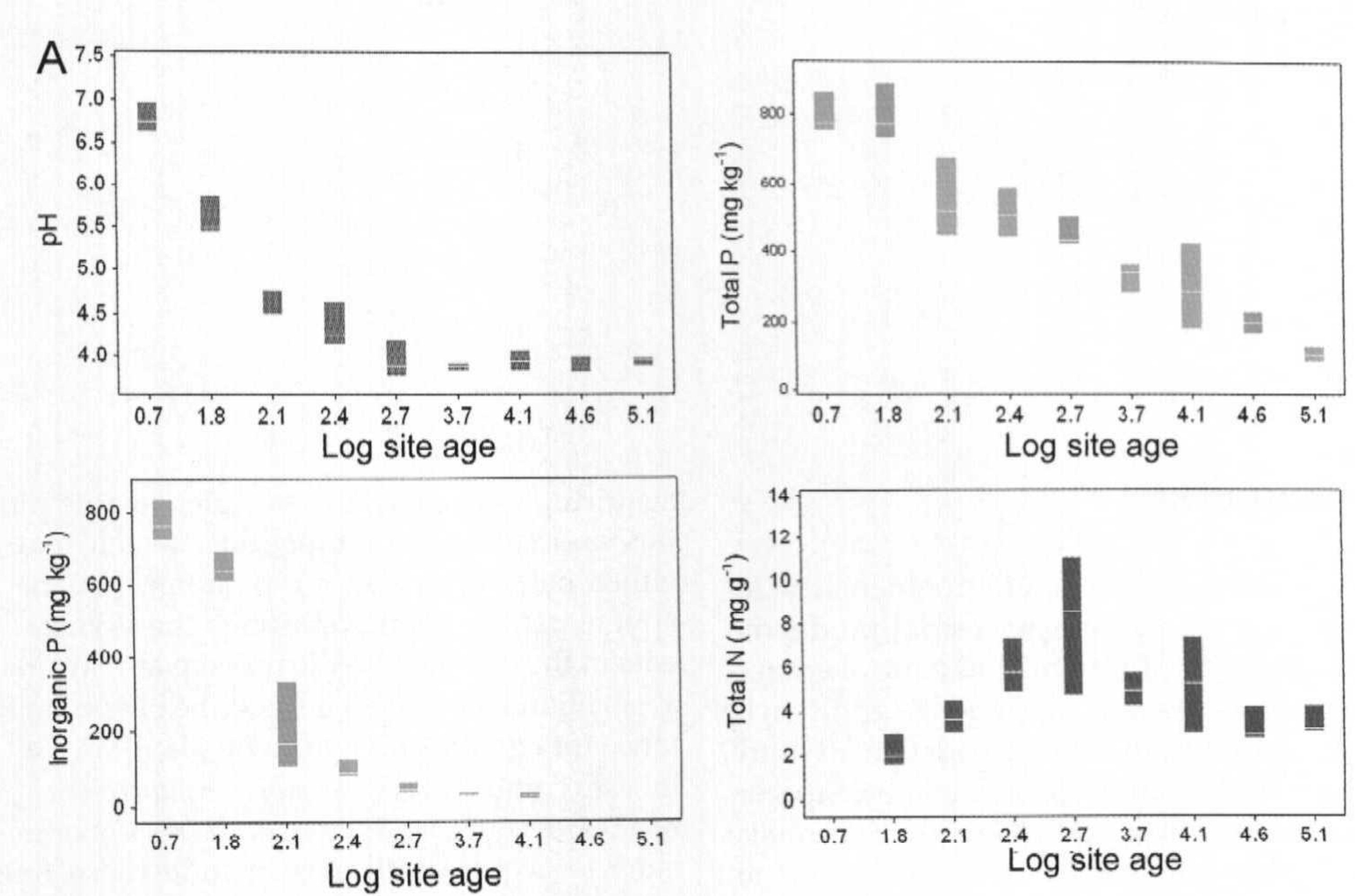
Ecophysiology

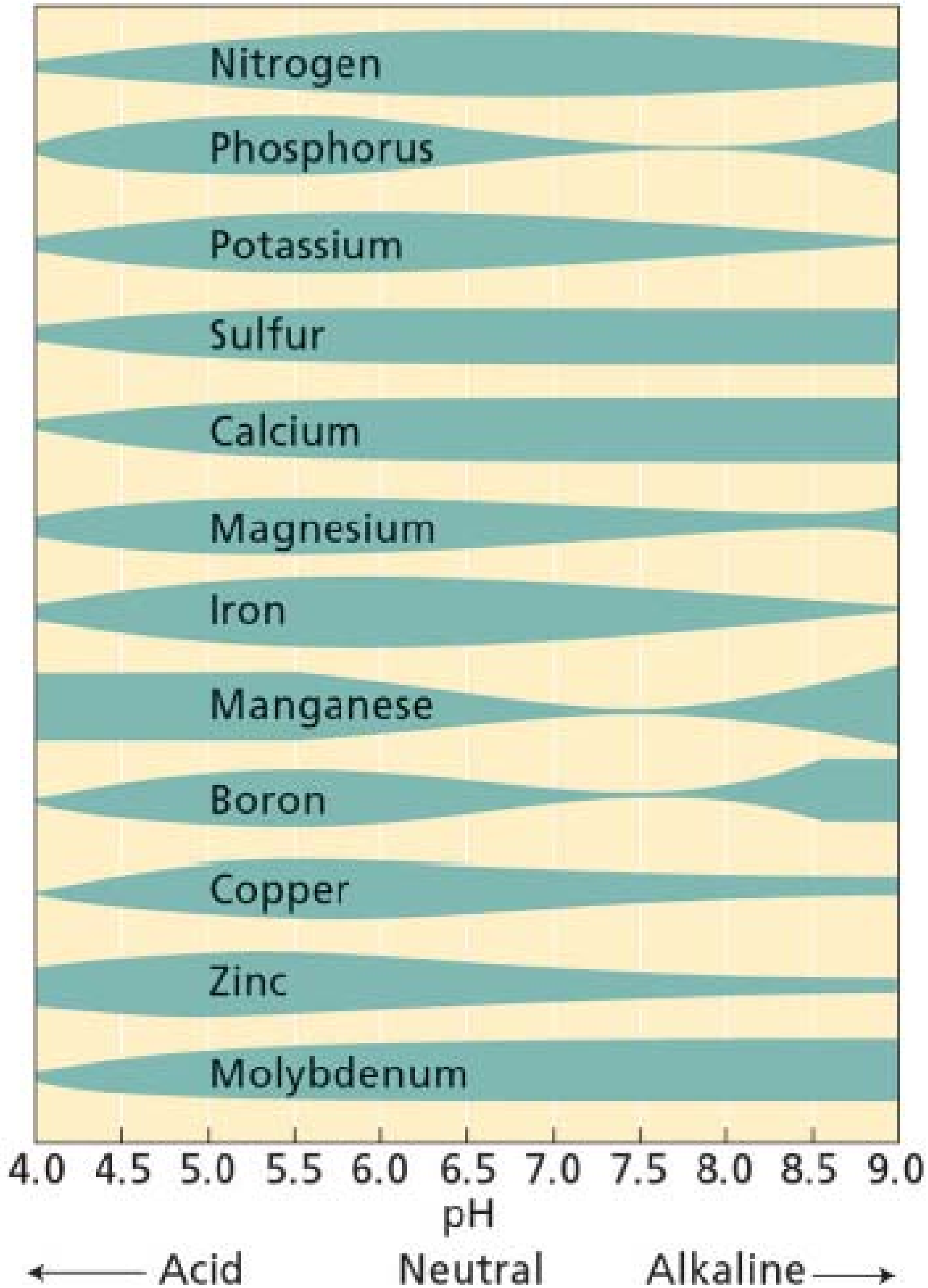
Please Note: Some of the slides are Animated and are best viewed as a Slide Show; some slides have attached notes below the slides and these are best viewed in Normal (editing) view.

5. Mineral Nutrition & Ionic Stress

Soil Acidity Increases With Age...



...and Nutrient Ion Availability is pH Dependent



PLANT PHYSIOLOGY, Third Edition, Figure 5.4 © 2002 Sinauer Associates, Inc.

Relative Elemental Analysis of Plants

H_2O or CO_2

Soil

Element	Chemical symbol	Concentration in dry matter (% or ppm)	Relative number of atoms with respect to molybdenum
Hydrogen	H	6 %	60,000,000
Carbon	C	45 %	40,000,000
Oxygen	O	45 %	30,000,000
Nitrogen	N	1.5 %	1,000,000
Potassium	K	1.0 %	250,000
Calcium	Ca	0.5 %	125,000
Magnesium	Mg	0.2 %	80,000
Phosphorus	P	0.2 %	60,000
Sulfur	S	0.1 %	30,000
Silicon	Si	0.1 %	30,000
Chlorine	Cl	100 ppm	3,000
Iron	Fe	100 ppm	2,000
Boron	B	20 ppm	2,000
Manganese	Mn	50 ppm	1,000
Sodium	Na	10 ppm	400
Zinc	Zn	20 ppm	300
Copper	Cu	6 ppm	100
Nickel	Ni	0.1 ppm	2
Molybdenum	Mo	0.1 ppm	1

Essential Nutrients

- **Essential mineral nutrients**:
  - one whose absence prevents a plant from completing its life cycle (classic definition),
  - or, one that has a clear physiological role (current modification of classic definition).
- **Macronutrient:** required in relatively large amounts,
- **Micronutrient:** required in relatively small amounts.

Table 37.1 Essential Nutrients in Plants

Element	Form Available to Plants
Macronutrients	
Carbon	CO_2
Oxygen	CO_2
Hydrogen	H_2O
Nitrogen	NO_3^-, NH_4^+
Sulfur	SO_4^{2-}
Phosphorus	$H_2PO_4^-$, HPO_4^{2-}
Potassium	K^+
Calcium	Ca^{2+}
Magnesium	Mg^{2+}
Micronutrients	
Chlorine	Cl^-
Iron	Fe^{3+}, Fe^{2+}
Boron	$H_2BO_3^-$
Manganese	Mn^{2+}
Zinc	Zn^{2+}
Copper	Cu^+, Cu^{2+}
Molybdenum	MoO_4^{2-}
Nickel	Ni^{2+}

Table 37.1 Essential Nutrients in Plants

Table 37.1 Essential Nutrients in Plants

Element	Form Available to Plants	Major Functions
Macronutrients 9		
Carbon	CO_2	Major component of plant's organic compounds
Oxygen	O_2	Major component of plant's organic compounds
Hydrogen	H_2O	Major component of plant's organic compounds
Nitrogen	NO_3^-, NH_4^+	Component of nucleic acids, proteins, hormones, and coenzymes
Sulfur	SO_4^{2-}	Component of proteins, coenzymes
Phosphorus	$H_2PO_4^-$, HPO_4^{2-}	Component of nucleic acids, phospholipids, ATP, several coenzymes
Potassium	K^+	Cofactor that functions in protein synthesis; major solute functioning in water balance; operation of stomata
Calcium	Ca^{2+}	Important in formation and stability of cell walls and in maintenance of membrane structure and permeability; activates some enzymes; regulates many responses of cells to stimuli
Magnesium	Mg^{2+}	Component of chlorophyll; activates many enzymes
Micronutrients >8		
Chlorine	Cl^-	Required for water-splitting step of photosynthesis; functions in water balance
Iron	Fe^{3+}, Fe^{2+}	Component of cytochromes; activates some enzymes
Boron	$H_2BO_3^-$	Cofactor in chlorophyll synthesis; may be involved in carbohydrate transport and nucleic acid synthesis
Manganese	Mn^{2+}	Active in formation of amino acids; activates some enzymes; required for water-splitting step of photosynthesis
Zinc	Zn^{2+}	Active in formation of chlorophyll; activates some enzymes
Copper	Cu^+, Cu^{2+}	Component of many redox and lignin-biosynthetic enzymes
Molybdenum	MoO_4^{2-}	Essential for nitrogen fixation; cofactor that functions in nitrate reduction
Nickel	Ni^{2+}	Cofactor for an enzyme functioning in nitrogen metabolism

Diffusion of Ions to Root Surface Decreases with Soil j_{H2O} and can Limit Acquisition

Ion	Diffusion Coefficient (m^2 s^{-1}) @ j_{H2O} -0.1 MPa	Diffusion Coefficient (m^2 s^{-1}) @ j_{H2O} -1.0 MPa
Cl^-	$\sim 5 . 10^{-10}$	$\sim 5 . 10^{-12}$
NO_3^-	$\sim 1 . 10^{-10}$	$\sim 1 . 10^{-12}$
SO_4^{2-}	$\sim 2 . 10^{-10}$	$\sim 2 . 10^{-12}$
$H_2PO_4^-$	$\sim 2 . 10^{-13}$	$\sim 2 . 10^{-15}$
K^+	$\sim 15 . 10^{-12}$	$\sim 15 . 10^{-14}$

Traits for Increasing Nutrient Ion Acquisition

Maximizing Root / Shoot Ratio

Root Surface Area

(Root Hairs ~200% Increase in Surface Area for 2% Carbon Investmnent

Increasing Root Surface Area is Not the Only Important Trait

Pi Acquisition in Some Species, Root Hairs Important

..but for Si Acquisition in Rice, Root Hair Density has Little Effect

TABLE 4. Phosphorus uptake of seven plant species in relation to morphological root properties (root radius and root hairs).

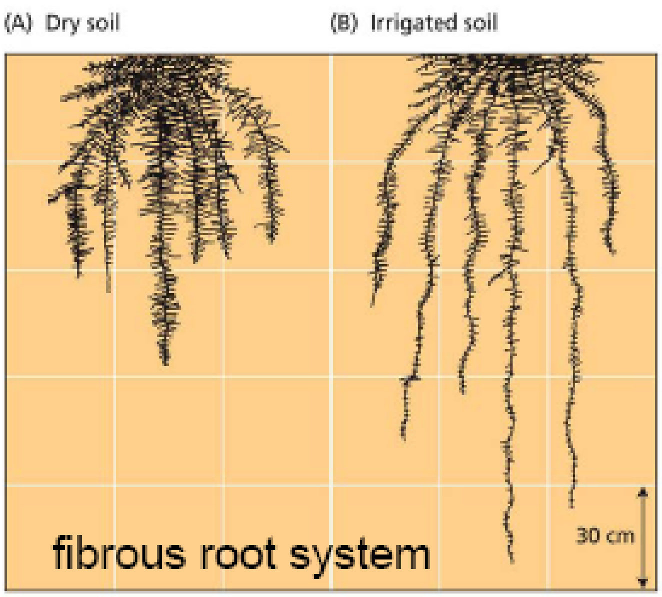
Species	P_i uptake (10^{-12} mol m^{-1} s^{-1})	Root radius (μm)	Root hairs: Number per mm	Root hairs: Average length (mm)	Root hairs: Surface area of root hairs (m^2 m^{-2})
Allium cepa	84	2290	1	0.05	6.5×10^{-3}
Lolium perenne	69	660	45	0.34	1.2
Triticum aestivum	91	770	46	0.33	1.2
Brassica napus	320	730	44	0.31	1.3
Solanum lycopersicum	186	1000	58	0.17	0.6
Spinacia oleracea	485	1070	71	0.62	1.9
Phaseolus vulgaris	60	1450	49	0.20	0.4

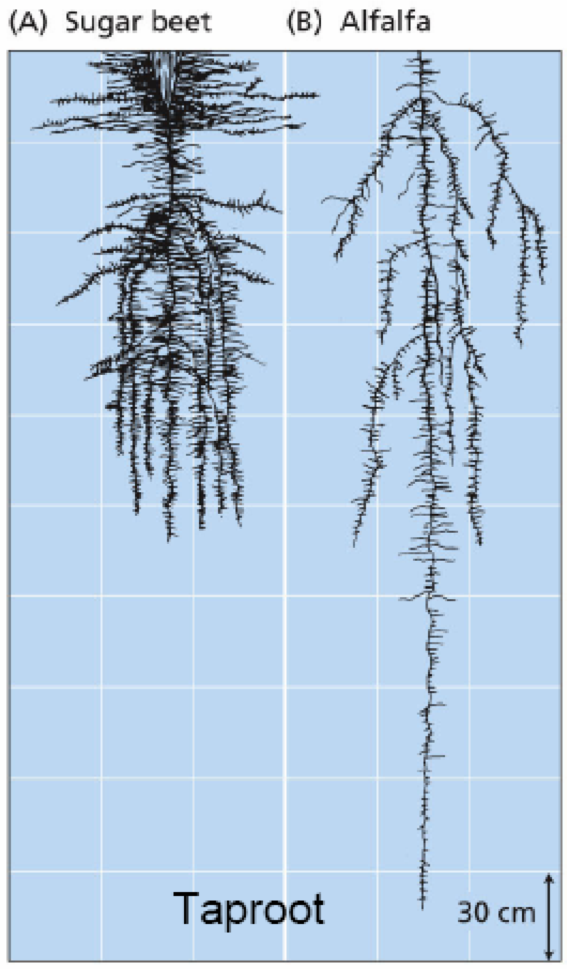
Source: Föhse et al. 1991.

Root Structure is Determined by Genetics & The Environment

Roots, the hidden half

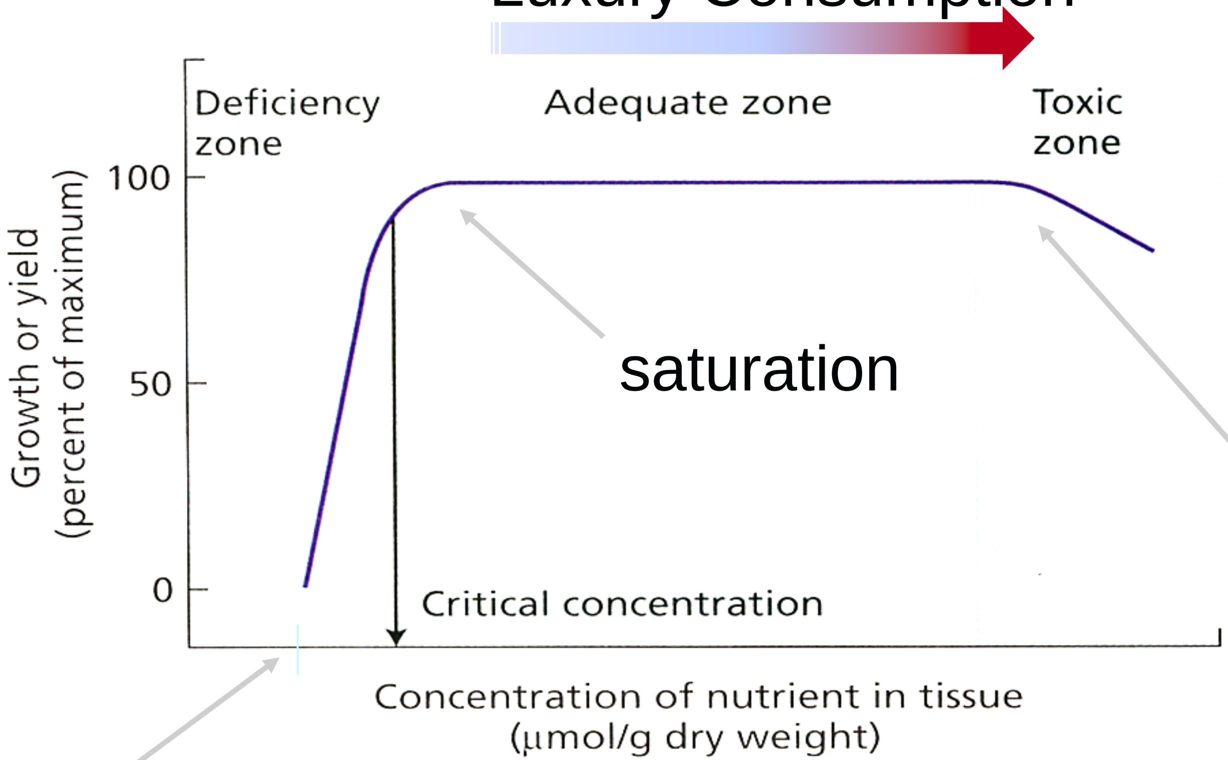
- One Rye plant can have 200 m^2 root surface area and 300 m^2 root hair surface area
- The total length of the root of a tree can be 18 km
- In desert, root of some plants can penetrate 50 m deep.
- Monocot: fibrous root system with pirmary roots and adventitious root
- Dicot: Taproot with primary root and lateral root





Dose Response Curves

Luxury Consumption

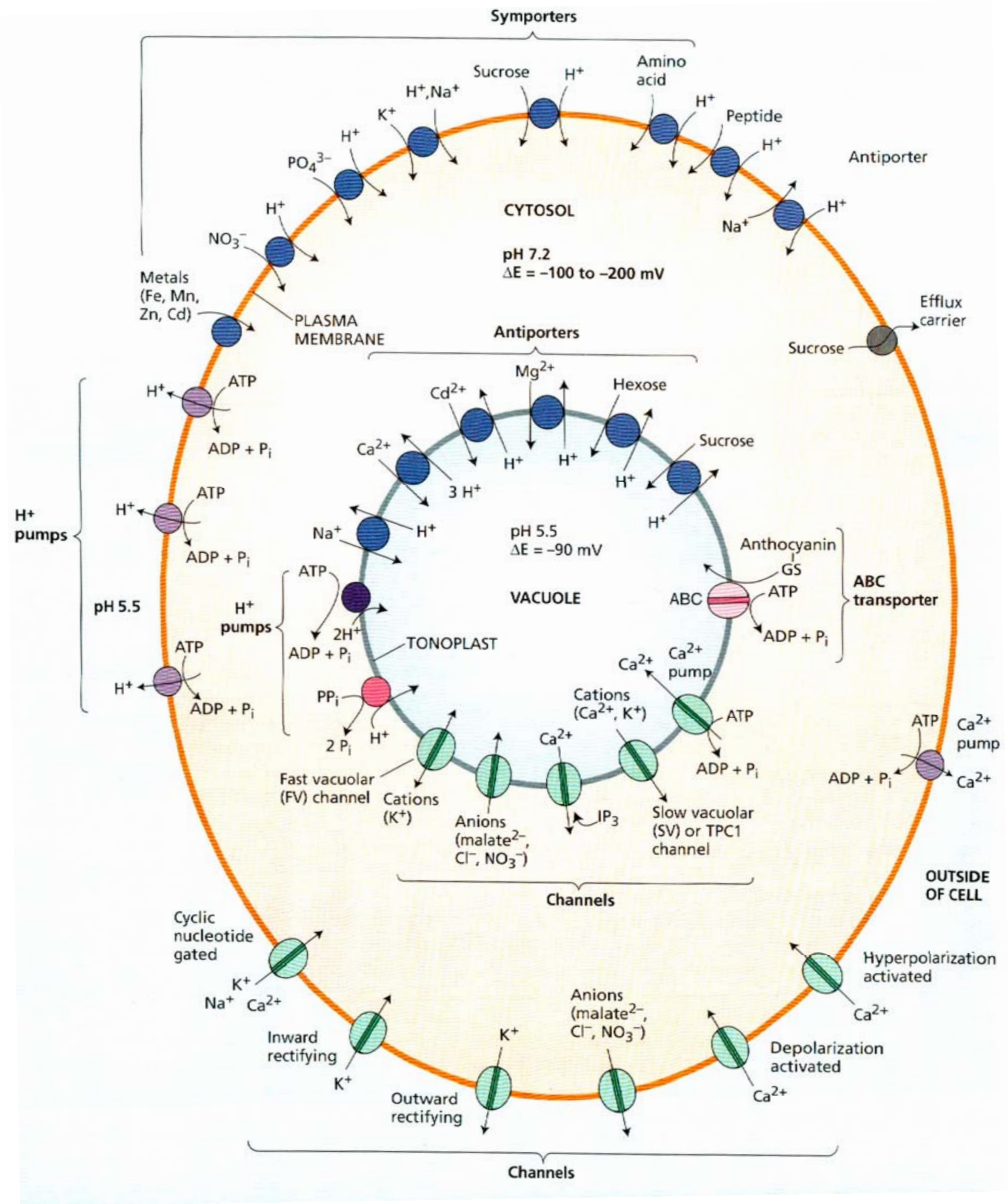


saturation

Toxic: suppression of uptake may be beneficial

threshold

Overview of Transport Processes in Plant Cells



Note:

H^+ Pumps

- P-type H^+-ATPase
- V-type H^+ ATPase
- H^+ PPiase (pyrophosphatase)

Carriers

- Symport & Antiport

Channels

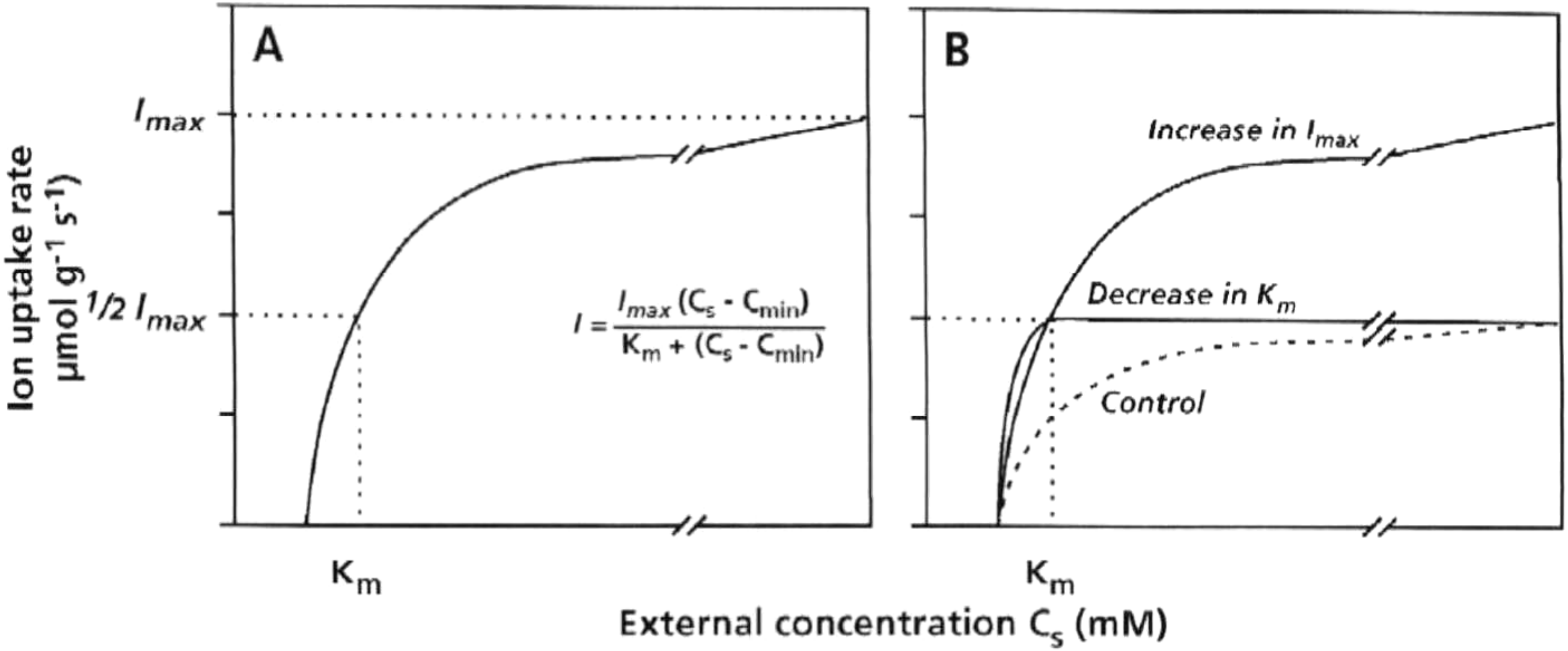
- Outward & Inward

Uptake of Nutrient Ions Approximates to Michaelis-Menten Kinetics for Enzymes

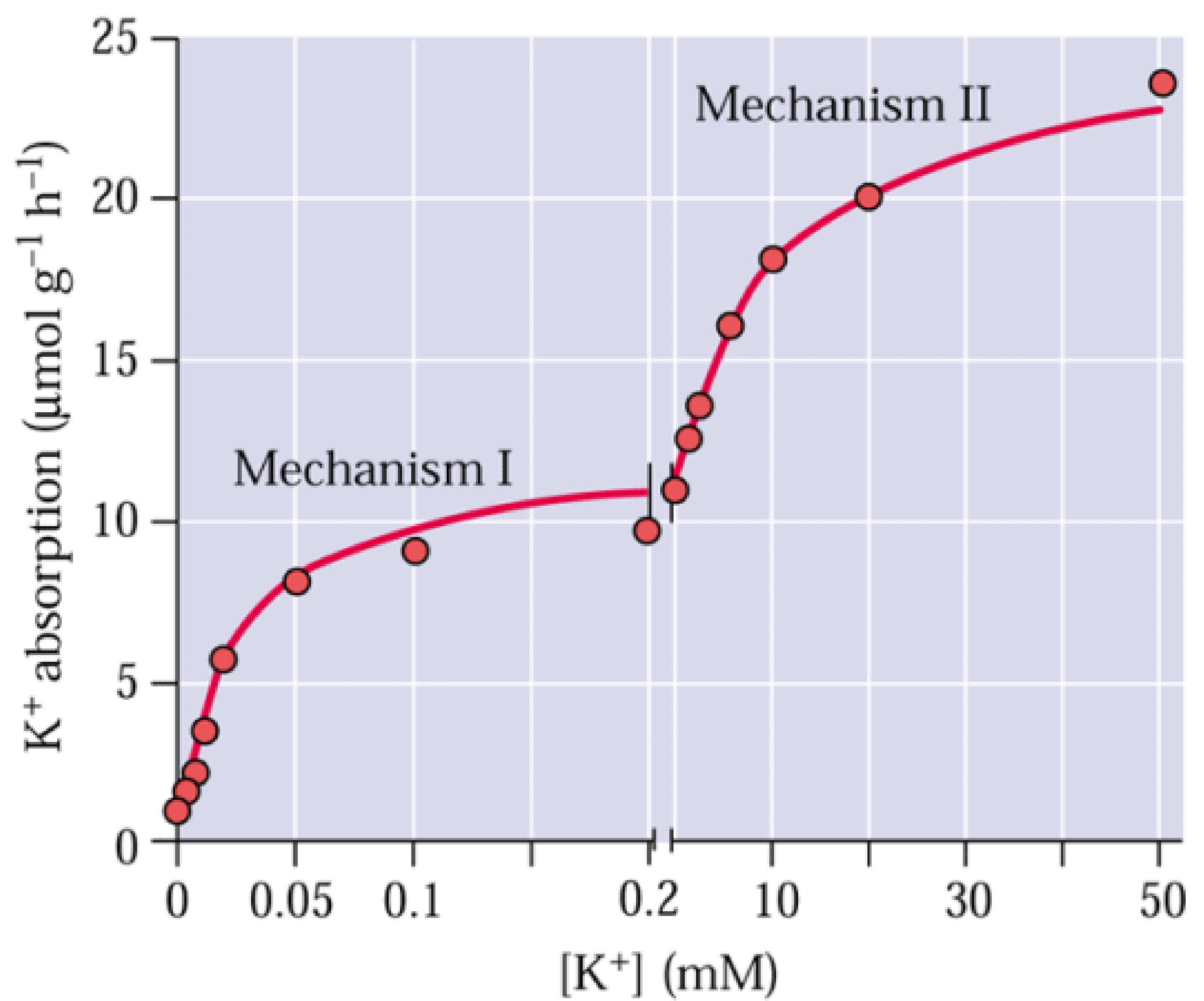
Increased Uptake by:

