Pflanzliche Anpassung an Phosphorverfügbarkeit

9. November 2016

Leibniz-Institute für Pflanzenbiochemie, Halle

Stress- und Entwicklungsbiologie
(Scheel)

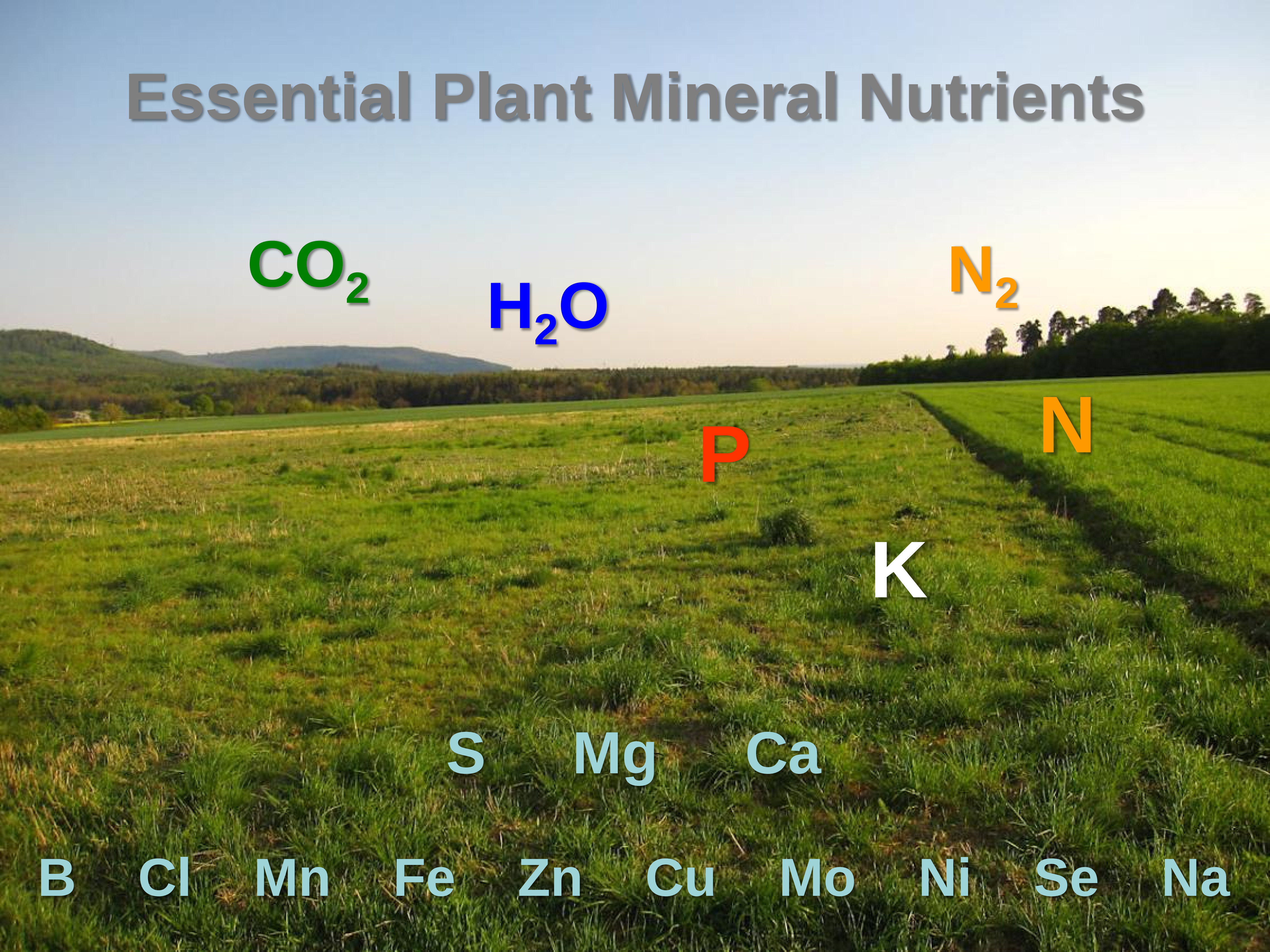
Stoffwechsel- und Zellbiologie
(Tissier)

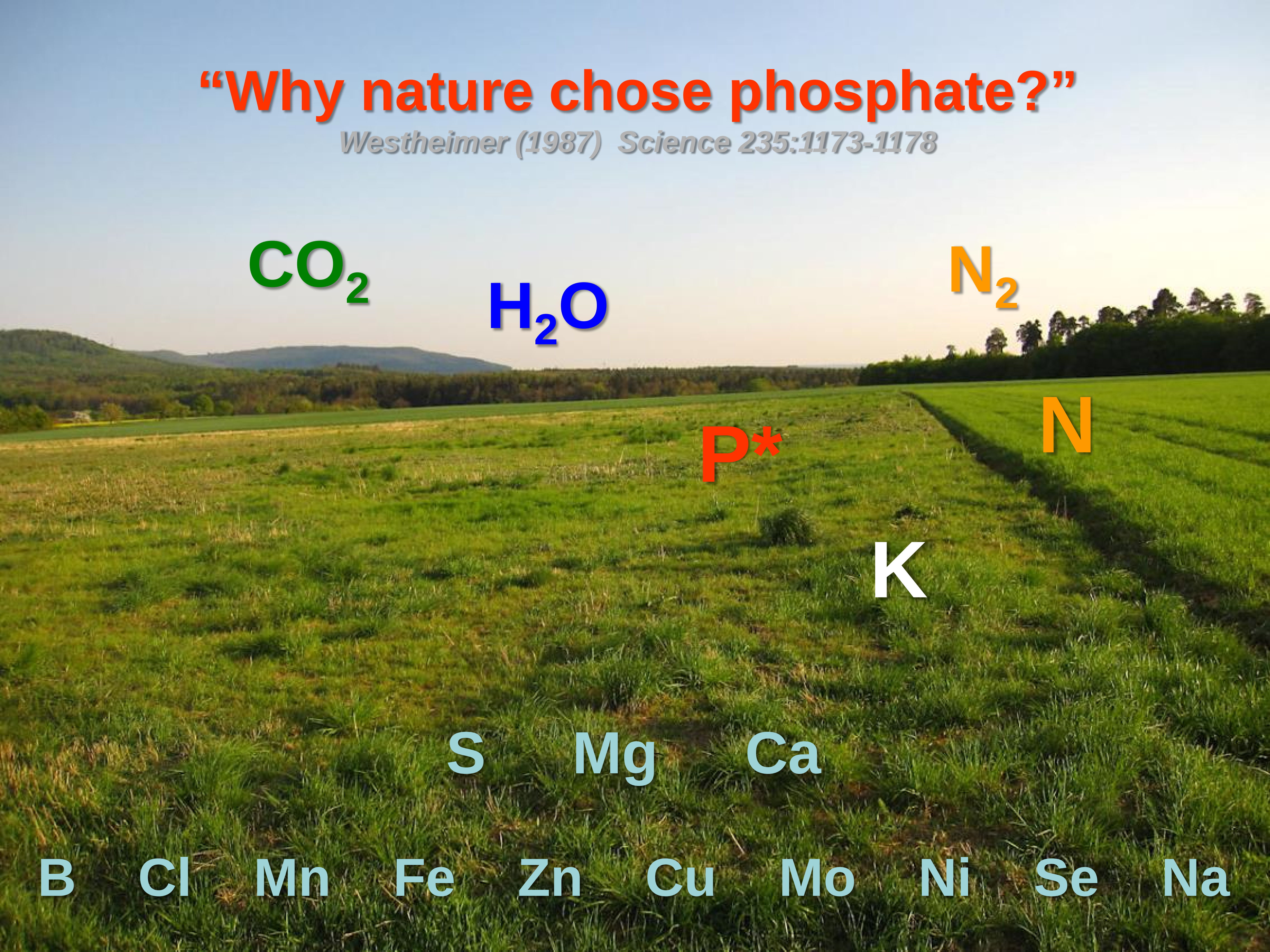
Molekulare Signalverarbeitung
(Abel)

Natur- und Wirkstoffchemie
(Wessjohann)

IPB

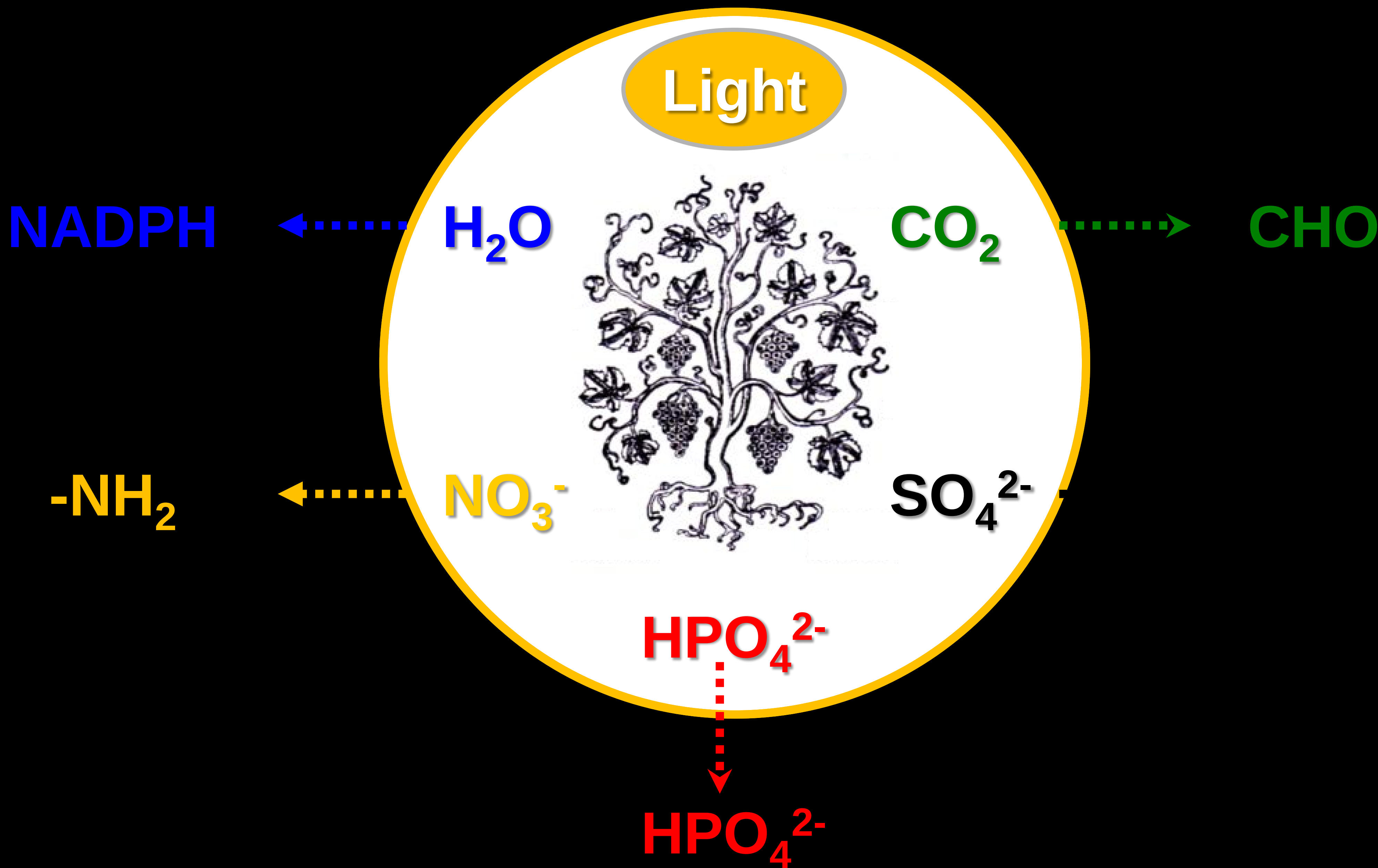
Essential Plant Mineral Nutrients




"Why nature chose phosphate?"
Westheimer (1987) Science 235:1173-1178
CO_2
H_2O
N_2
N
P*
K
S Mg Ca
B Cl Mn Fe Zn Cu Mo Ni Se Na

“Why nature chose phosphate?”

Westheimer (1987) Science 235:1173-1178



“Bioenergetics” of Macronutrient Assimilation

Electronegativity		***Energy Requirements for Reduction***		
3.4	O• •O			
3.0	N •• O	NO_3^-	NAD(P)H →	NH_3
2.6	S •• O	SO_4^{2-}	NAD(P)H + ATP →	H_2S
2.6	C •• O	CO_2	NAD(P)H + ATP →	CHO
2.2	H •• O	H_2O	*Solar Energy* →	$\{H_2\}$
2.1	P •• O	PO_4^{3-}	? ⋯→	PH_3
	Polarity (X→O)		***Reduction*** (X• •O)	

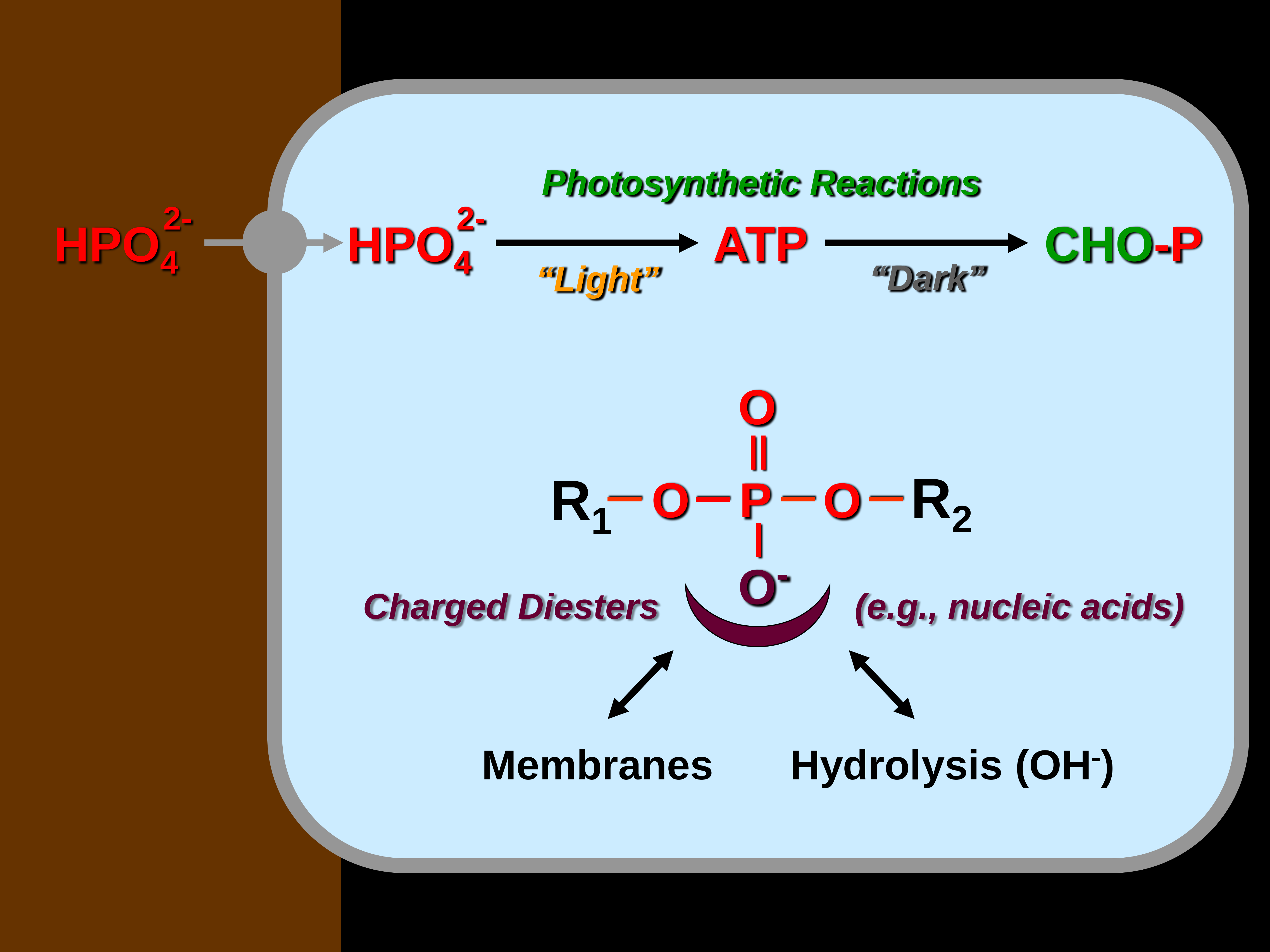
Photosynthetic Reactions

HPO_4^{2-} → HPO_4^{2-} —"Light"→ ADP~P —"Dark"→ CHO-P

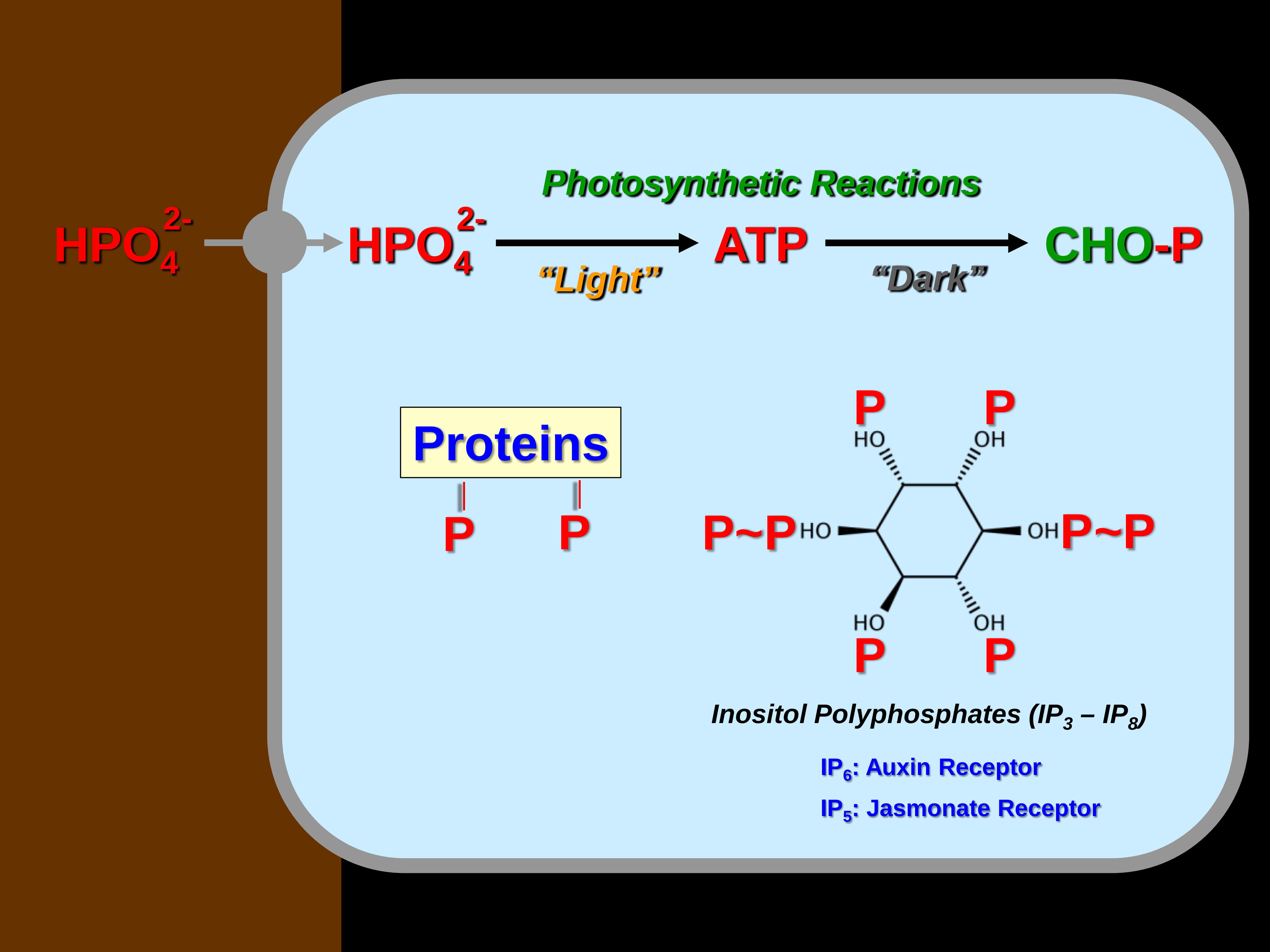
Phosphorus and Hesperus

Evelyn De Morgan (1889)

Phōsphoros: "The bearer of light"



Photosynthetic Reactions
HPO4 2-
HPO4 2-
"Light"
ATP
"Dark"
CHO-P
O
R1 O P O R2
O-
Charged Diesters
(e.g., nucleic acids)
Membranes
Hydrolysis (OH-)


Photosynthetic Reactions
HPO₄²⁻
HPO₄²⁻
"Light"
ATP
"Dark"
CHO-P
Proteins
P
P
P
P
P~P
HO
OH
P~P
HO
OH
HO
OH
P
P
Inositol Polyphosphates (IP3 – IP8)
IP6: Auxin Receptor
IP5: Jasmonate Receptor

Lithosphere

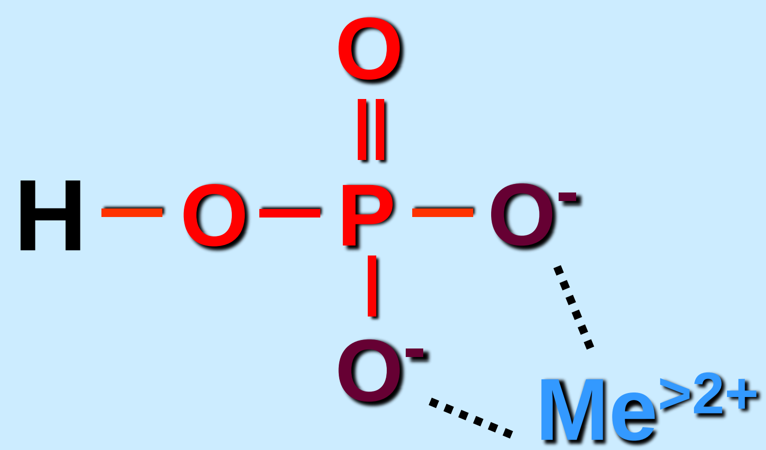
Elemental Abundance (%)

O	46.6
Si	27.7
Al	8.1
Fe	5.0
Ca	3.6
Na	2.8
K	2.6
Mg	2.1
P	0.1

K_{sp} of **Phosphates** (10^{-20}...10^{-44})

Photosynthetic Reactions

HPO_4^{2-} —"Light"→ **ATP** —"Dark"→ **CHO-P**



Ca^{2+}

Chemical Rationale for Calcium Signaling

Lithosphere

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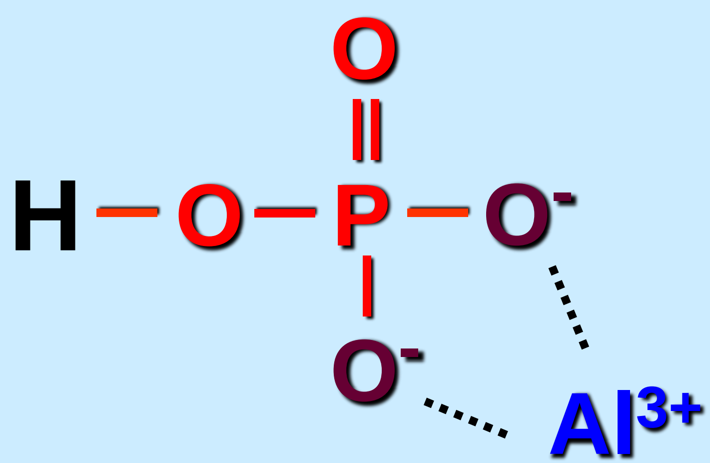
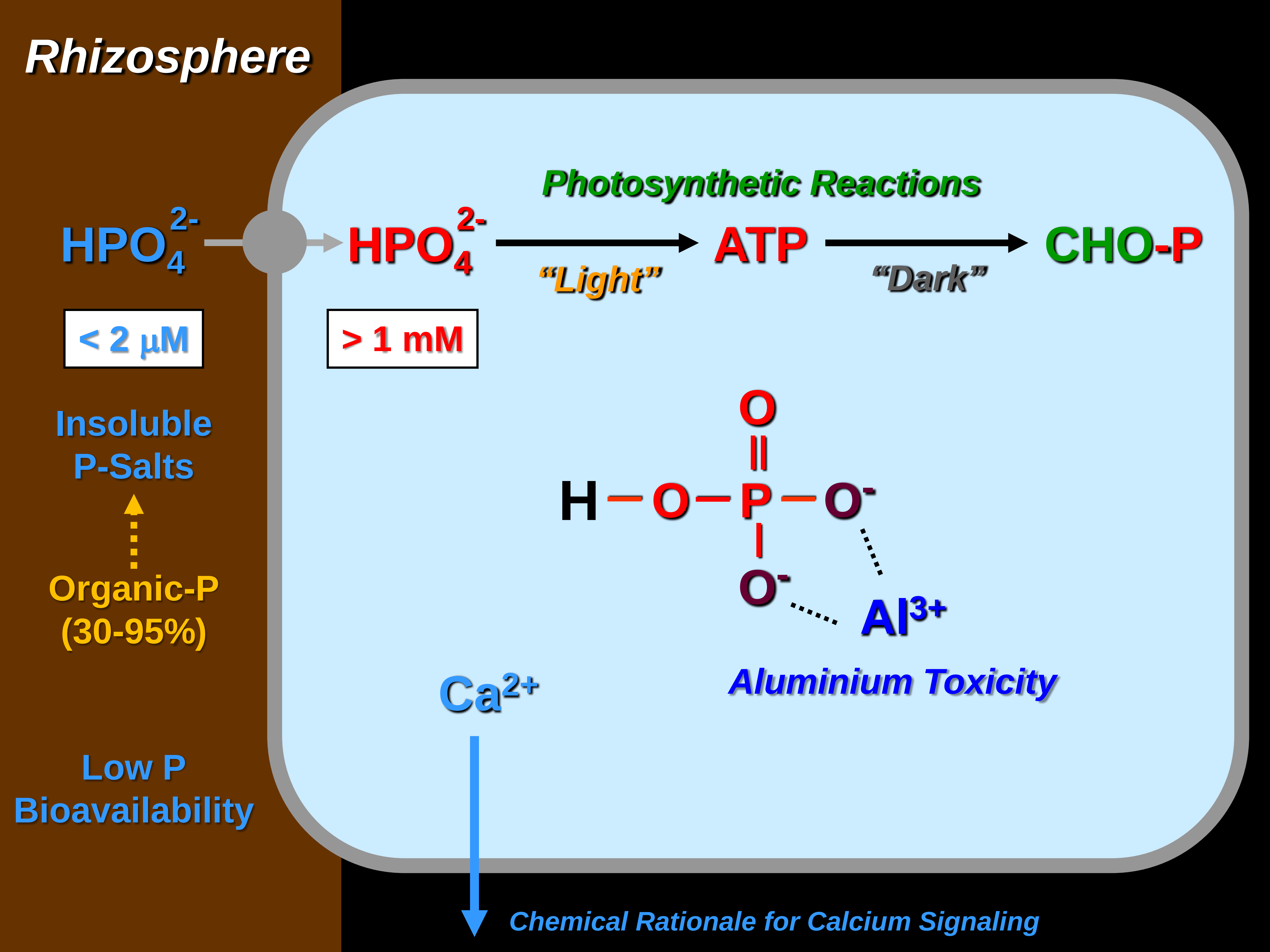


Aluminium Toxicity

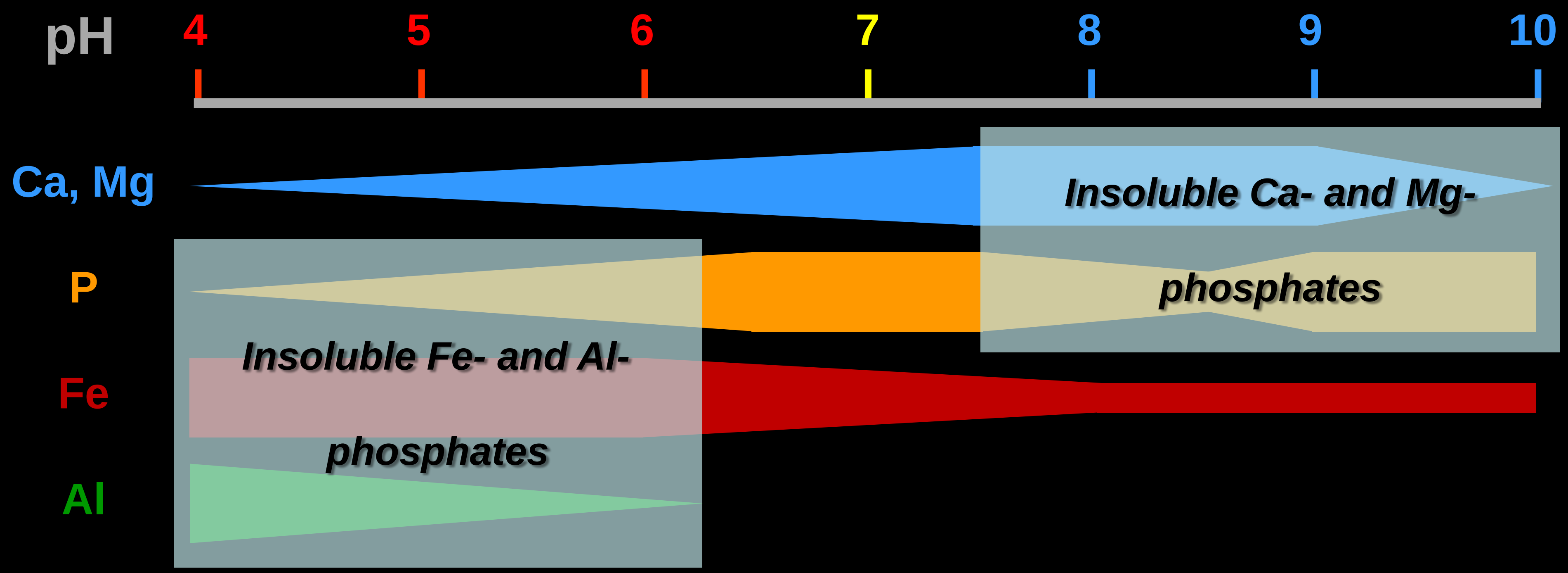
Ca^{2+}

Chemical Rationale for Calcium Signaling



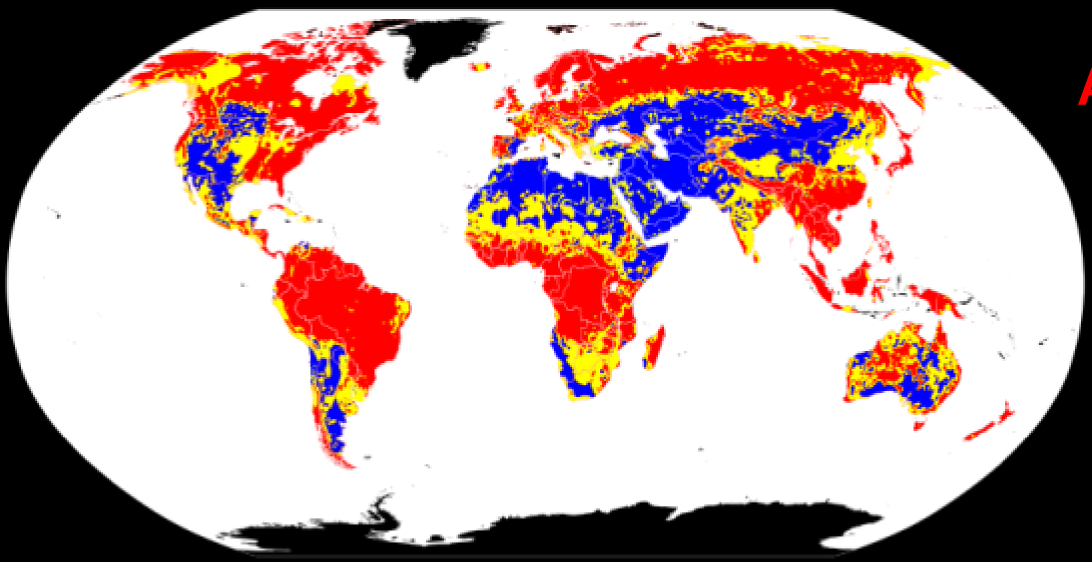
Rhizosphere
HPO4 2-
< 2 μM
Insoluble P-Salts
Organic-P (30-95%)
Low P Bioavailability
Photosynthetic Reactions
HPO4 2-
> 1 mM
"Light"
ATP
"Dark"
CHO-P
O
H O P O-
O-
Al3+
Aluminium Toxicity
Ca2+
Chemical Rationale for Calcium Signaling

Limited P Bioavailability on a Global Scale



World Soils

(Source: FAO)



Acidic (low P)

Neutral

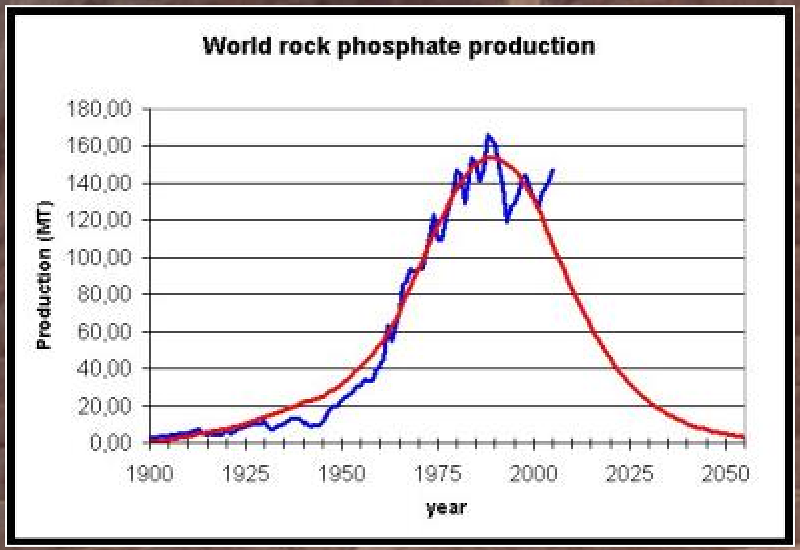
Basic (low P)

No P-Fertilization ***Australia*** **P-Fertilization**

https://www.agric.wa.gov.au/mycrop/phosphorus-deficiency-wheat

Hypericum hidcote (Großblumiges Johanniskraut)

No P-Fertilization http://www.manna.de **P-Fertilization**



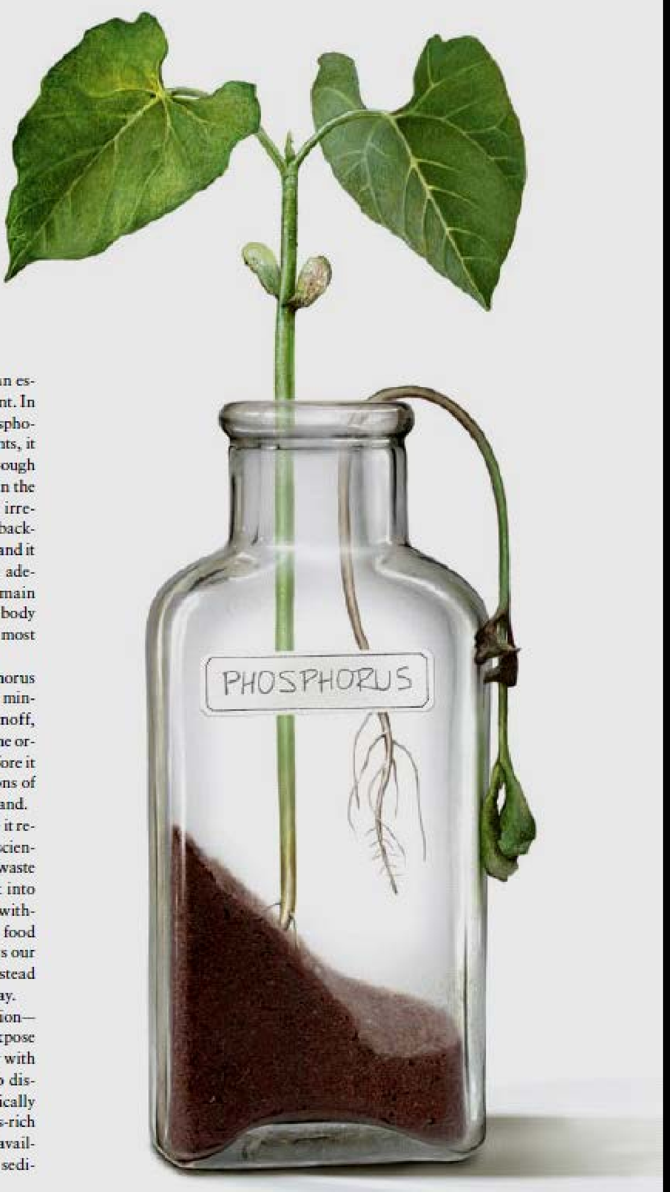
THE DISAPPEARING NUTRIENT

Phosphate-based fertilizers have helped spur agricultural gains in the past century, but the world may soon run out of them. **Natasha Gilbert** investigates the potential phosphate crisis.

Nature, October 2009

Phosphorus: A Looming Crisis

This underappreciated resource—a key part of fertilizers—is still decades from running out. But we must act now to conserve it, or future agriculture will collapse • By David A. Vaccari



KEY CONCEPTS

- Mining phosphorus for fertilizer is consuming the mineral faster than geologic cycles can replenish it. The U.S. may run out of its accessible domestic sources in a few decades, and few other countries have substantial reserves, which could also be depleted in about a century.
- Excess phosphorus in waterways helps to feed algal blooms, which starve fish of oxygen, creating "dead zones."
- Reducing soil erosion and recycling phosphorus from farm and human waste could help make food production sustainable and prevent algal blooms.

—*The Editors*

As complex as the chemistry of life may be, the conditions for the vigorous growth of plants often boil down to three numbers, say, 19-12-5. Those are the percentages of nitrogen, phosphorus and potassium, prominently displayed on every package of fertilizer. In the 20th century the three nutrients enabled agriculture to increase its productivity and the world's population to grow more than sixfold. But what is their source? We obtain nitrogen from the air, but we must mine phosphorus and potassium. The world has enough potassium to last several centuries. But phosphorus is a different story. Readily available global supplies may start running out by the end of this century. By then our population may have reached a peak that some say is beyond what the planet can sustainably feed.

Moreover, trouble may surface much sooner. As last year's oil price swings have shown, markets can tighten long before a given resource is anywhere near its end. And reserves of phosphorus are even less evenly distributed than oil's, raising additional supply concerns. The U.S. is the world's second-largest producer of phosphorus (after China), at 19 percent of the total, but 65 percent of that amount comes from a single source: pit mines near Tampa, Fla., which may not last more than a few decades. Meanwhile nearly 40 percent of global reserves are controlled by a single country, Morocco, sometimes referred to as the "Saudi Arabia of phosphorus." Although Morocco is a stable, friendly nation, the imbalance makes phosphorus a geostrategic ticking time bomb.

In addition, fertilizers take an environmental toll. Modern agricultural practices have tripled the natural rate of phosphorus depletion from the land, and excessive runoff into waterways is feeding uncontrolled algal blooms and throwing aquatic ecosystems off-kilter. While little attention has been paid to it as compared with other elements such as carbon or nitrogen, phosphorus has become one of the most significant sustainability issues of our time.

Green Revelation

My interest in phosphorus dates back to the mid-1990s, when I became involved in a NASA program aiming to learn how to grow food in space. The design of such a system requires a careful analysis of the cycles of all elements that go into food and that would need to be recycled within the closed environment of a spaceship. Such know-how may be necessary for a future trip to Mars, which would last almost three years.

Our planet is also a spaceship: it has an essentially fixed total amount of each element. In the natural cycle, weathering releases phosphorus from rocks into soil. Taken up by plants, it enters the food chain and makes its way through every living being. Phosphorus—usually in the form of the phosphate ion PO_4^{3-}—is an irreplaceable ingredient of life. It forms the backbone of DNA and of cellular membranes, and it is the crucial component in the molecule adenosine triphosphate, or ATP—the cell's main form of energy storage. An average human body contains about 650 grams of phosphorus, most of it in our bones.

Land ecosystems use and reuse phosphorus in local cycles an average of 46 times. The mineral then, through weathering and runoff, makes its way into the ocean, where marine organisms may recycle it some 800 times before it passes into sediments. Over tens of millions of years tectonic uplift may return it to dry land.

Harvesting breaks up the cycle because it removes phosphorus from the land. In prescientific agriculture, when human and animal waste served as fertilizers, nutrients went back into the soil at roughly the rate they had been withdrawn. But our modern society separates food production and consumption, which limits our ability to return nutrients to the land. Instead we use them once and then flush them away.

Agriculture also accelerates land erosion—because plowing and tilling disturb and expose the soil—so more phosphorus drains away with runoff. And flood control contributes to disrupting the natural phosphorus cycle. Typically river floods would redistribute phosphorus-rich sediment to lower lands where it is again available for ecosystems. Instead dams trap sedi-

JEN CHRISTIANSEN

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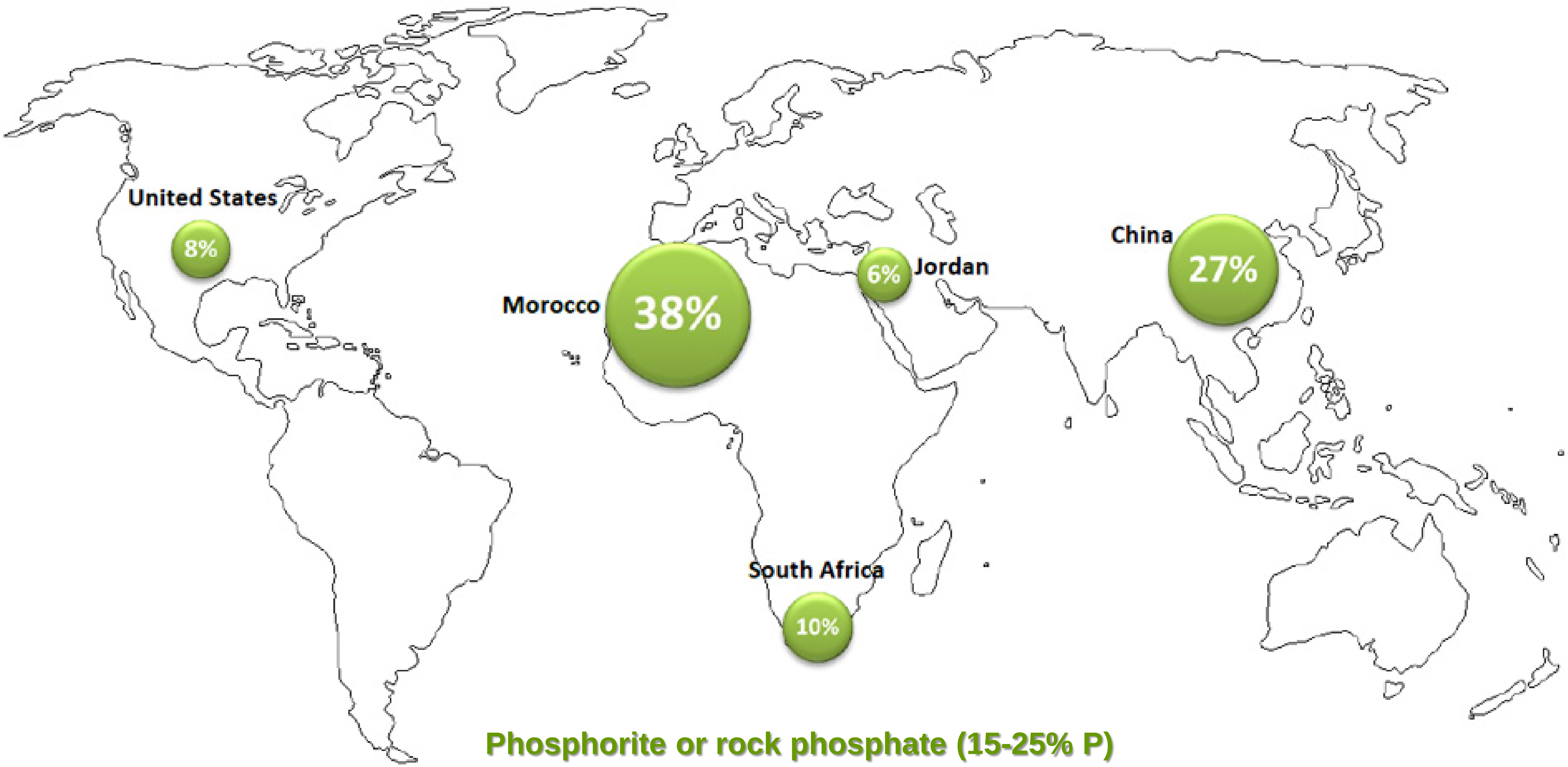
Scientific American, June 2009

Global distribution of phosphate reserves



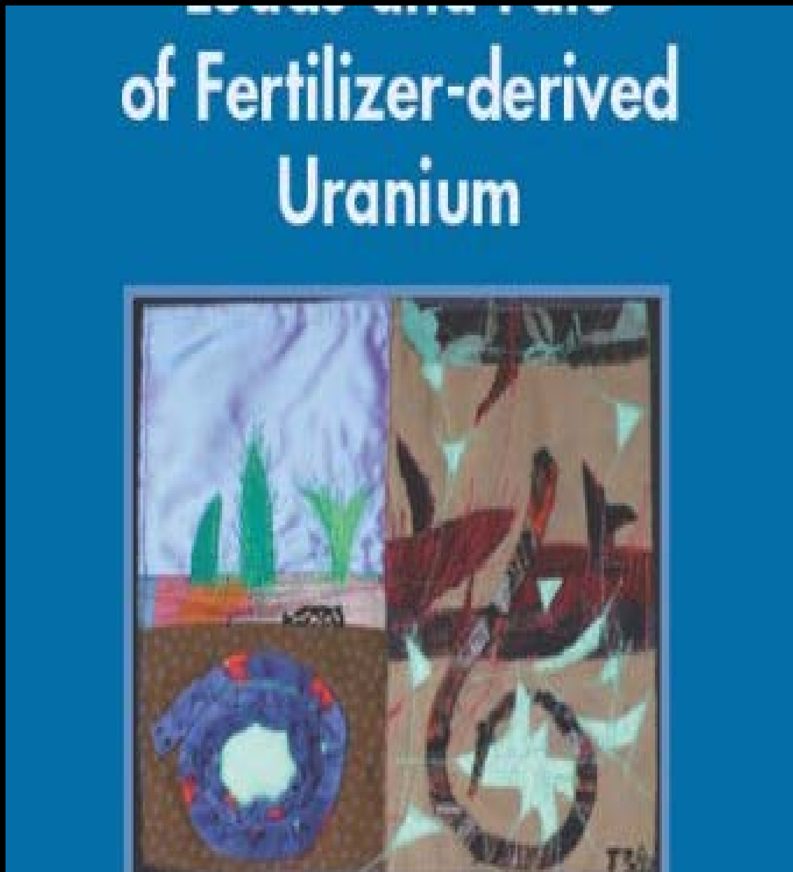
Phosphorite or rock phosphate (15-25% P)

Typical sedimentary rock (<0.2% P)

Source: 2009 USGS

Annual use of P-fertilizers worldwide: <u>> 40 Million tons (ca. $25 Billion)</u>

Heavy Metal Contamination and Eutrophication



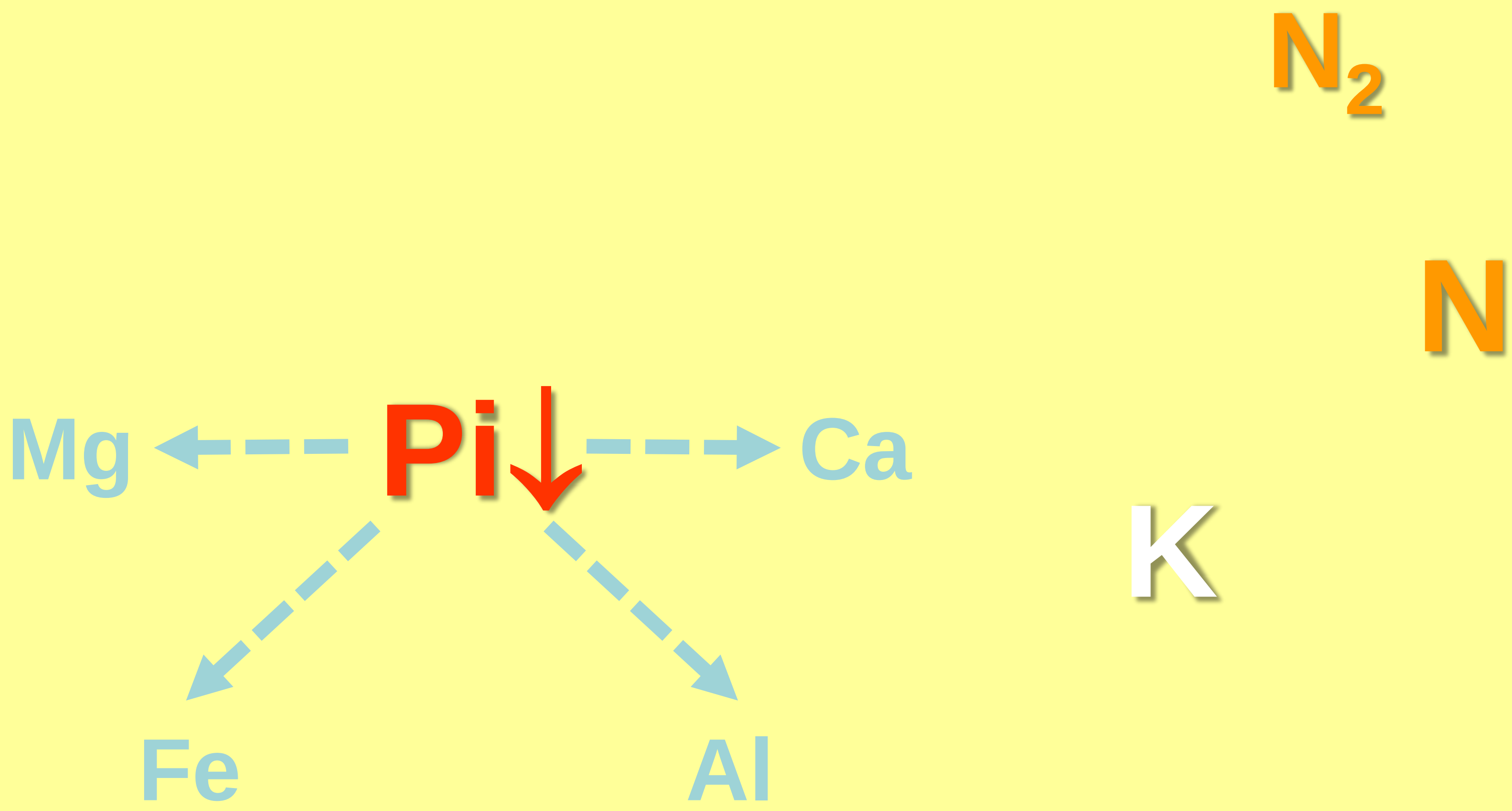
Cadmium and Uranium in German and Brazilian Phosphorous Fertilizers

Geerd A. Smidt, Franziska C. Landes, Leandro Machado de Carvalho, Andrea Koschinsky, Ewald Schnug

Abstract. A collection of phosphorous (P) fertilizers used in Germany (N = 75) and southern Brazil (N = 39) was analyzed for cadmium (Cd) and uranium (U). Both collections show high mean concentrations of Cd (12.0 and 18.6 mg/kg respectively) and U (61.3 and 70.16 mg/kg respectively), while maximum concentrations of 56 mg Cd/kg and up to 200 mg U/kg were found. Currently, up to 42 t Cd and 228 t U are distributed annually on German and 611 t Cd and 1614 t on Brazilian agricultural soils by mineral P fertilizers.