Increased Imax (*i.e.* More Transporters)

Decreased Km (*i.e.* Altered Efficiency of Existing Transporters)



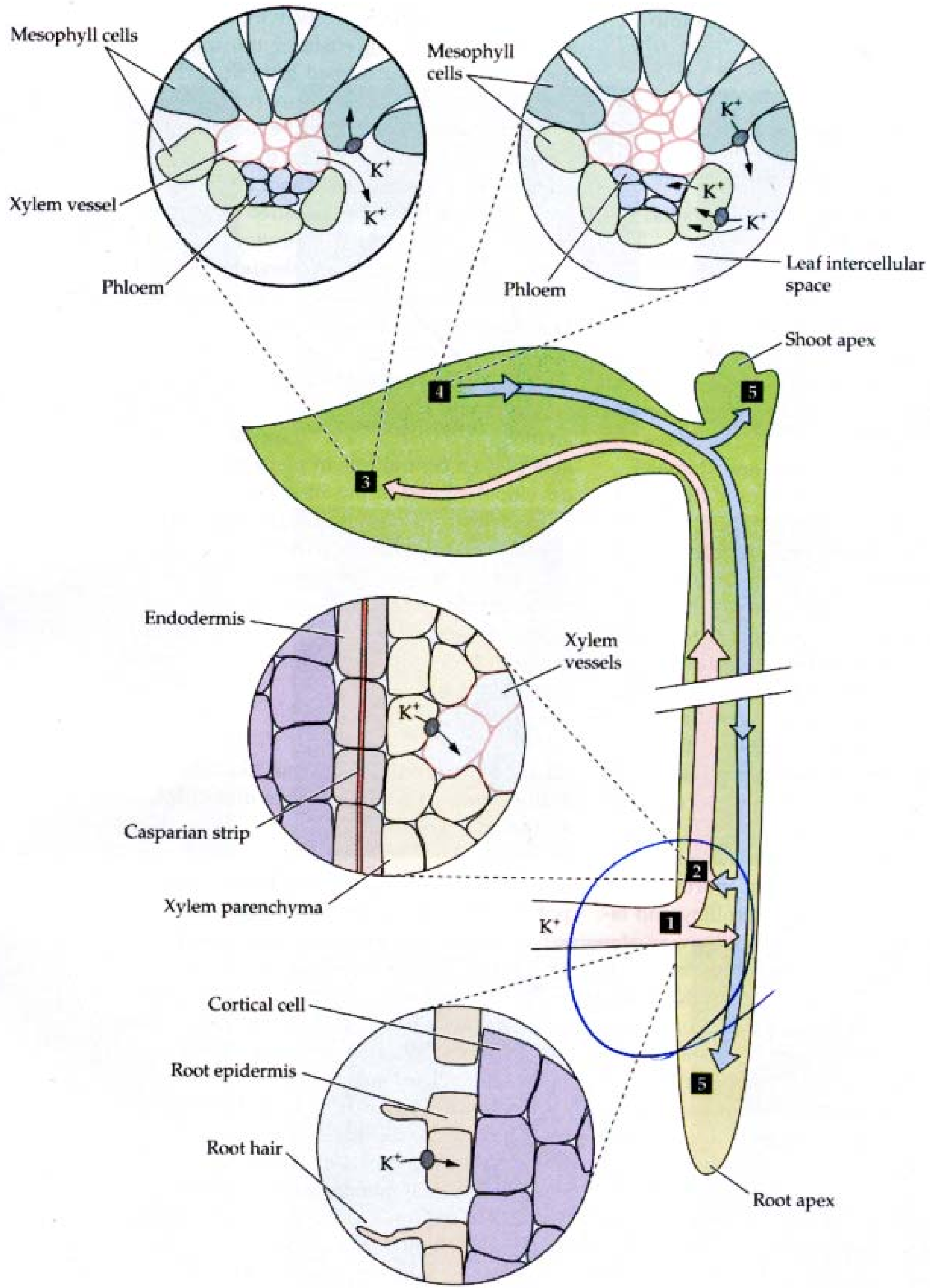
Dual Kinetics Profile



Ion Transporters are Located at Many Sites in Plants

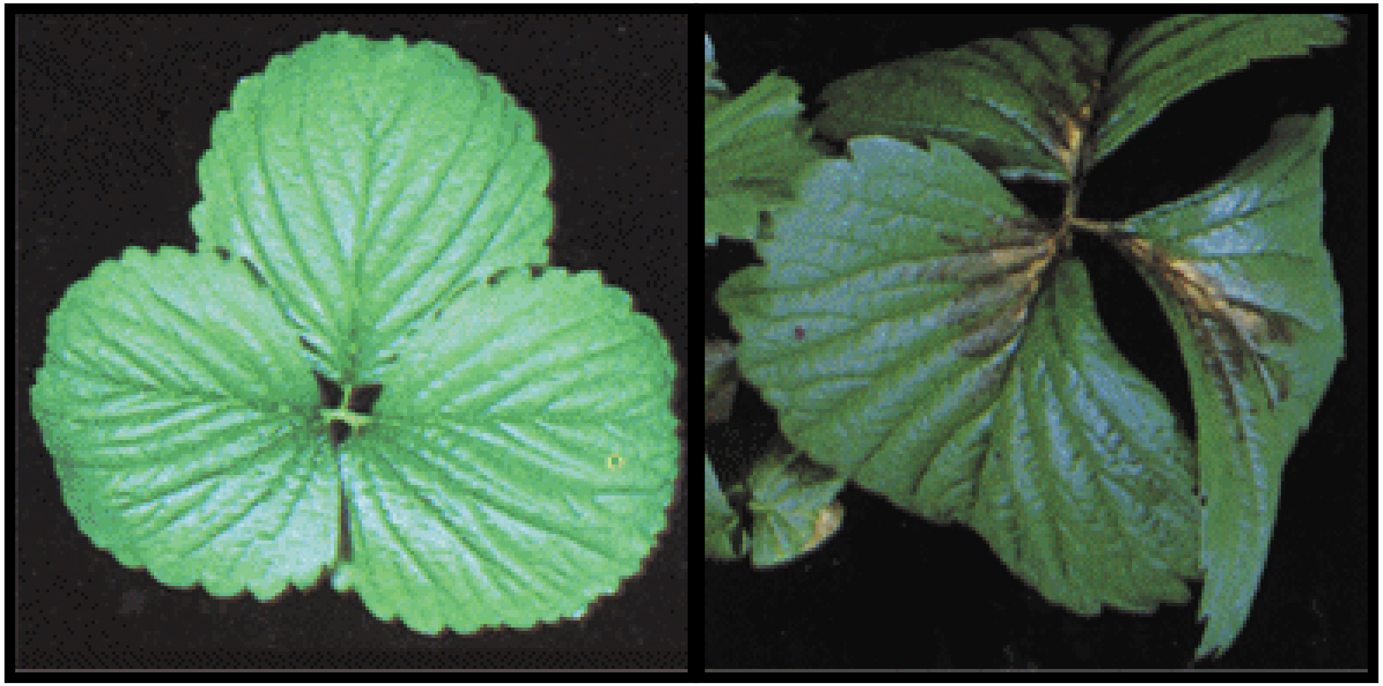
Root Membranes
- Epidermis
- Cortex
- Endodermis
- Xylem Parenchyma
- *etc.,*

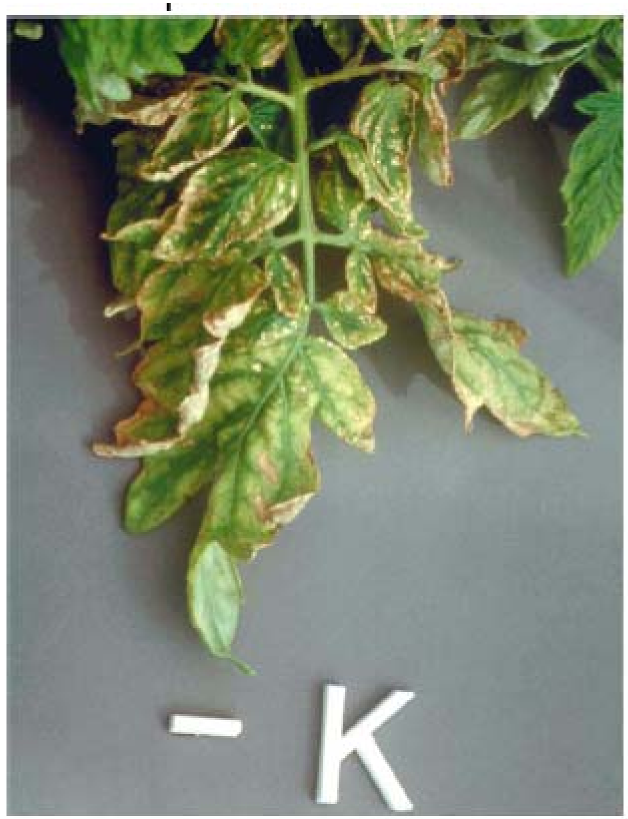
Shoot Membranes
- Xylem Parenchyma
- Mesopohyll Cells
- Guard Cells
- *etc.,*



K^+ Assimilation

Potassium Nutrition Status





K^+ Sufficient (Replete)

K^+ Deficient (Deplete)

- Marginal chlorosis
- Curl and crinkle
- Slender and weak stem
- Short internodal region

Energetics of K^+ Uptake

Soil levels of K^+ vary from
~1 M (deplete) ⇨ >1 mM (replete)

Cytoplasmic levels of K^+ are ~ 80 - 100 mM

How do plants accumulate K^+ against a >1000-fold concentration range?

They utilize *ELECTROCHEMICAL* gradients

The Nernst Equation

$$Dm_{K+} = V_m - \frac{RT}{Z_j F} \ln ([K^{out}]/[K^{in}]$$

$$Dm_{K+} = V_m - 60 \log_{10} ([K^{out}]/[K^{in}]$$

for a monovalent cation

R = Gas Constant

T = temperature in K

Vm = membrane potential (mV)

F = Fraday constant

Z_j is valance of ion

$[j^{out}]$ and $[j^{in}]$ = concentrations of j outside and inside the cell

Please Note: Sometimes the Membrane Potential, Vm is Written as Dj

What Vm is required to establish $[K^+]^{in}$ of 100 mM if $[K+]^{out}$ is….

1. 10 mM… -240 mV
2. 100 mM… -180 mV
3. 1 mM… -120 mV
4. 10 mM… -60 mV

Is this feasible…?

Believed Vm more –ve than –150 mV not possible.

Plant Growing in K^+ Deplete Soils Require Additional Active K^+ Transport Component

If

$[K^+]^{out}$ is = 10 mM,

$[K^+]^{in}$ = 100 mM

Vm = -150 mV

then at equilibrium, $Dm_{K+} = 0$, and $V_m = -60 \log_{10} ([K^{out}]/[K^{in}]$

$$Dm_{K+} = V_m - 60 \log_{10} ([K^{out}]/[K^{in}]$$

$$Dm_{K+} = -150 - 60 \log_{10} ([100]/[0.01]$$

$$-90 \text{ mV} = -150 \text{ mV} - 240 \text{ mV} \quad (\text{or } 8.96 \text{ KJ / mol})$$

Here, K can not be acquired PASSIVELY

ACTIVE COUPLED transport is required using a H^+ Pump and a K^+ Carrier

For a CATION ACTIVE TRANSPORT usually required if CONCENTRATION GRADIENT is > 100:1 (In:Out)

What Vm is required to establish $[H_2PO_4^-]^{in}$ of 10 mM if $[H_2PO_4^-]^{out}$ is….

1. 1 mM… +240 mV
2. 10 mM… +180 mV
3. 100 mM… +120 mV
4. 1 mM… +60 mV

Is this feasible…?

No, Vm are always –ve (cytoplasm –ve), -60 to –150 mV

For an ANION ACTIVE TRANSPORT is usually required

Note: the sign in the Nernst Equation switches from a '-' to a '+' when an Anion is considered (see slide 19)

Plant Growing in K^+ Deplete Soils Require Additional Active K^+ Transport Component

If

$[Pi]^{out}$ is = 1 mM,

$[Pi]^{in}$ = 10 mM

Vm = -60 mV then we can calculate

then at equilibrium, $Dm_{Pi-} = 0$, and $V_m = – 60 \log_{10} ([Pi^{out}]/[Pi^{in}]$

$$Dm_{K+} = V_m + 60 \log_{10} ([Pi^{out}]/[Pi^{in}]$$

$$Dm_{K+} = -60 + 60 \log_{10} ([10]/[0.001]$$

+180 mV = -60 mV + 240 mV (or 17.3 KJ / mol)

Here, Pi can not be acquired PASSIVELY

ACTIVE COUPLED transport is required using a H^+ Pump and a Pi Carrier

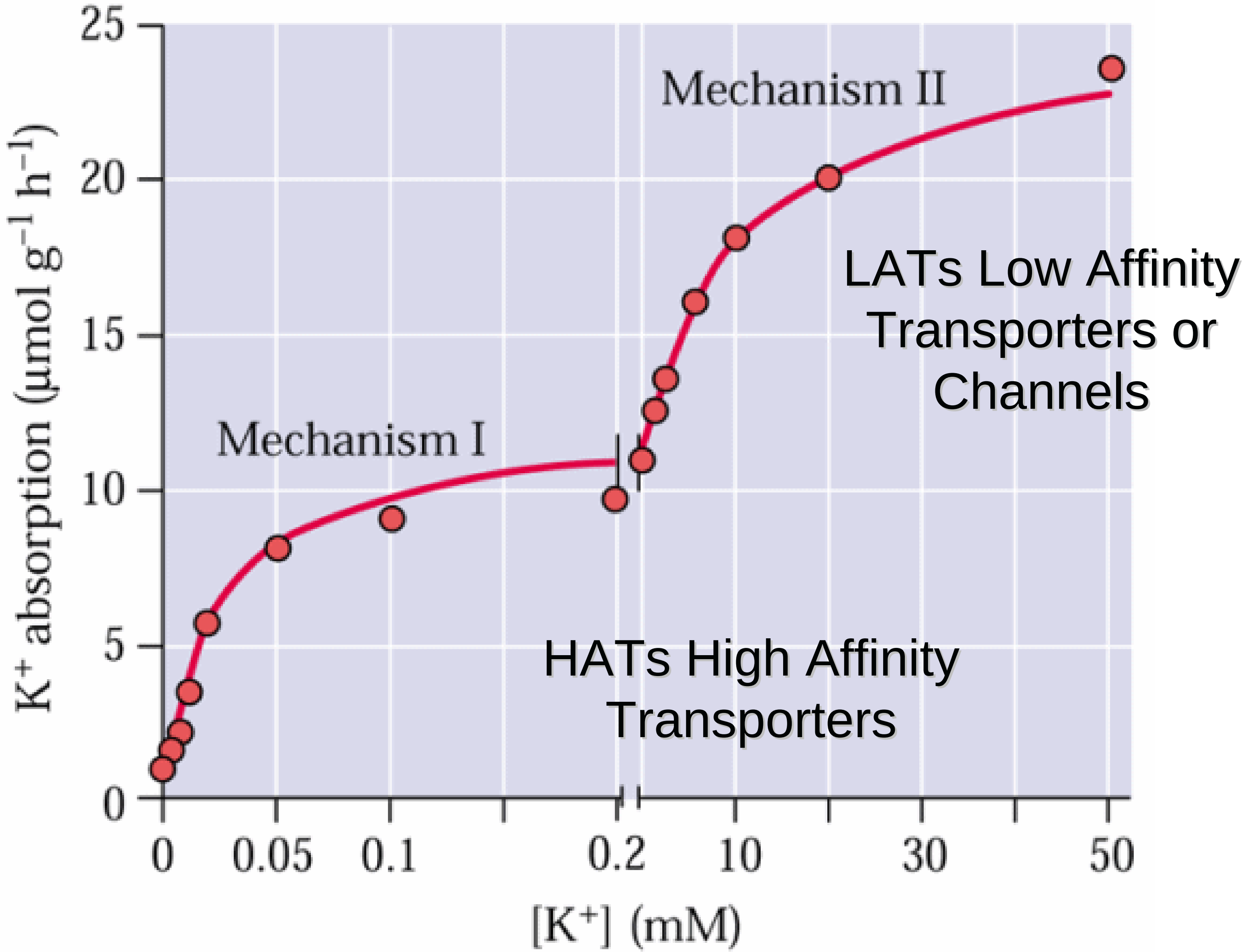
Summary of '*Theortetical*' K^+ Transport..

High Affinity Transporters (HATs) operate in the $[K^+]^{out}$ < 200 mM range (utilize DmH$^+$ and DmK$^+$)

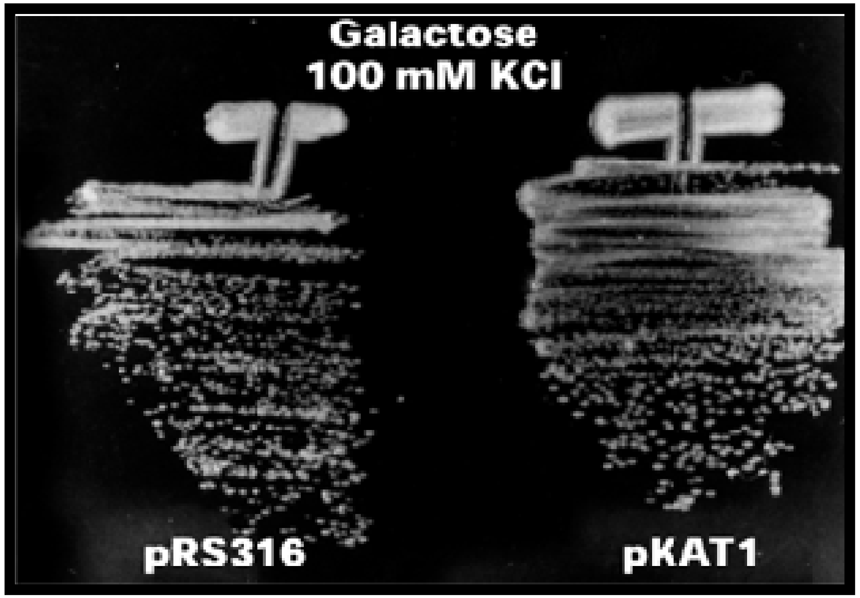
Low Affinity Transporter (channels) operate in the $[K^+]^{out}$ >200 mM range (utilize DmK$^+$ only)

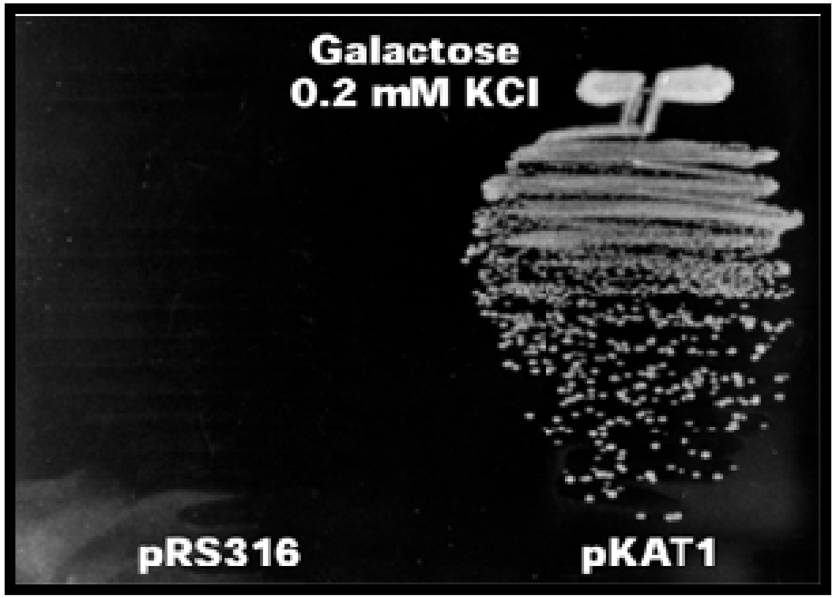
Note: There is Accumulating Evidence that Some HATs can be converted to LATs – but these are Carriers not Channels

Dual Kinetics Profile



AKT1 and KAT1 were Cloned by Heterologous Expression in *S. cerevisiae* strain CY162 (D*trk1-2*)

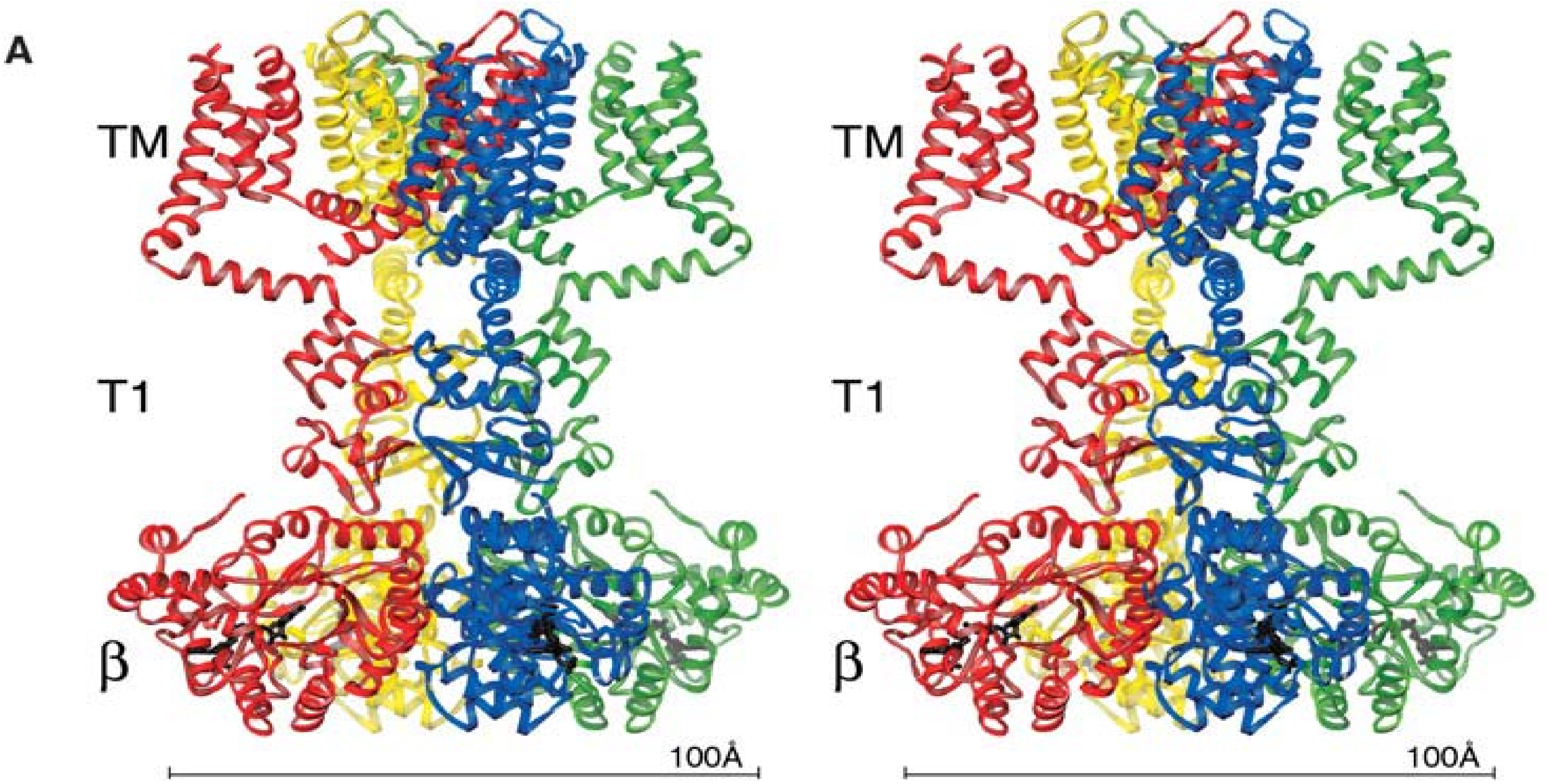




Conclusion…

an *Arabidopsis* sequence restores high affinity uptake in CY162

Structure of Kv1.2, a *Shaker* K^+ Channel



Long *et al.* (2005) Science 309:897-903
Long *et al.* (2005) Science 309:903-908

K^+ Channel Summary

Several homologues of AKT1 have now been cloned

Most are located in root epidermis / cortex, but also elsewhere

Homologues also found in other species (*e.g.* SKT1-3 from *Solanum tuberosum*)

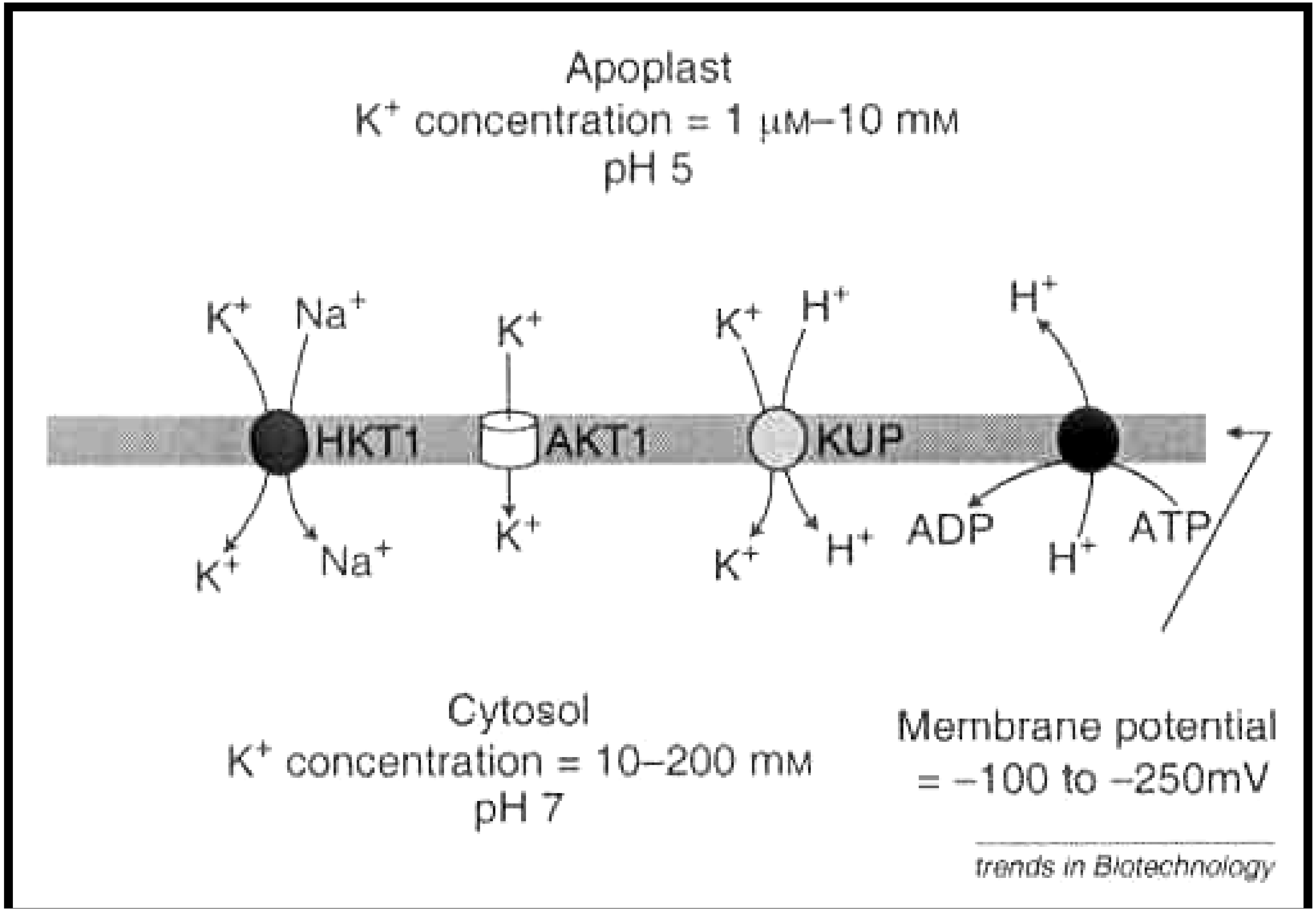
Cloning HKT1 and KUP High Affinity Transporters