Only 15-30% of applied fertilizer P is taken up
USE
IN
LOW LAND PADDY

Plant Responses to Phosphate (Pi) Limitation



Plant Responses to Phosphate (Pi) Limitation

- Reduced photosynthesis
- Reduced shoot growth

Plant Responses to Phosphate (Pi) Limitation

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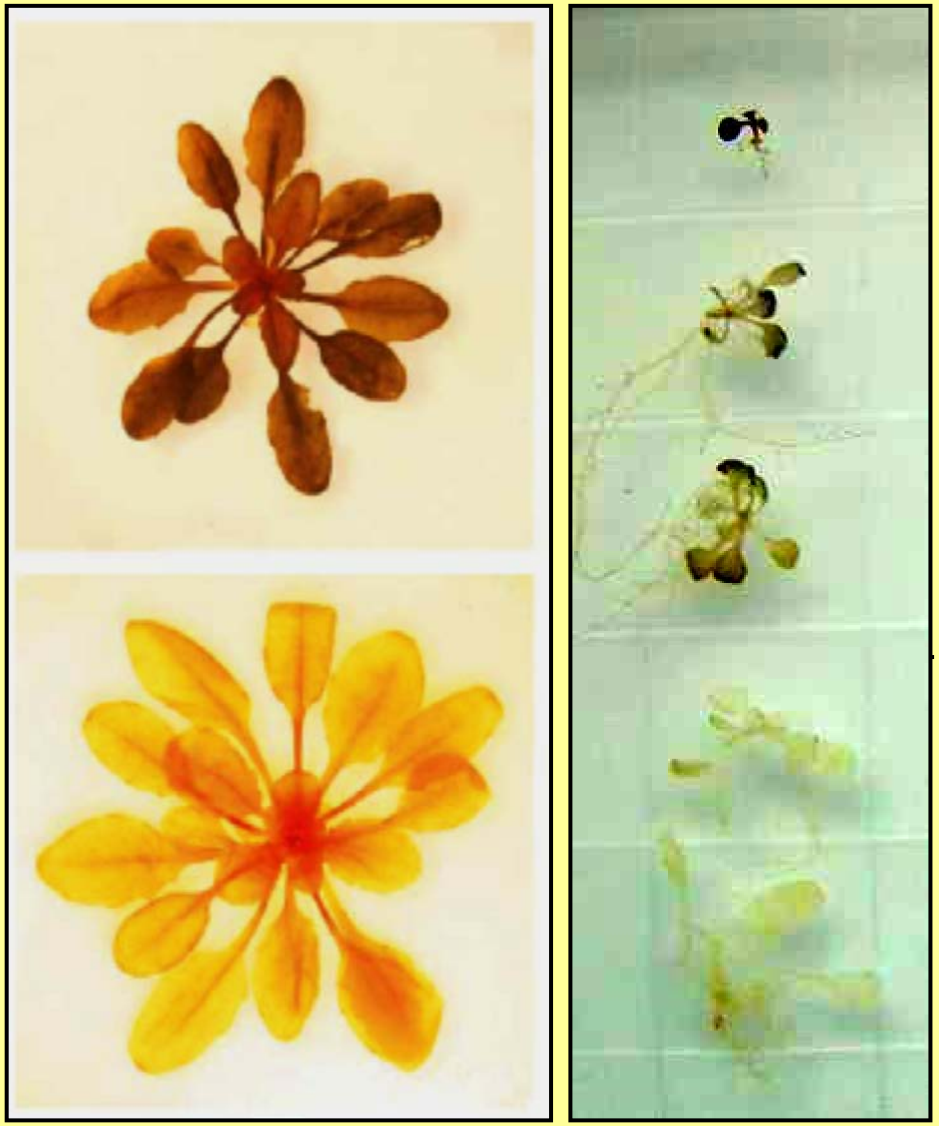
- Reduced shoot growth
- Anthocyanin synthesis

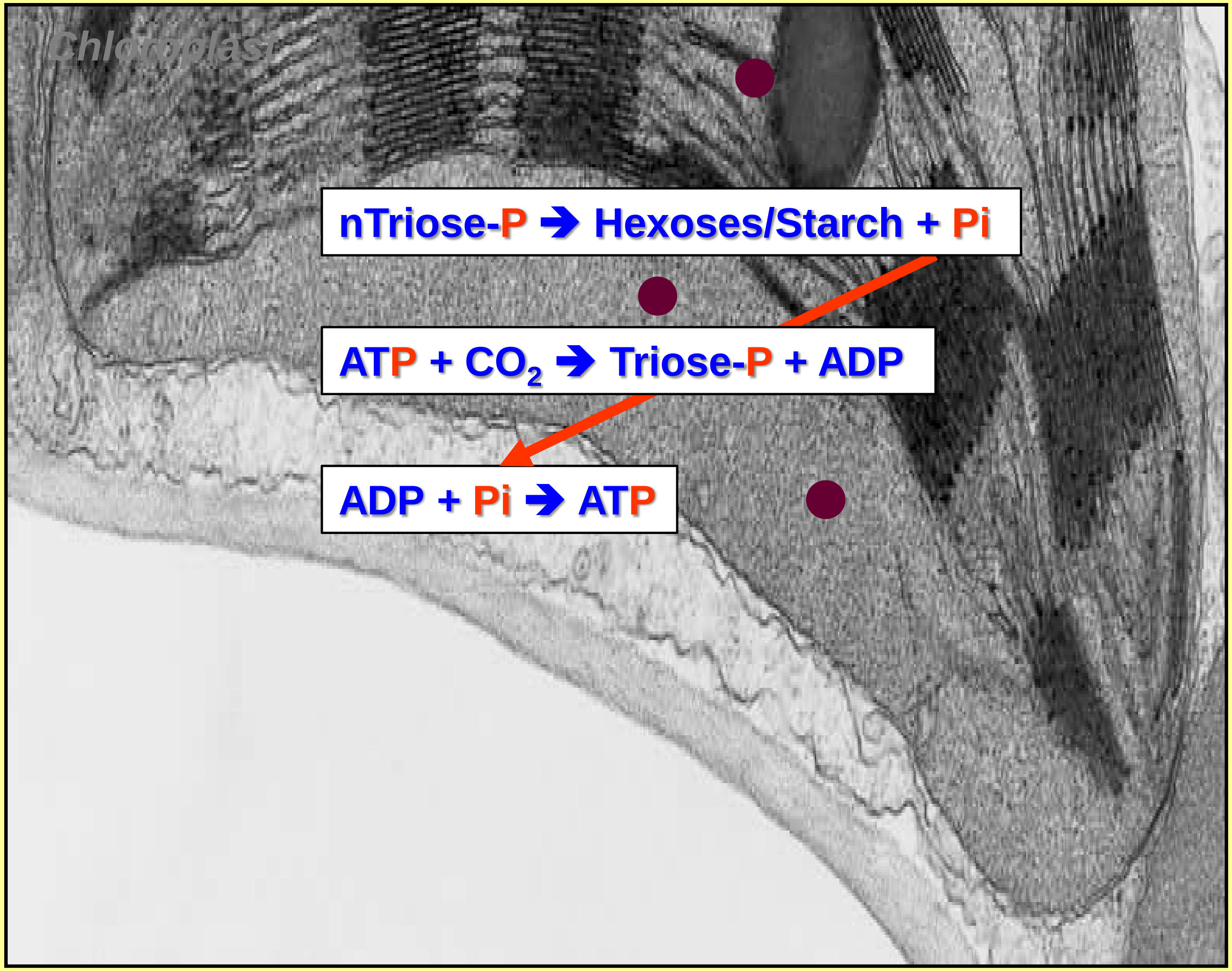
Plant Responses to Phosphate (Pi) Limitation



Transitory Starch

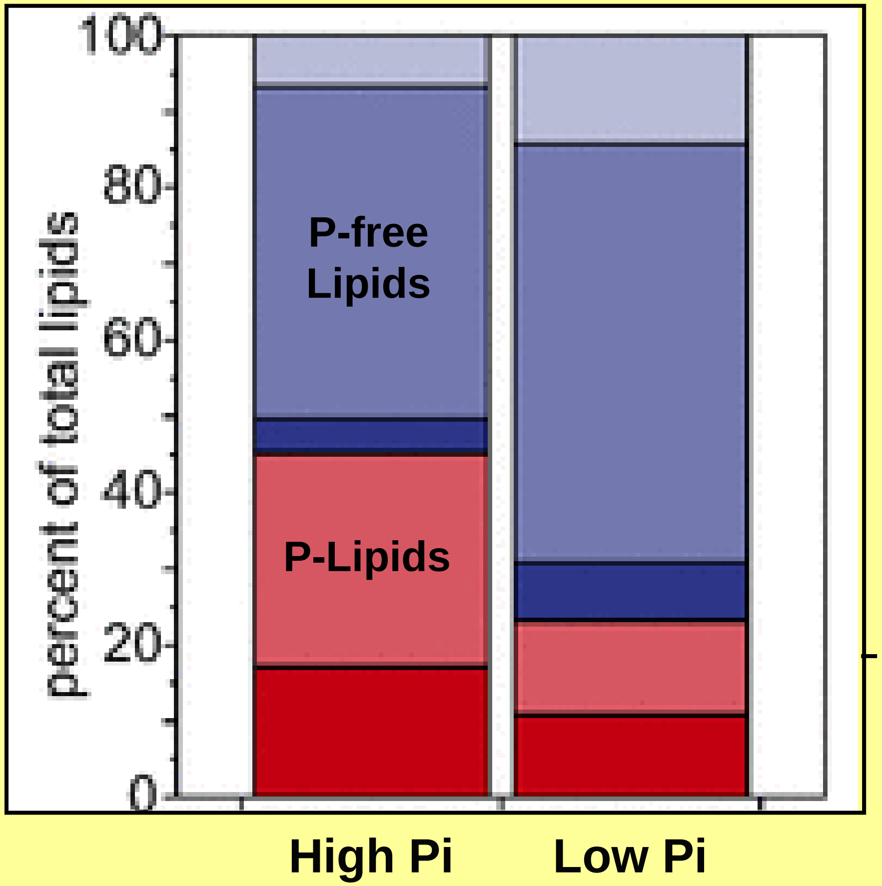
- Reduced photosynthesis
- Reduced shoot growth
- Anthocyanin synthesis
- Starch and sugar synthesis

Plant Responses to Phosphate (Pi) Limitation



Transitory Starch

Plant Responses to Phosphate (Pi) Limitation



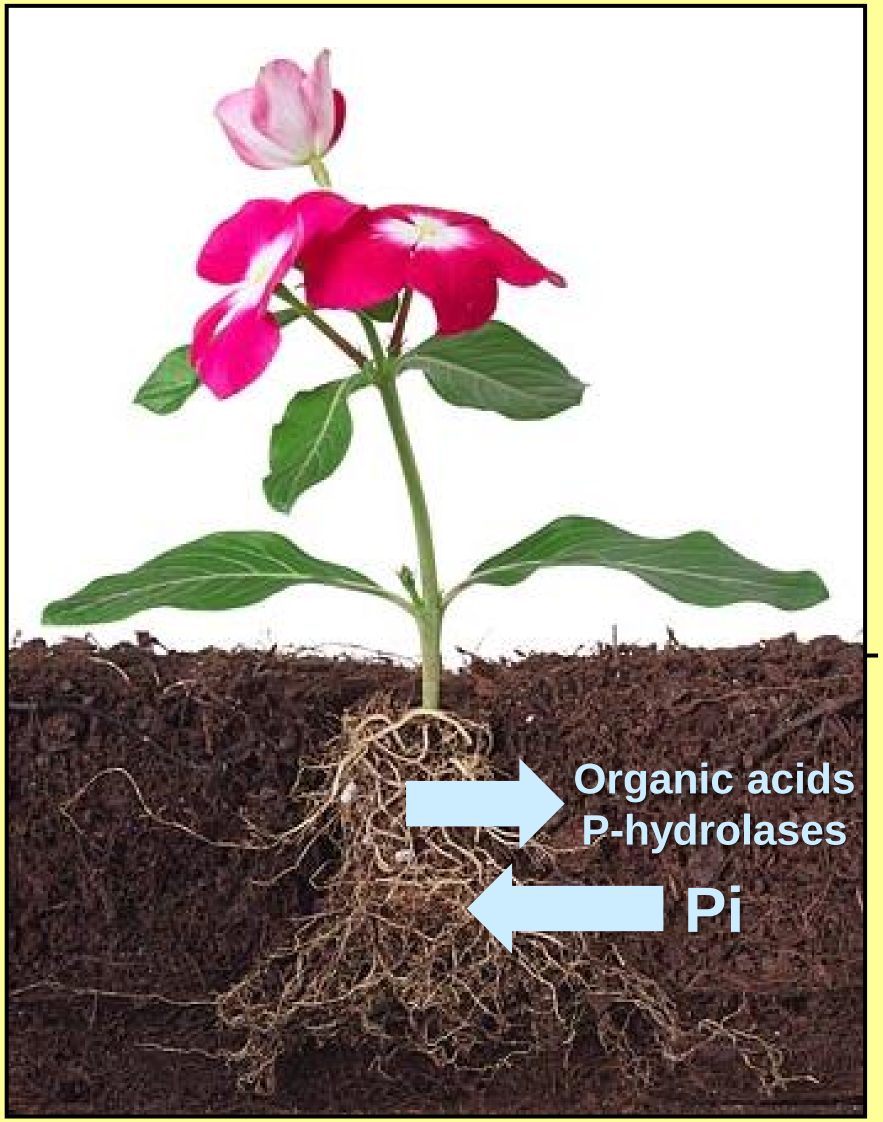
Carini et al. (2015) PNAS 112:7767-7772

- **Reduced photosynthesis**
- **Reduced shoot growth**
- **Anthocyanin synthesis**
- **Starch and sugar synthesis**
- **Lipid remodeling**

Plant Responses to Phosphate (Pi) Limitation

- Reduced photosynthesis
- Reduced shoot growth
- Anthocyanin synthesis
- Starch and sugar synthesis
- Lipid remodeling
- Pi recycling and remobilization

Plant Responses to Phosphate (Pi) Limitation



- Reduced photosynthesis
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- Anthocyanin synthesis
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- Lipid remodeling
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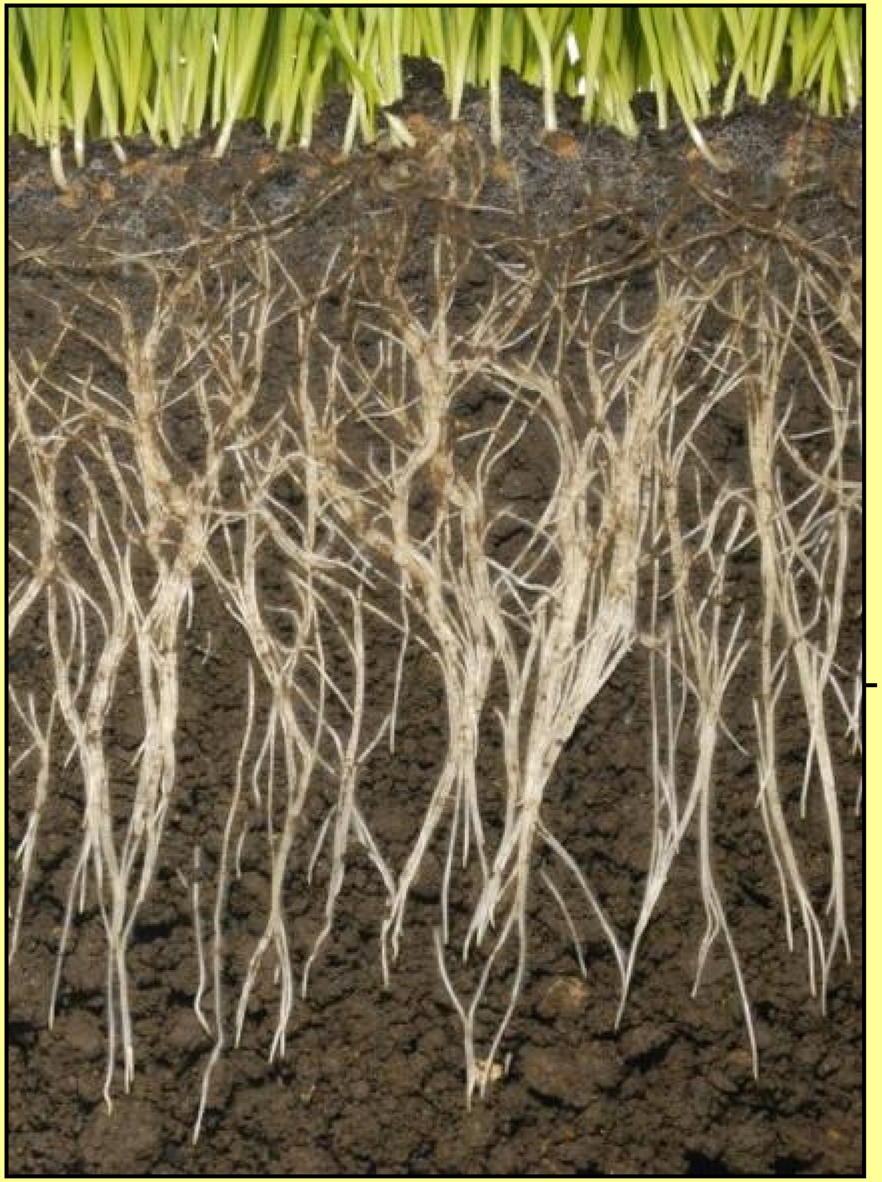
- Pi high affinity uptake
- Exudation (Pi mobilization)

Plant Responses to Phosphate (Pi) Limitation



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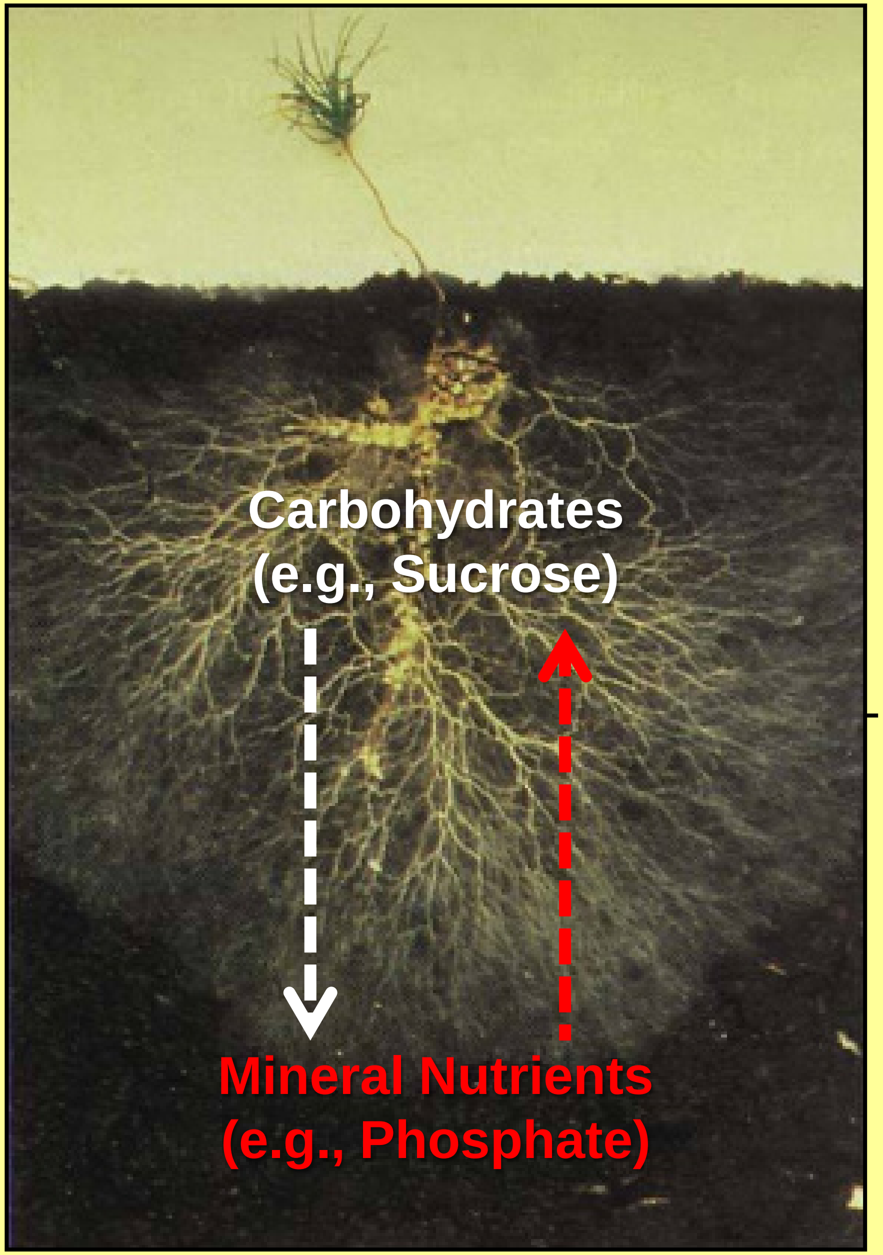
- Root system architecture

Plant Responses to Phosphate (Pi) Limitation



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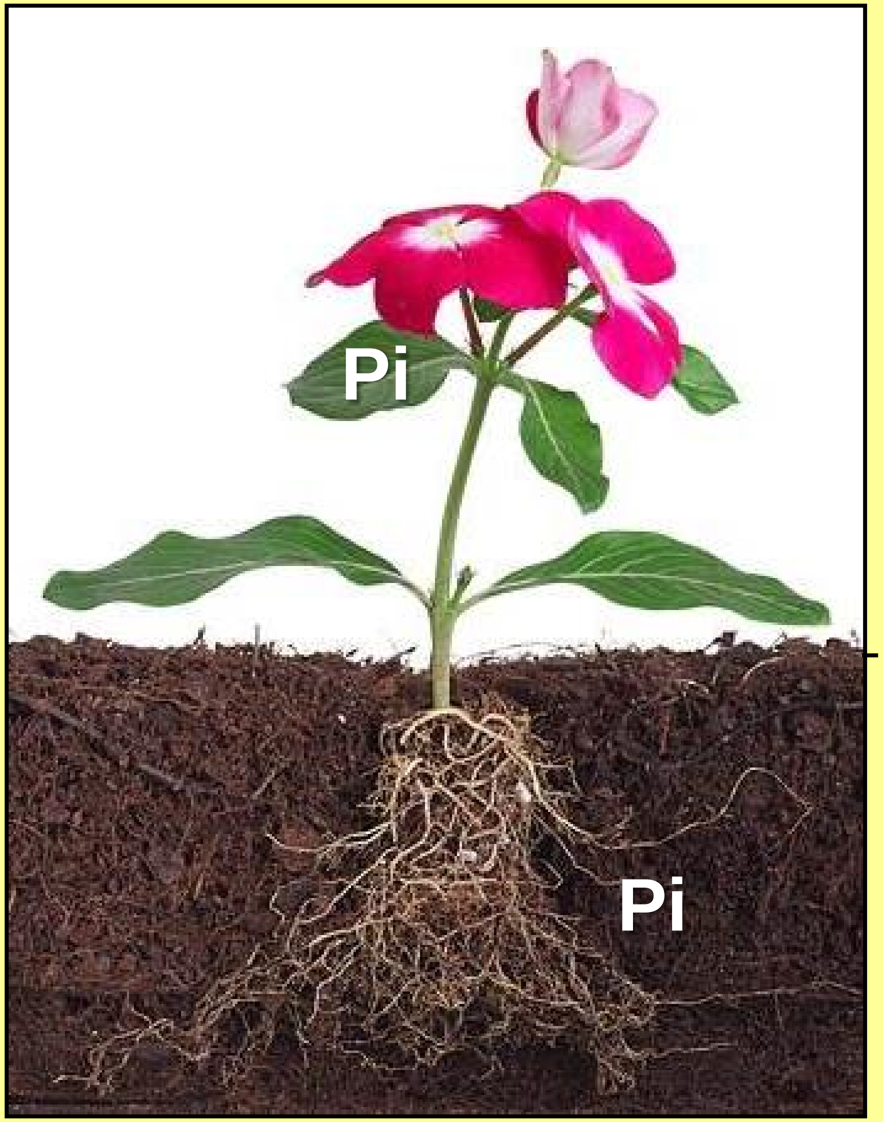
- Anthocyanin synthesis
- Starch and sugar synthesis
- Lipid remodeling
- Pi recycling and remobilization

- Pi high affinity uptake
- Exudation (Pi mobilization)
- Root system architecture
- Mycorrhiza formation