HKT1 cloned by screening (complementation) of wheat cDNA library in yeast strain CY162

AtKUP1/2 cloned by complementation of CY162 *and* by homology to *E. coli* HAK1

Both enriched in root tissue

Summary of K^+ Uptake



Nitrogen Assimilation

Figure 37.9 The role of soil bacteria in the nitrogen nutrition of plants (Layer 1)

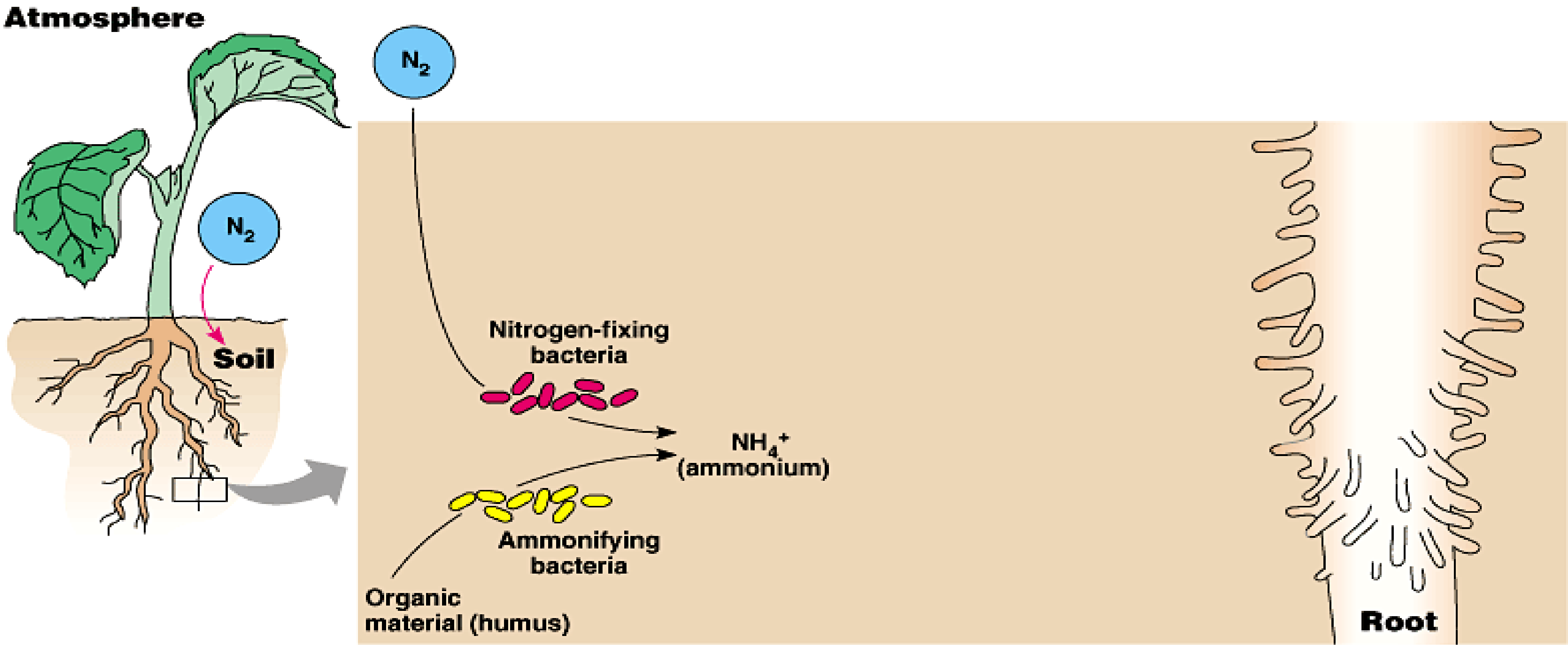


Figure 37.9 The role of soil bacteria in the nitrogen nutrition of plants (Layer 2)

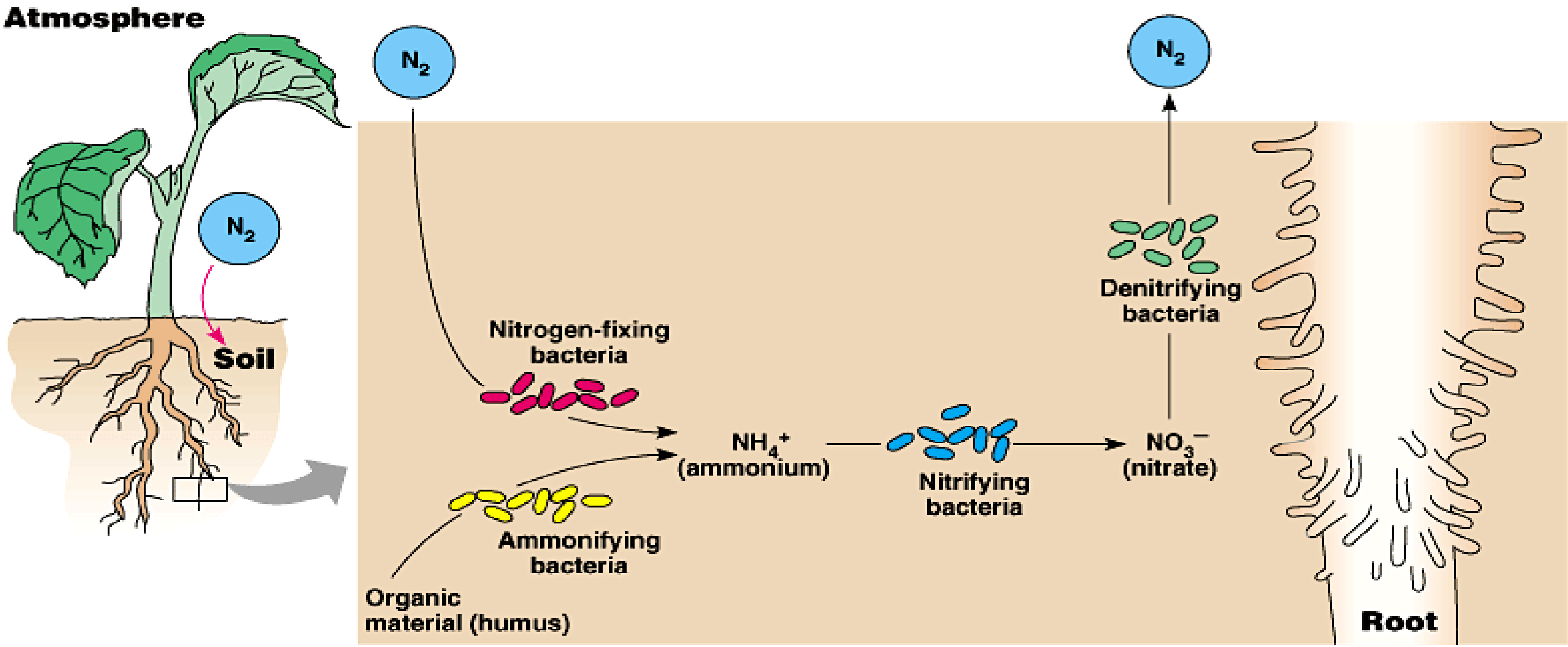
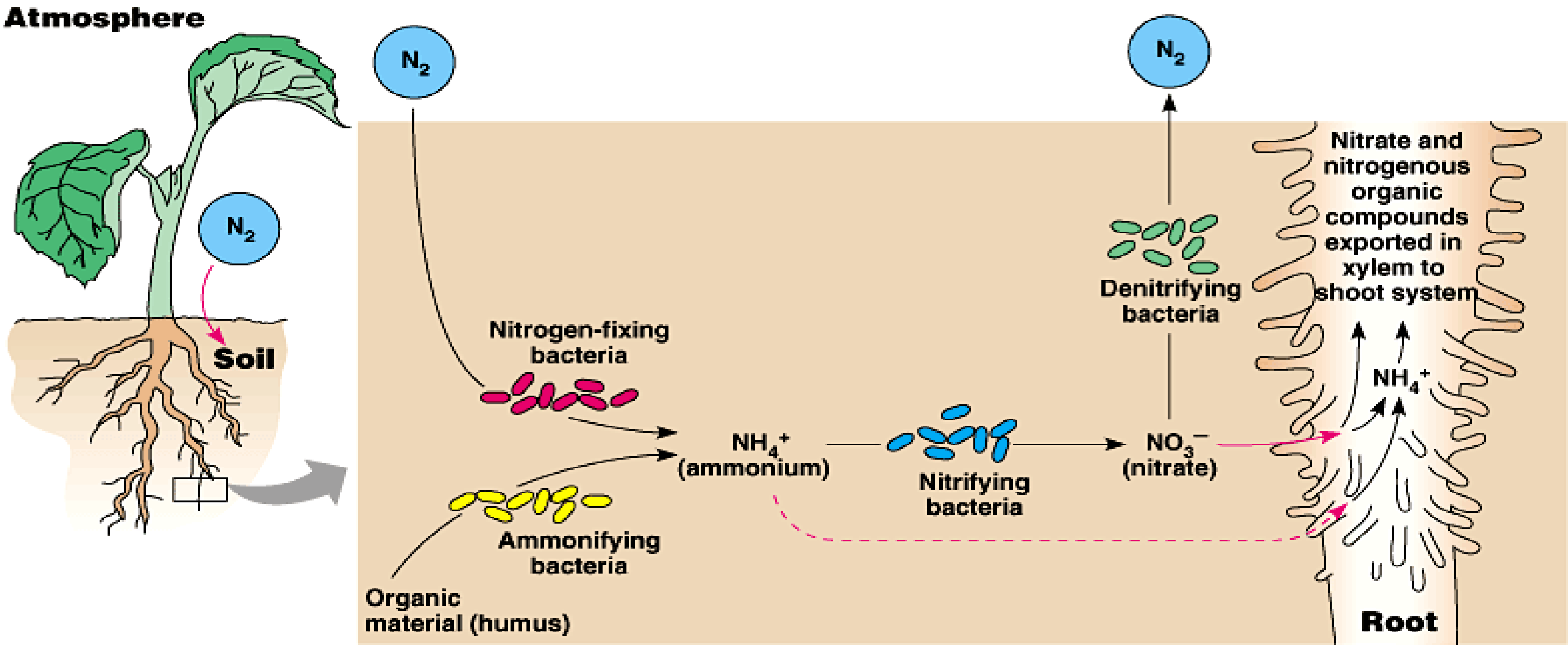


Figure 37.9 The role of soil bacteria in the nitrogen nutrition of plants (Layer 3)



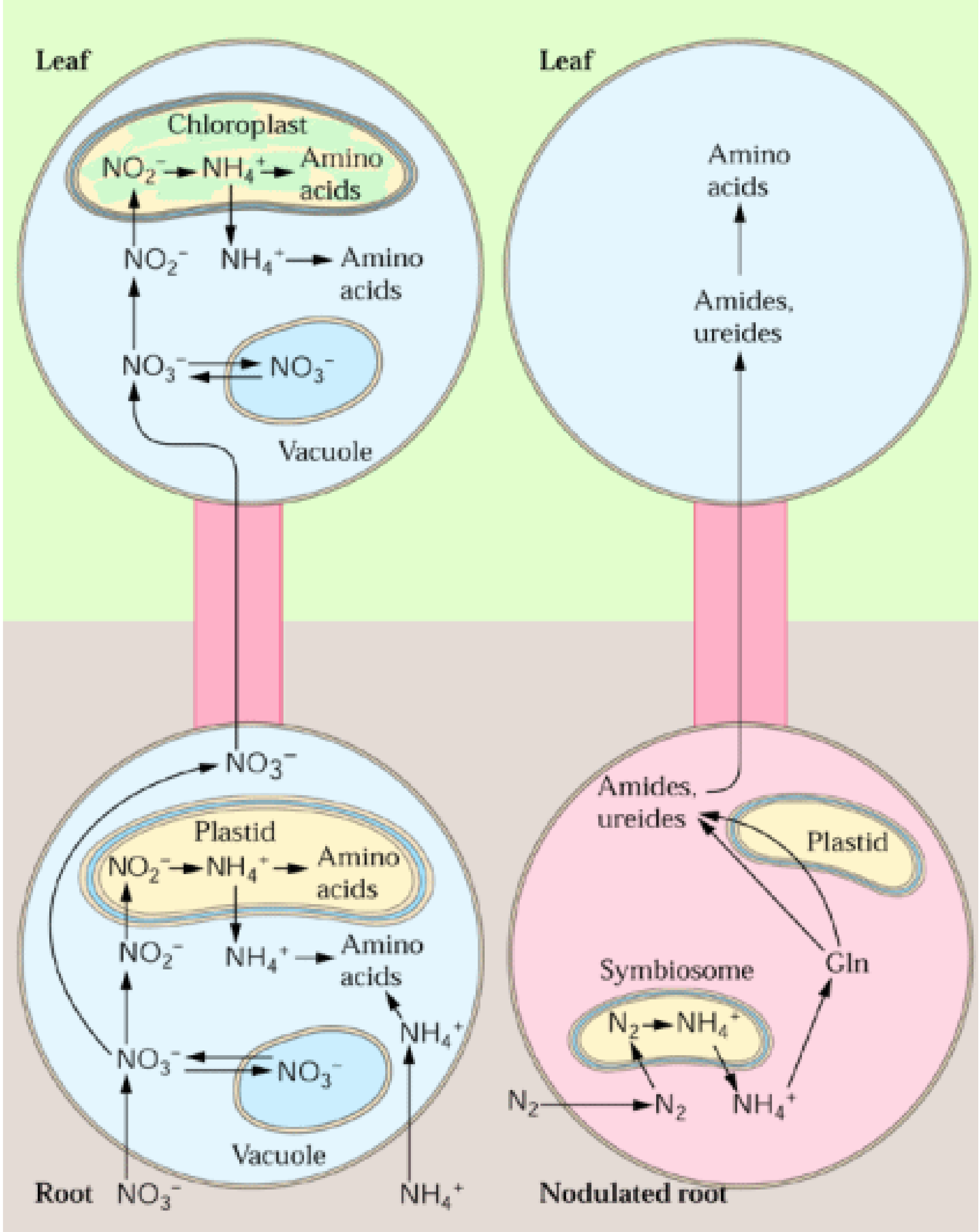
Nitrogen Assimilation in Plants

1. By uptake of NO_3^- & reduction to NH_4^+ by Nitrate Reductase (NR, – Energetically Expensive)

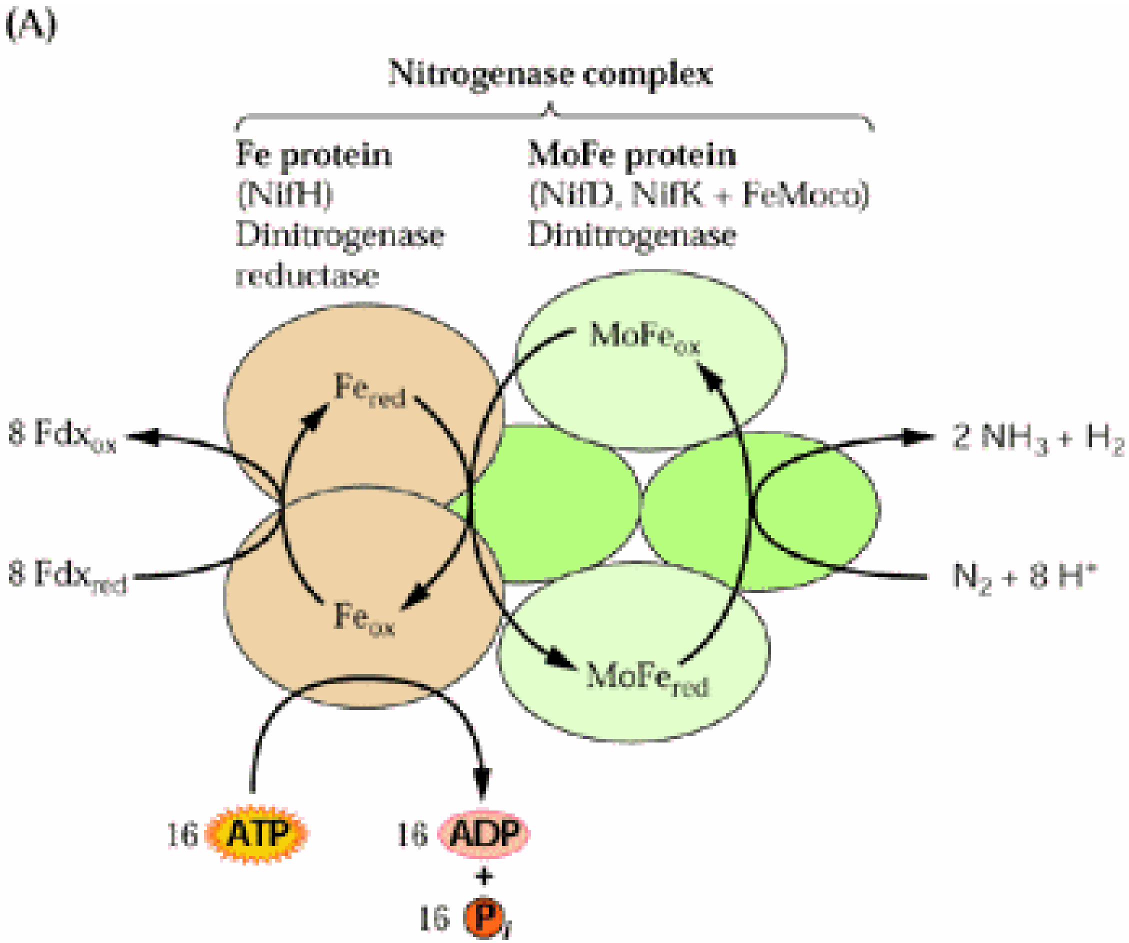
   Root – mainly Temperate, ~15% of Plant's Energy

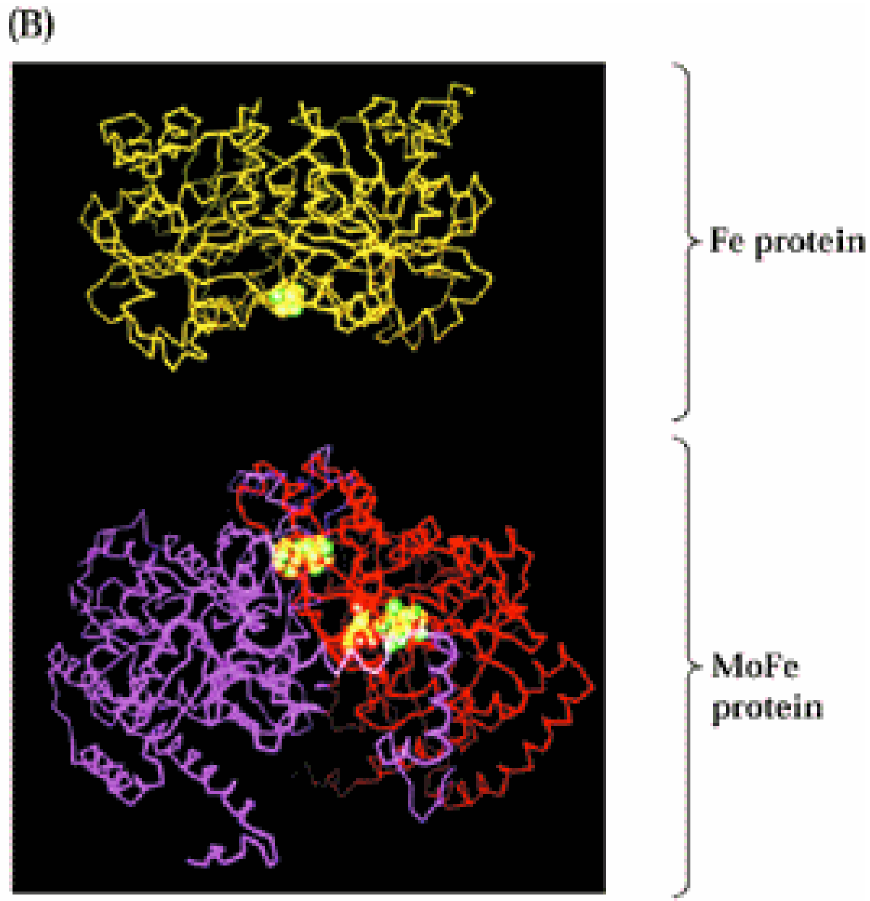
   Shoot – mainly Tropical, ~2% Plant's Energy

2. By direct uptake of NH_4^+
3. By symbiotic N_2 assimilation to NH_4^+



Symbiotic Dinitrogen Assimilation Requires the Action of the Enzyme Nitrogenase





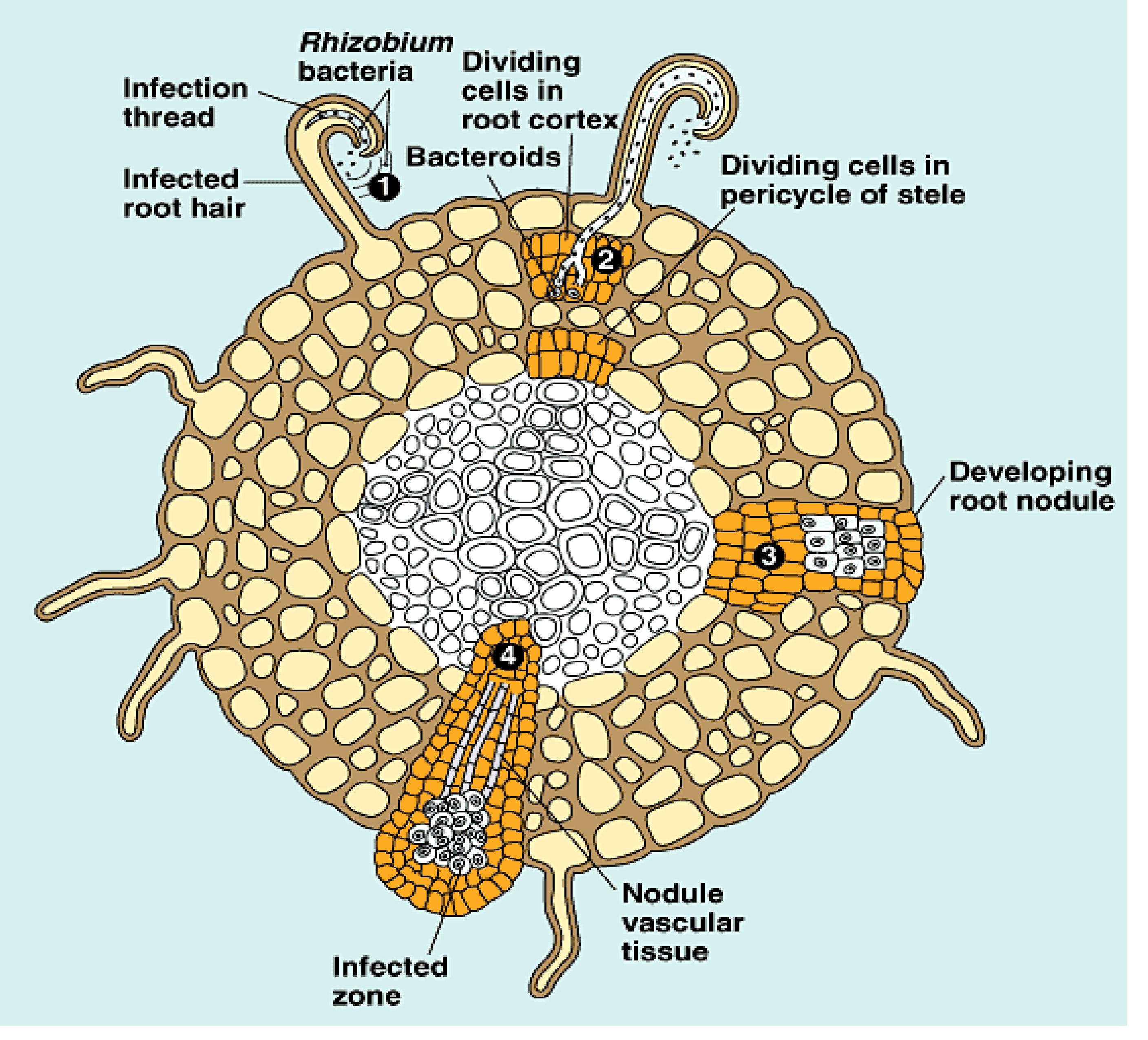
Main Nitrogen-fixing Symbiotic Associations

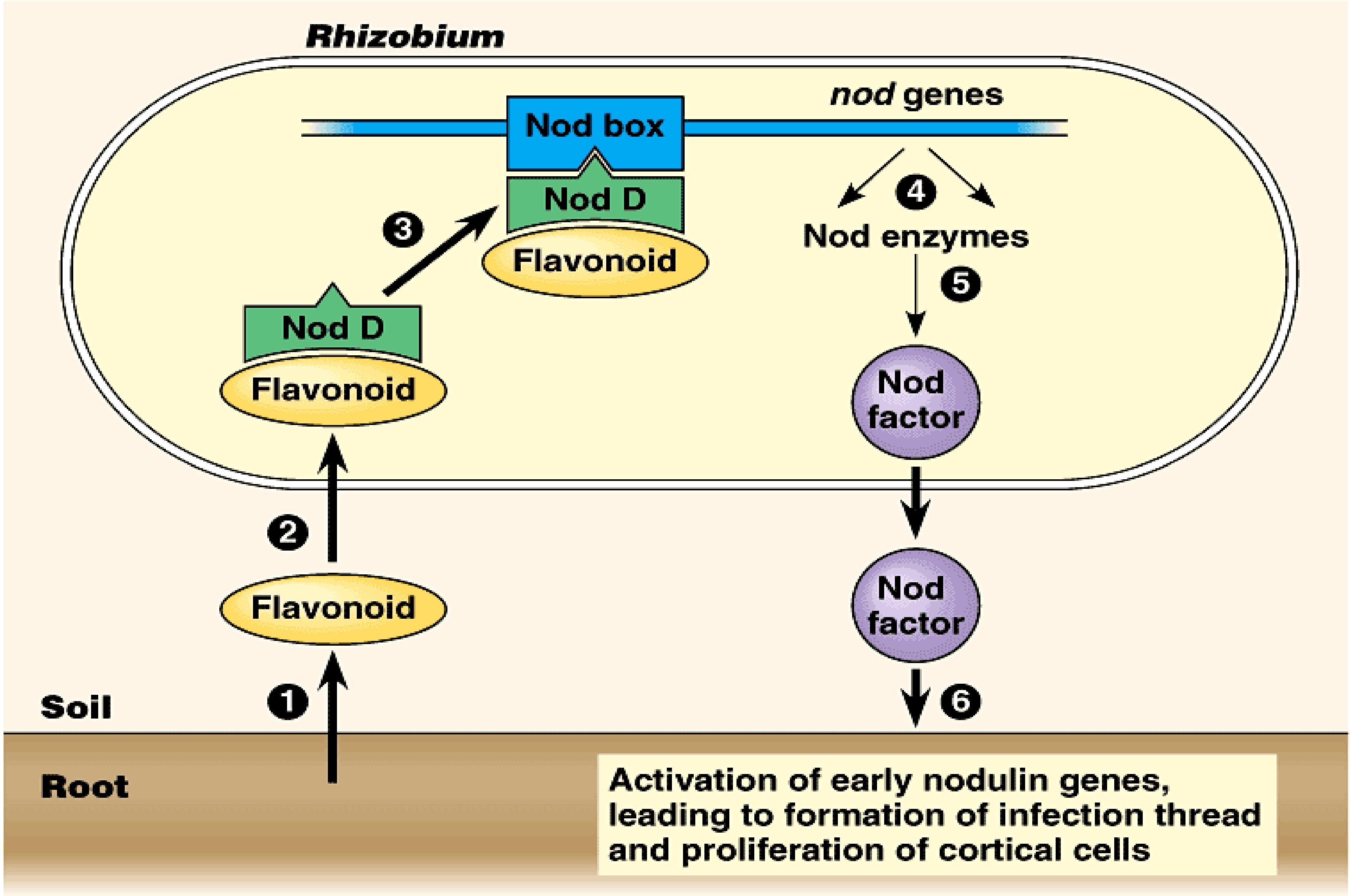
Rhizobium spp. with Legumes

Frankia spp. with*Alnus, Casuarina, Myrica, Ceanothus*

Cyanobacteria with *Gunera,* Cycads, ferns (*Azolla*)

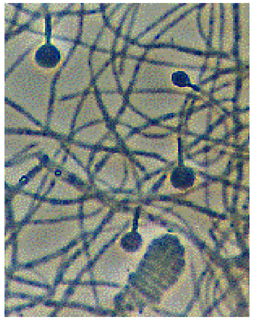
Figure 37.11 Development of a soybean root nodule



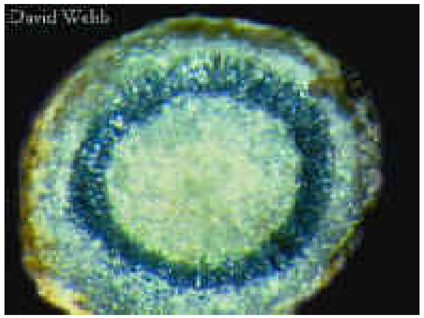

Rhizobium
nod genes
Nod box
Nod D
Flavonoid
3
4
Nod enzymes
5
Nod D
Flavonoid
Nod factor
2
Flavonoid
Nod factor
Soil
1
6
Root
Activation of early nodulin genes, leading to formation of infection thread and proliferation of cortical cells

Rhizobium – Legumes (Fabaceae)

Frankia - Alder, Myrica, Casuarina



Cyanobacteria – Azolla, Cycads, Gunnera



Carnivorous Plants

Sundew
(Drosera)

Pitcher
Plant

Fly Trap
(Dionaea)

Nitrate Transporters

Two gene families have been identified in plants

NRT1 – identified by screen of *Arabidopsis* mutants on chlorate.

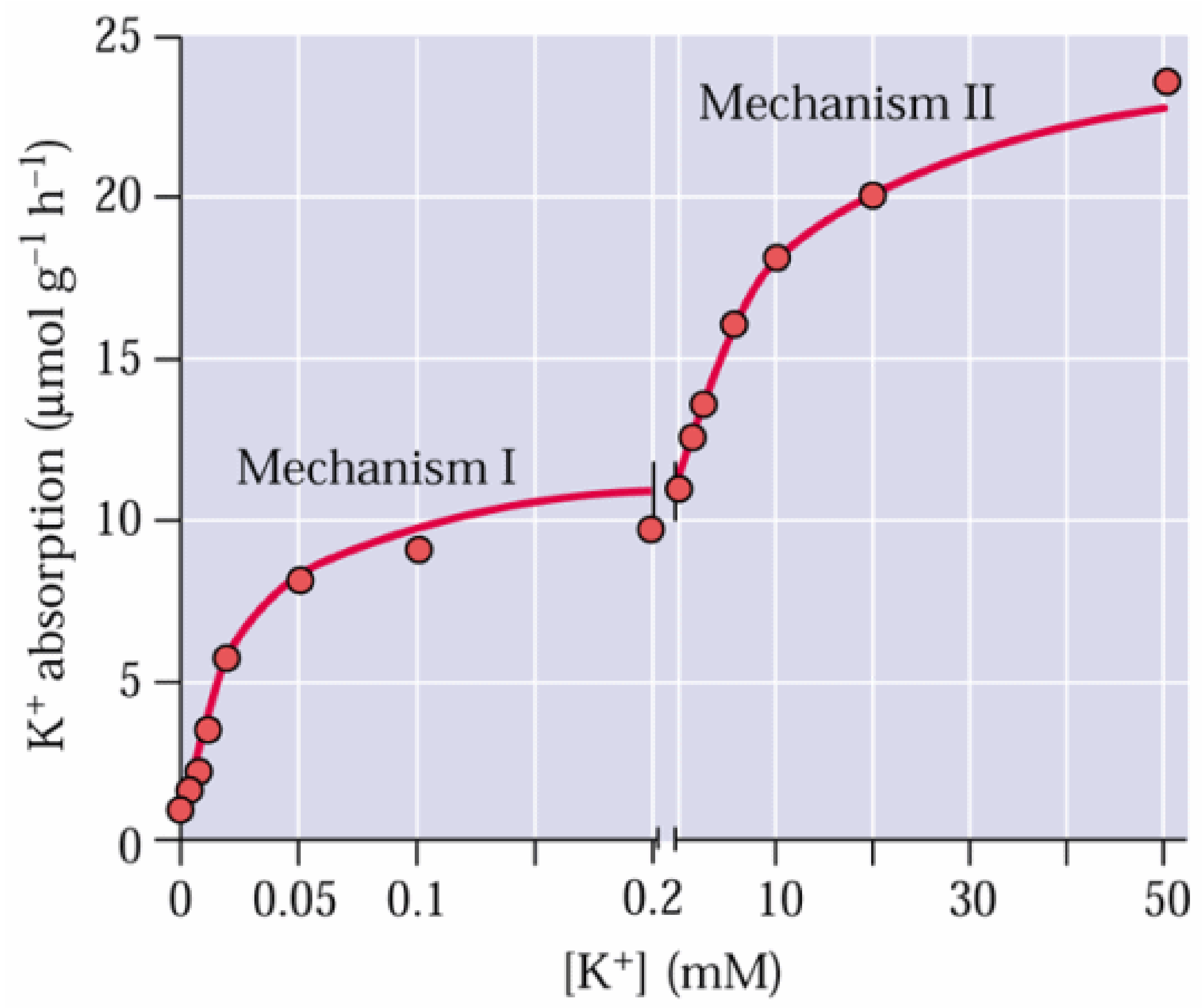
- 12 ms a-helices superfamily FDT
- Some members are inducible by low NO_3^-
- Some appear to mediate High & Low Affinity NO_3^- uptake

NRT2- protein structurally unrelated to NRT1

- Induced by low external NO_3^-
- Loss of NTR2 appears to be lethal

Both NRT1 & NRT2 believed to be $2H^+/NO_3^-$ symporters

Like K Uptake, NO_3 Uptake Shows 'Dual Kinetics' in Plants.



Structure of NRT1 Family of Proteins

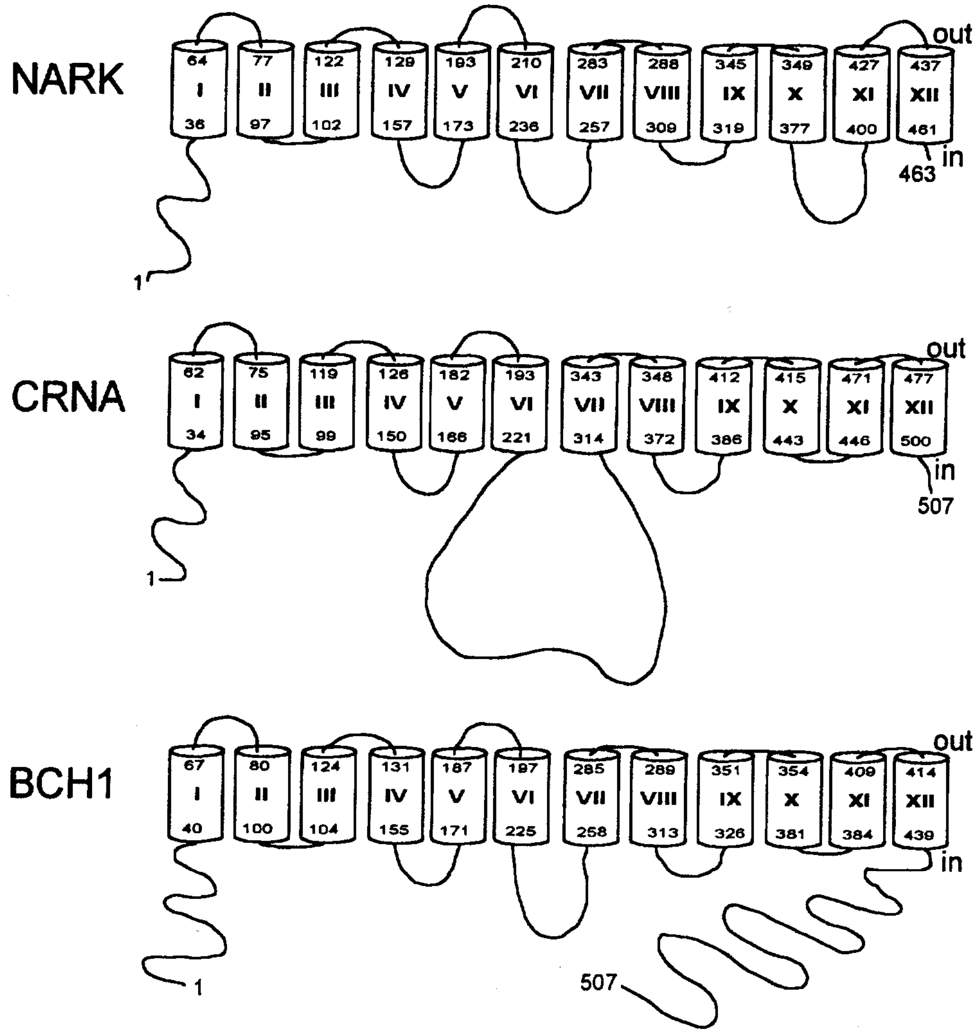


Fig. 4. Models for the membrane topologies of the NARK, CRNA and BCH1 polypeptides. The locations of the twelve transmembrane domains are as predicted by the TMAP programme (Persson and Argos, 1994).

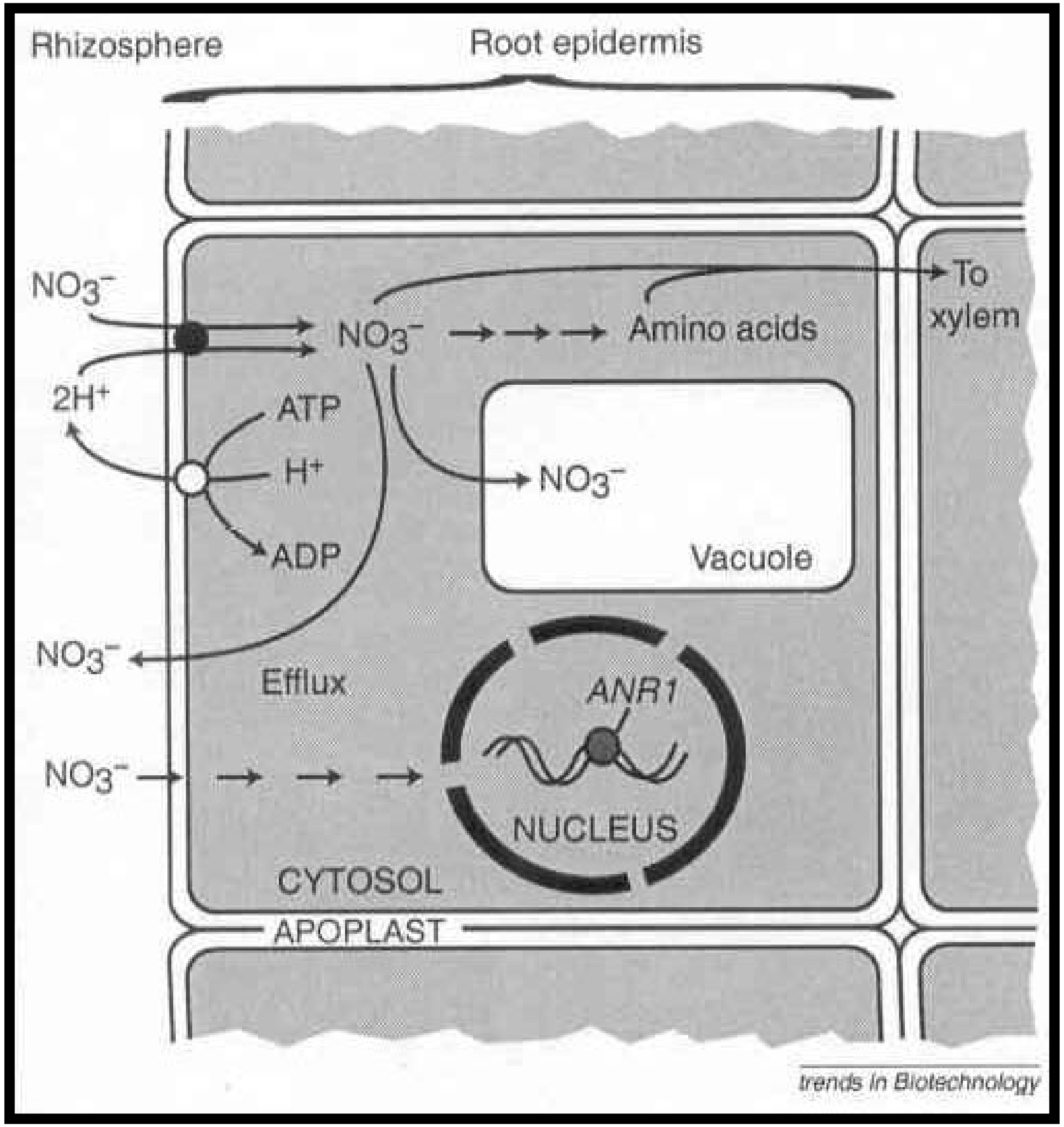
Improving NO_3^- Assimilation

Overexpression of *NTR1 and NTR2* genes does <u>not</u> increase NO_3^- uptake

ANR1 a is a low NO_3^- activated MADS-box transcription factor

believed to cause root hair proliferation

Summary of NO_3^- Uptake



Phosphorus Assimilation

Phosphorus Acquisition & Assimilation.

HPO_4^{2-} / $H_2PO_4^-$ are usual forms in pH 4-9

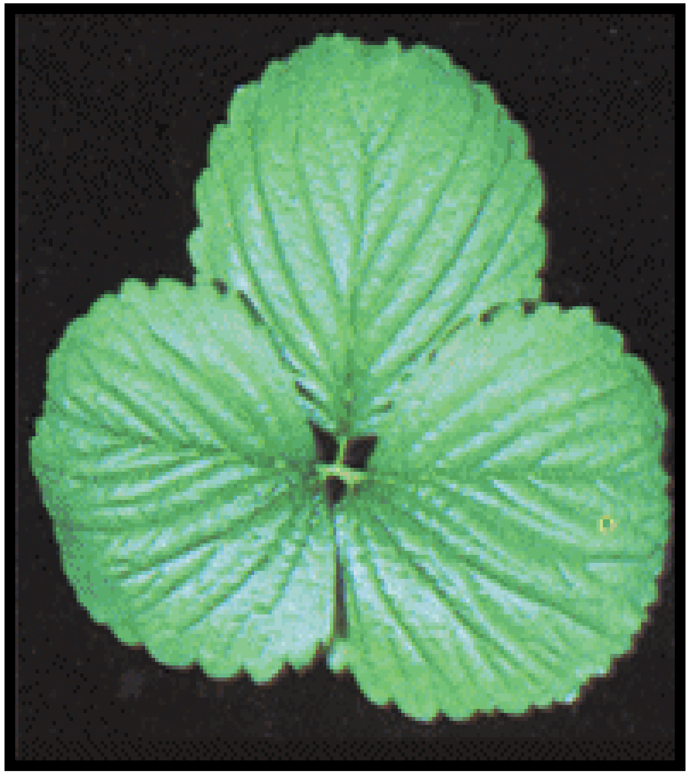
Many salts of phosphate are insoluble (Ca^{2+}, Fe^{3+}, etc.) at alkaline pH

Most phosphate in soil is complexed to carbon or in insoluble form (high pH)

Phosphate levels in soil vary from <1 mM to >1 mM

Mobilization of phosphate is required in many unfertilized soiils

Symptoms of P Deficiency



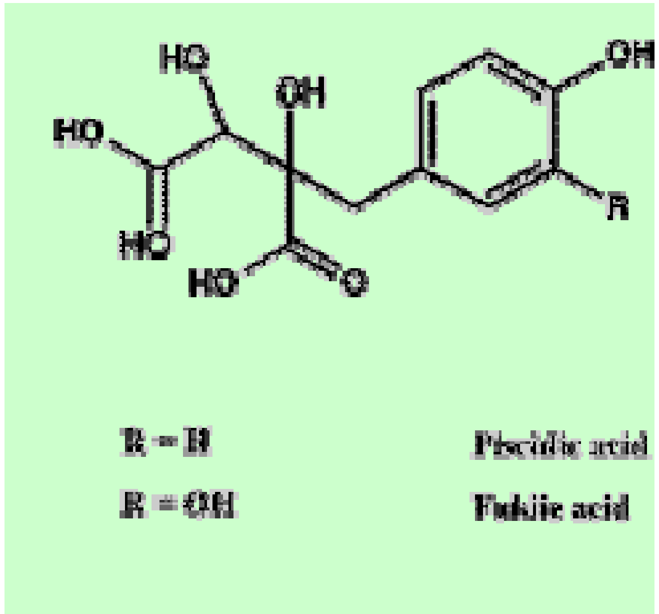
Nutrient Sufficient

Phosphorus Deficient (-P)

Many Plants Exude Organic Acids into the Rhizosphere to Mobilize P

Cajanus cajan
(Pigeonpea)

Secretes piscidic acid into rhizosphere



Many Plants Secrete Phosphatases into the Rhizosphere

Mycorrhizal fungi secrete phosphatases into the soil to release organic P into solution (as phosphate) – some of these genes have been cloned

No plant homologues have been identified yet but they do exist

Should be possible to genetically manipulate crops to exploit this mechanism of P acquisition

Phosphate Transporters have been identified in Plants

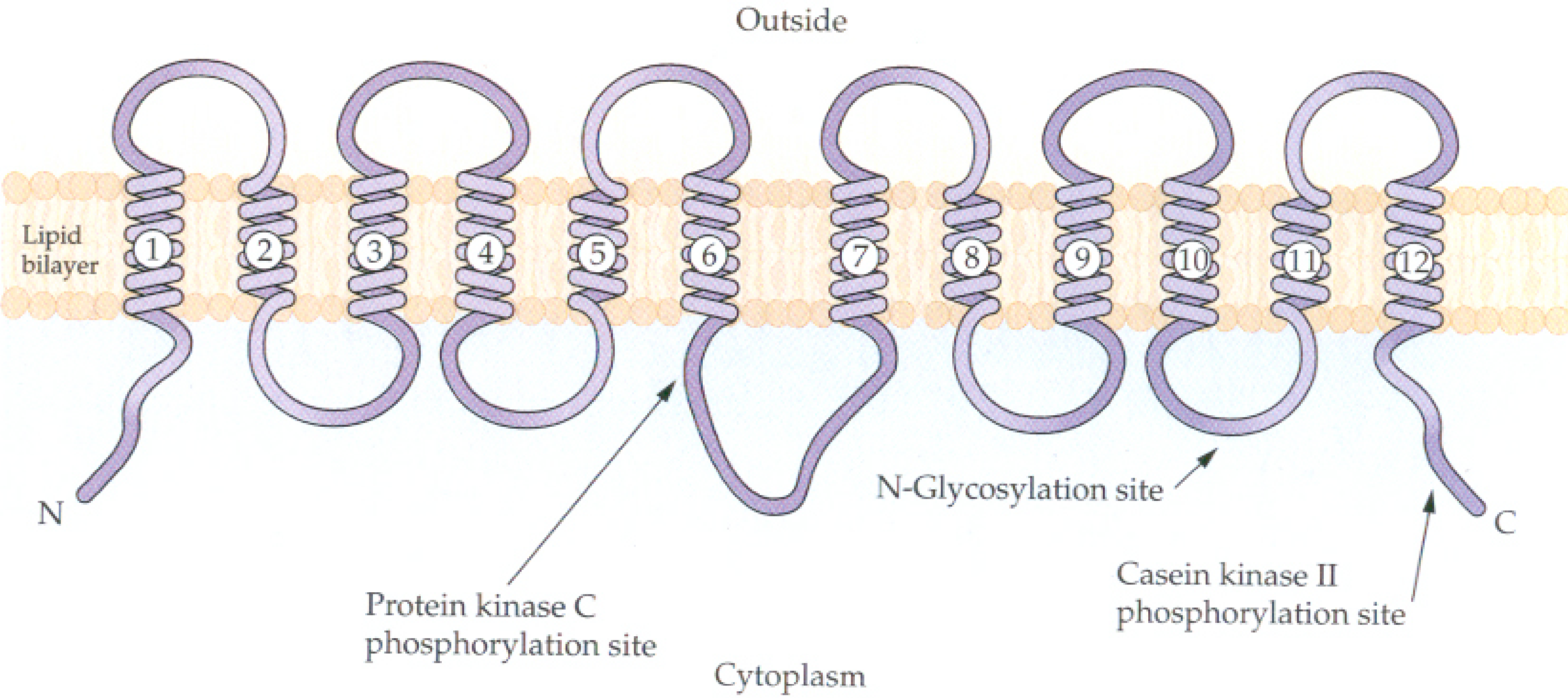
Phosphate transport is multiphasic in Plants

Phosphate uptake is carrier-mediated and active

PT1 & PT2 have now been cloned from *Arabidopsis*, & *L. esculentum* and *S. tuberosum* – similar in structure to well characterized yeast PHO84

PT1 and PT2 are induced by low P

PT1 & PT2 are believed to be H^+ / PO_4 symporters but the evidence is contradictory



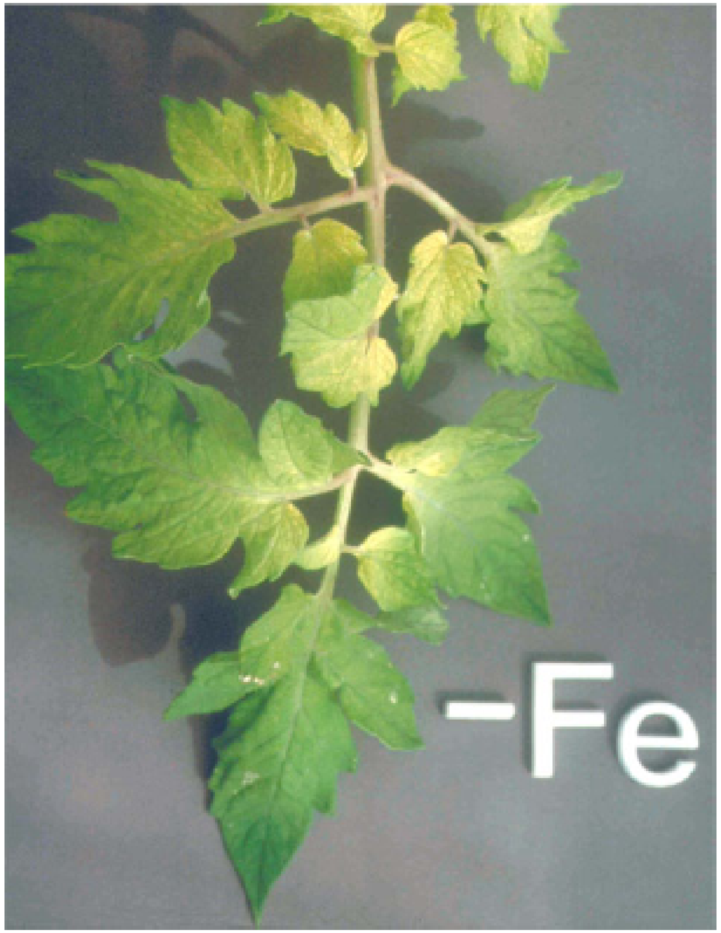
Iron Assimilation

Symptoms of Fe Deficiency

Iron Sufficient

Iron Deficient

Group IV: deficiencies in mineral nutrients that are involved in redox reactions



- intervenous chlorosis
- Younger leaves

- Dark green leves with necrotic spots
- Leaves are twisted

Iron Acquisition

Fe^{3+} is the major form in soil

Fe^{3+} is very insoluble > pH 7

Two strategies have evolved in plants to take up Fe from the rhizosphere

- Type 1 Dicots & monocots (excluding graminae) reduce $Fe^{3+} \Rightarrow Fe^{2+}$ *explanta,* then take up Fe^{2+}

- Type 2 – the graminae release ***phytosiderophores***, proteins that adsorb Fe^{3+}, and then take up the complexed Fe^{3+}.

Type 1 Fe Accumulators

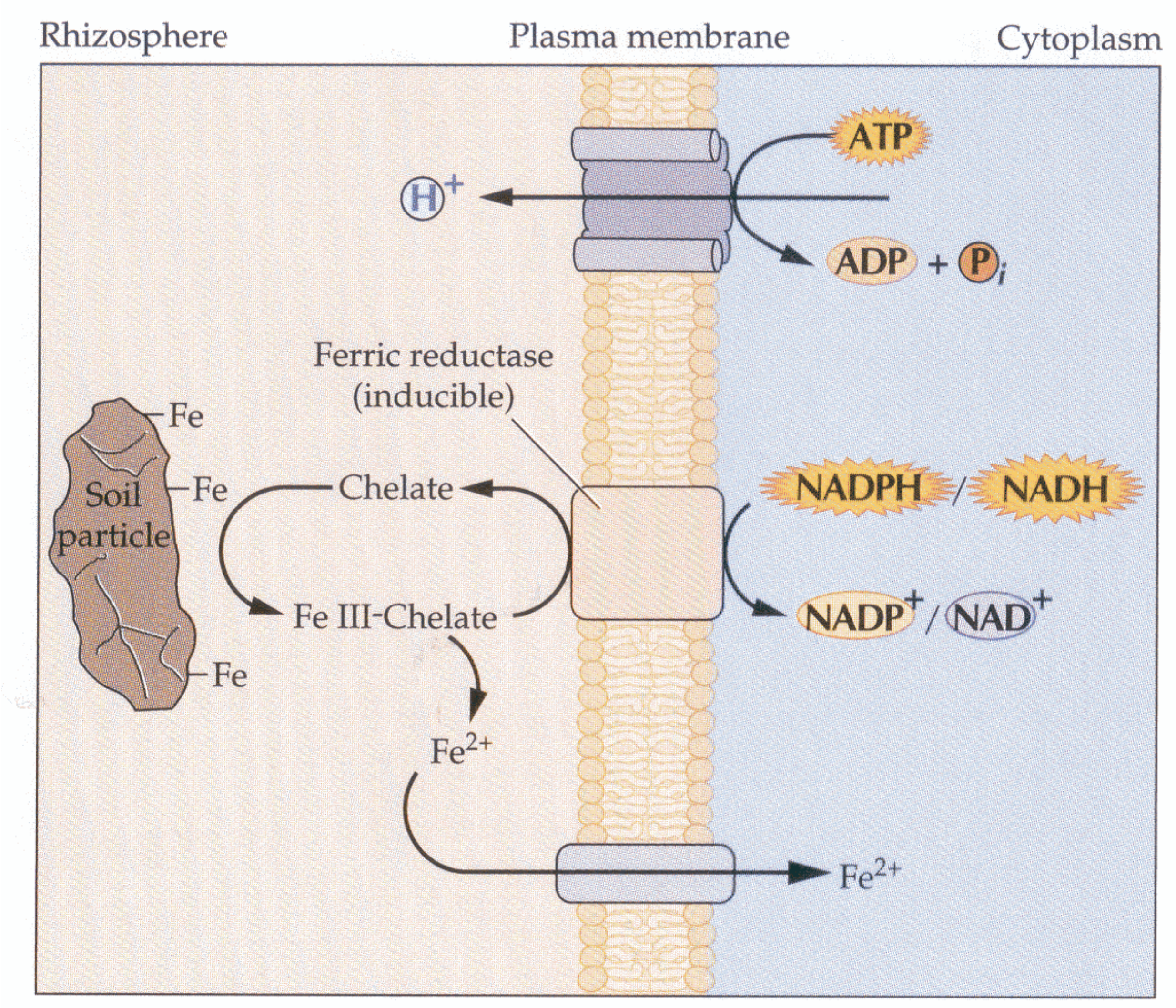
IRT1 from *Arabidopsis* has been identified that mediates Fe^{2+} uptake in yeast