Plant Responses to Phosphate (Pi) Limitation

Systemic Responses: Internal Pi Status



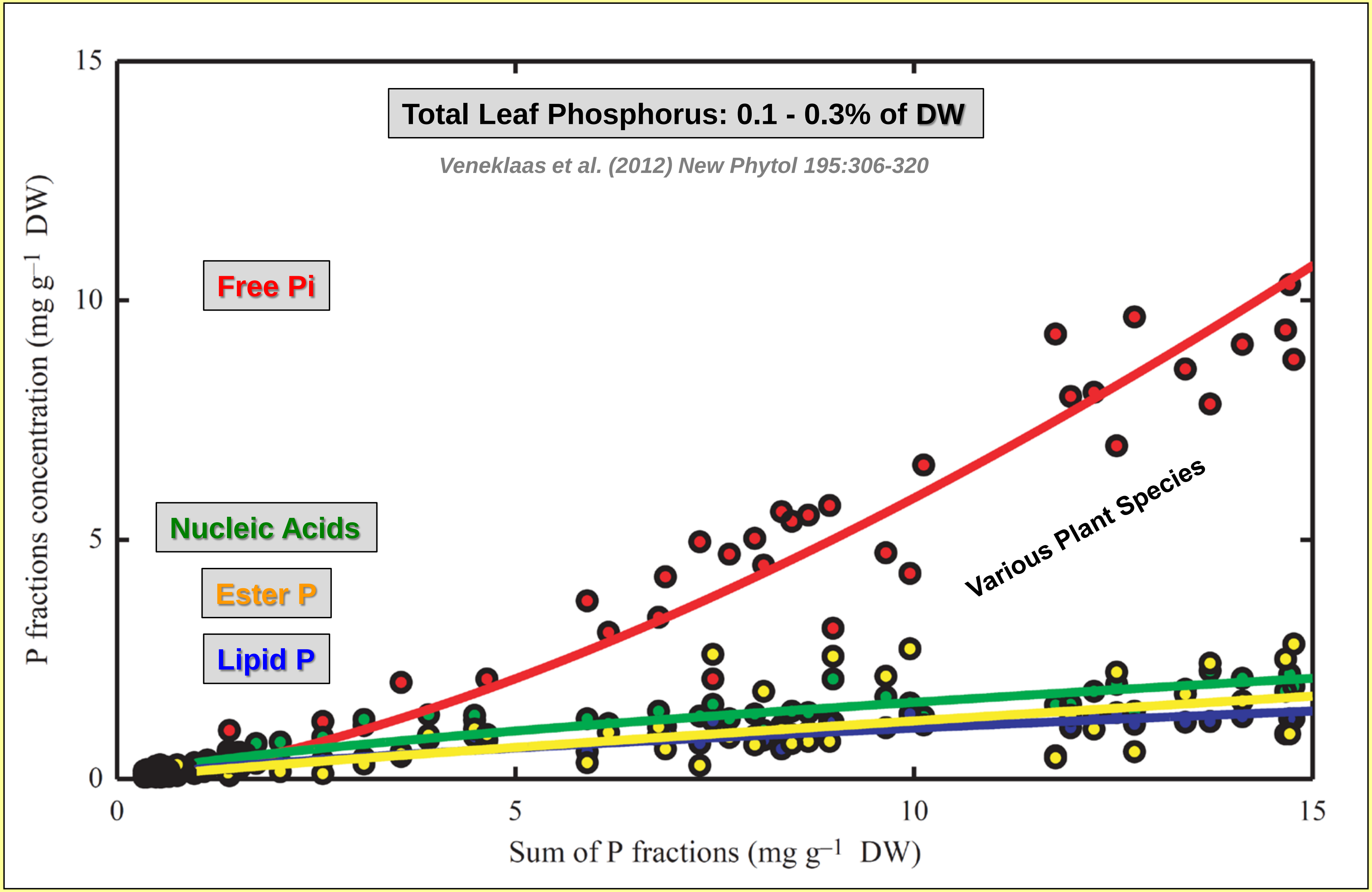
Pi Recycling

Pi Acquisition

Local Responses: External Pi Supply

Plant Responses to Phosphate (Pi) Limitation

Systemic Responses: Internal Pi Status



Plant Responses to Phosphate (Pi) Limitation

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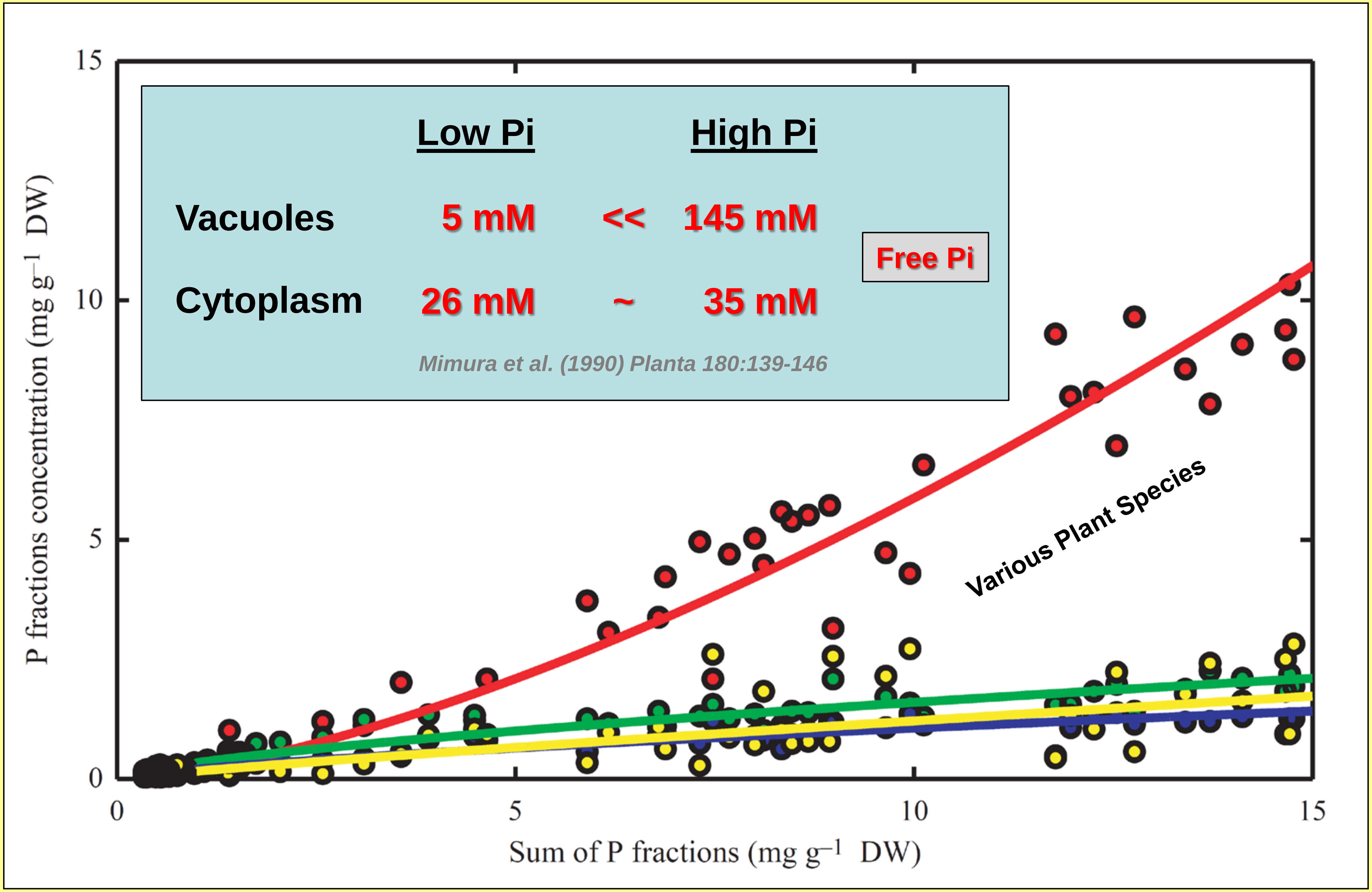
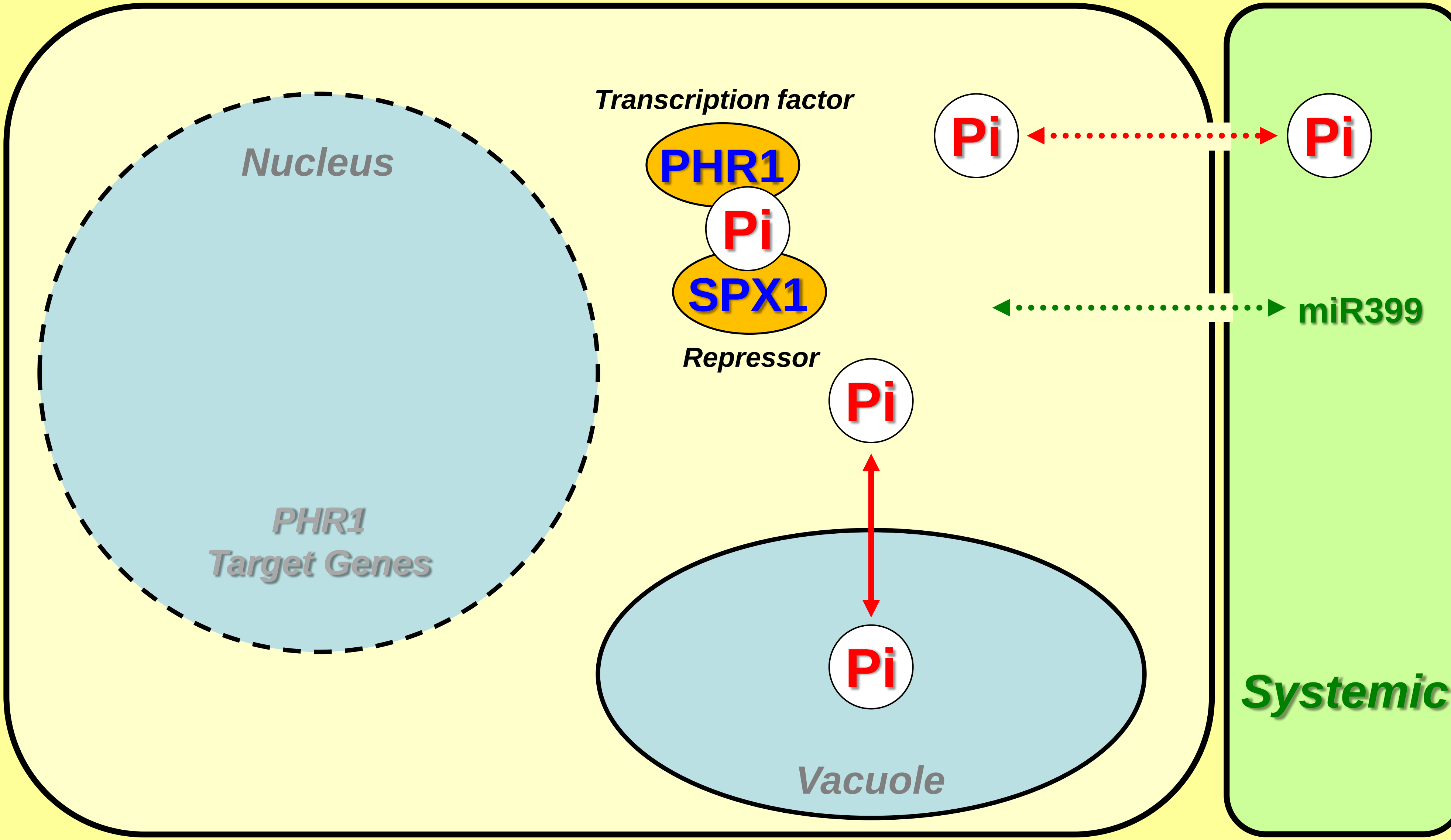


Plant Responses to Phosphate (Pi) Limitation

Systemic Responses: Internal Pi Status



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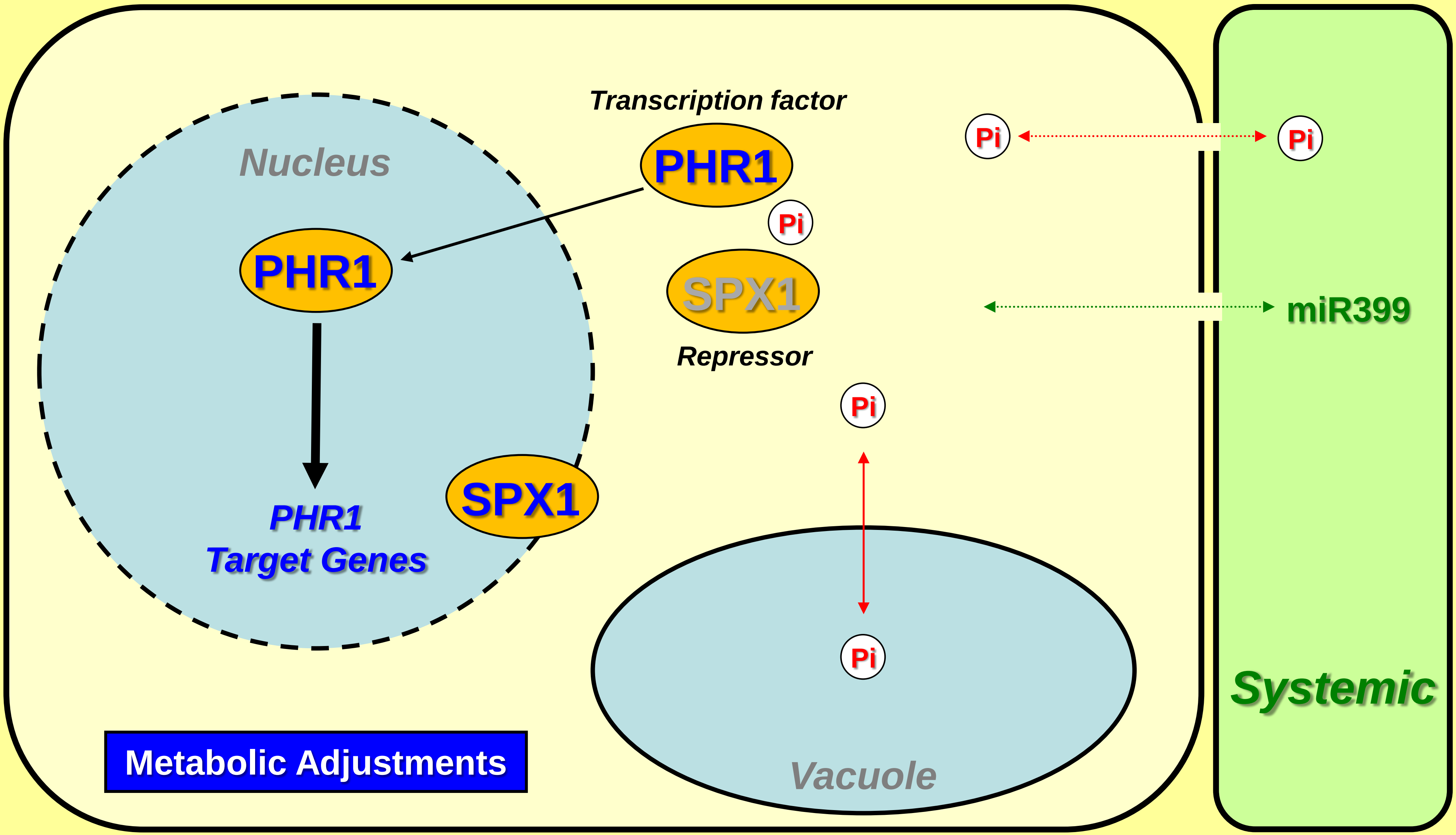

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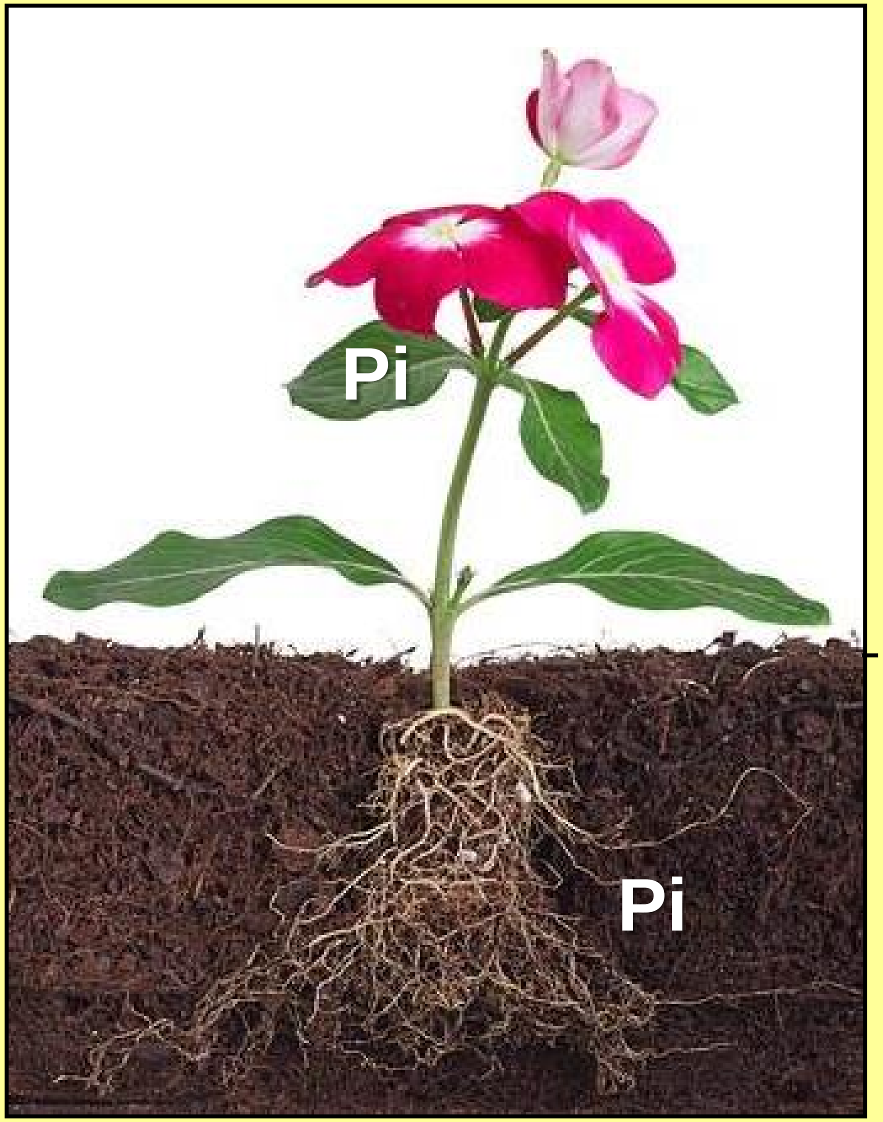

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Pi Acquisition

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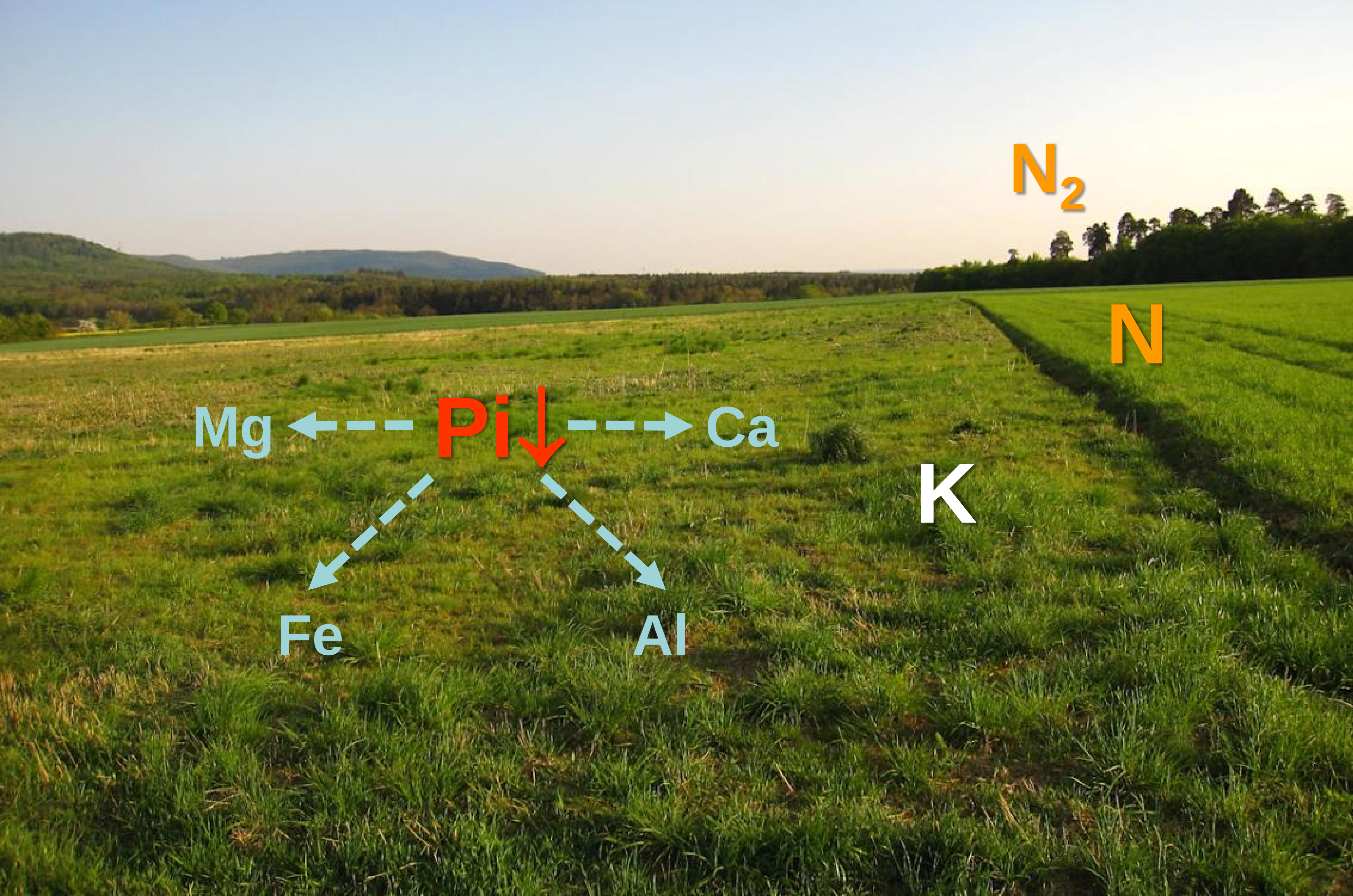
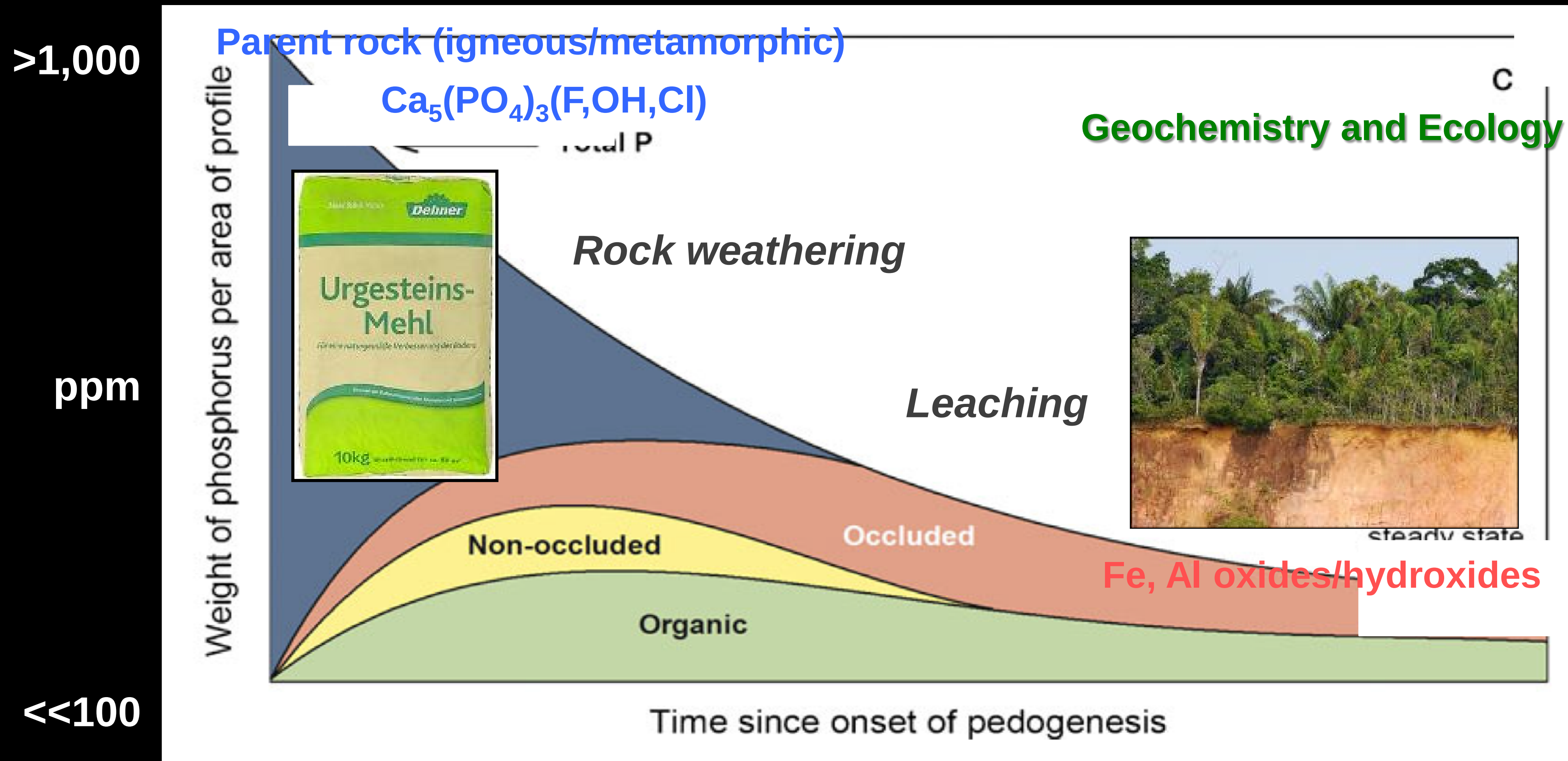