IRT1 is expressed in roots & induced by low external Fe

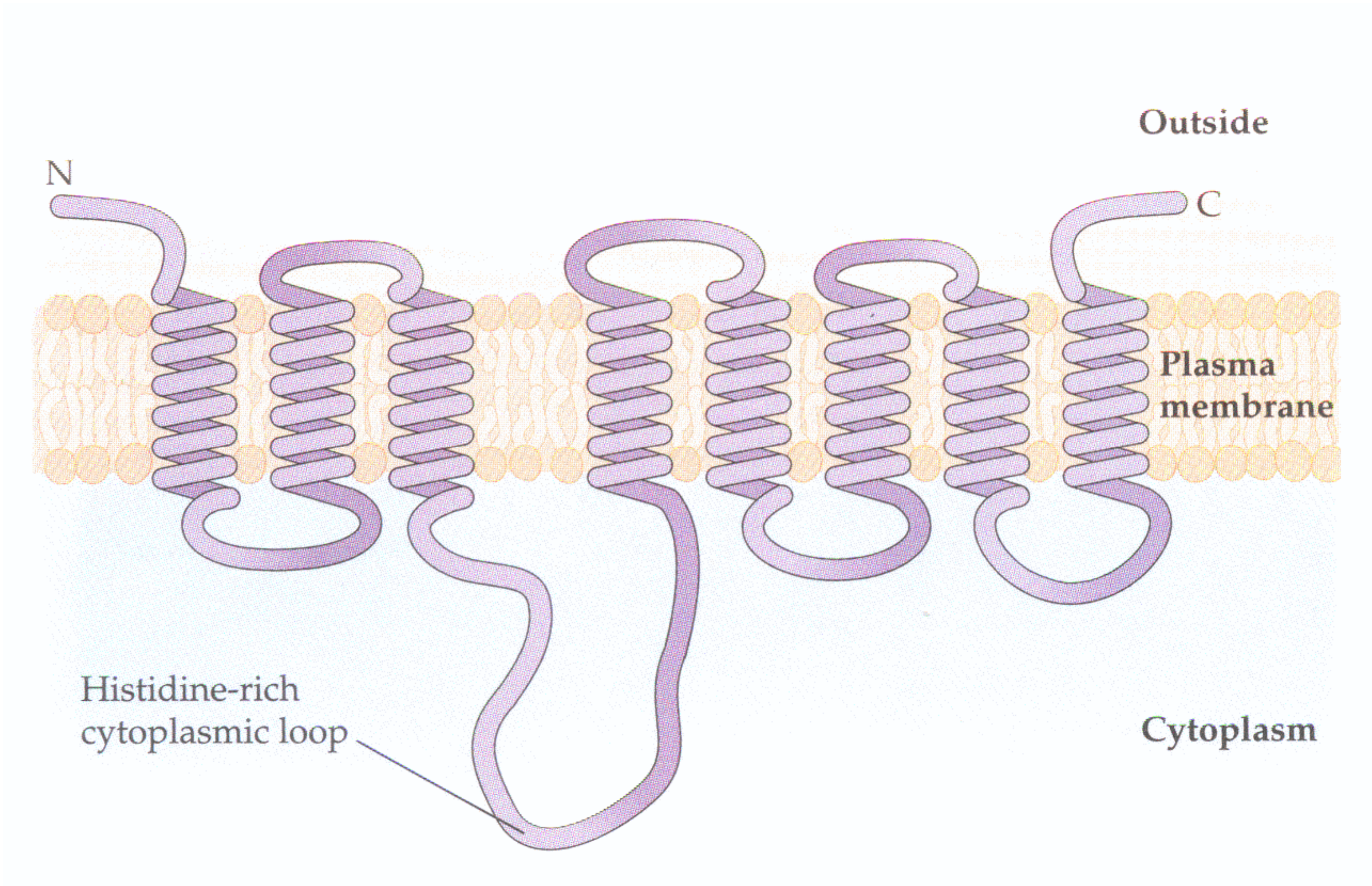
FRO2 - cloned from *Arabidopsis* – codes for a root Ferric Chelate Reductase

IRT1 & FRO2 are co-regulated

Type 1 – IRT1/FRO2 Mediated Fe^{2+} Uptake



IRT1 Represents a New Family of Transporters



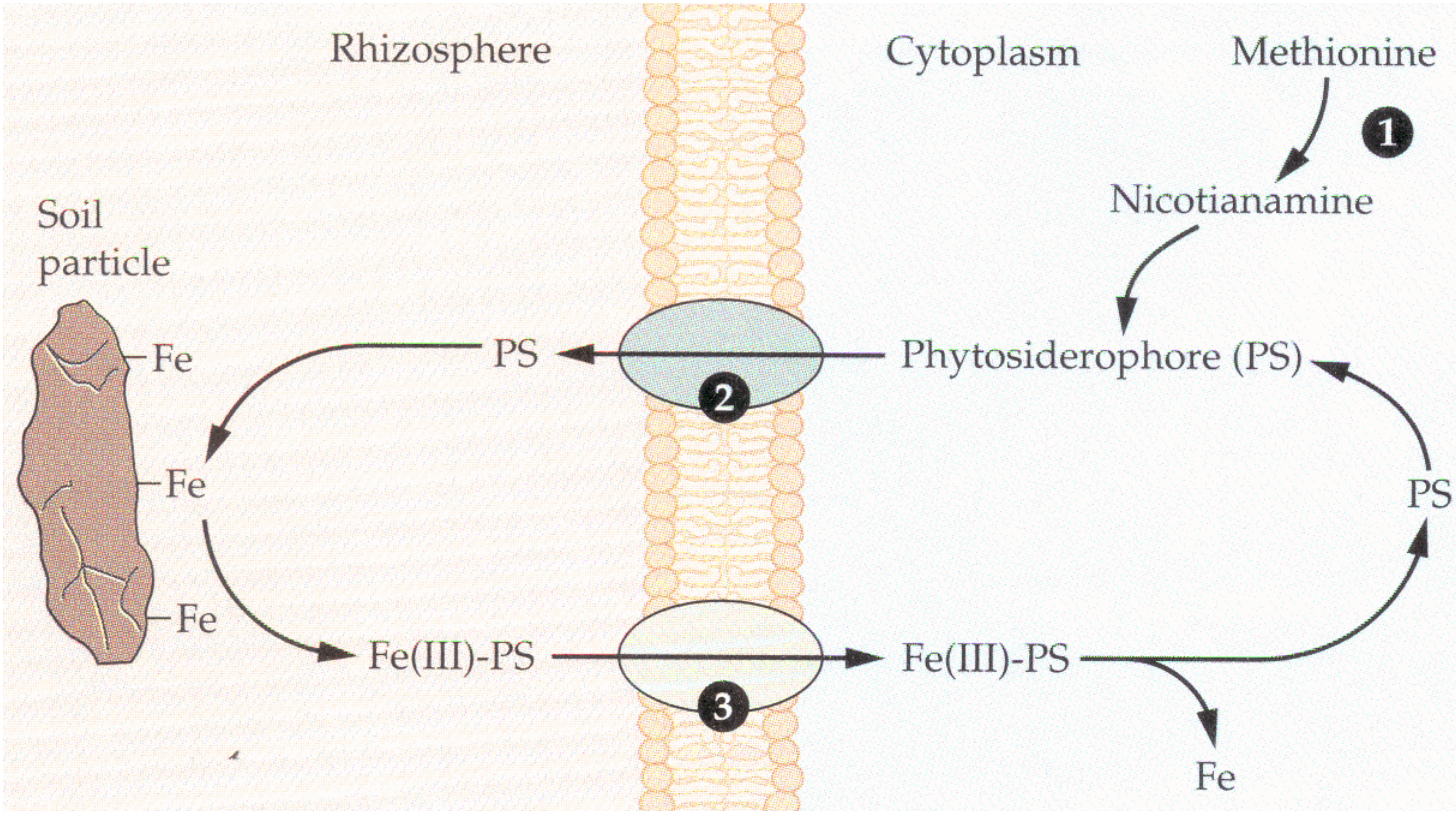
Type 2 Fe Accumulators

Grasses release Mugeneic acids (small acidic N-containing compounds) called phytosiderophores into the rhizosphere

Ligands form between MA and Fe^{3+}, and these complexes are taken up by unknown mechanisms

Genes for MAs synthesis have now been identified

Type 2 - Phytosiderophore Mechanism for Fe^{3+} Uptake



Mugeneic Acids are synthesised from Methionine

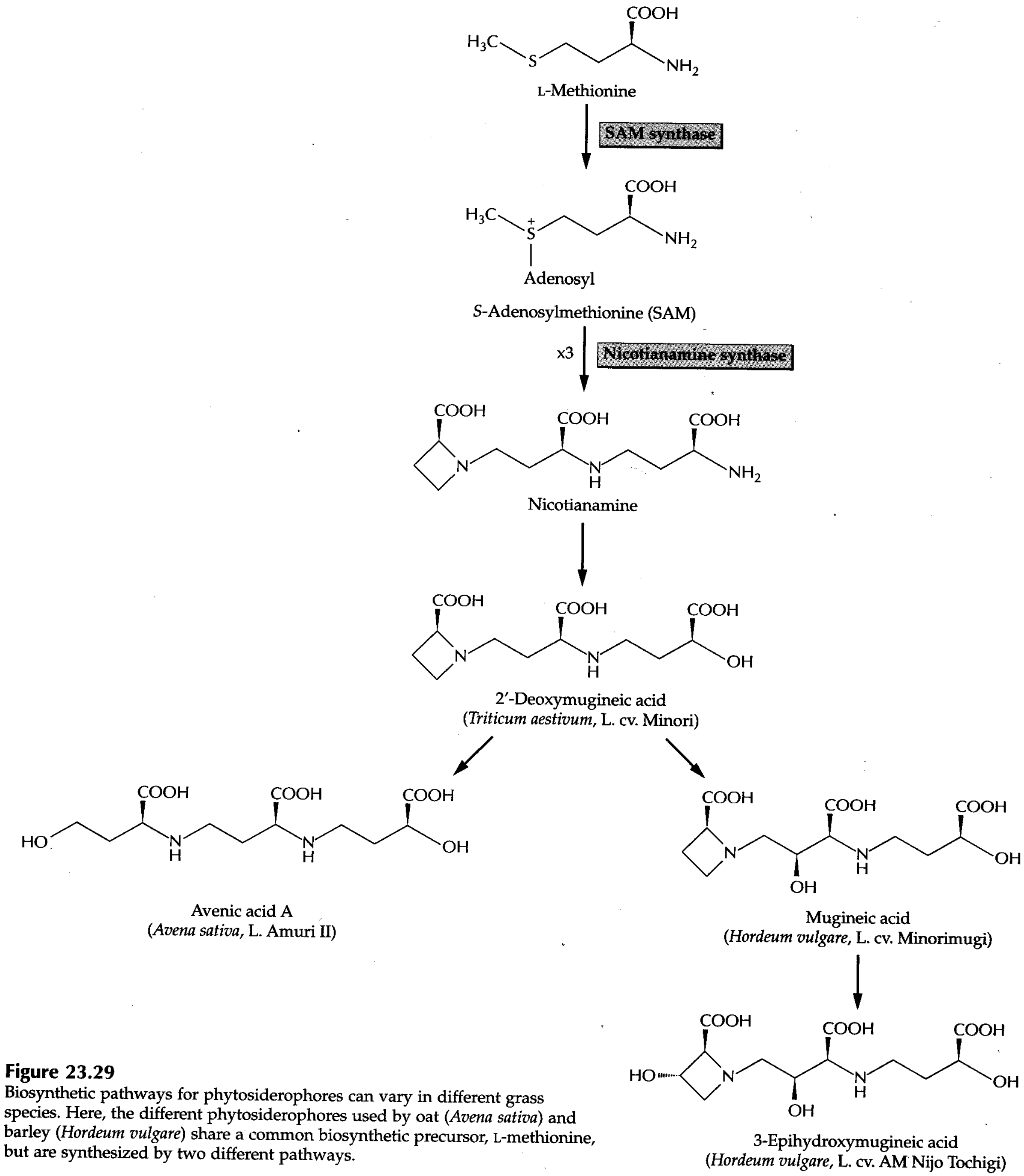


Figure 23.29
Biosynthetic pathways for phytosiderophores can vary in different grass species. Here, the different phytosiderophores used by oat (*Avena sativa*) and barley (*Hordeum vulgare*) share a common biosynthetic precursor, L-methionine, but are synthesized by two different pathways.

Micorrhizal Associations

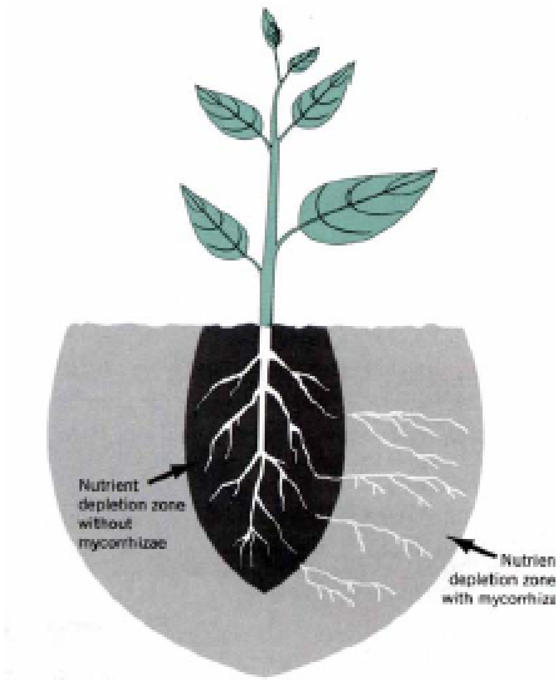
Mycorrhizal fungi facilitate nutrient uptake by roots

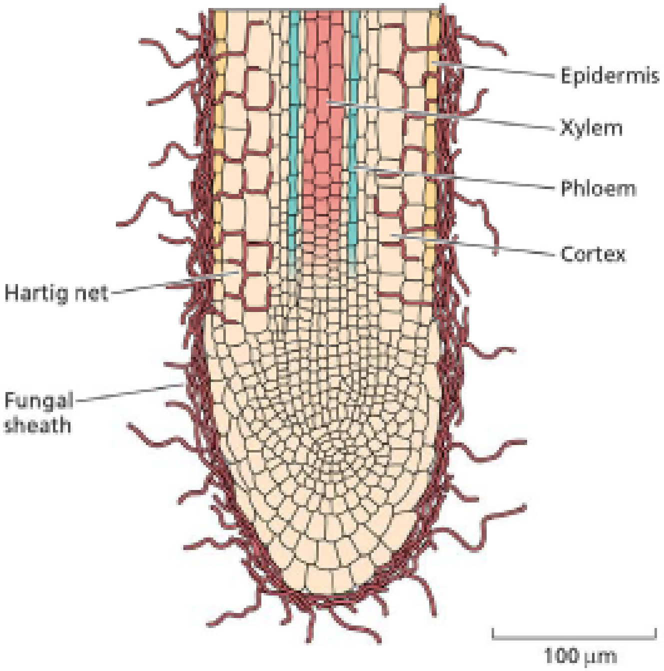
83% of dicots, 79% of monocots and all gymnosperms regularly form mycorrhizal assciation. Two types:

- Ectotrophic Mycorrhizae fungi: Gymnosperms and woody angiosperms,
  1) form thick sheath; 2) don't penetrate plant cell (only form hartig between cells)
- Vescular arbusular mycorrhizae fungi: 草本植物
  1) don't form sheath, less than 10 % of root weight; 2) penetrate epidermis or root hair for either vesicles or arbuscule (branched structure)

Function:

- Use external fungal hyphae to increase nutrient depletion zone
- Facilitate absorption of phosphate, Zn, Cu
- Can increase phosphate uptake by four times





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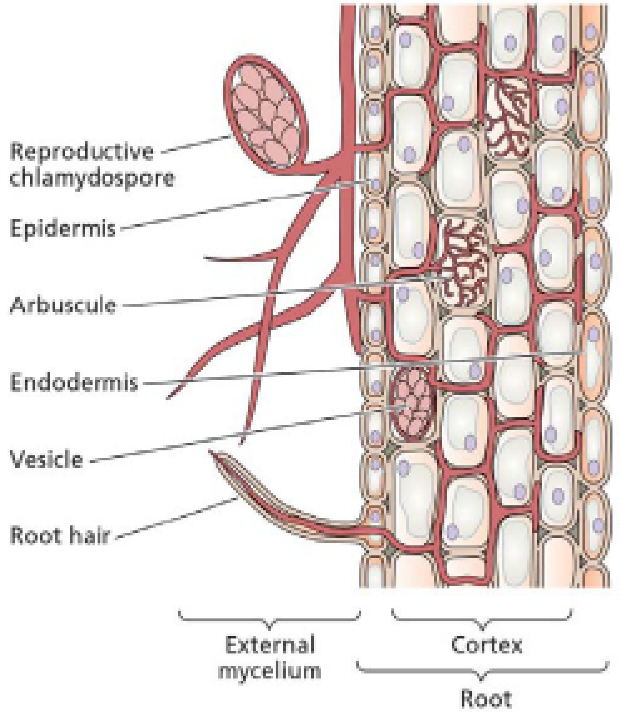

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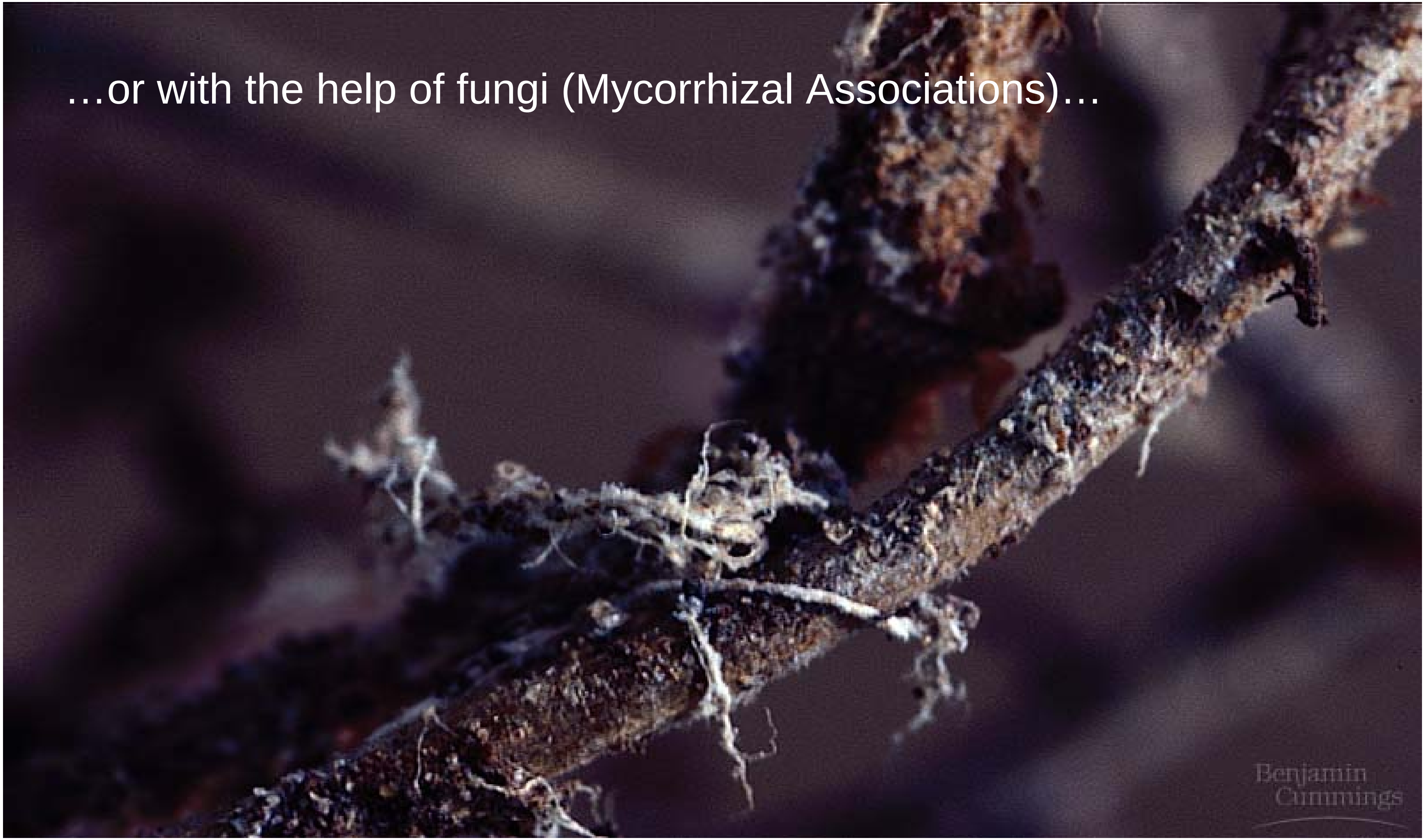
Figure 36.8 Mycorrhizae, symbiotic associations of fungi and roots



…or with the help of fungi (Mycorrhizal Associations)…

Ascomycetes, Basidiomycetes and Glomales form Mycorrhizal

Associations with plants

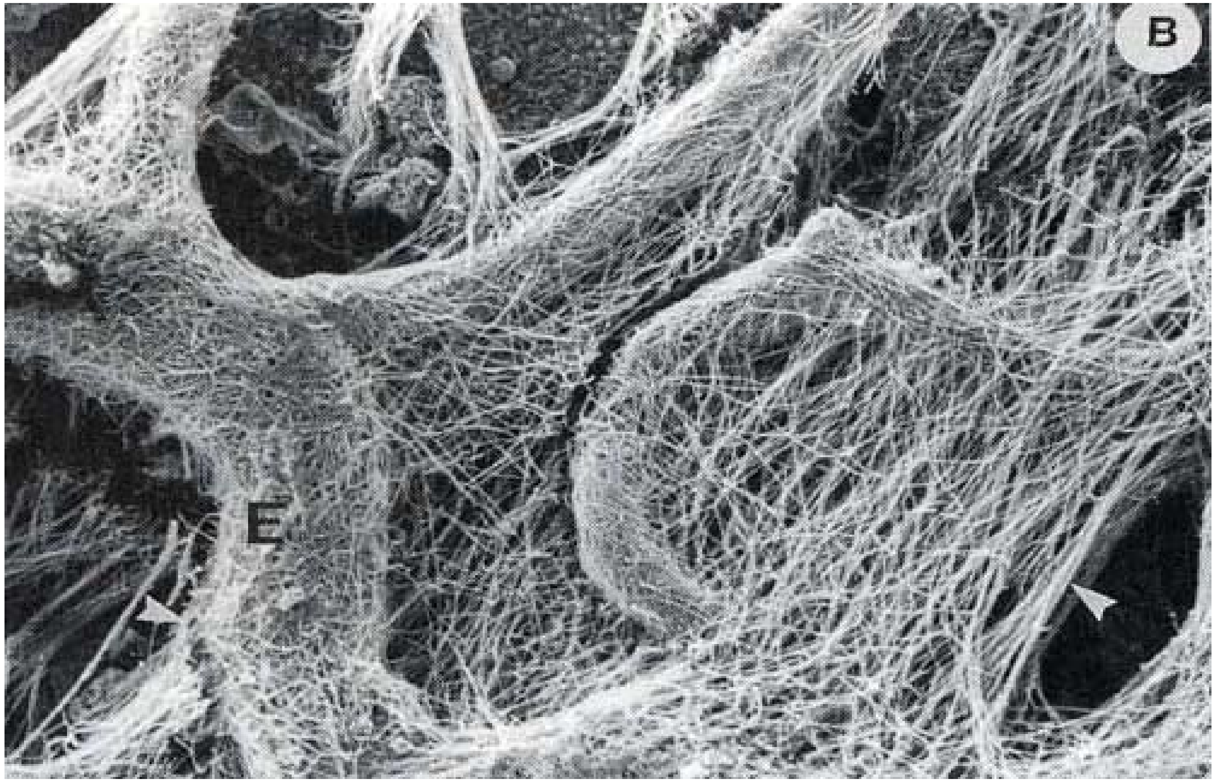
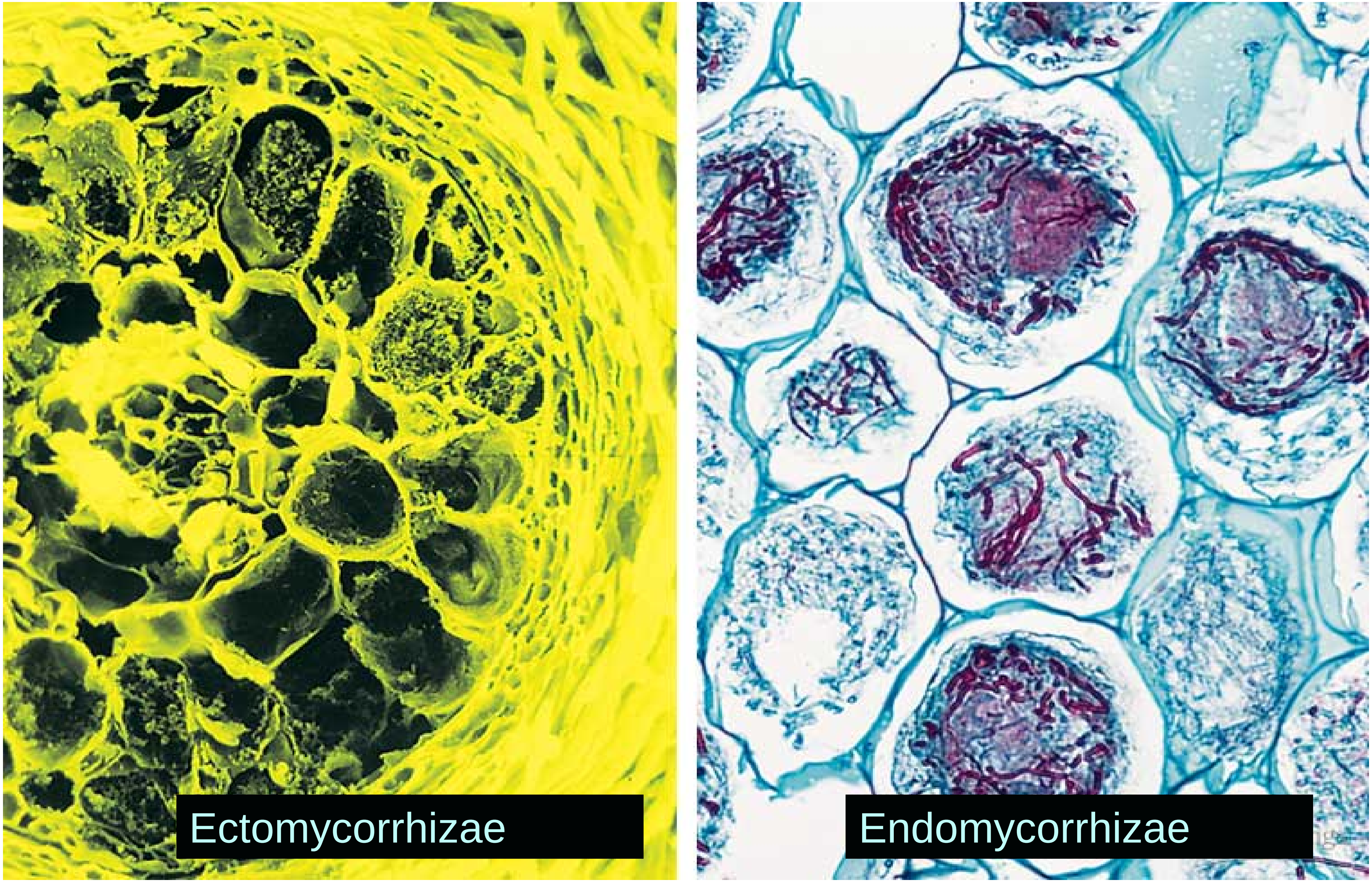