Fate of Phosphorus during Soil Development

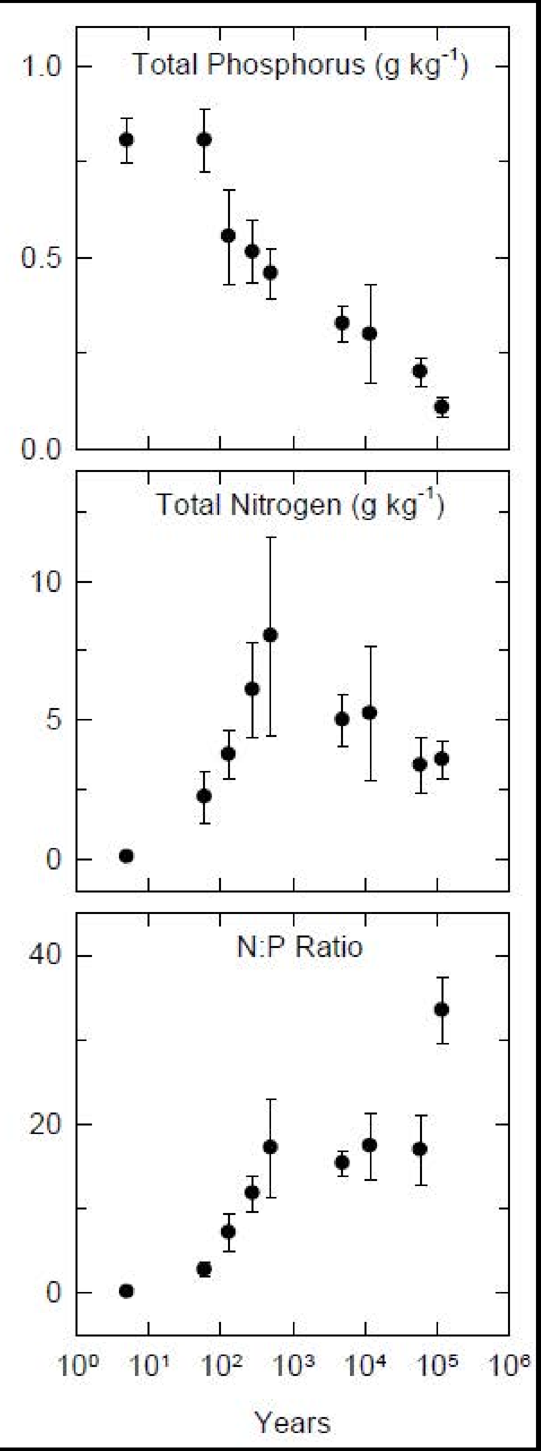


Rock —— *Pedogenesis* → >2,000,000 yrs

Basic Soils *Acidic Soils*

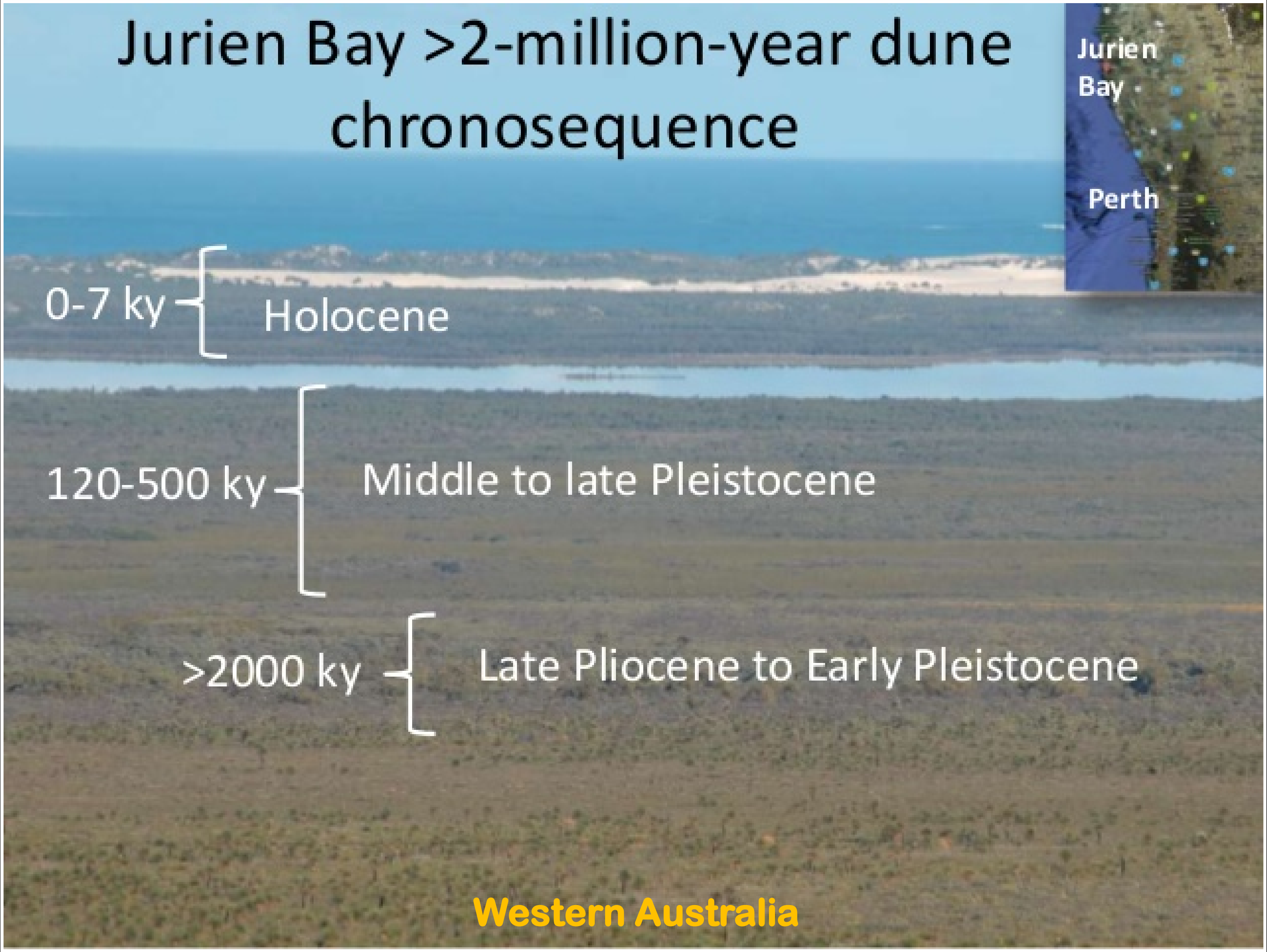
Walker and Syers (1976) Geoderma

Example: Franz Josef Gacier Soil Chronosequence



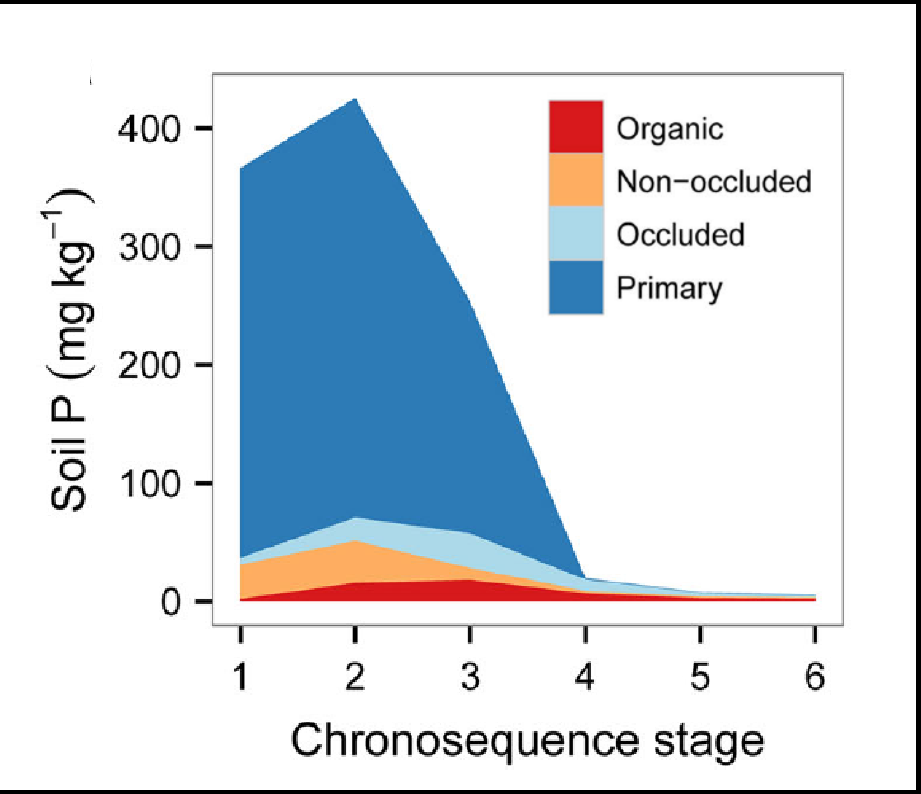
Richardson et al. (2004) Oecologia

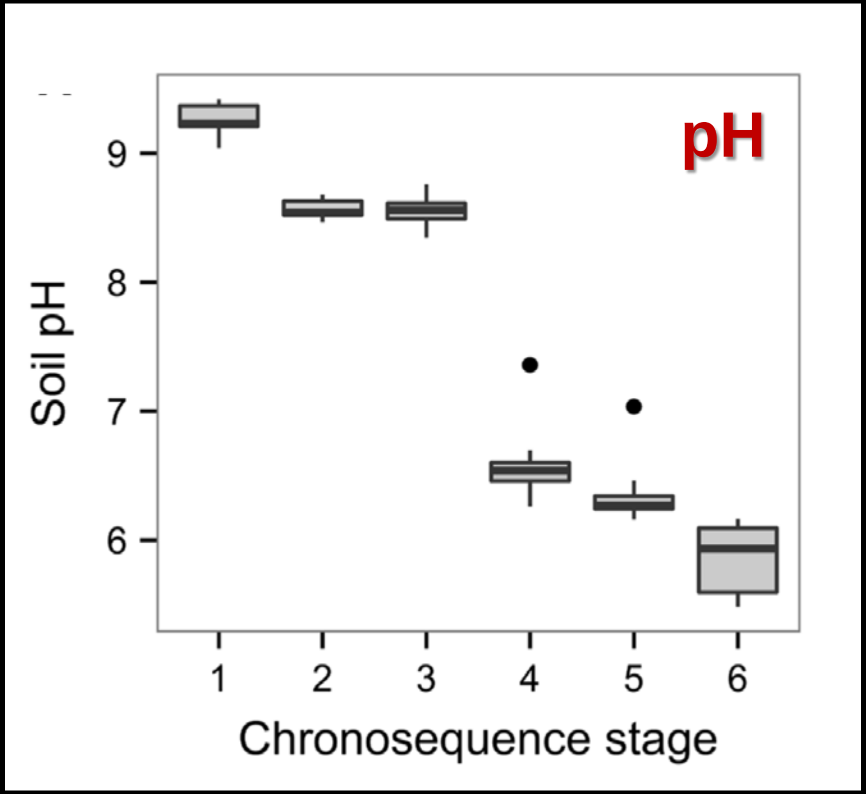
Example: The Jurien Bay Soil Chronosequence

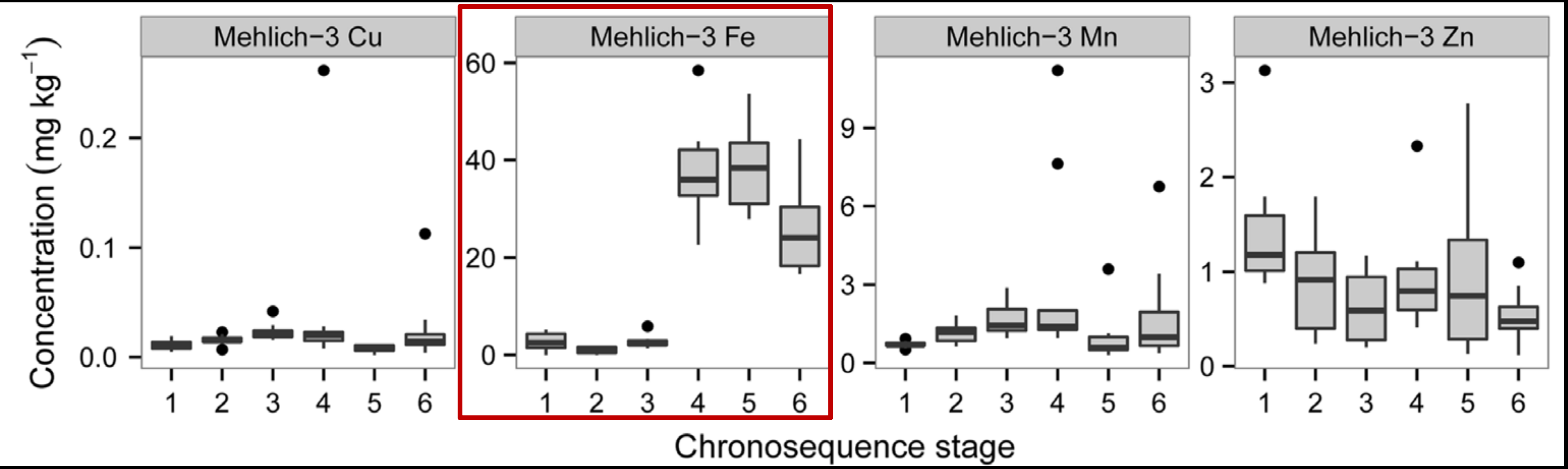


Turner and Laliberté (2015) Ecosystems

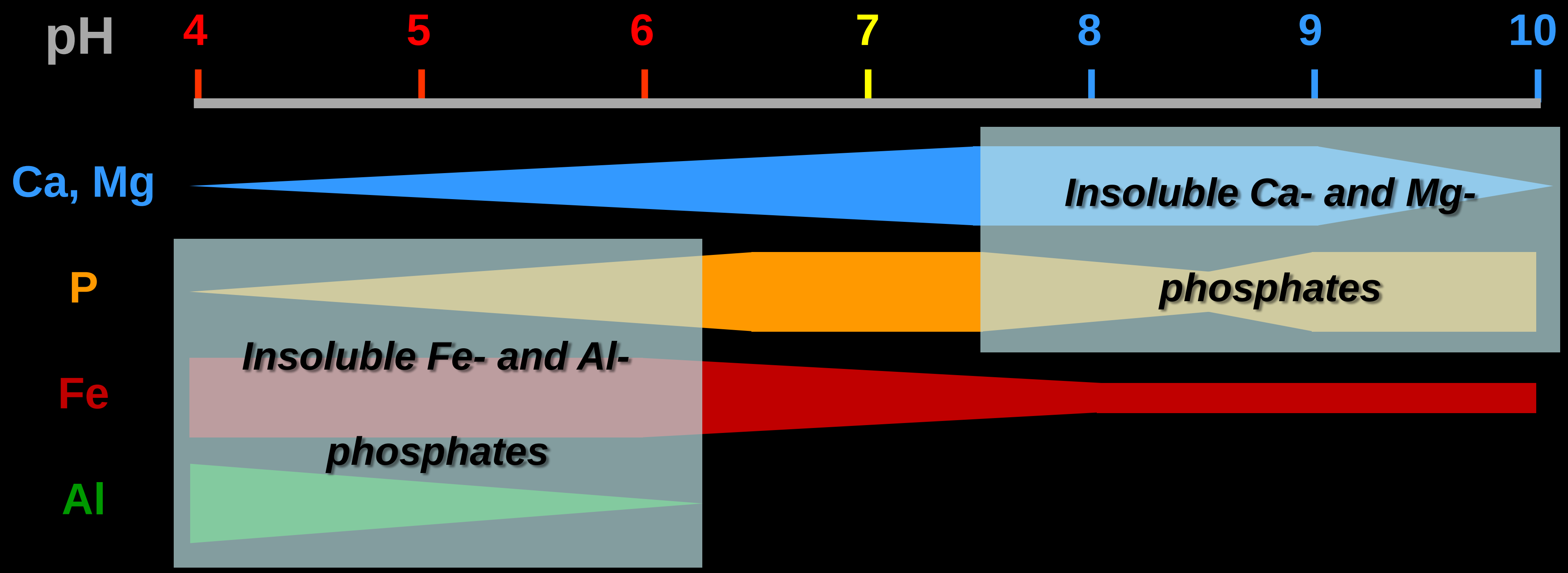
Example: The Jurien Bay Soil Chronosequence





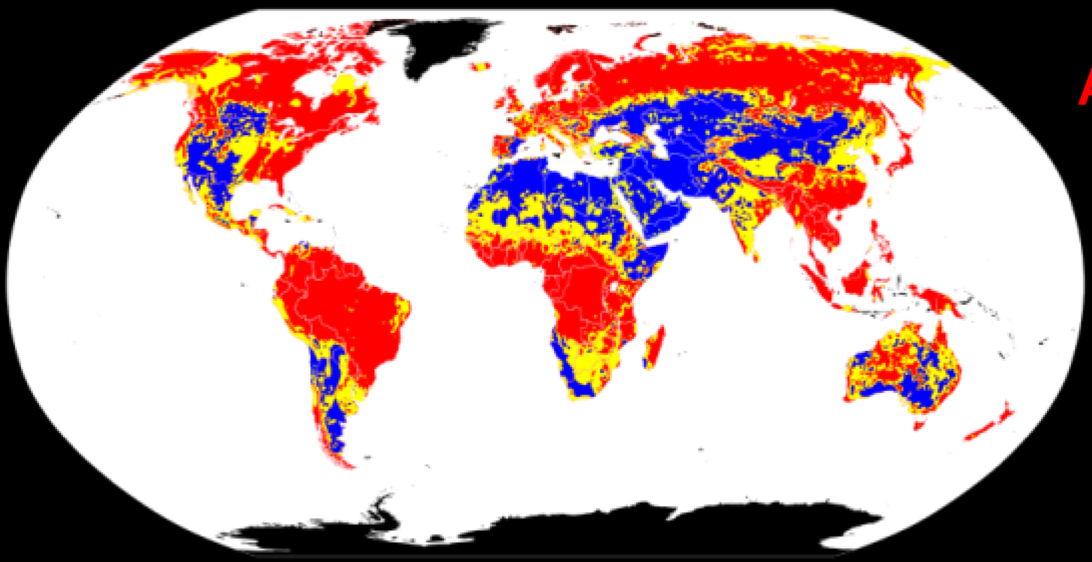


Limited P Bioavailability on a Global Scale



World Soils

(Source: FAO)

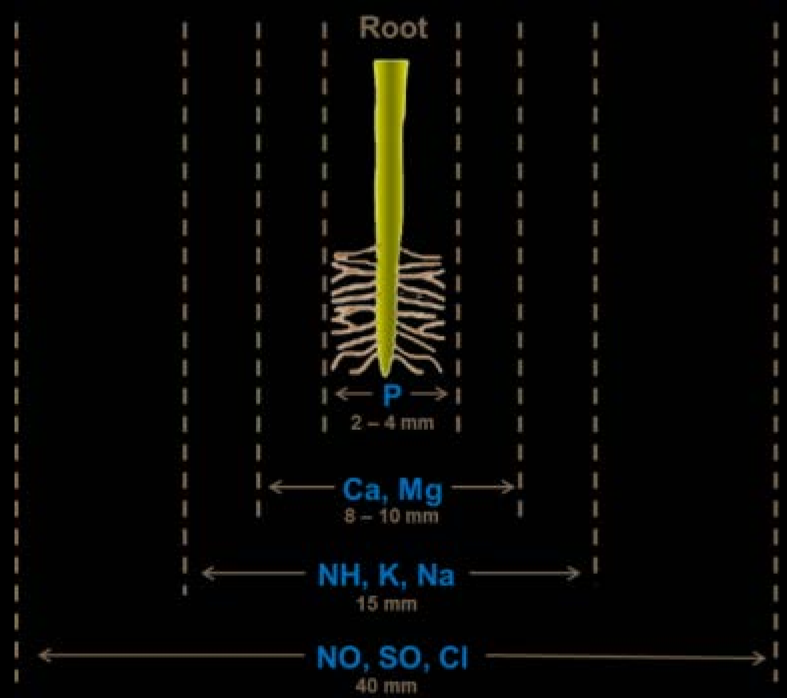


Acidic (low P)

Neutral

Basic (low P)

Different <u>Phosphate</u> (Pi) Acquisition Strategies



Pi-diffusion rate << Pi-uptake rate

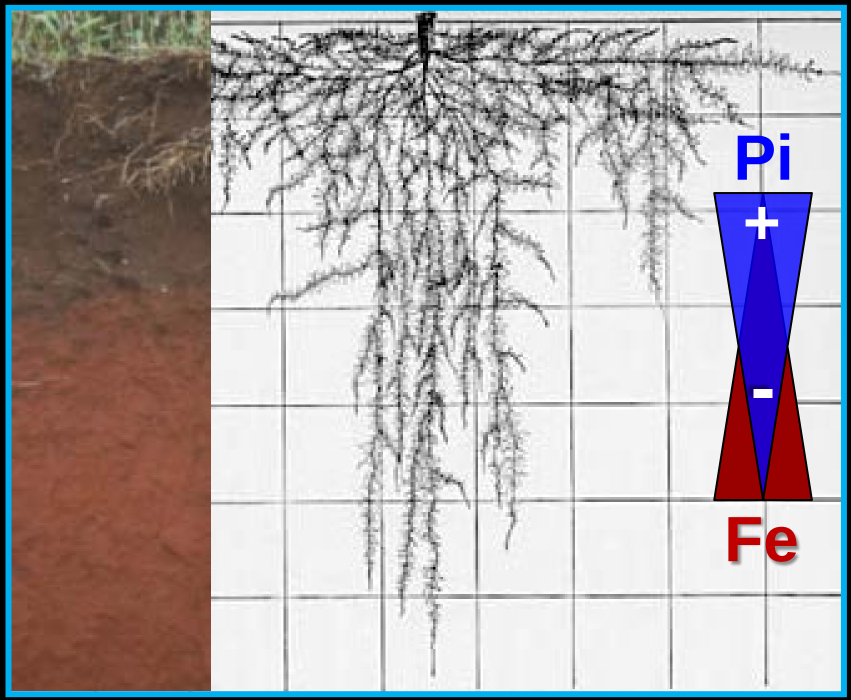
Competition with microorganisms

Root system expansion for
Pi interception

Different Phosphate (Pi) Acquisition Strategies

Brassicaceae-type

Proteaceae-type



Mycorrhiza

Cluster Roots

Topsoil Foraging

P Scavenging

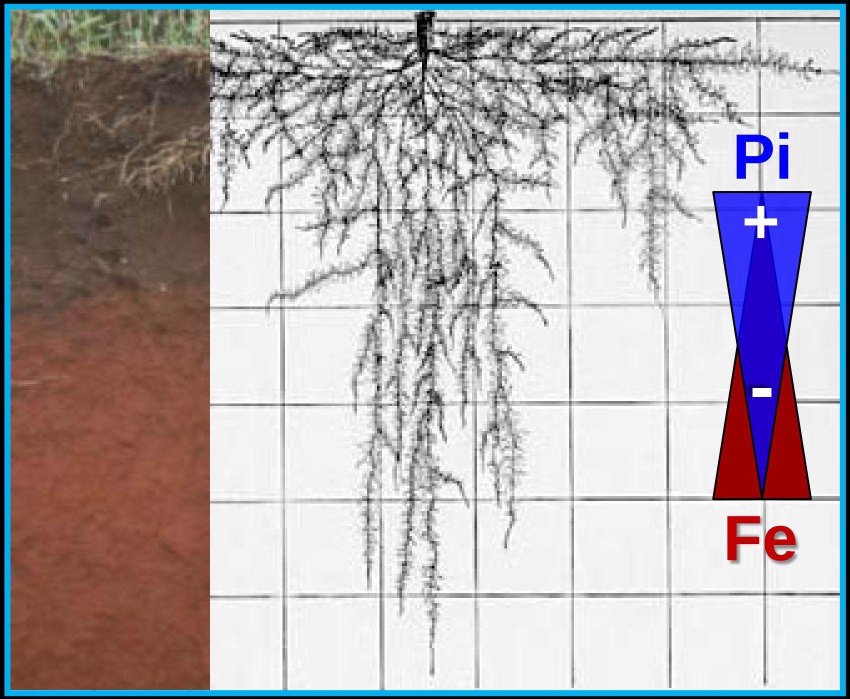
P Mining

7-20% *Carbon Cost* 25-50%

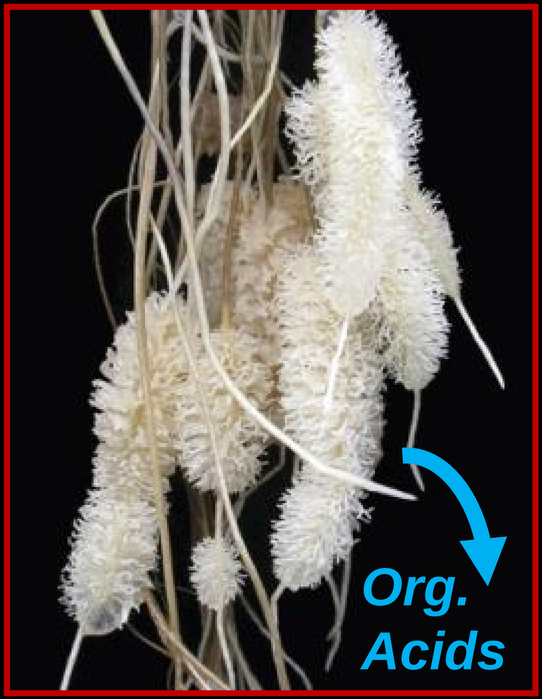
Different Phosphate (Pi) Acquisition Strategies

Brassicaceae-type

Proteaceae-type



Mycorrhiza



Cluster Roots

Topsoil Foraging

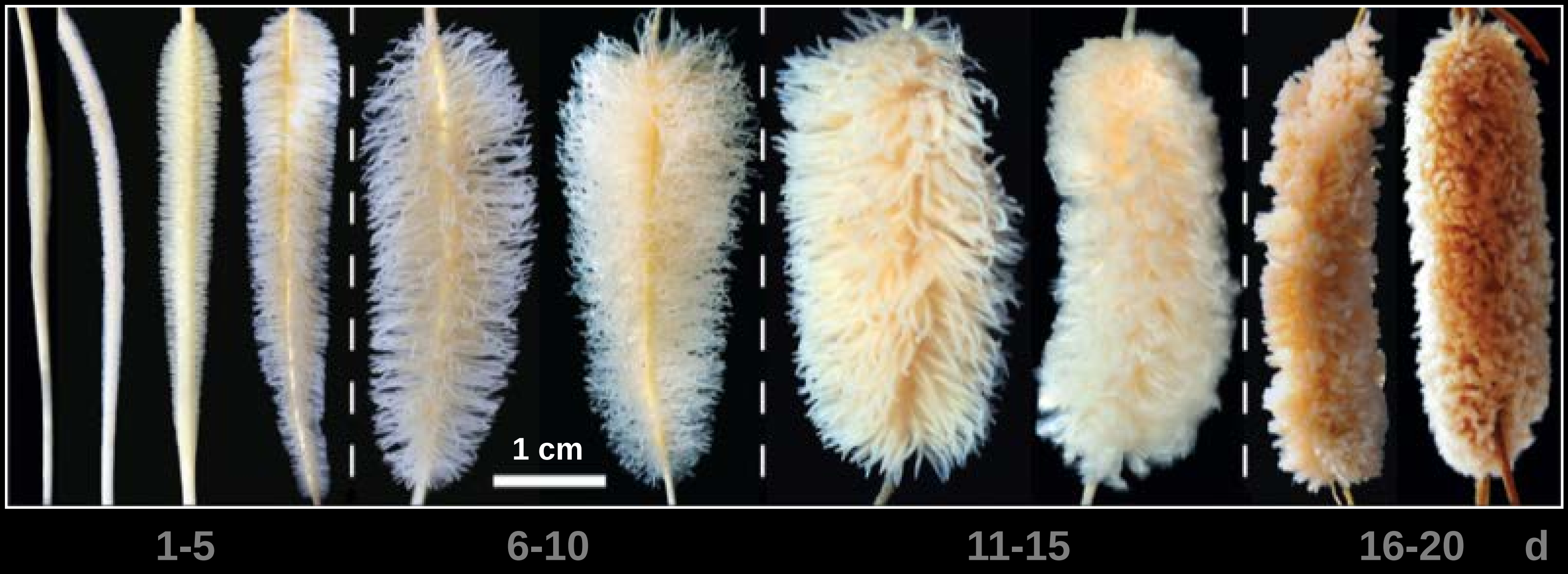
P Scavenging

P Mining

Responses to Pi Deficiency (Most Soils)

Adaptation to Pi Impoverished Soils

Adaptation of Proteaceae-type Species



Cluster Roots (*exudative burst*)

- Organic acids (anion exchange)
- Phospho-hydrolases
- Phenolics (antimicrobial)
- Cell wall-degrading enzymes

Shoot Pi Economy

- High P remobilization (senescence)
- Remodeling of membrane lipids
- Altered rRNA profiles
- Delayed greening
- Preferential P allocation to mesophyll
- High seed P content

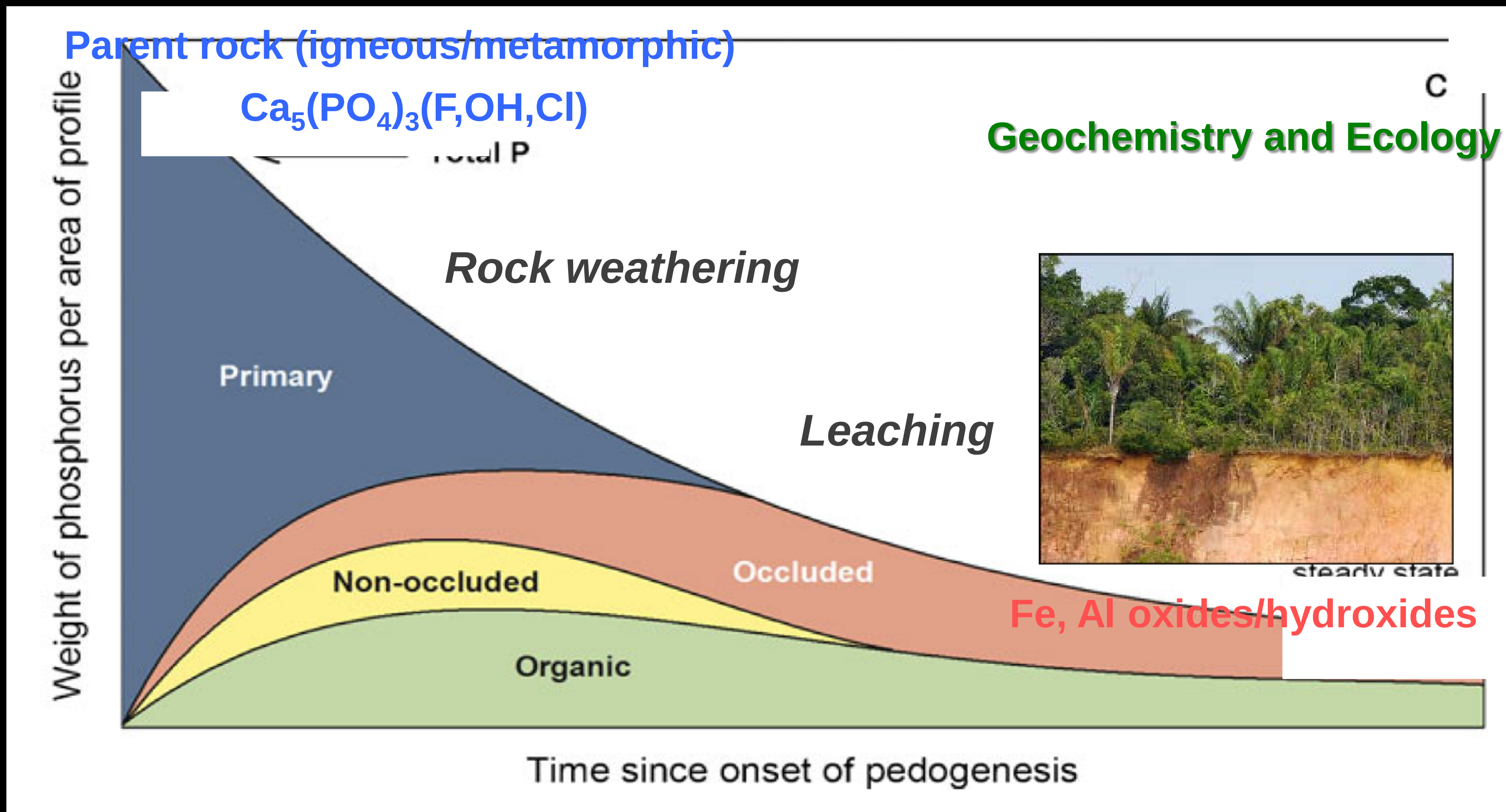
Lambers et al. (2015) Nat Plants

Different <u>Phosphate</u> (Pi) Acquisition Strategies

>1,000

ppm

<<100



non-mycorrhizal

P Mining

Proteaceae-type

Very small (5–150 nm) and poorly ordered crystals

Very large specific surface area (50-300 $m^2 g^{-1}$)

Fe oxides: <0.1% to >50% of total soil mass

Strong Pigments

Extremely low solubility

K_{sp}~10^{-40}

Fe(III) oxides

Iron oxyhydroxide (α-FeOOH)

Goethite

Rock weathering (O_2 exposure)

Fe(II) **Silicates, Sulfides** *Hypoxic Conditions*

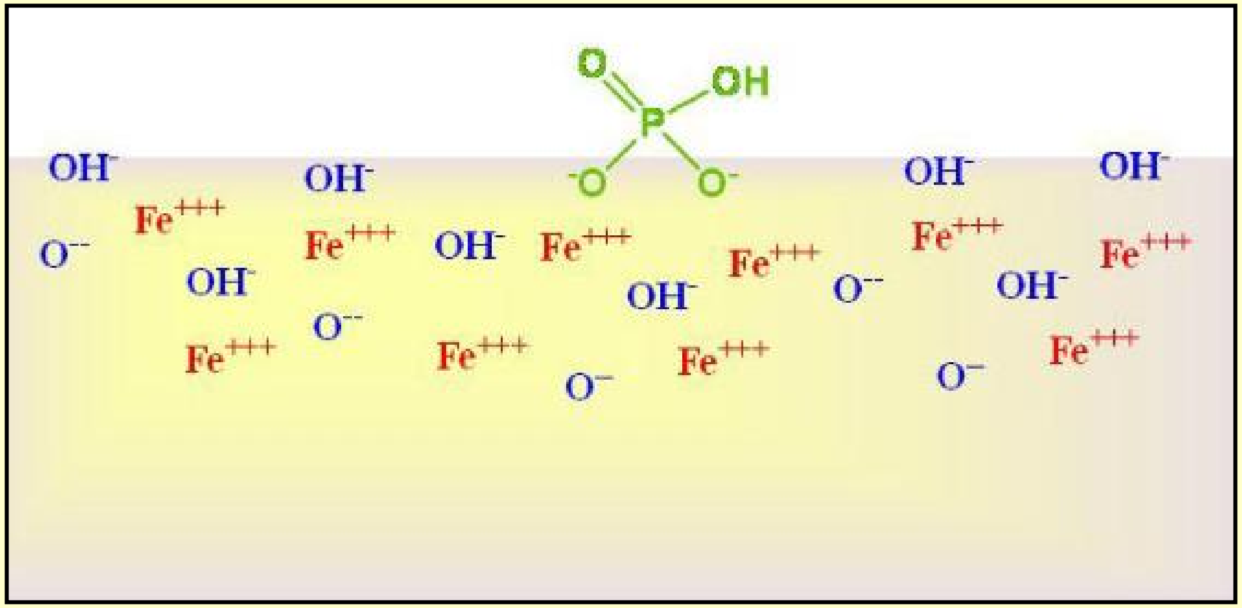
Fe(III) oxides

Adsorption of HPO_4^{2-} to Fe oxides

(Up to 2.5 μmol P m^{-2} or 0.75 mmol P g^{-1})

Competitive desorption by „natural organic matter“ (citric, malic, humic, fulvic acids), pH dependent

Ca^{2+} promotes HPO_4^{2-} adsorption



Only 30-60% of adsorbed HPO_4^{2-} is exchangeable, low mobility

Lambers et al. (2015) TIPS

Fe(III) oxides

Adsorption of HPO_4^{2-} to Fe oxides

(Up to 2.5 µmol P m^{-2} or 0.75 mmol P g^{-1})

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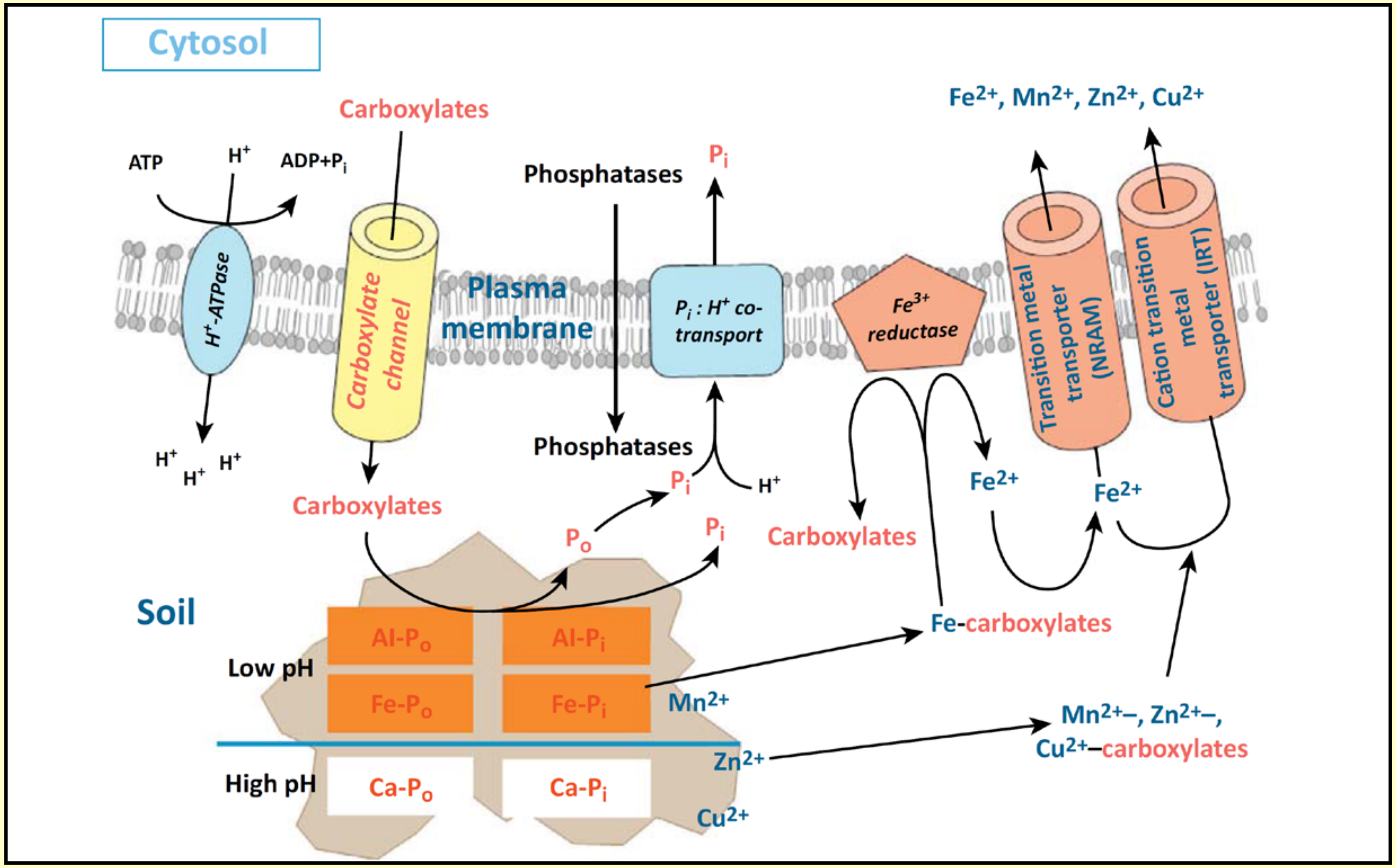

Lambers et al. (2015) TIPS

Different <u>Phosphate</u> (Pi) Acquisition Strategies

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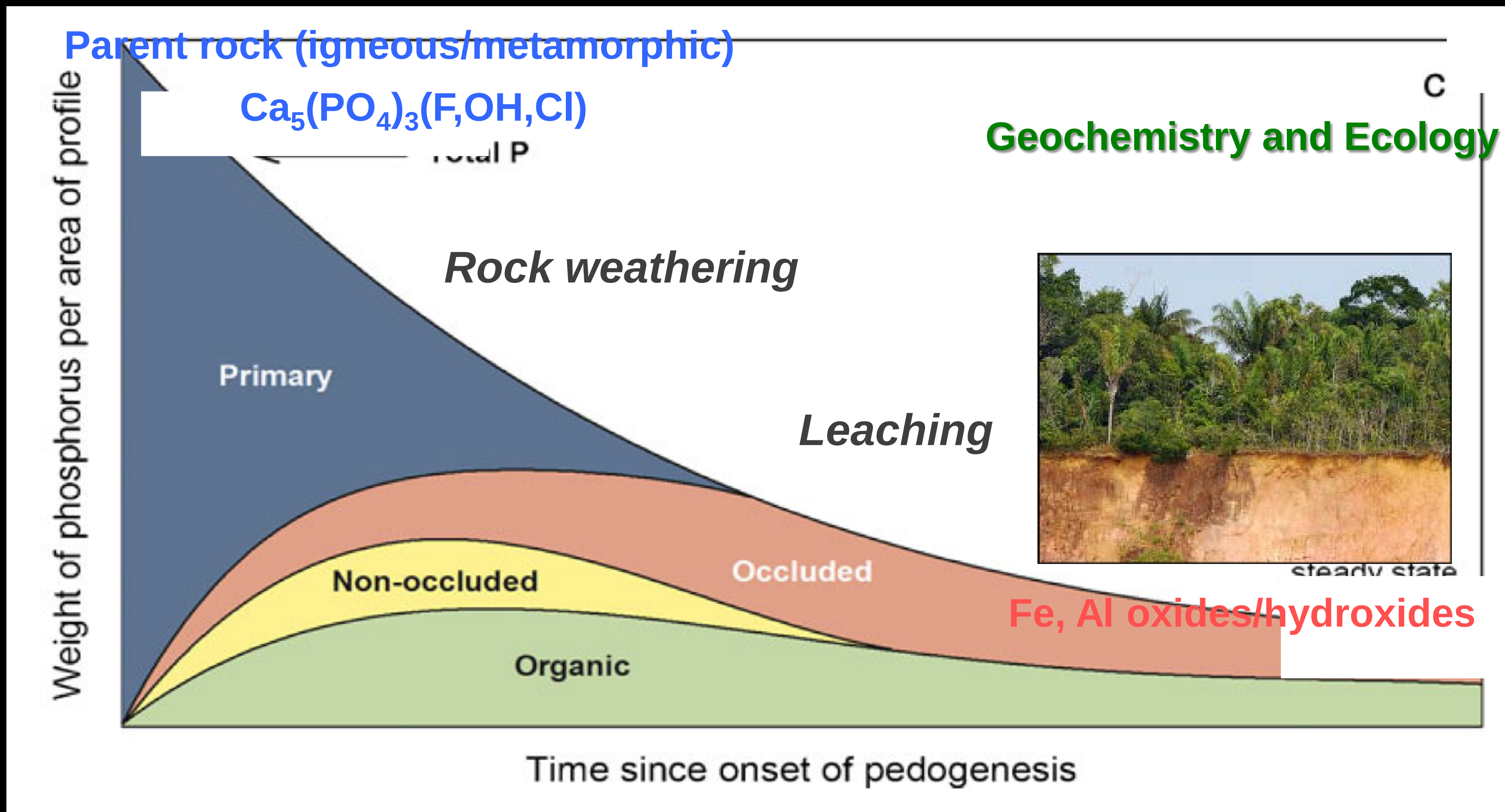
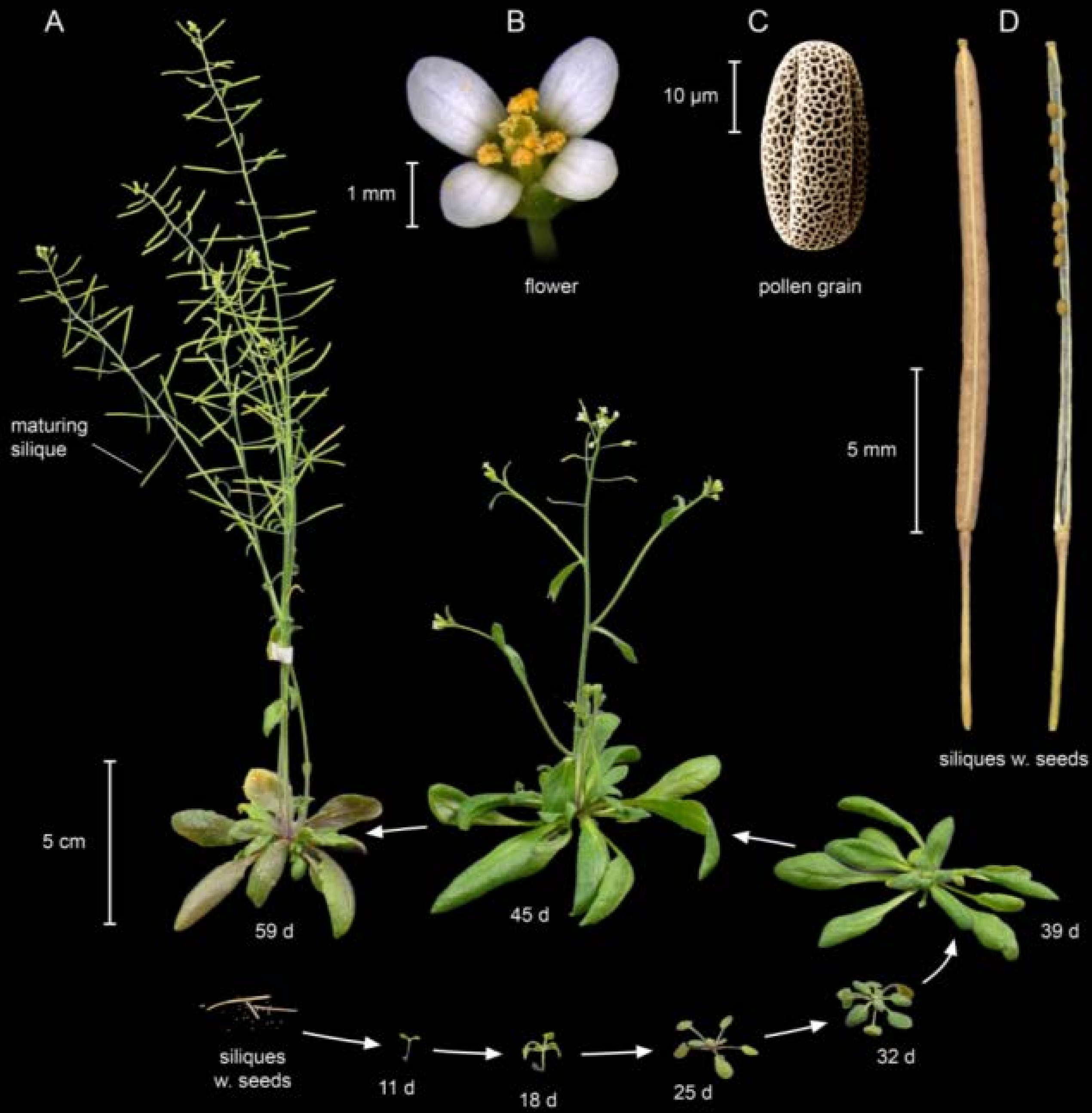


non-mycorrhizal 2 µM Pi *mycorrhizal* 0.5 µM Pi *non-mycorrhizal*

P Scavenging *P Mining*

Brassicaceae-type **Proteaceae-type**

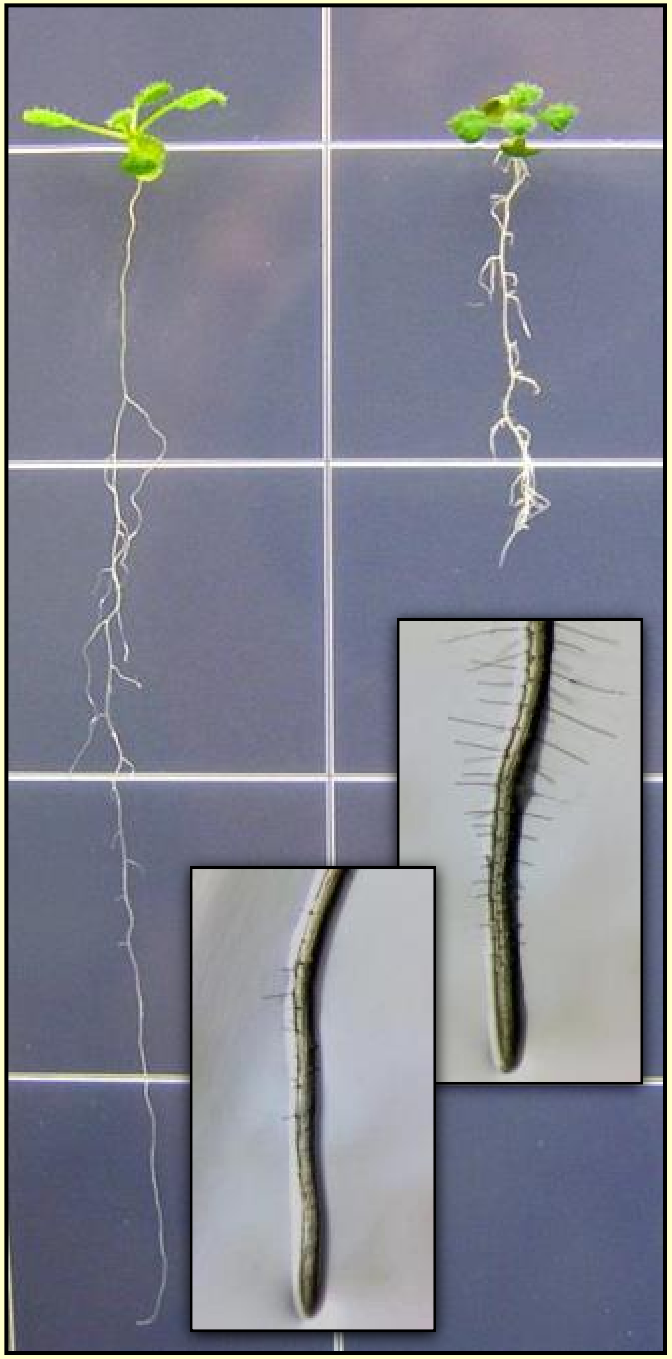
Arabidopsis thaliana (Ackerschmalwand)