Figure 37.14 Mycorrhizae

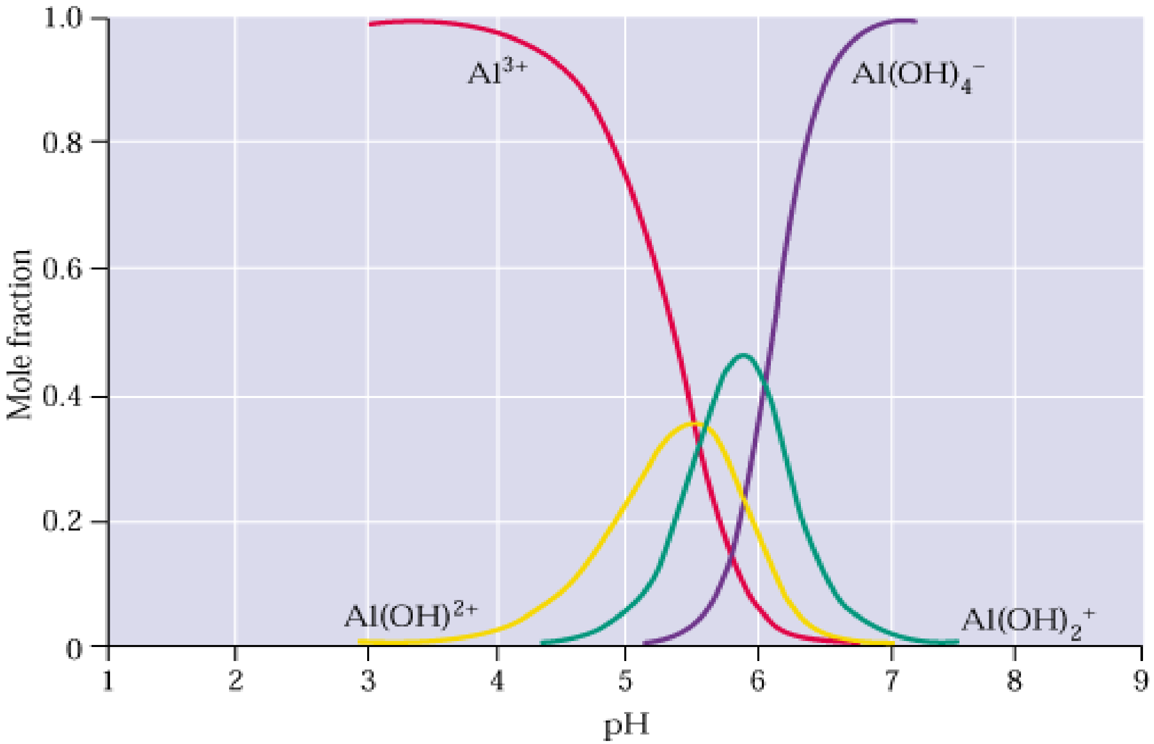


Ionic Stress – Metal Ions

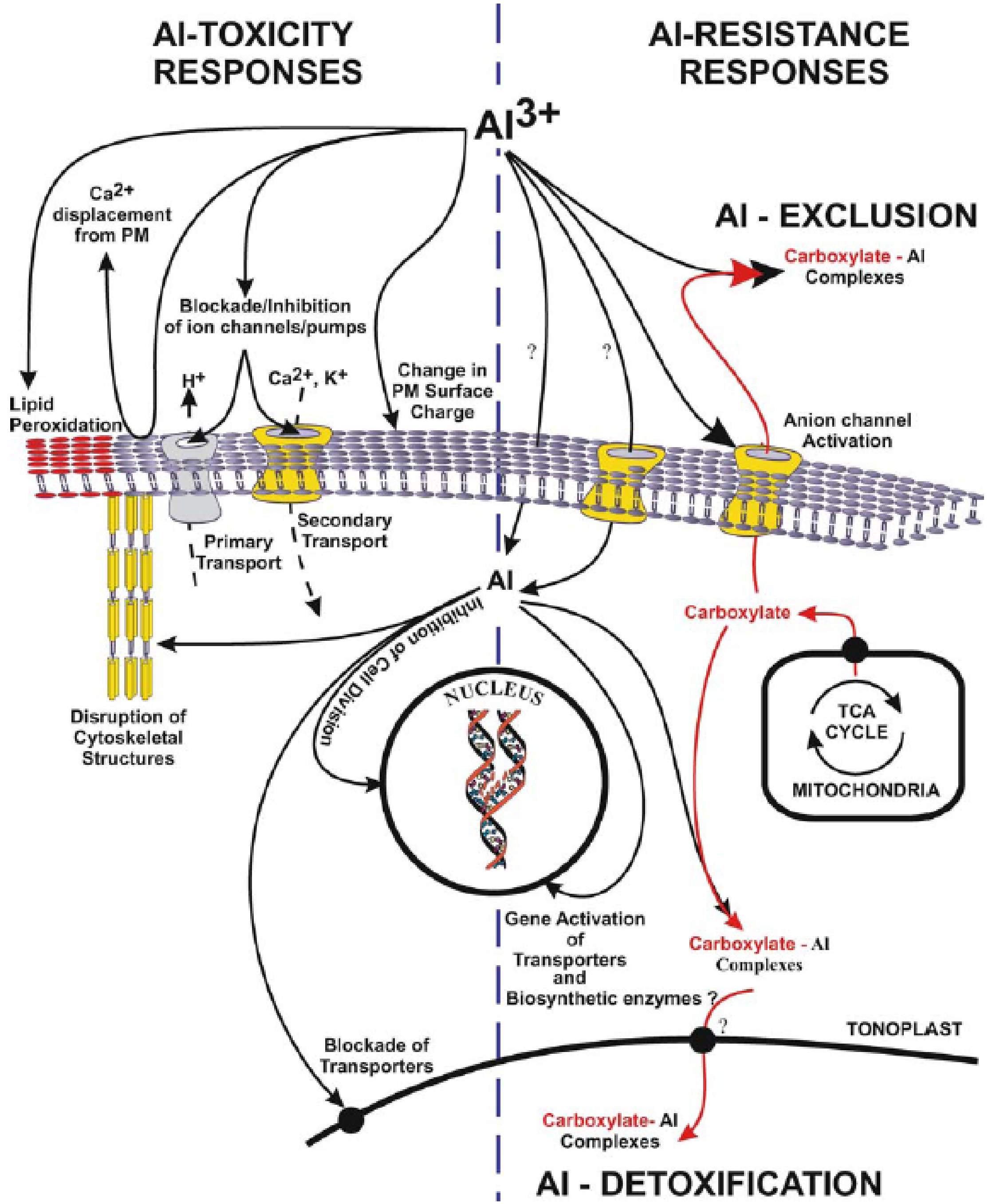
Growing Plants in Acid Soils

40% of the world's land is too acidic to grow crops

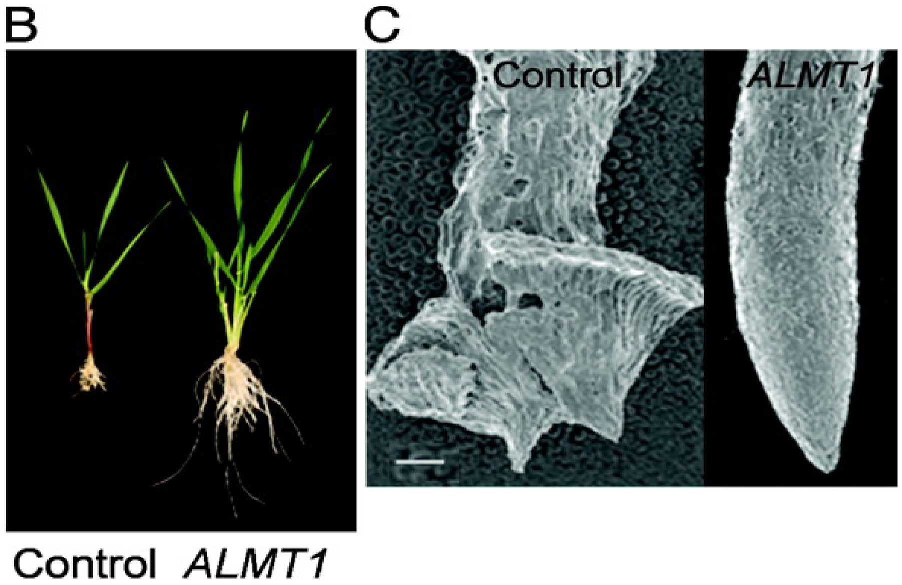
It is the mobilization of Al^{3+} that is toxic to plants

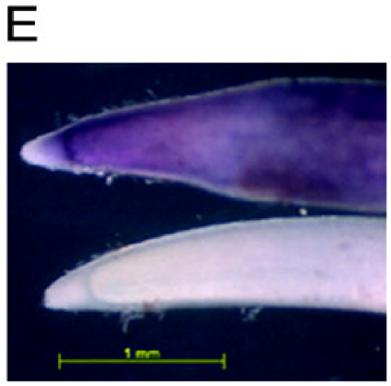


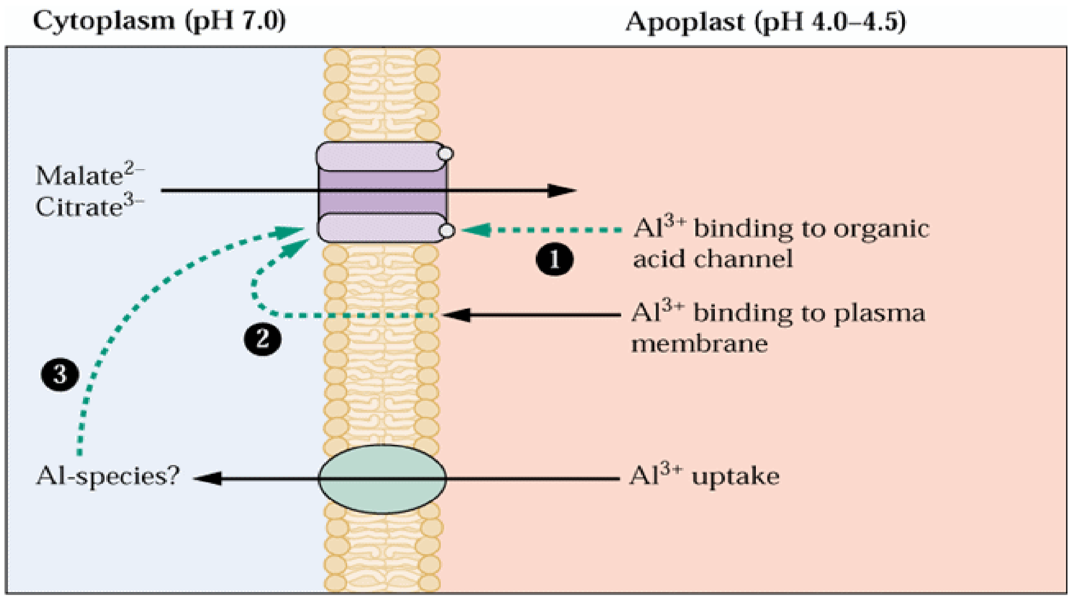
Targets for Al^{3+} Toxicity & Al^{3+} Resistance Mechanisms



Overexpression of a Malate Transporter (ALMT1) confers Al tolerance to barley







Delhaize, Emmanuel et al. (2004) Proc. Natl. Acad. Sci. USA 101, 15249-15254

Ionic Stress – Heavy Metal Ions

Co, Ca, Fe, Mn, Mo, Ni, Zn (essential nutrients)

Cd, Pb, Cr, Hg, Ag, U, Au (non-essential ions)

Strategies of Phyto-remediation

- Phytoextraction & Hyperacculululation

  -Cd, Pb, Ni, (radionuclides)

- Phytostabilization

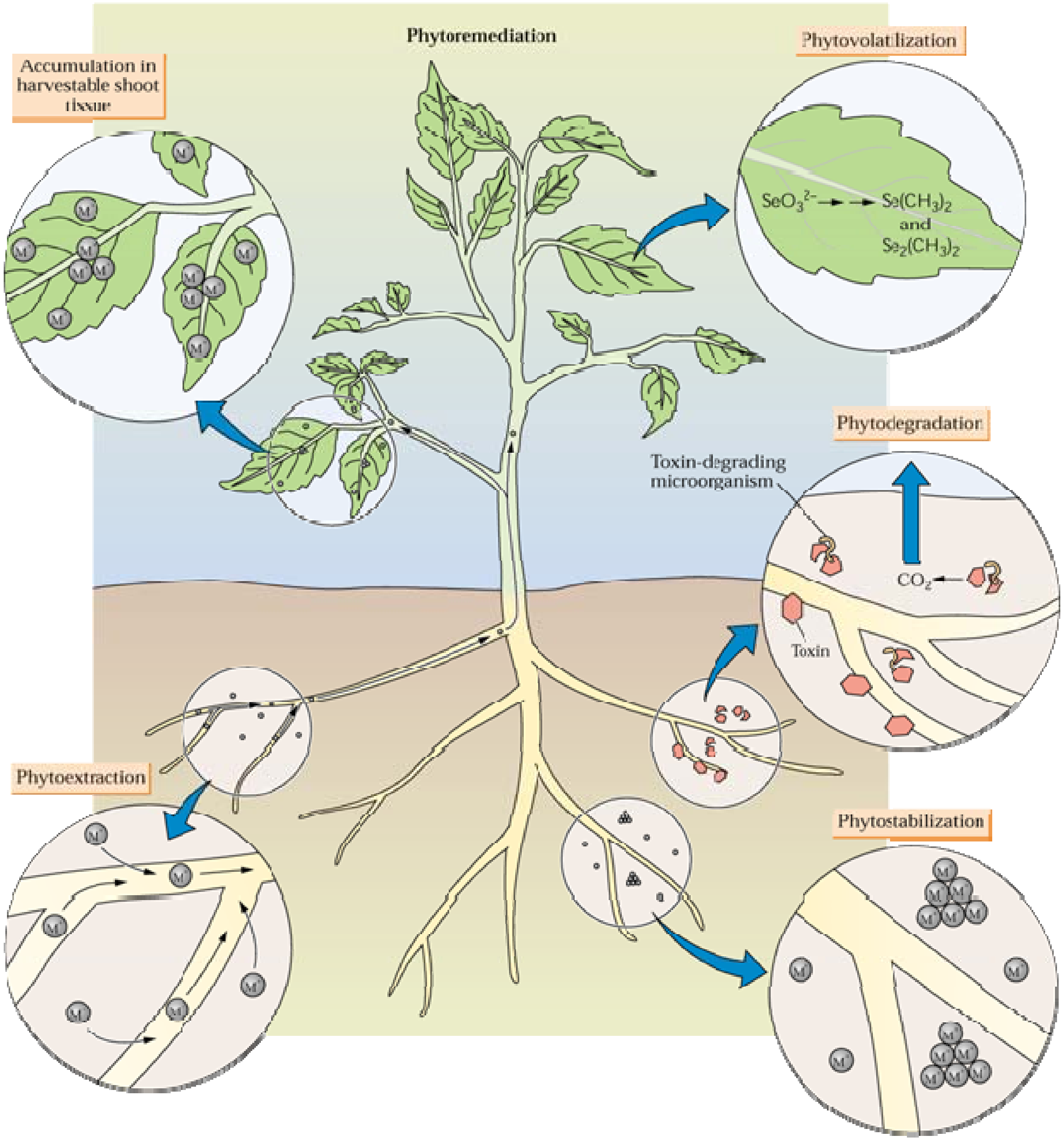
  - PCB, TNT,

- Phytodegradation

  - organics

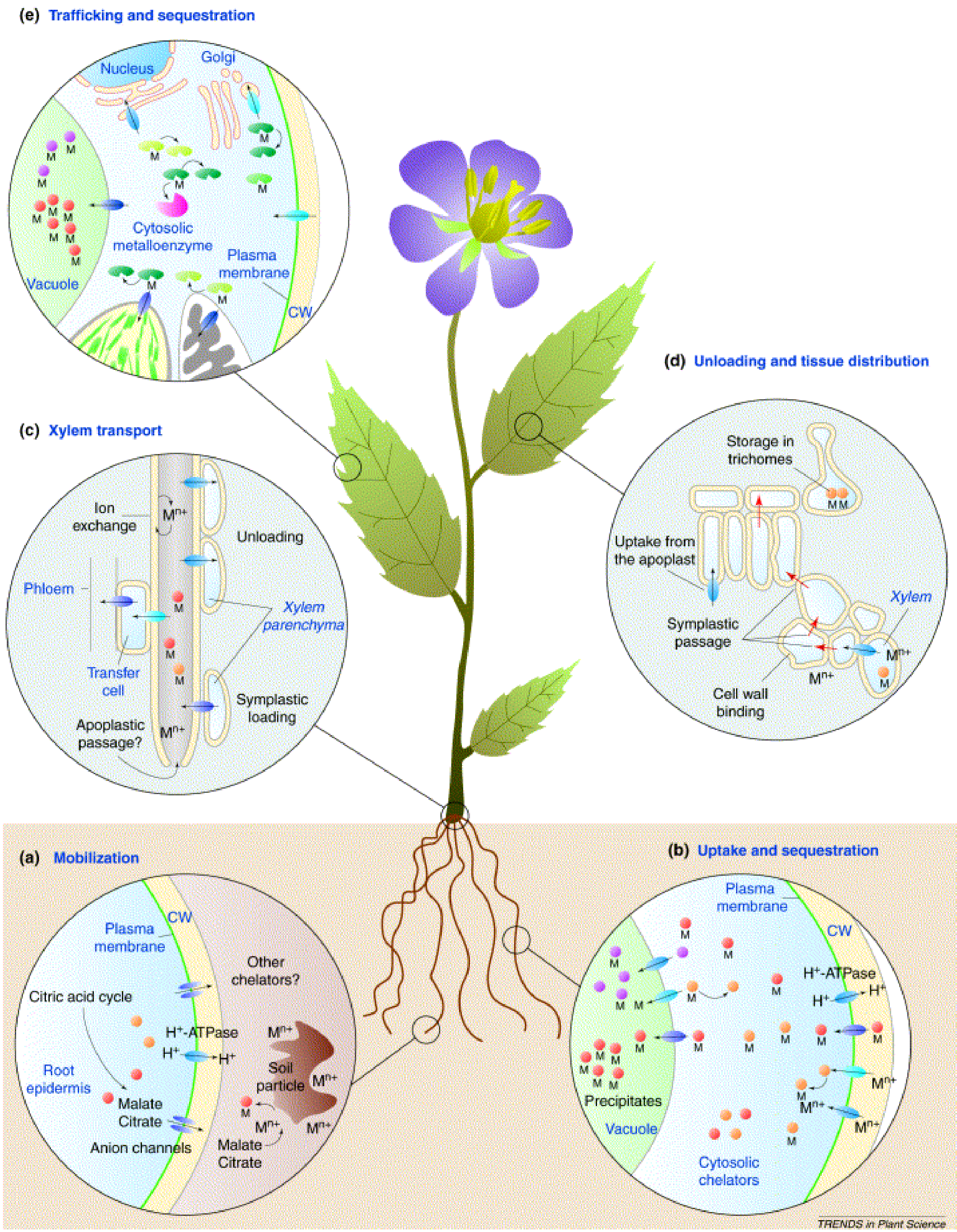
- Phytovolatilization

  -Se



Traits Required for Hyperaccumulation

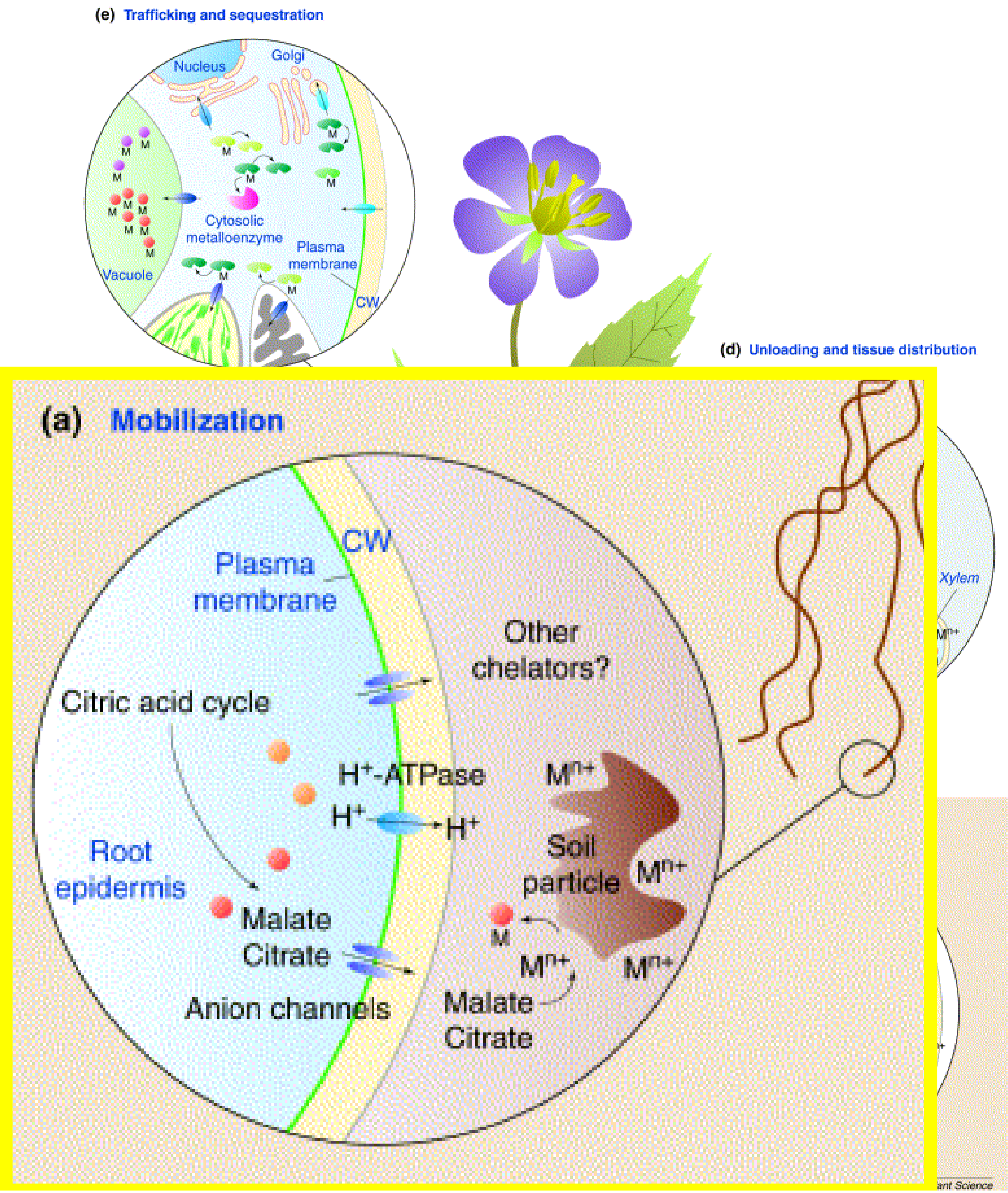
- Mobilization
- Uptake & root sequestration
- Xylem transport
- Unloading & tissue distribution
- Trafficking & sequestration



Mobilization

acidification of rhizosphere (H^+ pumps on plasma membrane)

Secretion of organic anions (citrate, malate, etc.,)



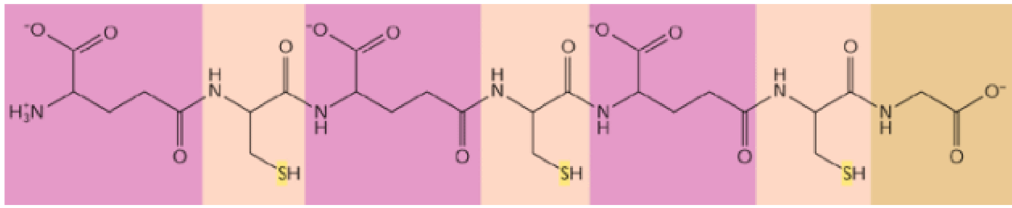
Uptake & sequestration

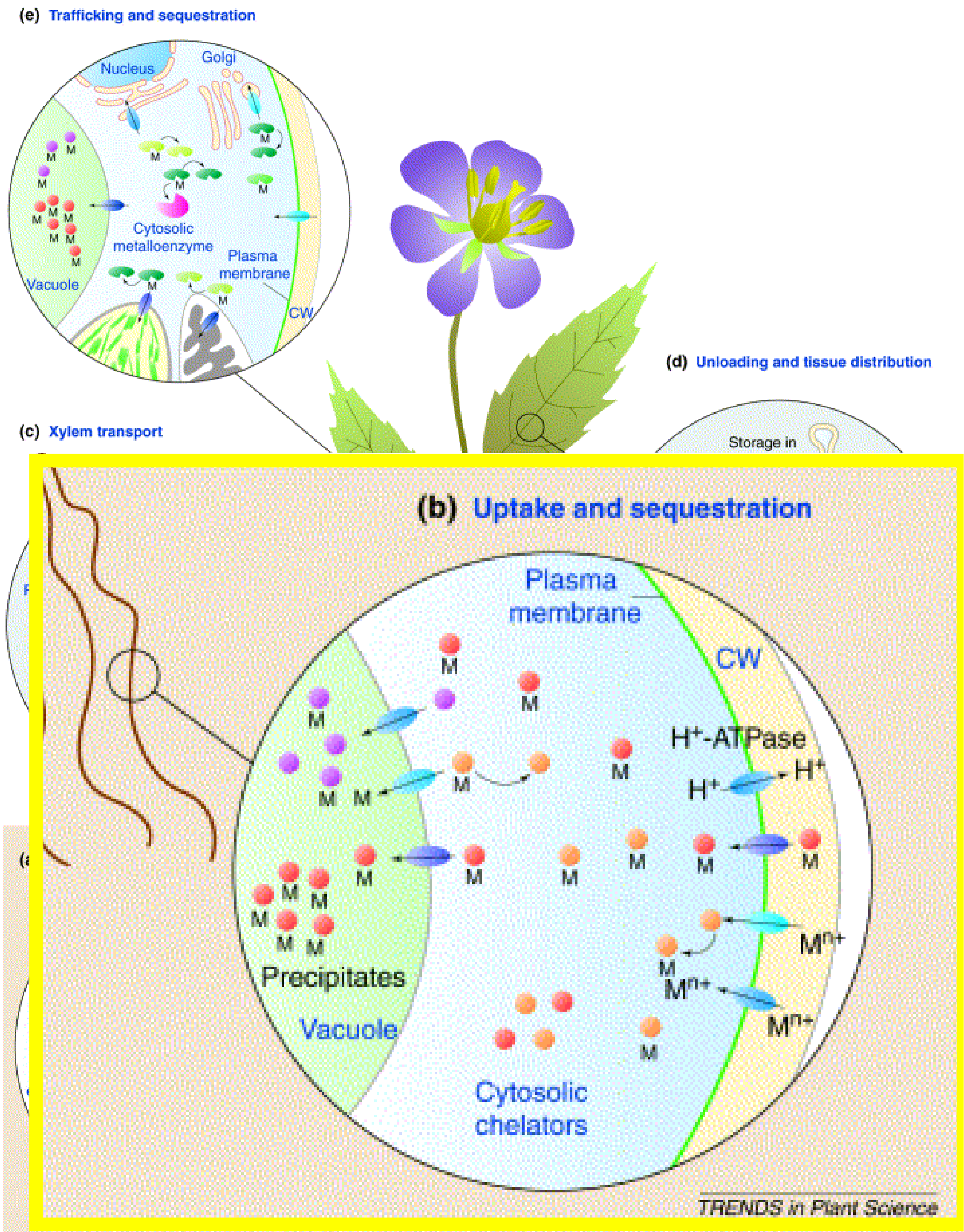
Through nutrient ion transporters

IRT1 – single amino acid change causes Cd^{2+} and Zn^{2+} (but no longer Fe^{2+} & Mn^{2+}) to be transported

Phytochelatins – peptide chains of

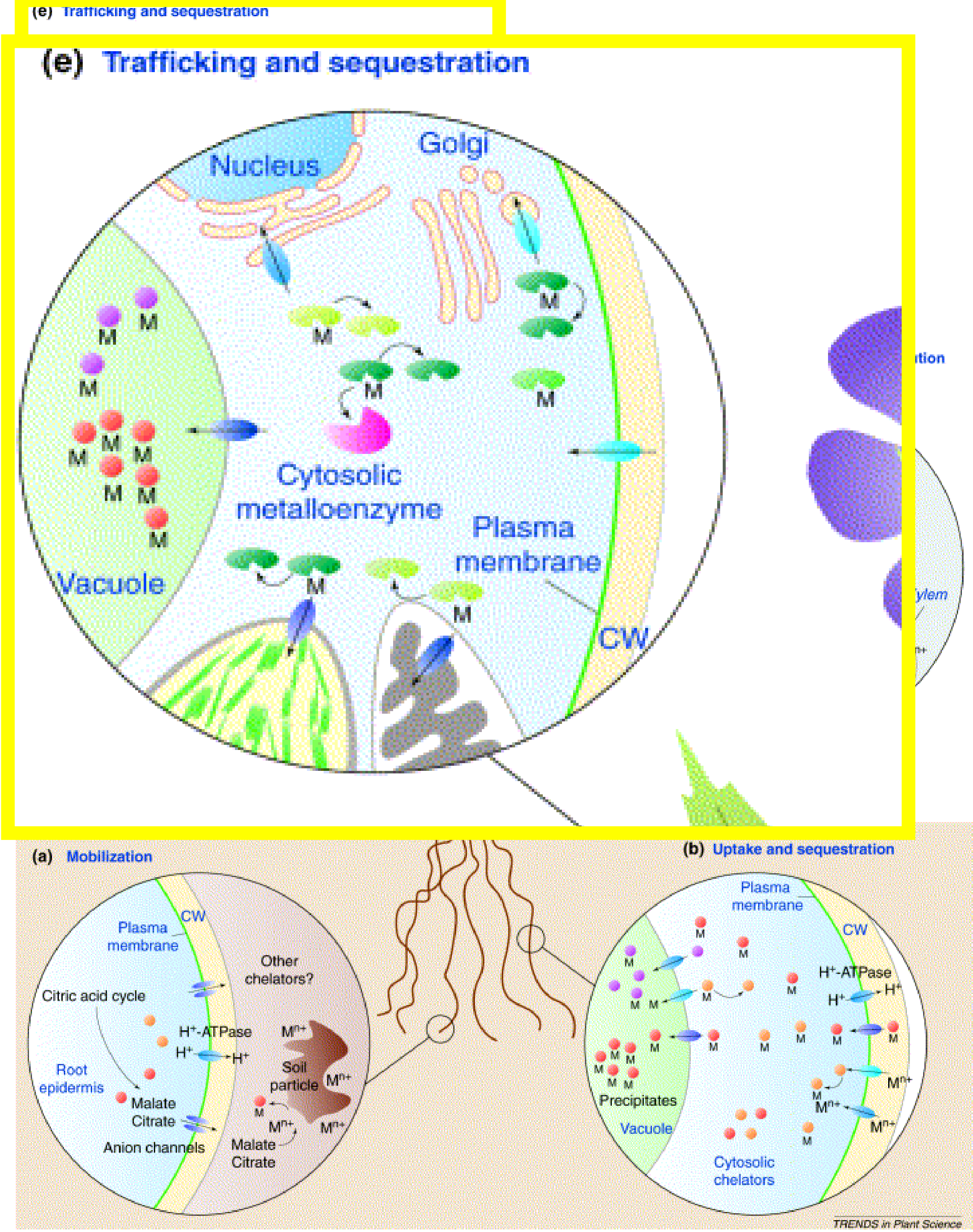
(g-Glu-Cys)$_n$-Gly





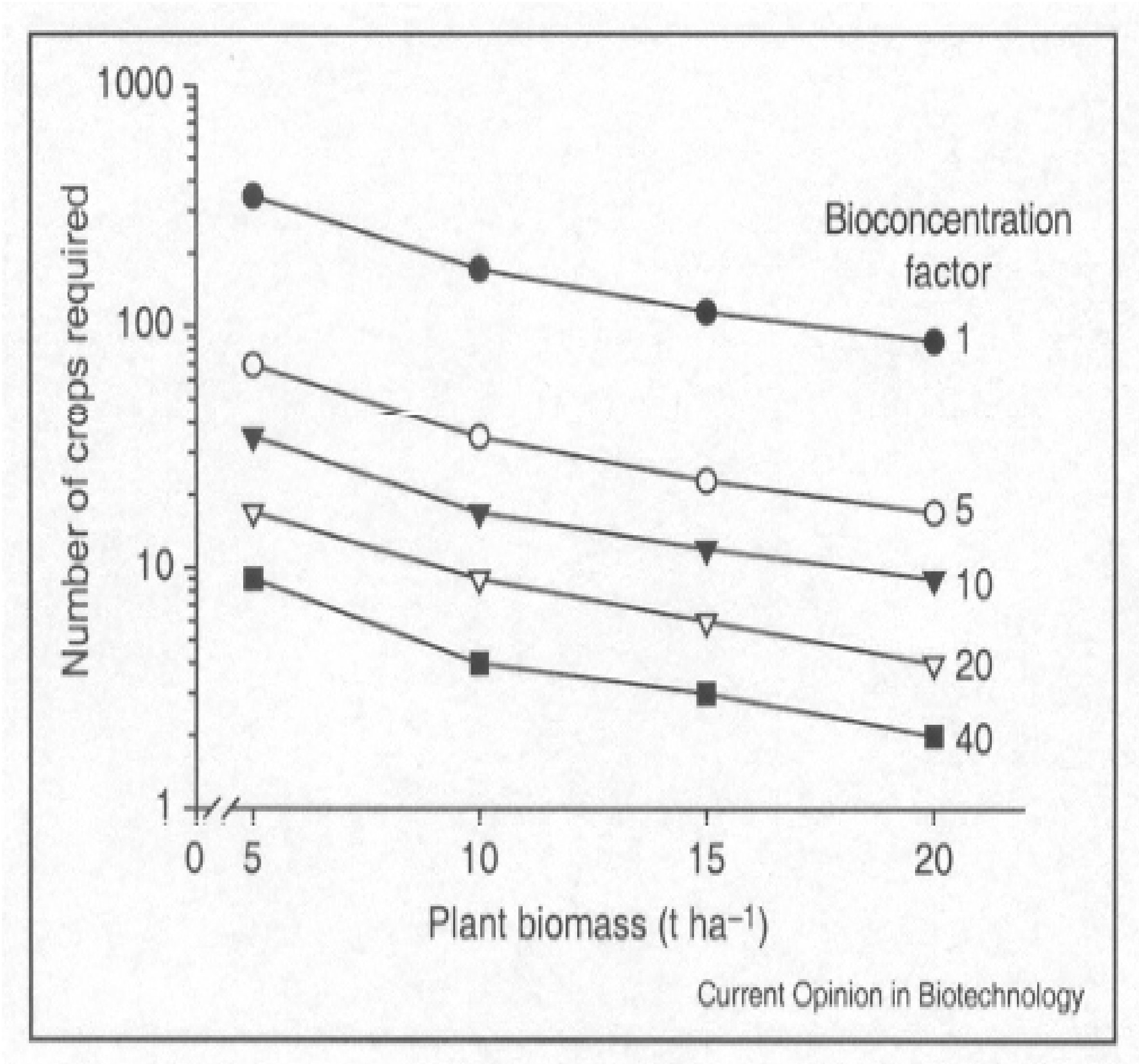
Trafficking & Storage

Excess metals in cytoplasm are pumped into vacuoles – in some species of mesophyll cells, in others in epidermis

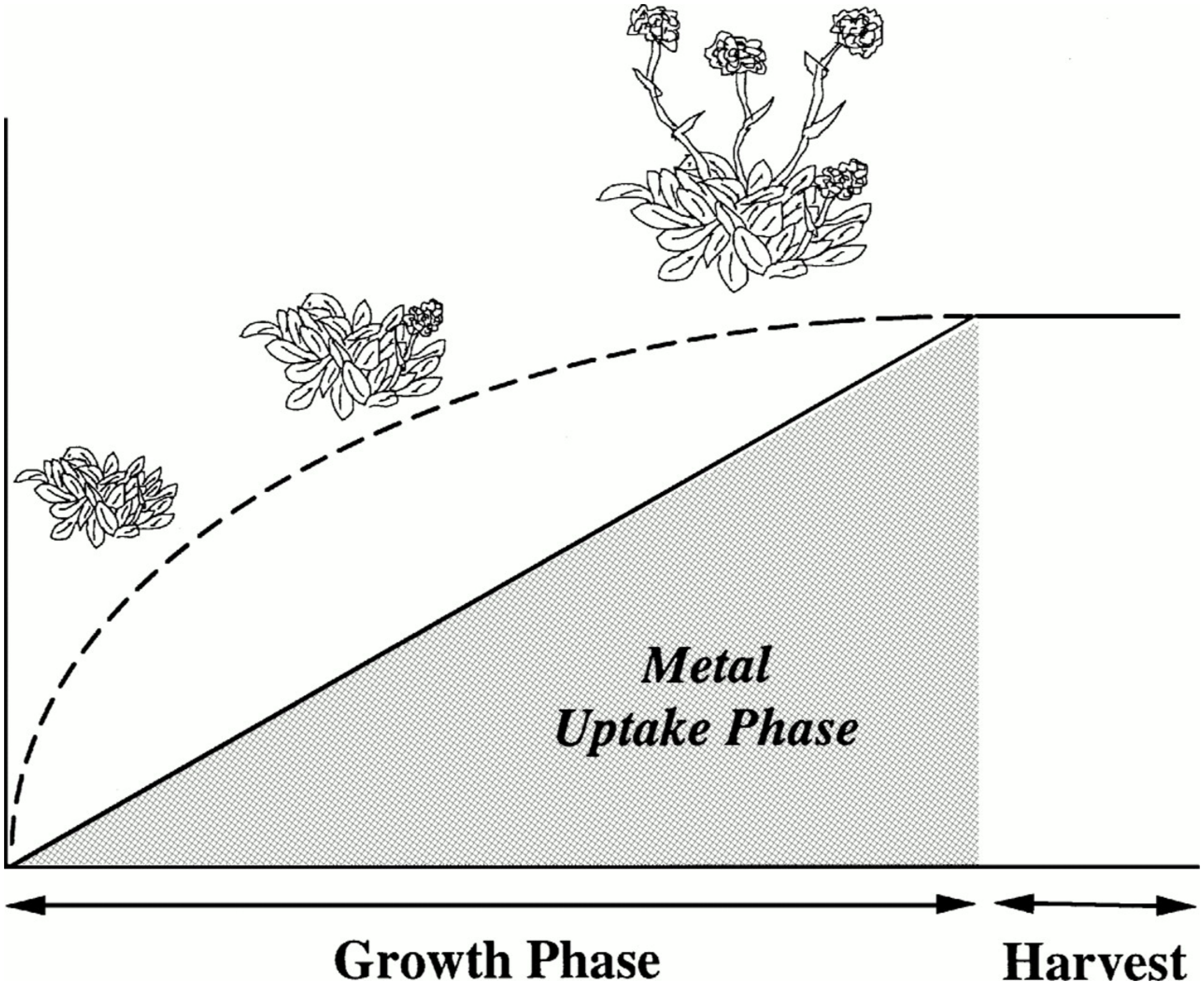


Feasibility of Phytoextraction

- Bioconcentration Factor – $[Metal]^{shoot}/[Metal]^{soil}$ determines feasibility
- Most plants BC < 1.0, hyperaccumulators 5-20
- Important traits for high BC
  - Metal phytomobilization in rhizosphere
  - Efficient metal uptake (extensive roots) and translocation to shoot
  - High shoot biomass
  - Detoxification mechanisms



Continuous Phytoextraction.



- Here the plant Hyperaccumulates the heavy metal by:
  - Mobilization from soil
  - Uptake of HM or HM-conjugate
  - Translocation in xylem to shoot
  - Sequestration in vacuole of leaf cells or trichomes

Model Metallophytes

- *Thalspi caerulescens* is a weedy *Brassica* closely related to the model plant *Arabidopsis thaliana.*
- *T. caerulescens* accumulates Cd & Zn to 1000-fold higher shoot concentrations than non-tolerant plants (~0.001% to 1% shoot dry wt).
- However, it is very slow growing!
- Over 400 heavy metal hyperaccumulating plants have been identified from 45 families

  (violet, mustards, *Alyssum, Fabacae,* etc.)

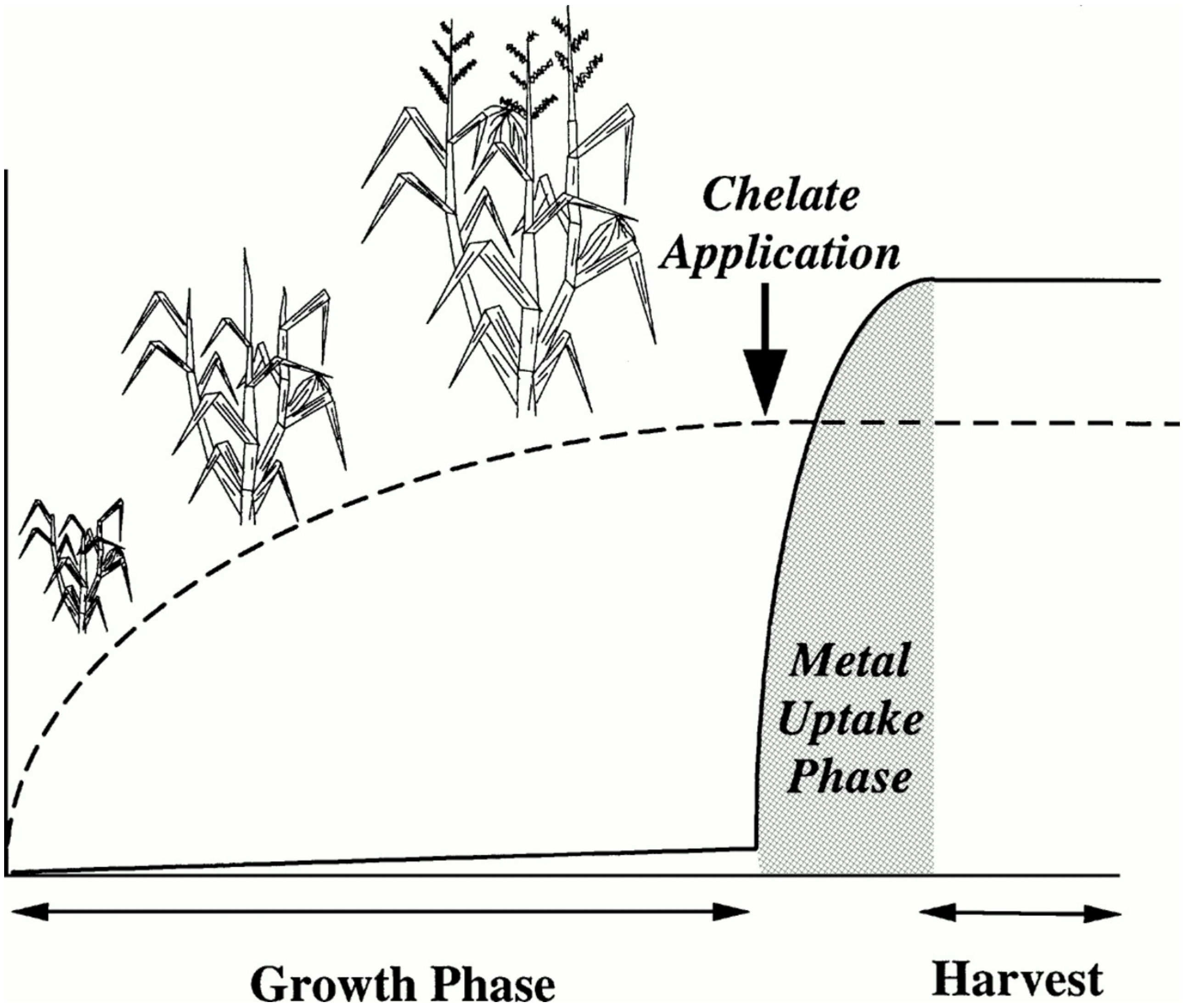
- *Alyssum spp.*
  - Hyperaccumulator o
    Ni

- *Arabidopsis halleri*

  Hyperaccumulator

  of Zn & Cd

Induced Phytoextraction.

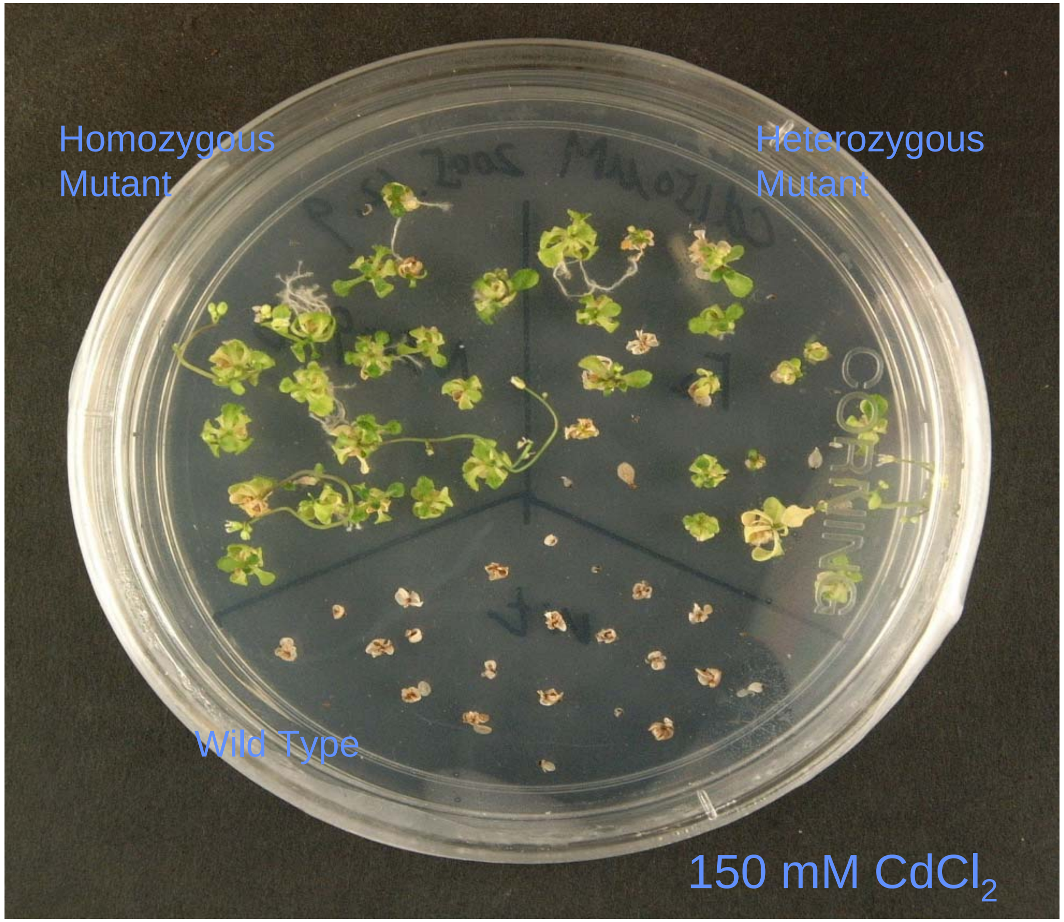


- Here the plant is first grown in the contaminated soil; initial uptake is low
  - lack of mobilization from soil particles
  - Formation of complexes *ex planta*
- After high plant biomass has established, chelate is added to soil…
- HM is mobilized, complexed and taken up into root
- MH-complex moves via xylem to leaves and sequestered in vacuoles

Biotechnology can be used to create mutants that are more tolerant of heavy metal pollutants

Lines of Arabidopsis can be created where a single random gene has been turned on or off. These lines can then be screened for genes that confer tolerance.

Opposite is a line identified here at Glasgow that is much more tolerant than wild type of the toxic heavy metal cadmium (Cd).



Salinity

Extent of Salt-Affected Soils

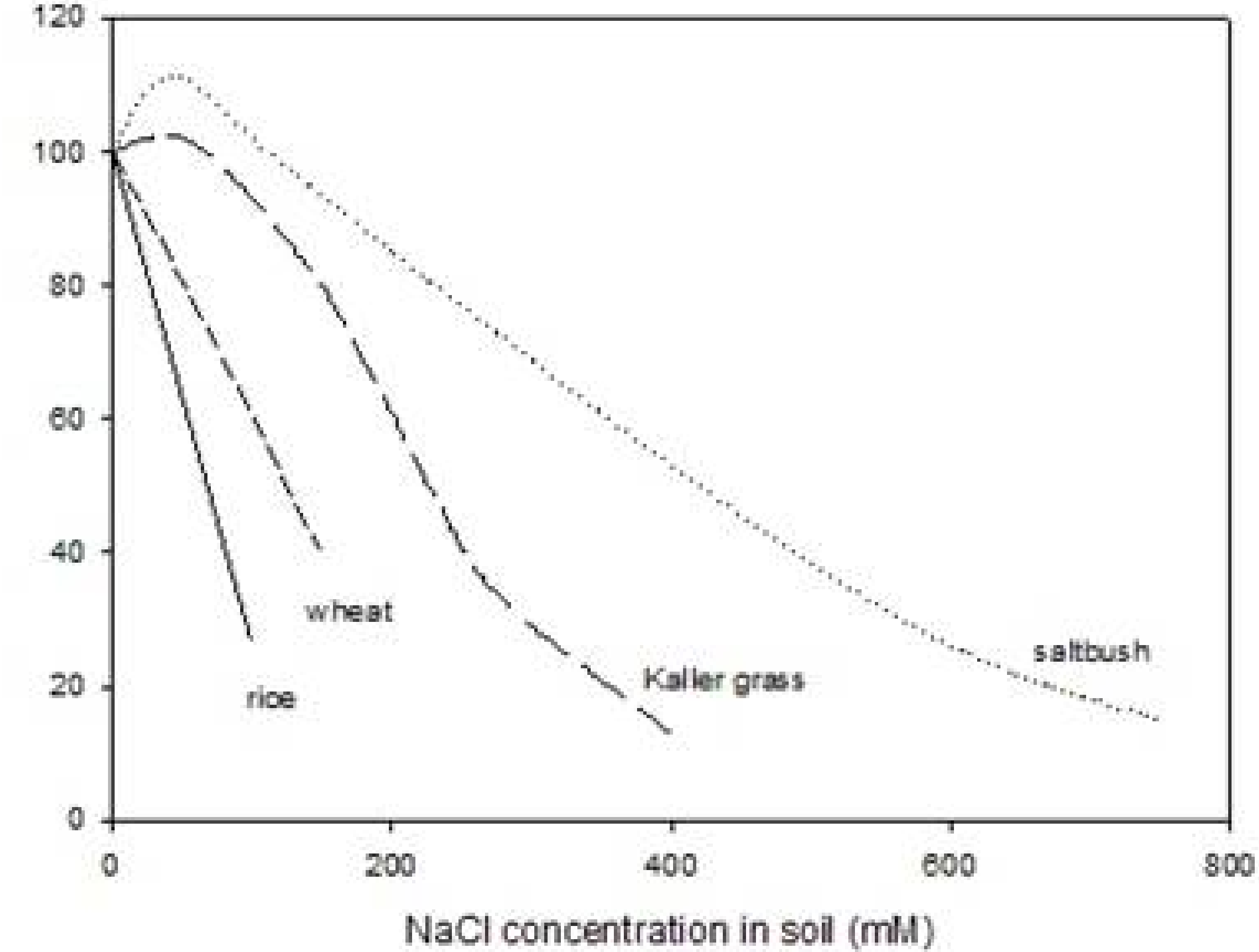
- > 6% World's land is 'salt-affected' (400 M Ha)
- 45 M Ha of Irrigated 230 M Ha
- 32 Ma of 1,500 MHa Under Dry Land Production
- EC of 4 dS/m or more (US Salinity Labs)
- Rainwater ~6 to 50 mg/kg of salt (decreases with distance from coast). 10 mg/kg, this would add 10 kg/ha for each 100 mm of rainfall per year

Table 1: Regional distribution of salt-affected soils, in million hectares

Regions	Total area	Saline soils		Sodic soils	
	Mha	Mha	%	Mha	%
Africa	1,899	39	2.0	34	1.8
Asia, the Pacific and Australia	3,107	195	6.3	249	8.0
Europe	2,011	7	0.3	73	3.6
Latin America	2,039	61	3.0	51	2.5
Near East	1,802	92	5.1	14	0.8
North America	1,924	5	0.2	15	0.8
Total	12,781	397	3.1%	434	3.4%

Source: FAO Land and Plant Nutrition Management Service

Pant Responses to Salinity



After Greenaway & Munns, 1980

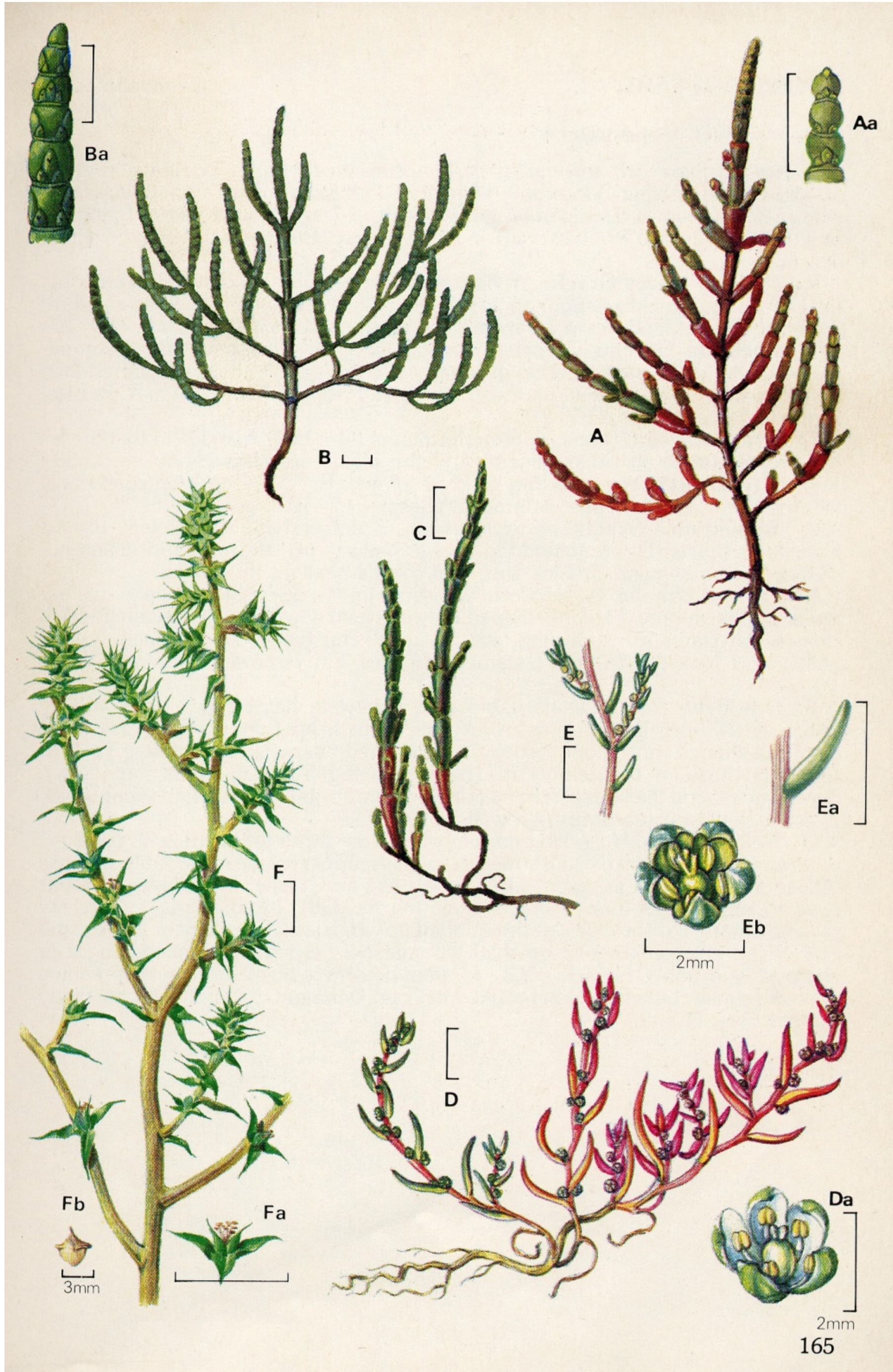
Salinity is Now as Important as Drought in Determining Global Crop Production

- Most crops will not flower in 100 mM NaCl - glycophytes
- Some plants will undergo a full life cycle in sea water (~550 mM NaCl) - halophytes

Halophytes from British Salt Marshes

Cheanopodiaceae.

- A. *Salicornia ramosissima*
- B. *Salicornia dolichostrachya*
- C. *Salicornia perennis*
- D. *Suaeda maritima*
- E. *Suaeda fruticosa*
- F. *Salsola kali*

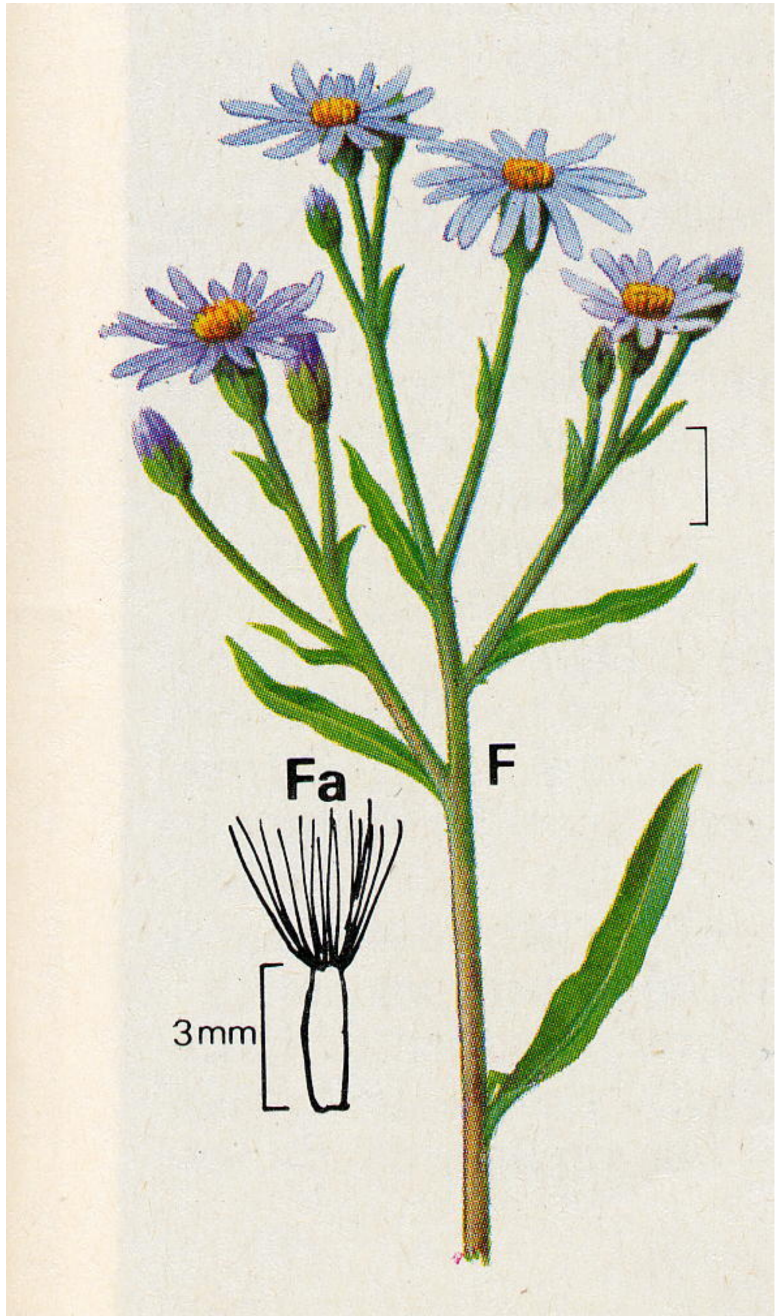


Halophytes from British Salt Marshes - *Cheanopodiaceae*

- A. *Atriplex hastata*
- B. *Atriplex patula*
- C. *Atriplex littoralis*
- D. *Atriplex glabriuscula*
- E. *Atriplex sabulosa*
- F. *Beta vulgaris* (sea beet)
- G. *Halimionie portulacoides*

Halophytes from British Salt Marshes

Aster tripolium (sea aster)



Most Crops are Salt Sensitive.

- Sugar beet (*Beta vulgaris* - opposite) is the only crop that can be said to be salt resistant - it will complete a full life cycle in >350 mM NaCl (70% sea water)
- Sugar beet was domesticated about 300 years ago from sea beet (*Beta vulgaris maritima*) which grows on salt marshes in Northern Europe.

Most Crops are Salt Sensitive.

- Barley (*Hordeum vulgare*) and to a lesser extent wheat (*Triticum aestivum*) will undergo a full life cycle in 150 mM NaCl, all other major crops will not survive in 100 mM NaCl.