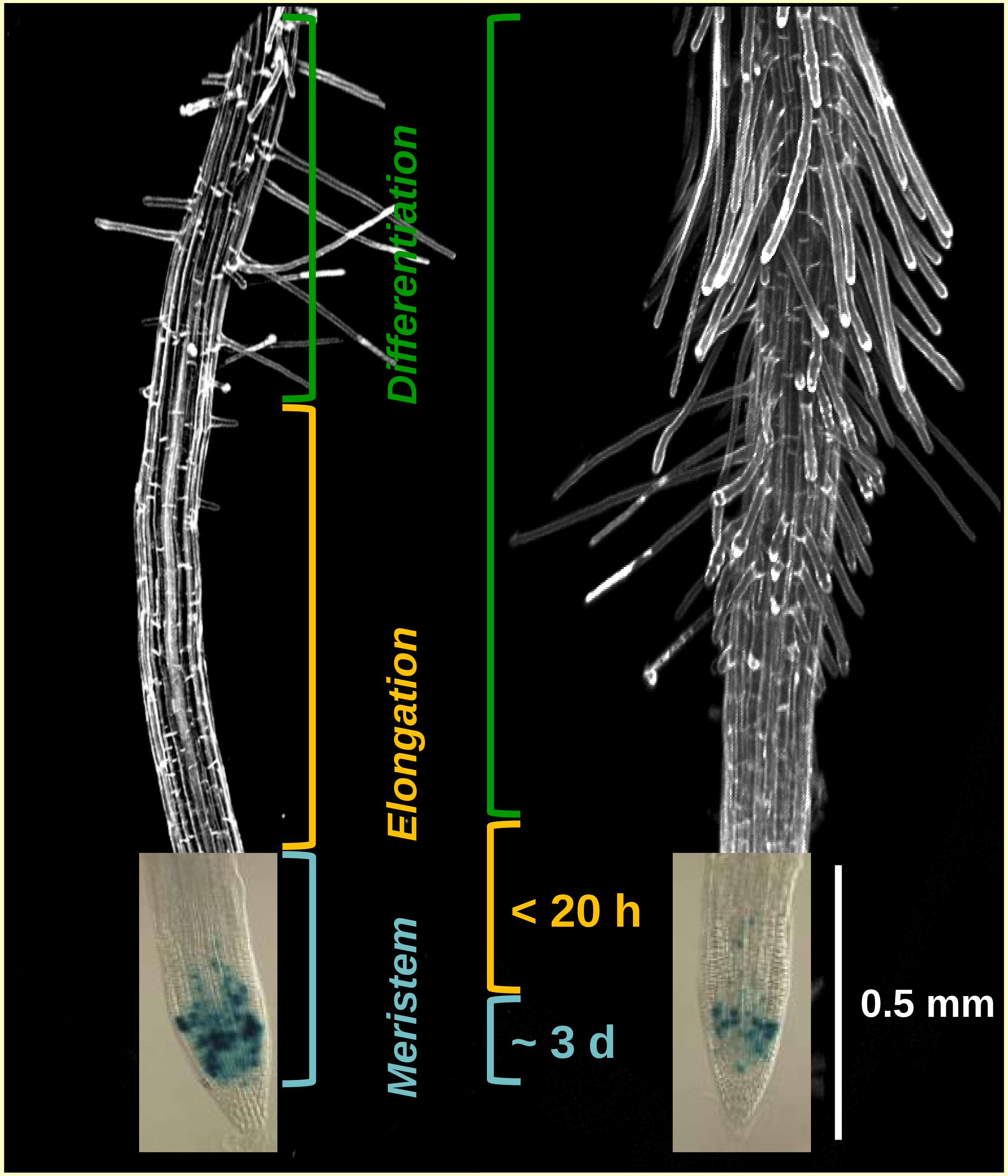


+Pi –Pi

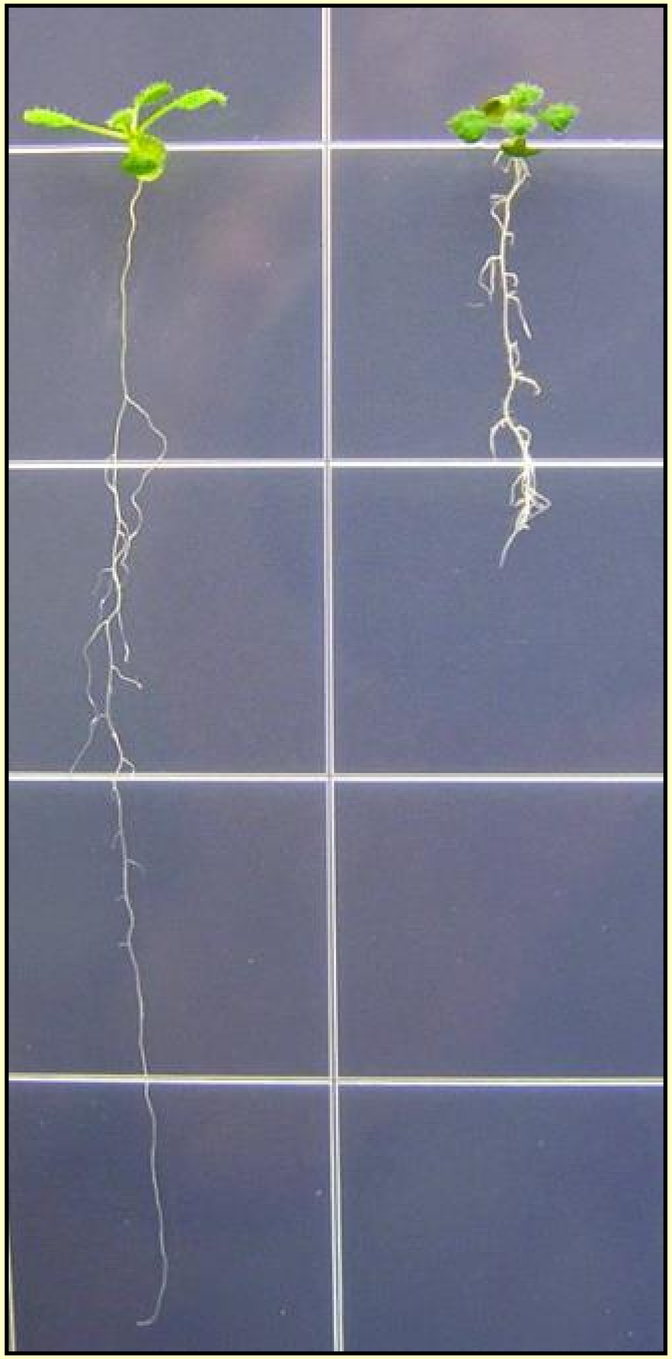
Arabidopsis thaliana (Ackerschmalwand)

Adaptation of *A. thaliana* (Brassicaceae-type)

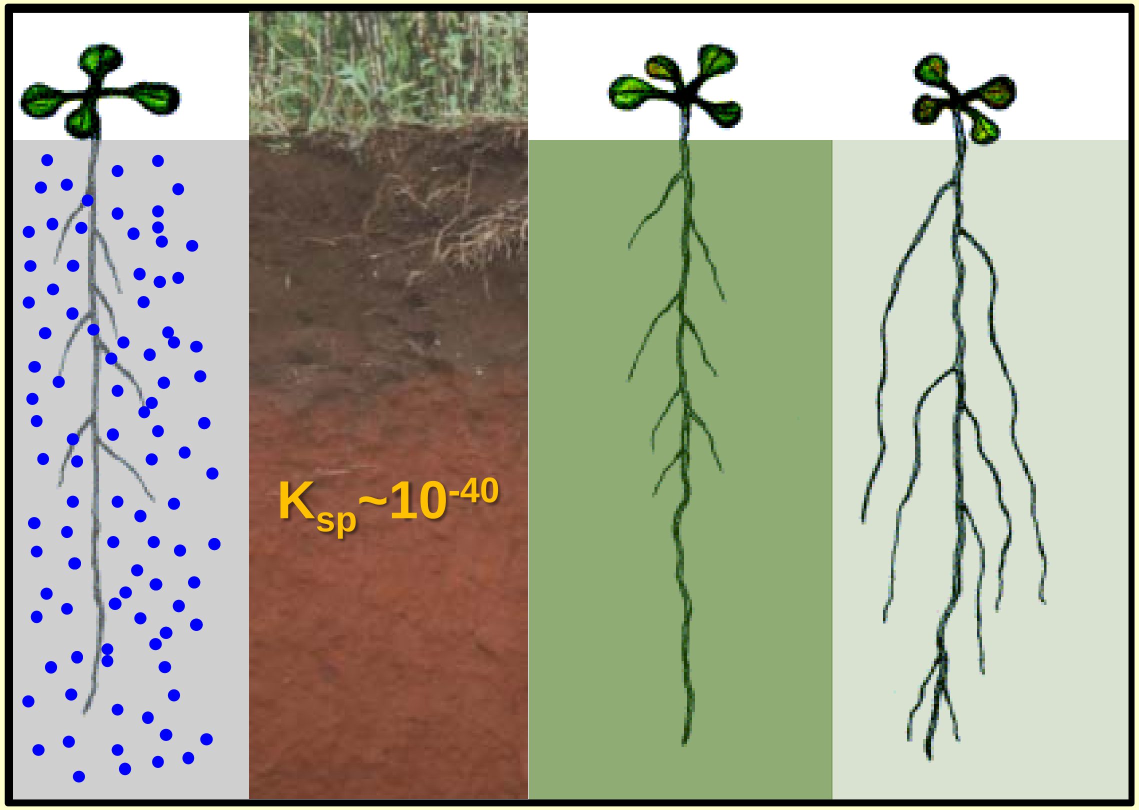




Topsoil Foraging (Brassicaceae-type Species)



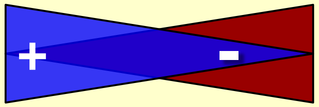
High Pi Low Pi



High Pi Low Pi High N Low N

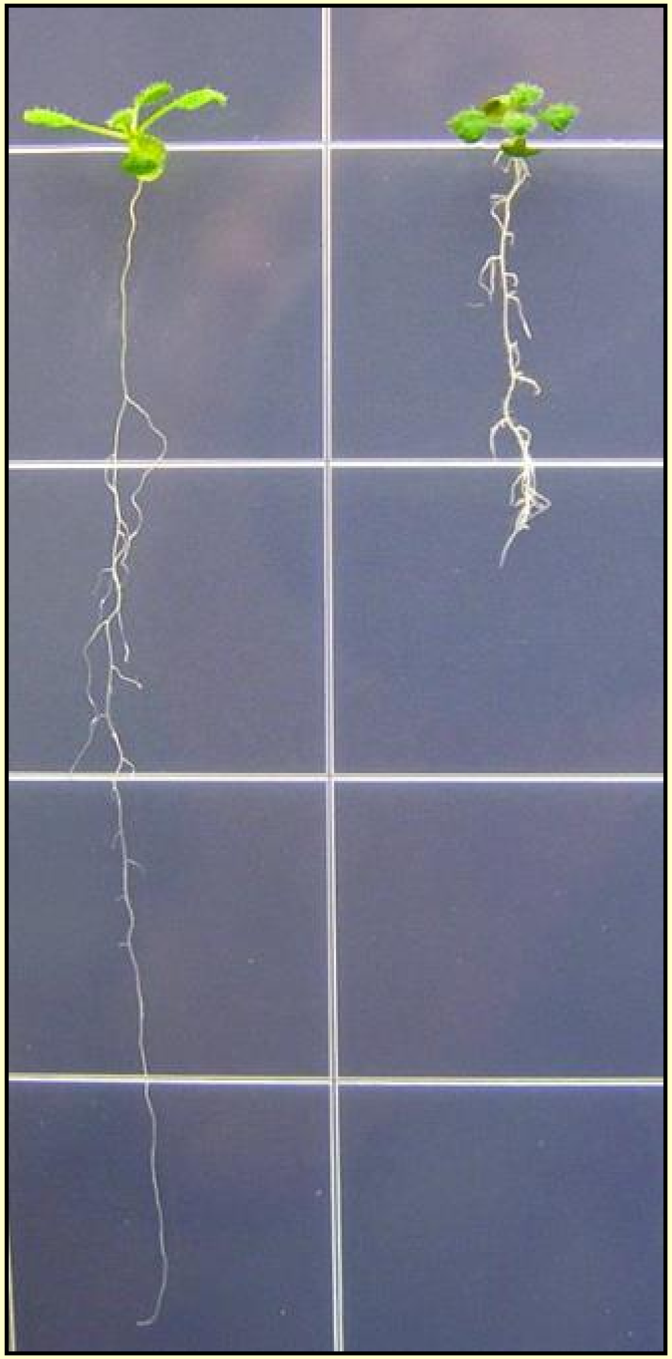
Insoluble ***Soluble***

Pi

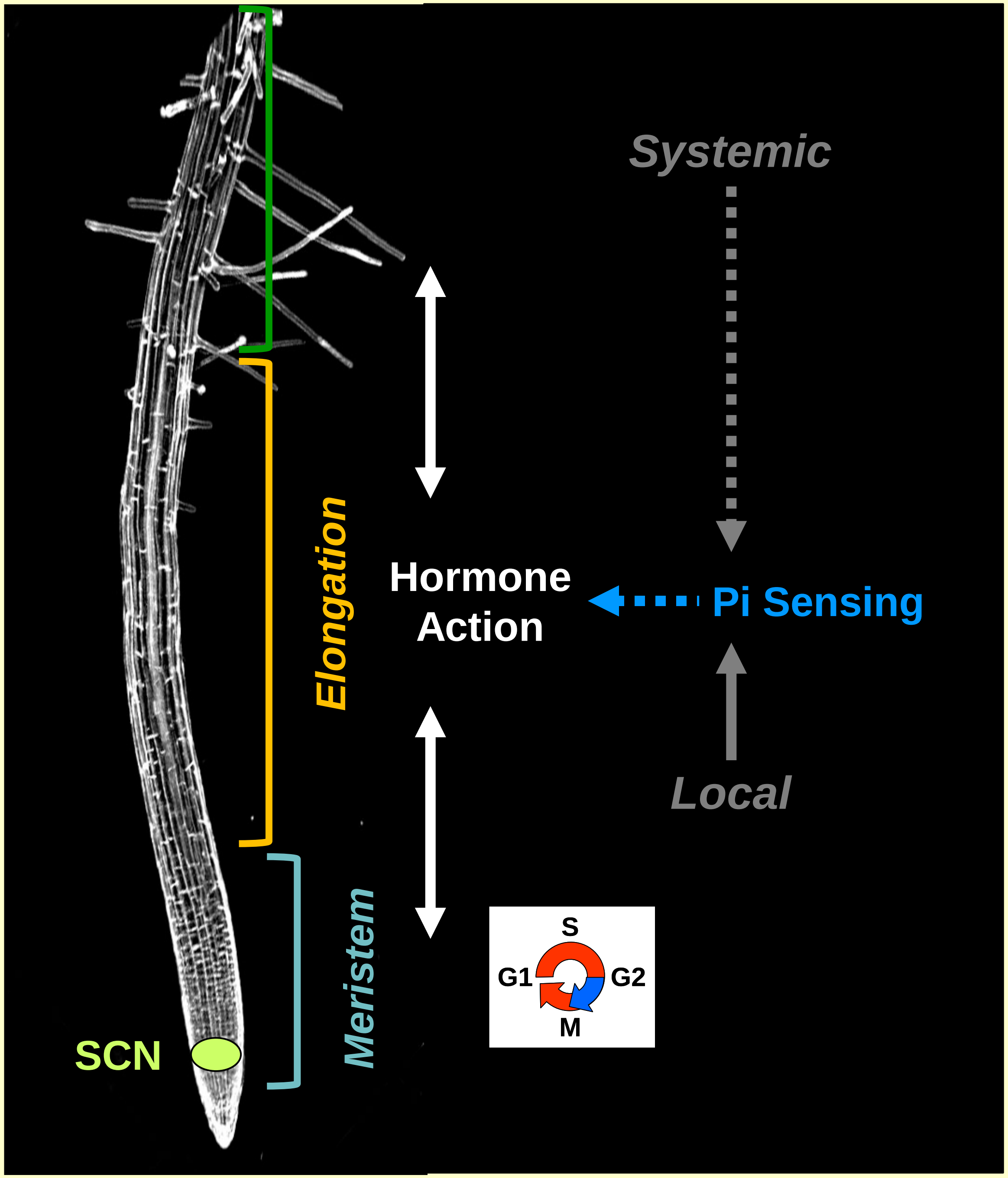


Fe

How is Pi sensed in root development ?

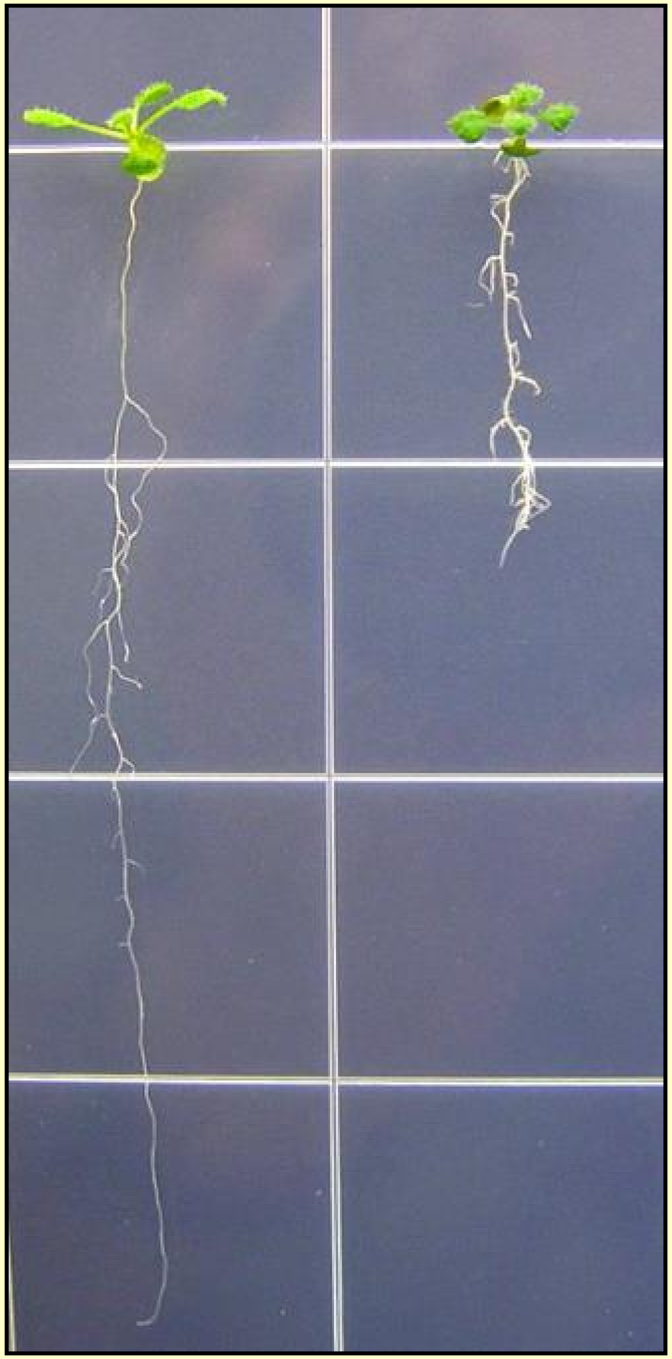


High Pi Low Pi

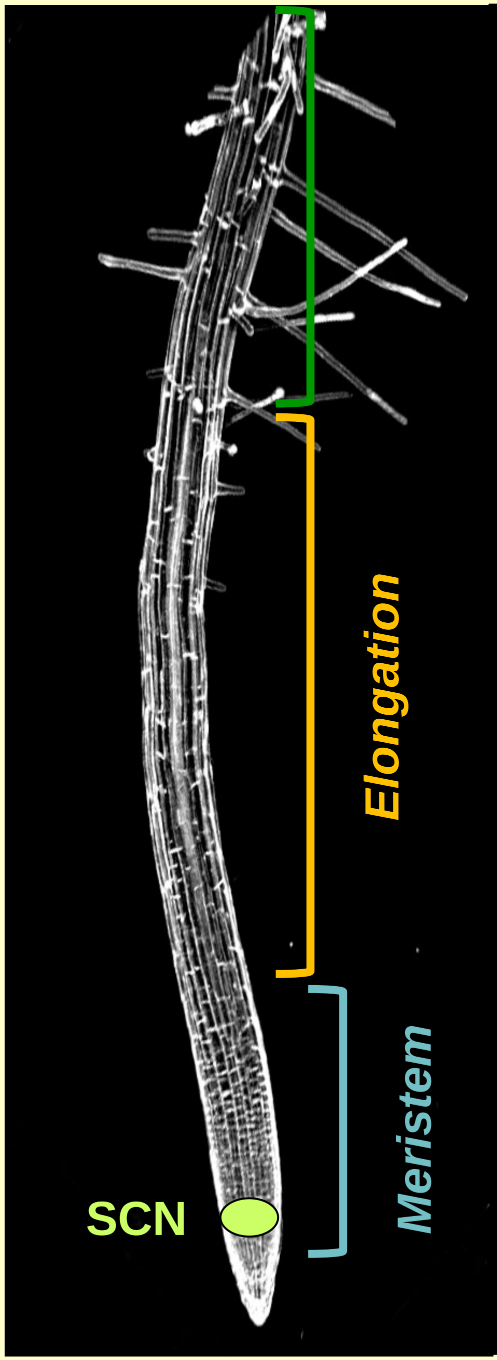


High ➔ Low

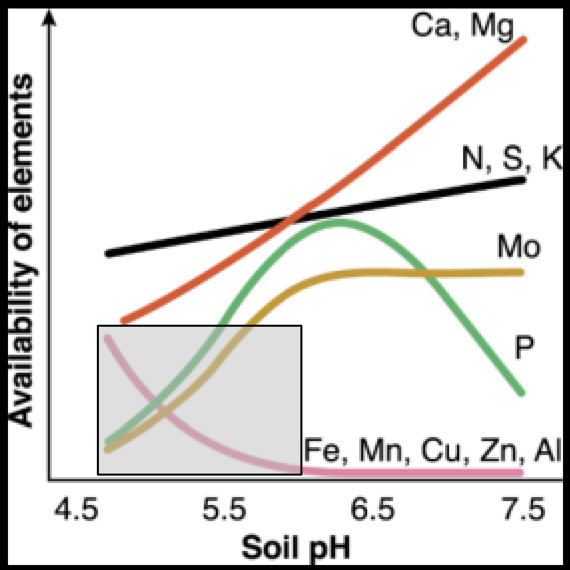
How is Pi sensed in root development ?