Relative Importance of Salt Stress Factors on Plants

[NaCl] (M)	0	100	200	300	400	500
Y_{H20} (MPa)	0	-0.49	-0.97	-1.46	-1.95	-2.44
	Pulses Rice Tomato Maize *etc.*	Barley Wheat Cotton	Sugar beet			

Ion Toxicity

Water Stress

It's the Ionic Component , not Water Stress, that's Toxic to Glycophytes

Essentially, 3 Key Physiological Strategies Confer Salinity Tolerance

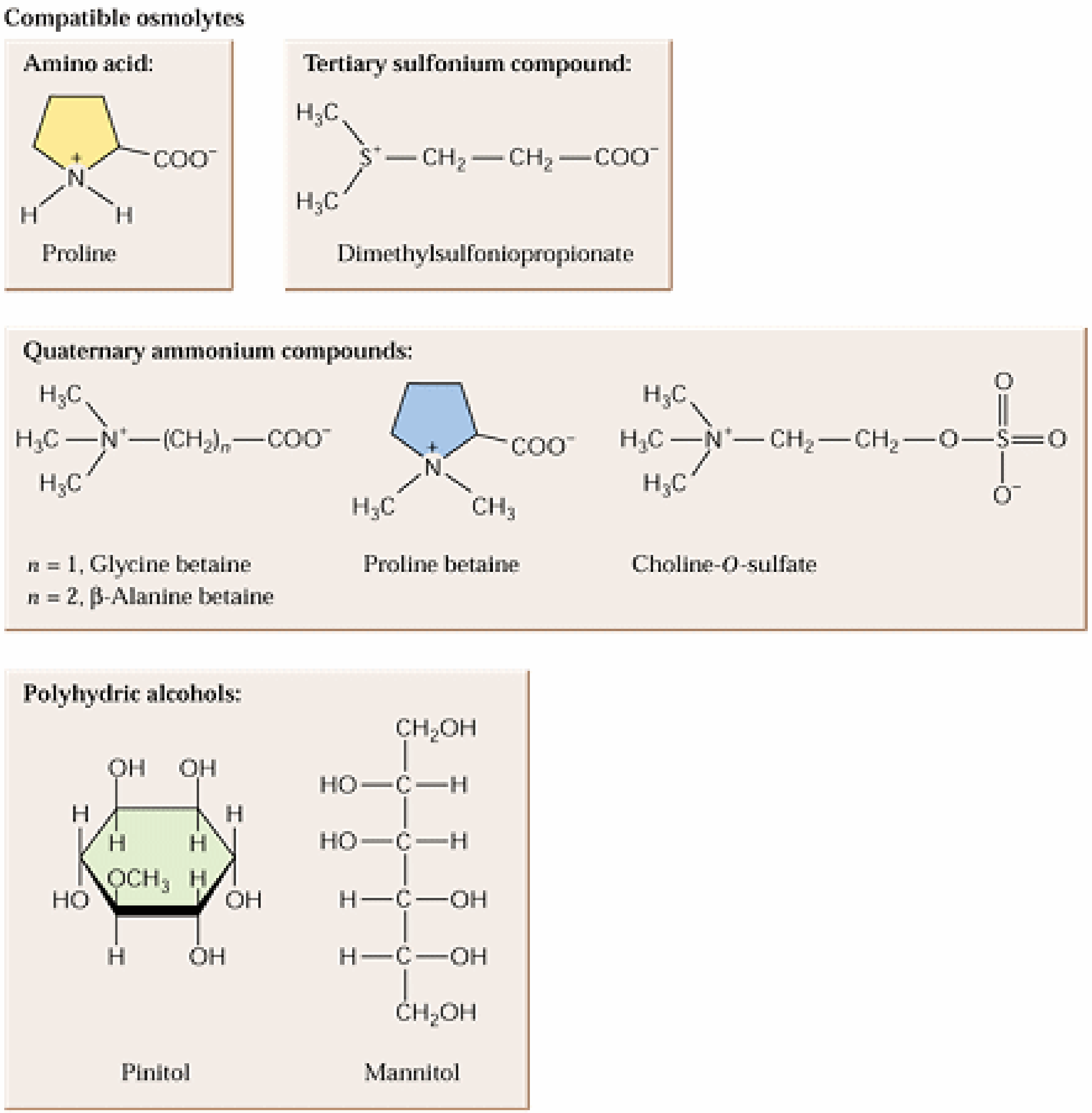
- Tolerate and/or avoid of desiccation (osmoregulation)

- Maintain a high cytoplasmic K^+ / Na^+ ratio

- Maintain a low cytoplasmic Cl^- concentration

Manipulating Compatible Solute Levels (Osmoregulation)

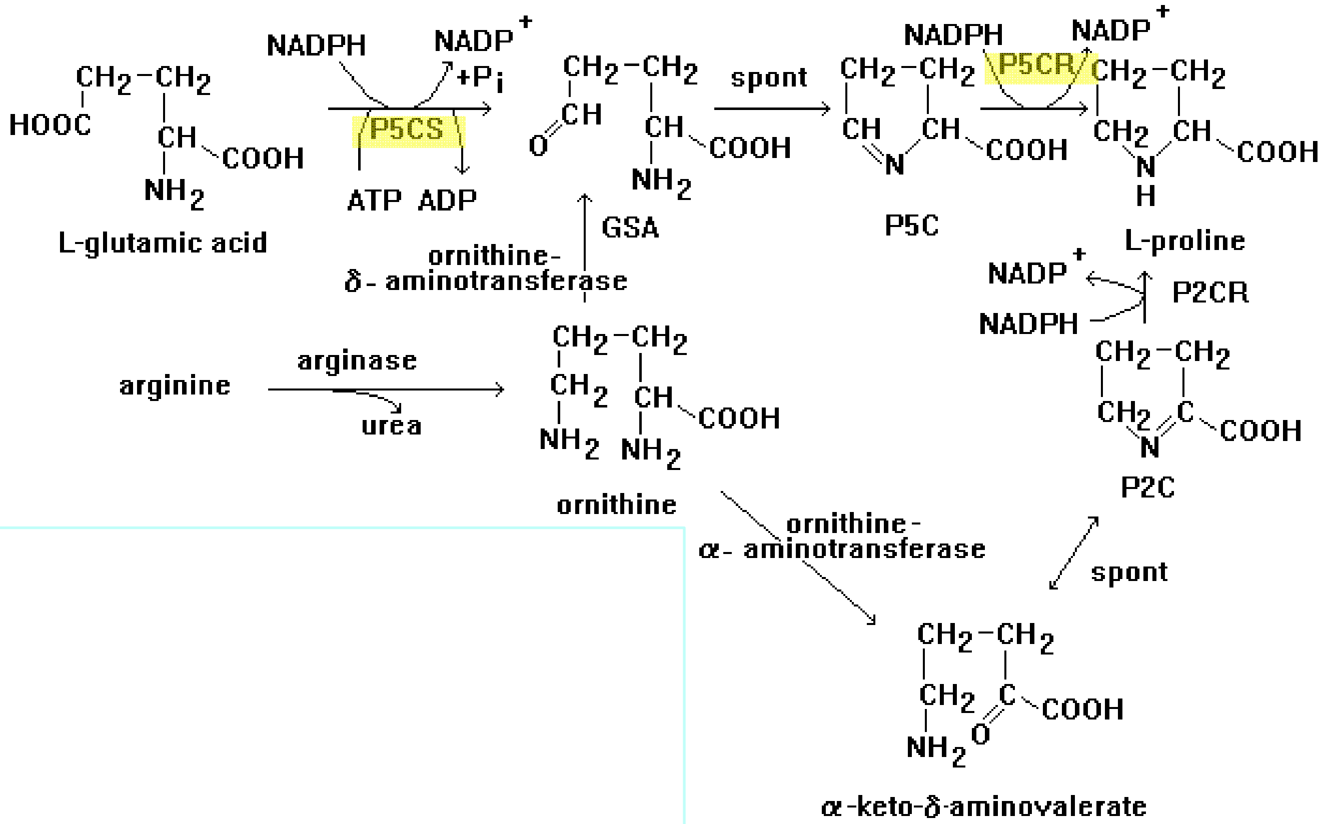
Plants Synthesize Compatible Solutes in Response to Water Stress



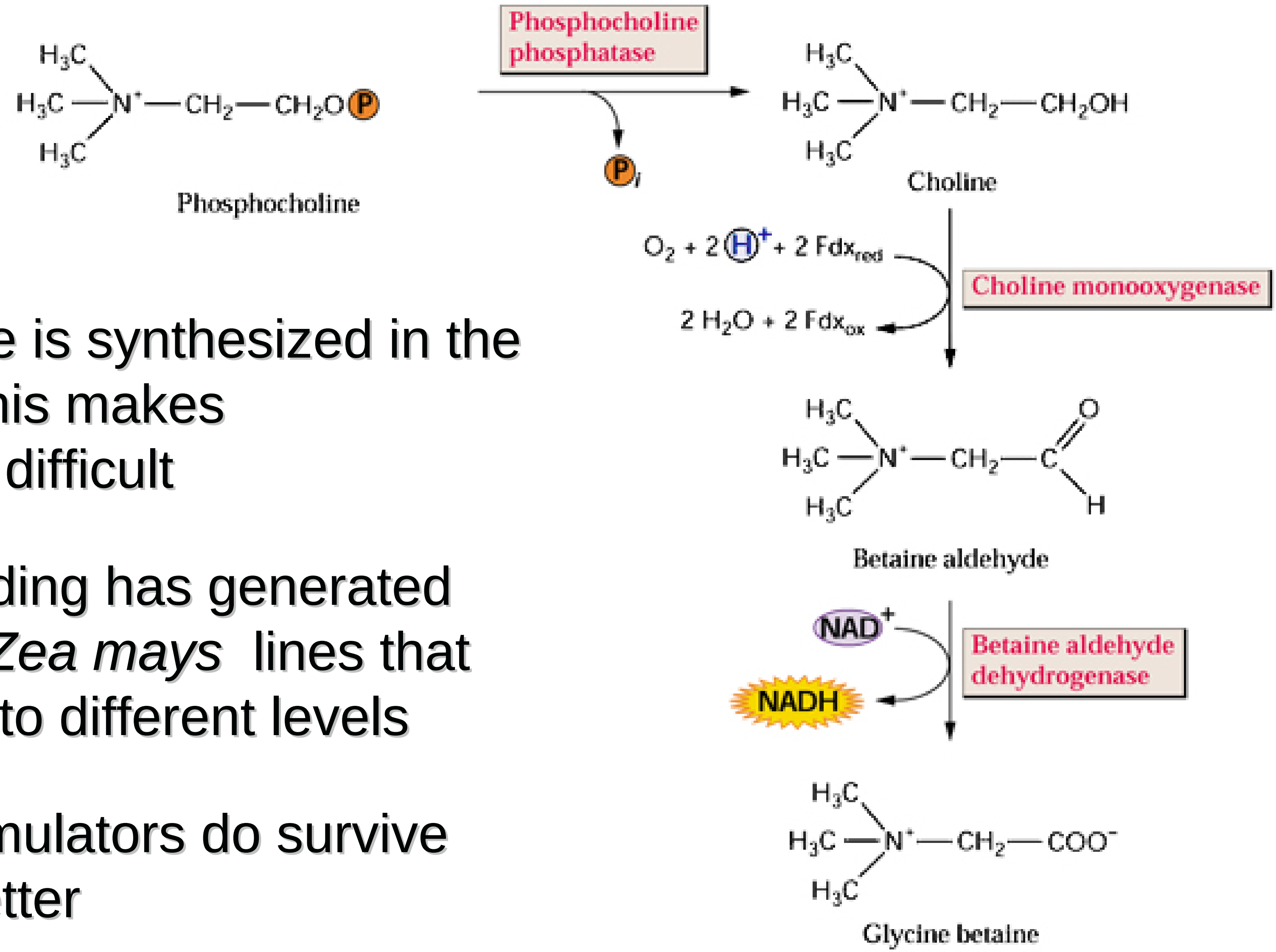
- Compatible solutes include:
  - proline
  - Tertiary Sulfonium Compounds (TSCs)
  - Quaternary Ammonium Compounds (QACs)
  - Polyhydric alcohols

Manipulating Compatible Solutes (I)

- Three genes from *E.* Coli (*proB, proA* (giving P5CS Acttivity) & P5C reductase) for the synthesis of proline have been over-expressed in plants....
- ....no improved resistance to drought / salinity has been observed due to accelerated breakdown in the plant



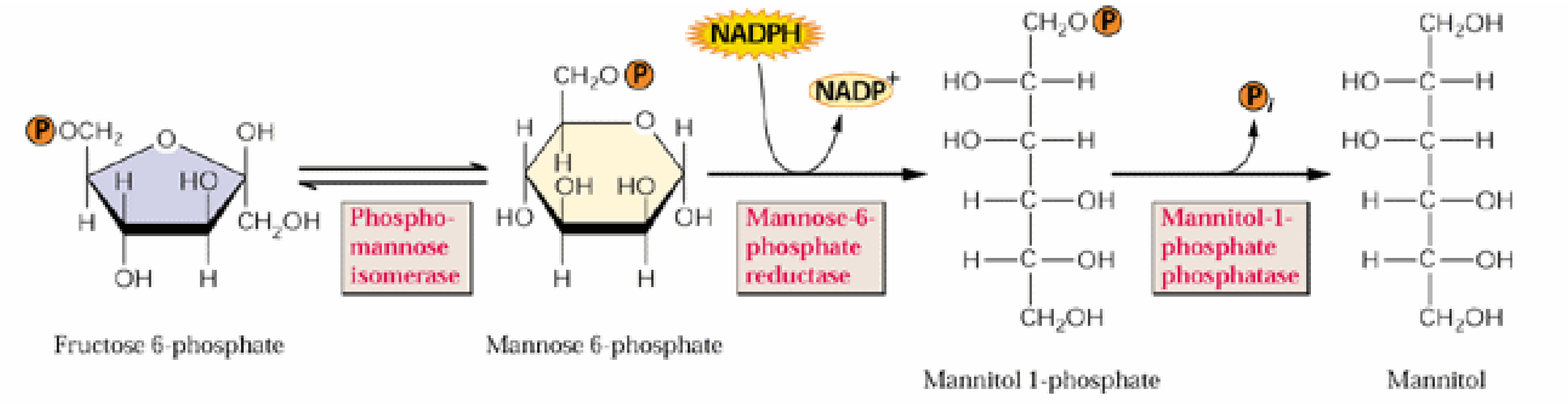
Manipulating Compatible Solutes (II)



- Glycine betaine is synthesized in the chloroplast....this makes transformation difficult
- Selective breeding has generated near-isogenic *Zea mays* lines that accumlate GB to different levels
- High GB accumulators do survive high salinity better

Manipulating Compatible Solutes (III)

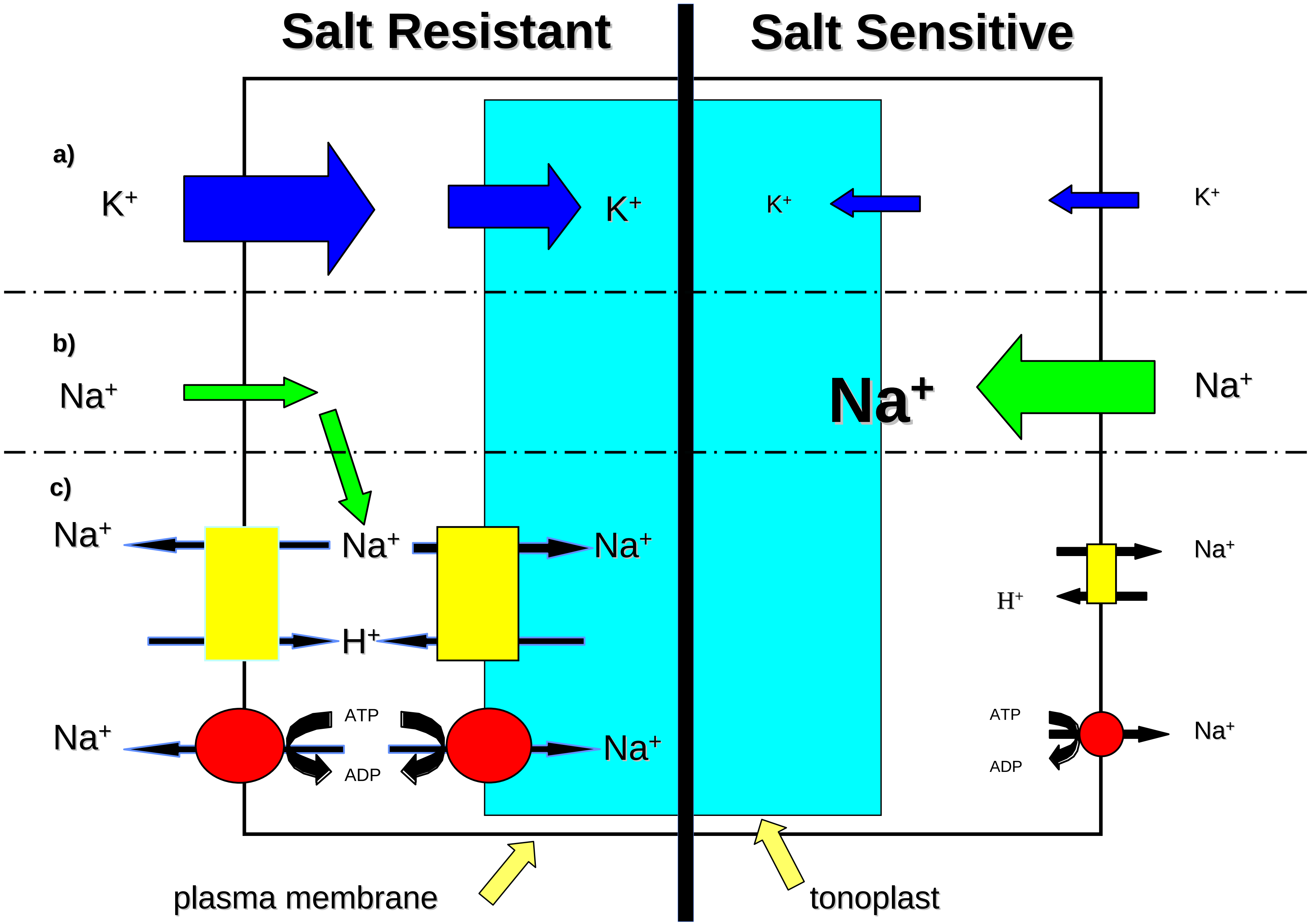
- Mannitol has been overexpressed in tobacco protoplasts
- A moderate resistance to salinity was observed



Manipulating Ion Transport Mechanisms

Essentially, 3 Key Physiological Strategies Confer Salinity Tolerance

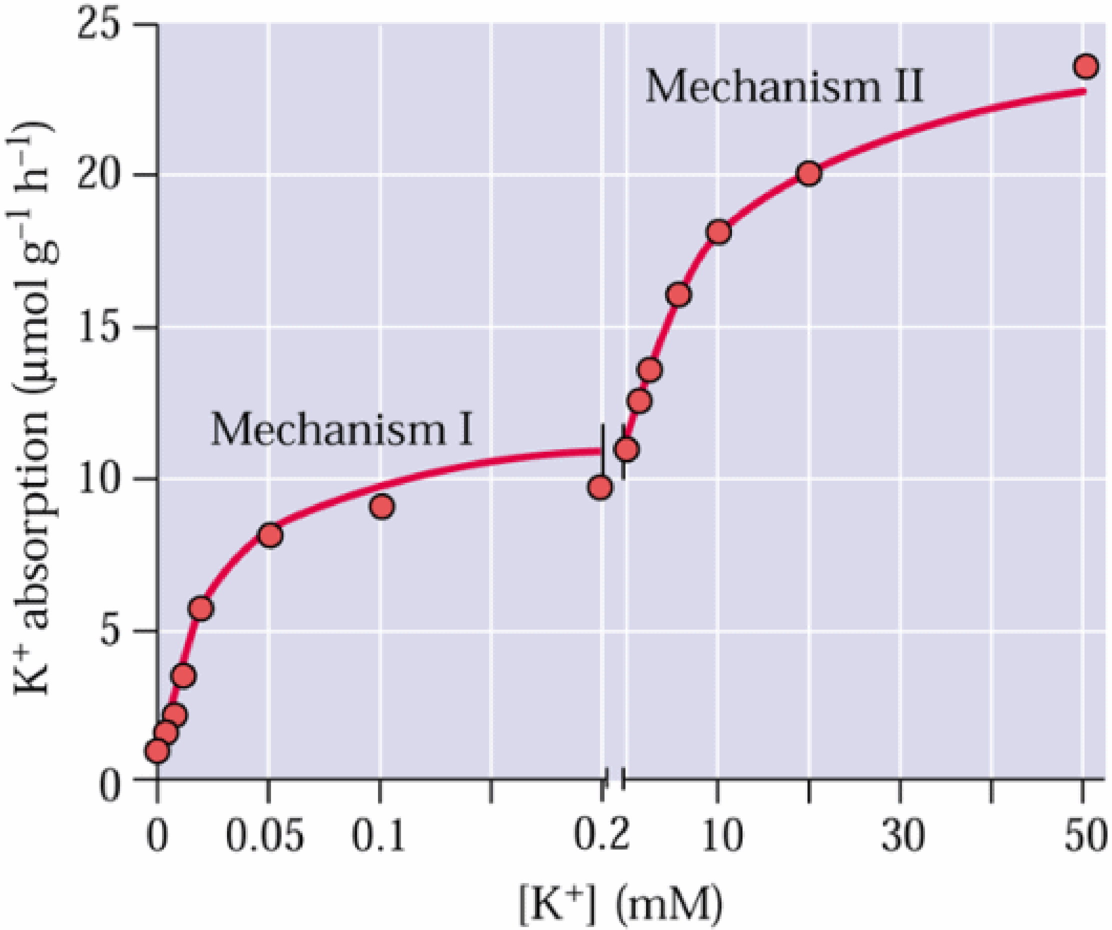
- Tolerate and/or avoid of desiccation (osmoregulation)
- Maintain a high cytoplasmic K^+ / Na^+ ratio
- Maintain a low cytoplasmic Cl^- concentration


Salt Resistant
Salt Sensitive
a)
K+
K+
K+
K+
b)
Na+
Na+
Na+
c)
Na+
Na+
Na+
H+
Na+
H+
Na+
ATP
ADP
Na+
ATP
ADP
Na+
plasma membrane
tonoplast

There are Multiple K^+ Uptake Mechanisms in Glycophytes; Does Na Enter Through Poor Discrimination for K?

- High Affinity Transport (HATs) operates at low external K^+ concentra-tions (10 - 200 mM)

- Low Affinity Transport (LATs) operates at higher external K^+ concentrations (>200 mM)



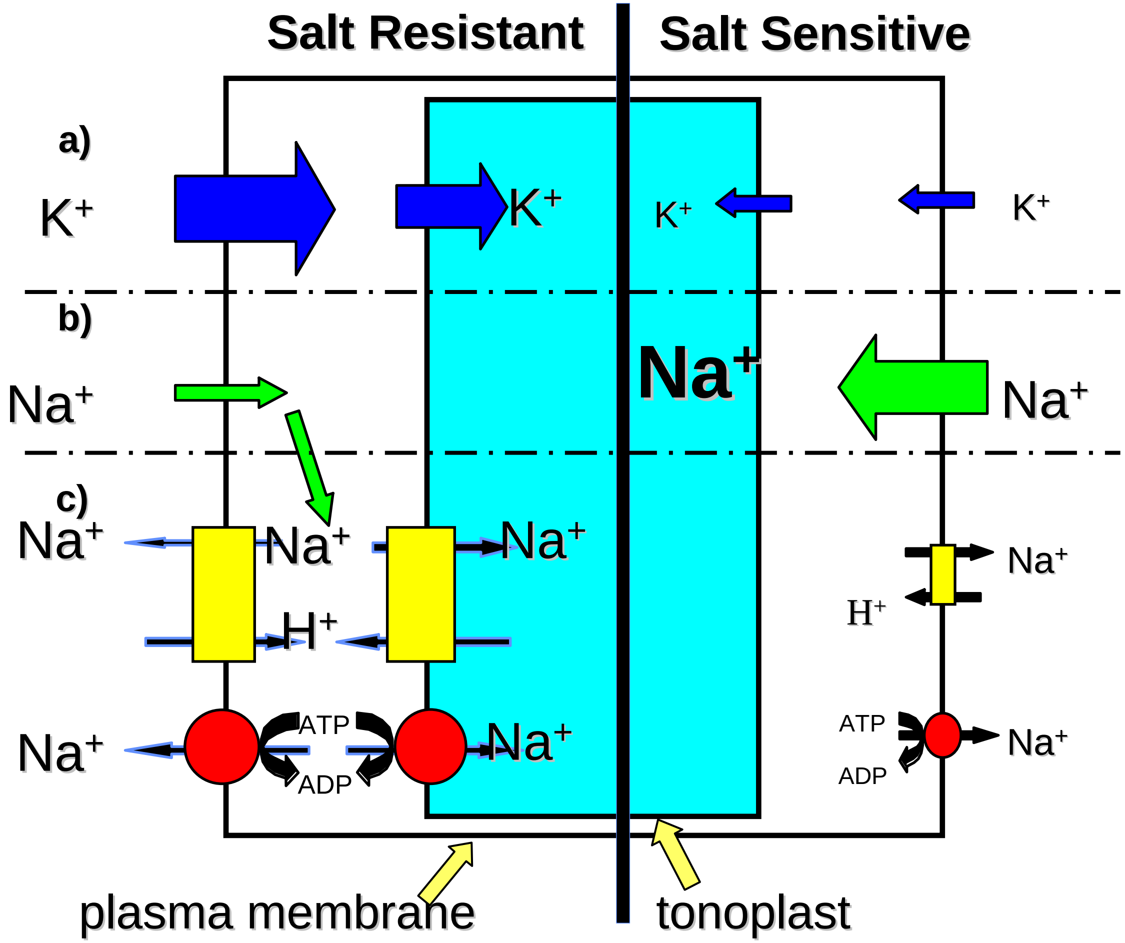
How do Salt Resistant Plants Maintain a High Cytoplasmic K^+ / Na^+ Ratio?

Resistant plants may be better at:

(a), maximizing K^+ uptake in high Na^+ backgrounds

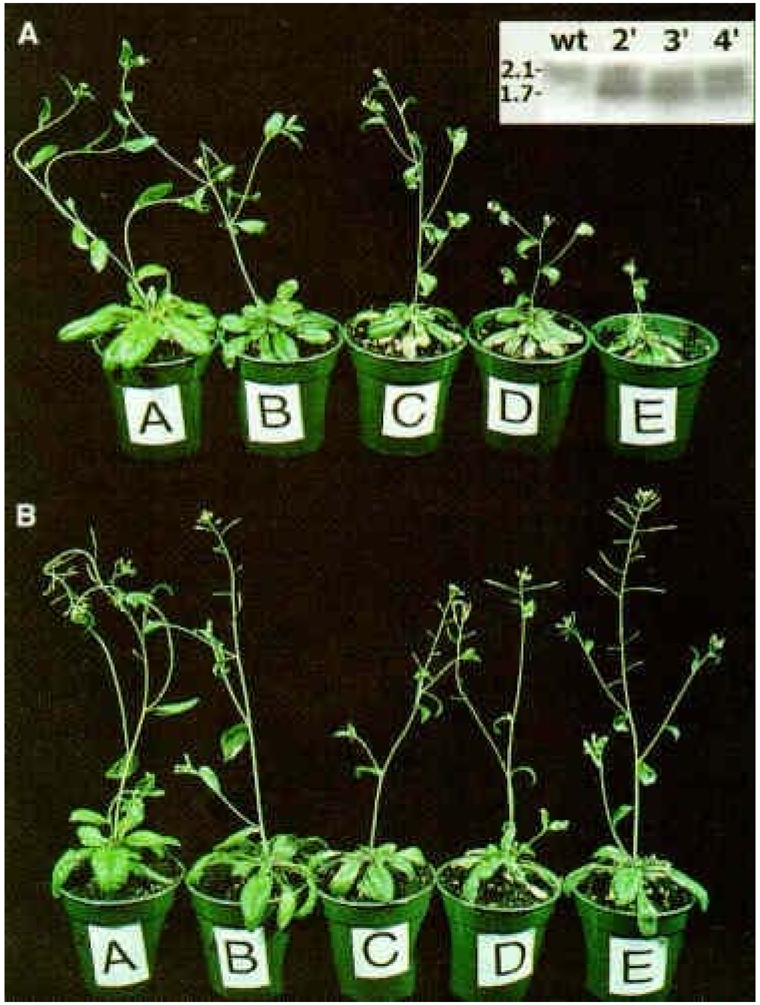
(b), minimizing Na^+ uptake

(c), Effecting Na^+ efflux by a Na^+/H^+ antiporter or a Na^+-ATPase



Manipulating Na^+ Balance in Plants Confers Resistance to Salinity

- A gene coding for a vacuolar Na^+ / H^+ antiporter (*AtNhx1*) has been identified...
- The gene product, AtNhx1, is believed to sequester cytosolic Na^+ into the vacuole..
- Transgenic *AtNhx1* lines are more salt resistant.



High Cytoplasmic K^+ / Na^+ Ratios can be Maintained by:-

- Better discrimination for K^+ Uptake

  High Affinity Transport - Km < 100 µM (HKT1?)

  Low Affinity Transport - Km > 20 mM (ATK1)

- Better discrimination against Na^+ Uptake

  Mechanism for Na^+ Uptake is unknown

- Actively Pumping Na^+ Out of the Cytoplasm

  Mechanism unknown in plants but some evidence for p-type Na^+ATPase in Fungi, and for pH-driven Na^+ / H^+ Antiporter