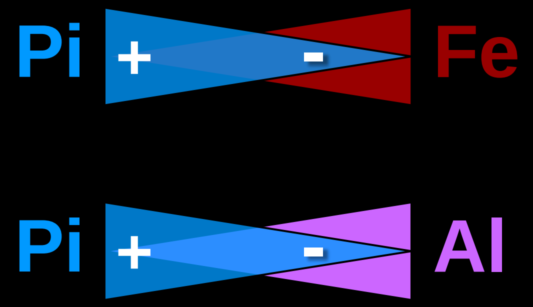


High Pi Low Pi



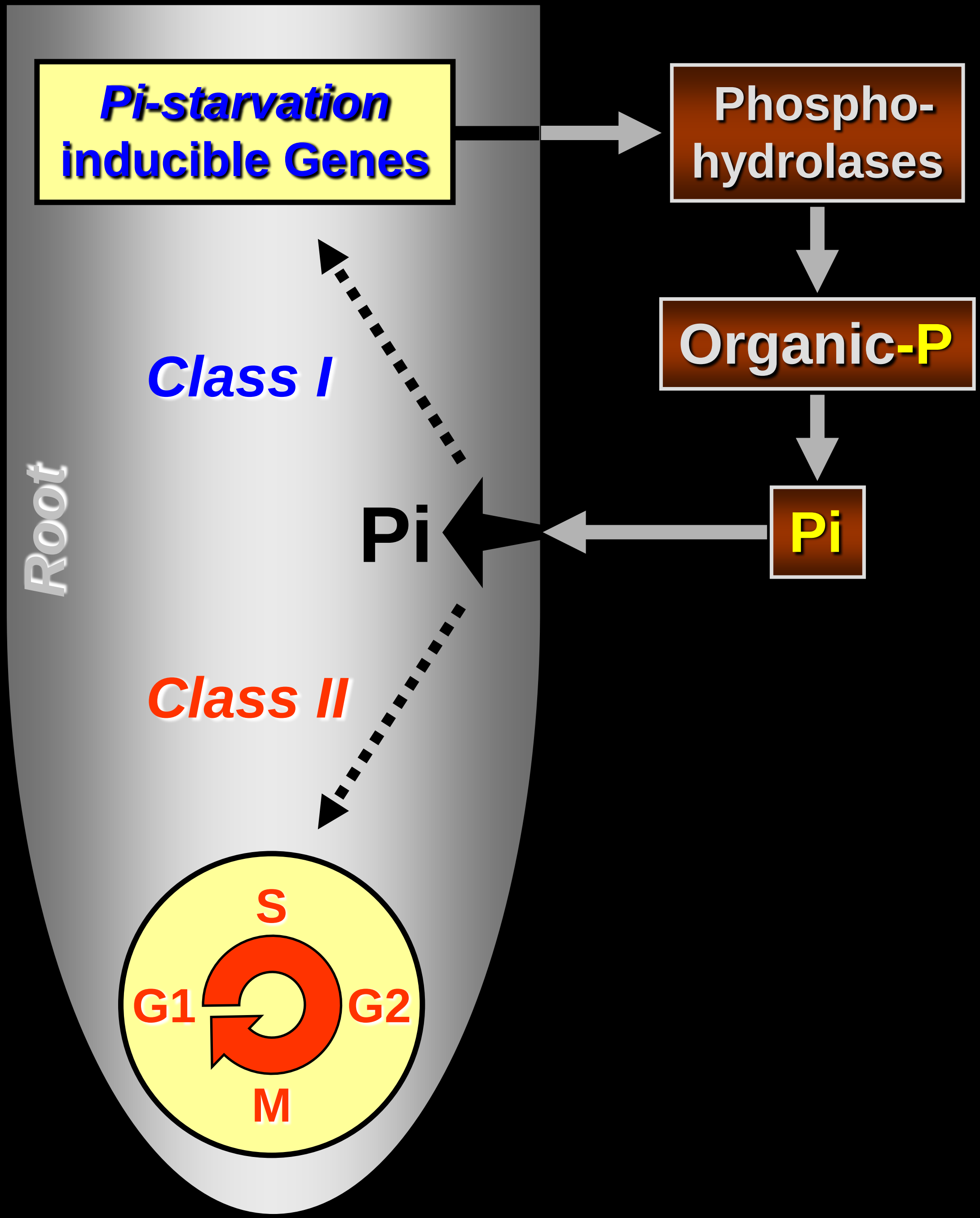
High ➔ Low

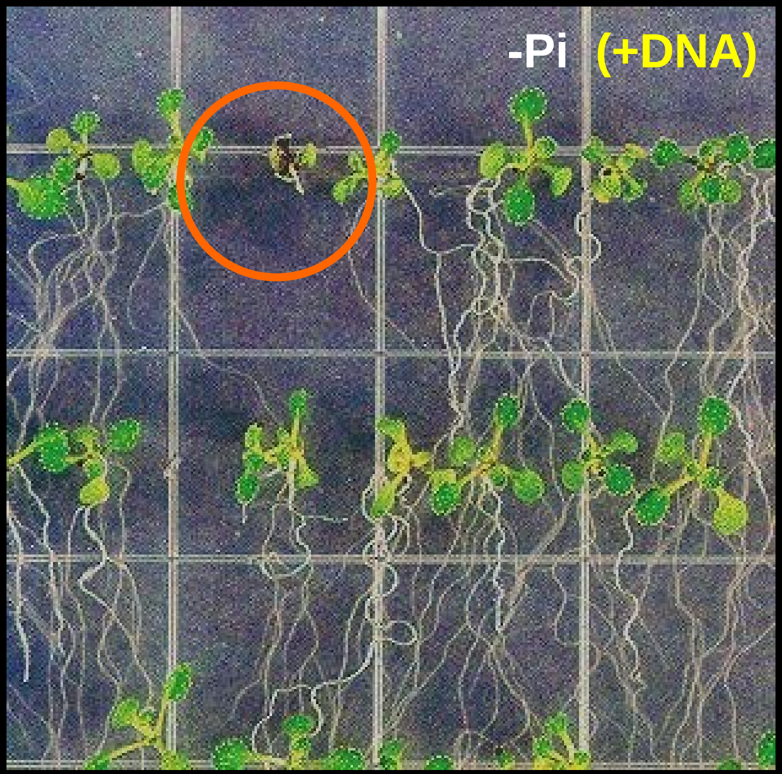


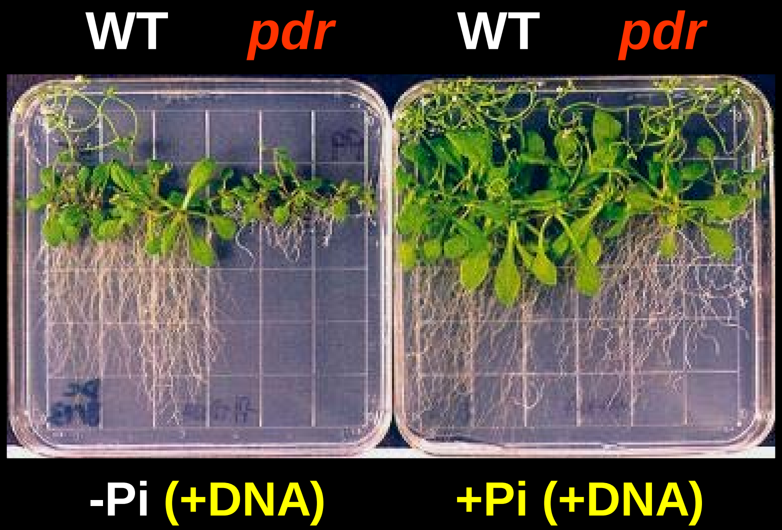


Role of Exudation
(organic acids
coumarines)

Screen for *Pi deficiency response* Mutants



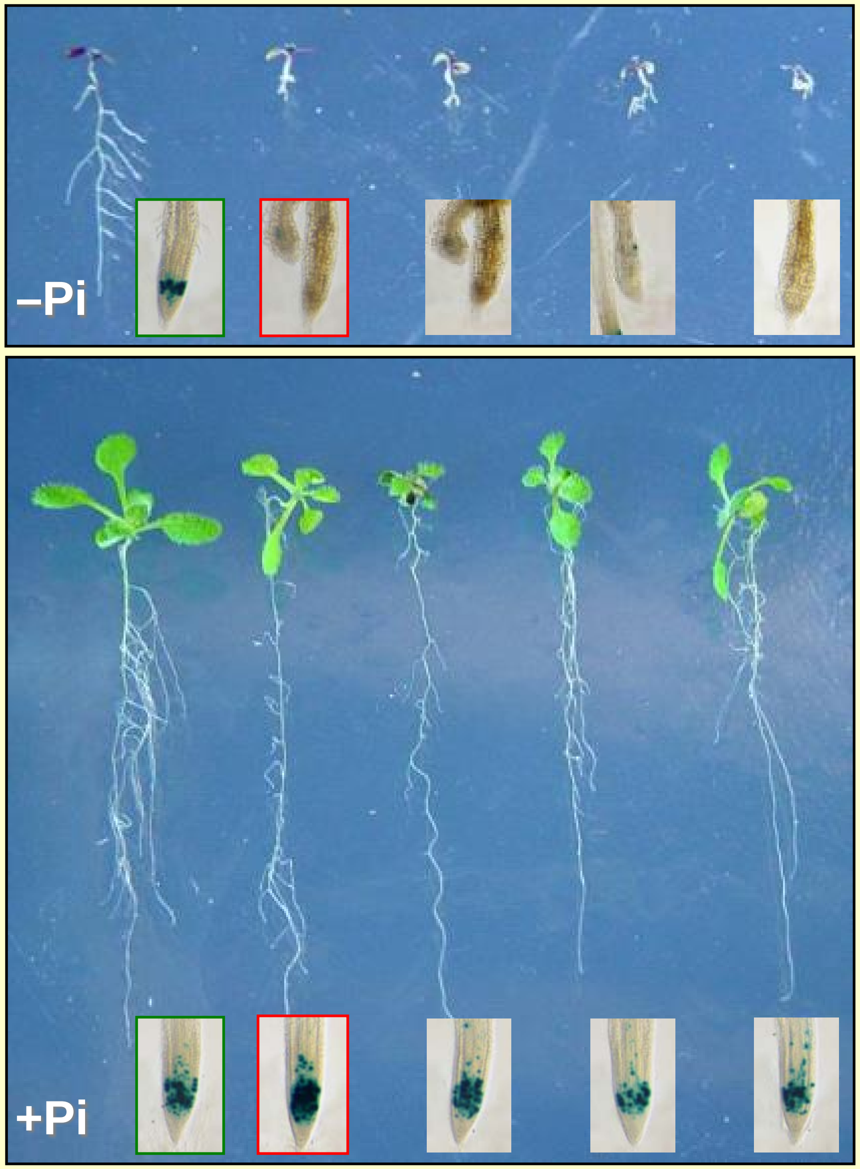




Forward Genetics

Pi-deficiency response (pdr) Mutants

Col ***pdr2*** ***pdr3*** ***pdr4*** ***pdr5***

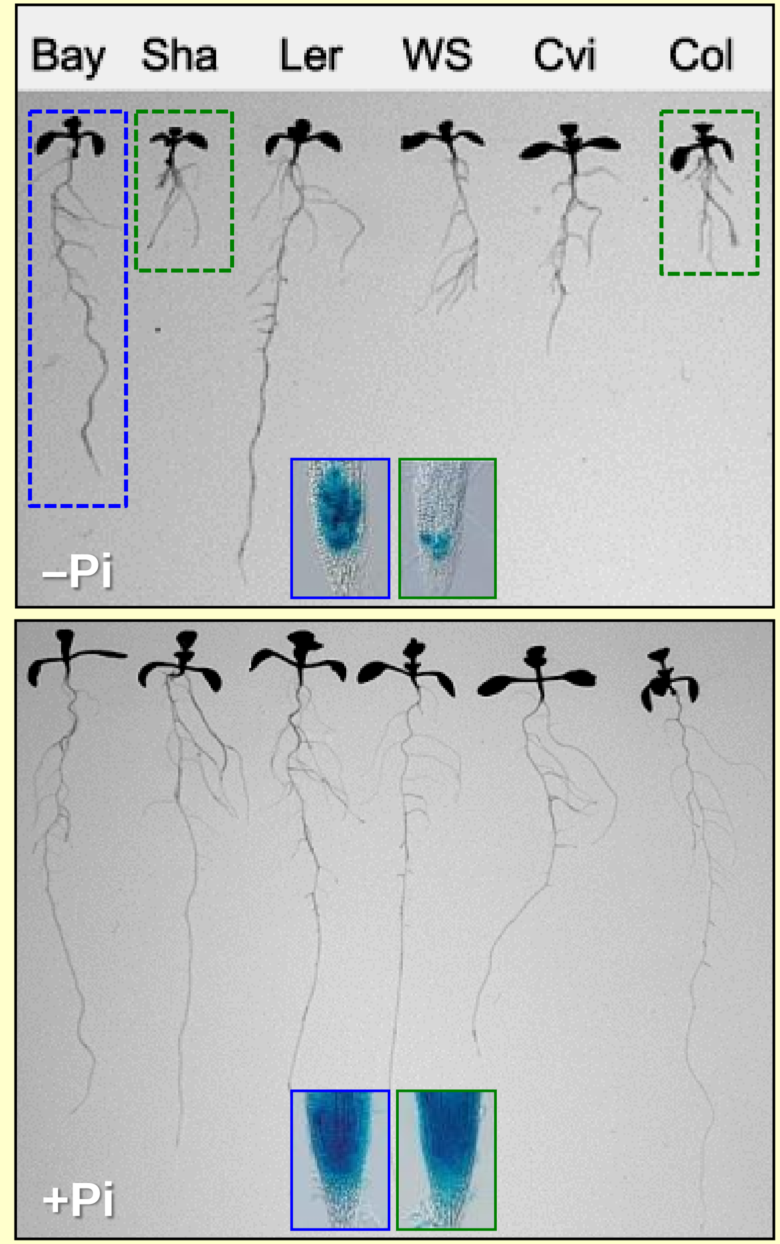


pCYCB1::GUS

Ticconi et al. (2004) Plant J

Natural Variation (QTL)

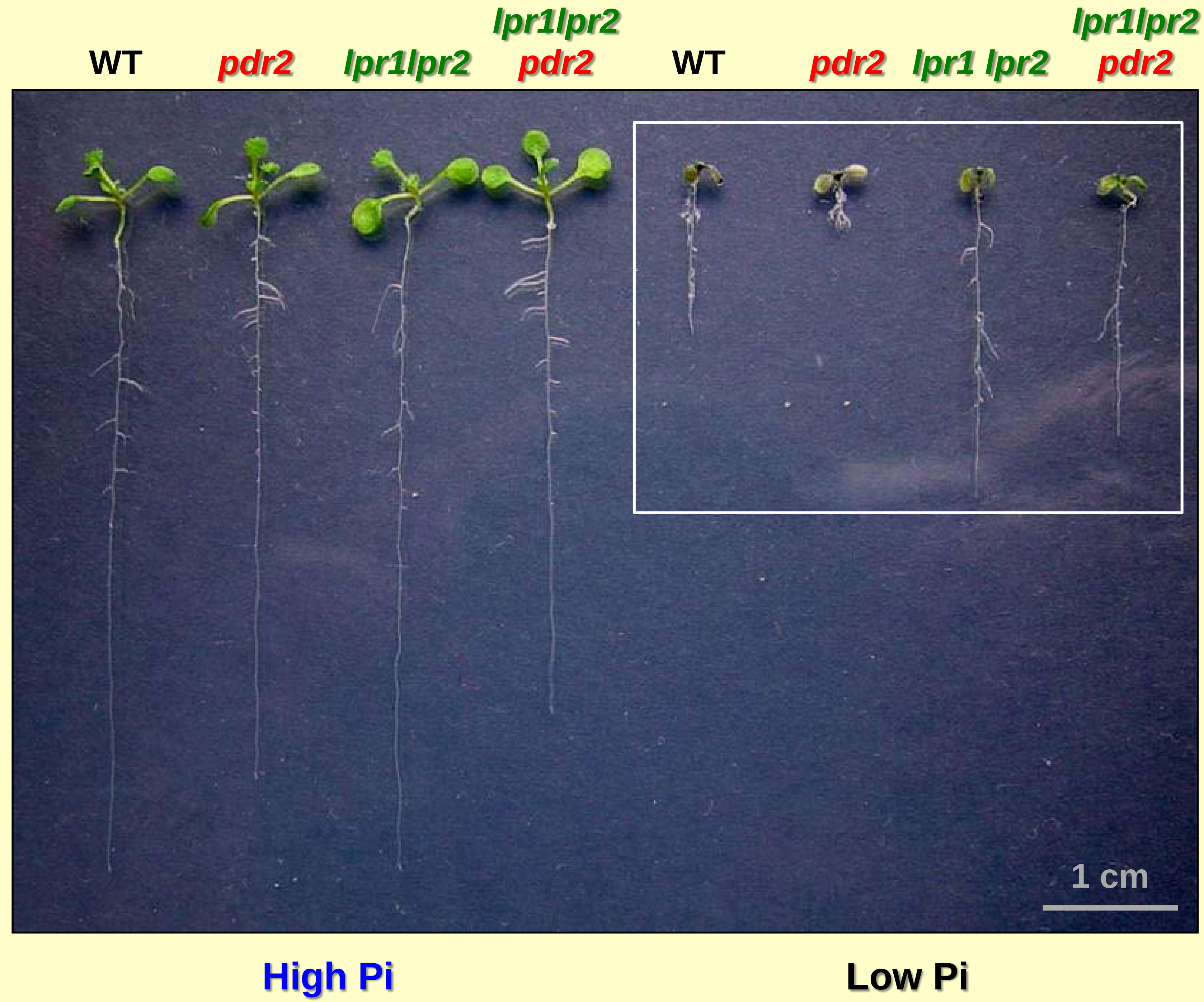
LOW Pi ROOT (LPR1/LPR2)



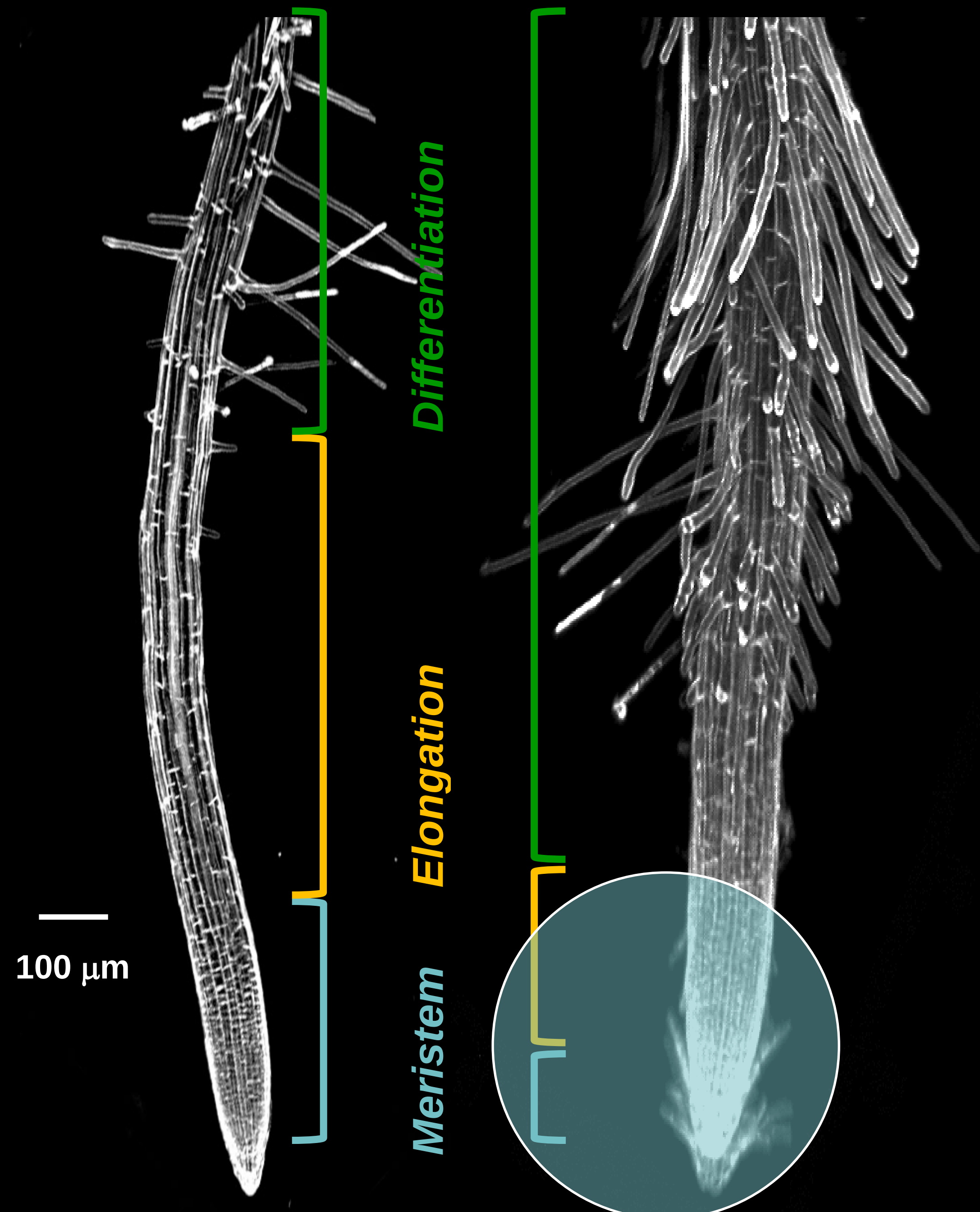
pCYCB1::GUS

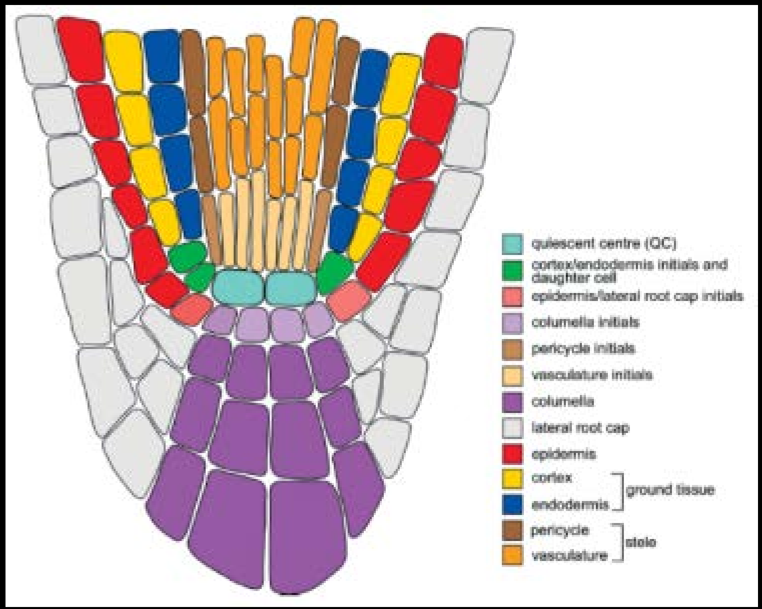
Svistoonoff et al. (2007) Nat Genetics

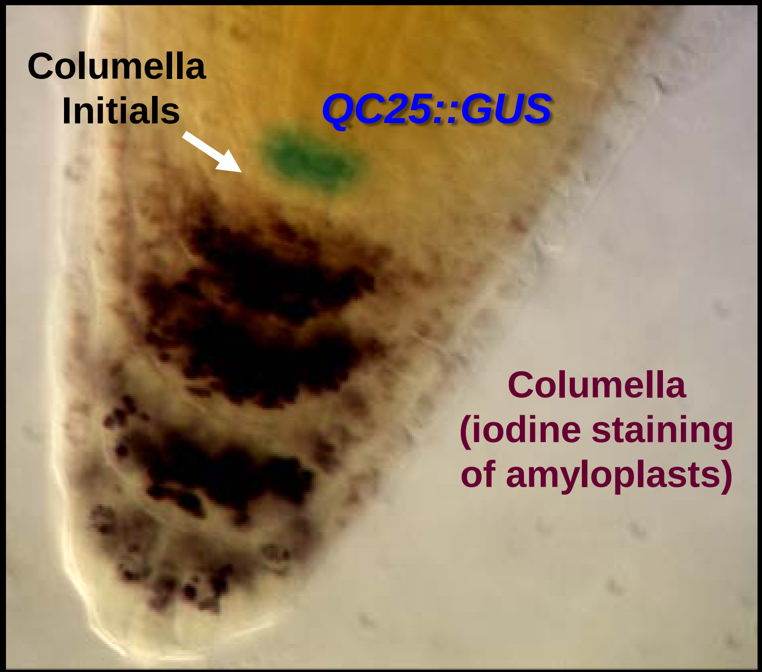
LPR1-PDR2: A Bridgehead in Pi Sensing



Pi-dependent Inhibition of Root Meristem Activity

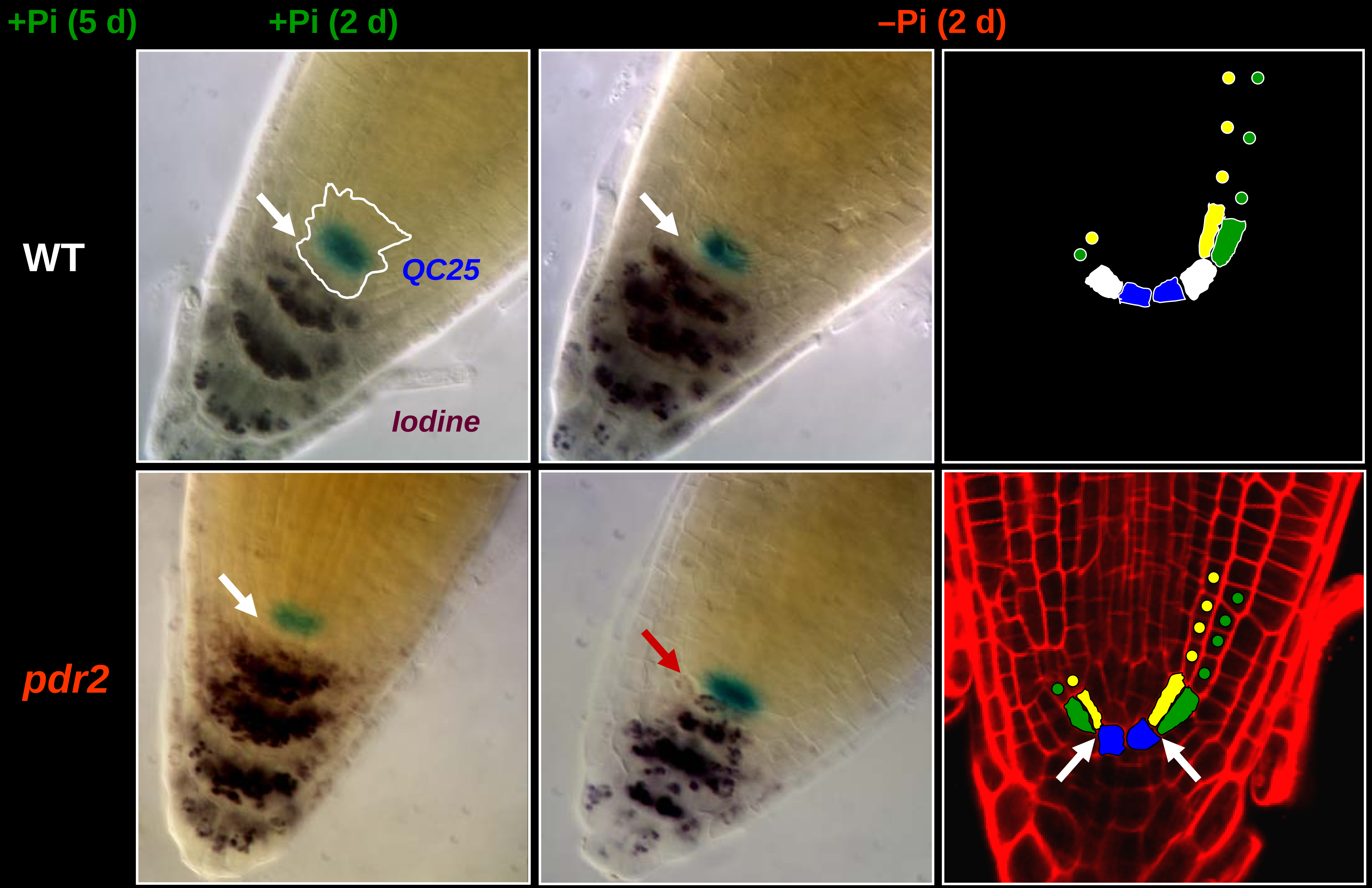


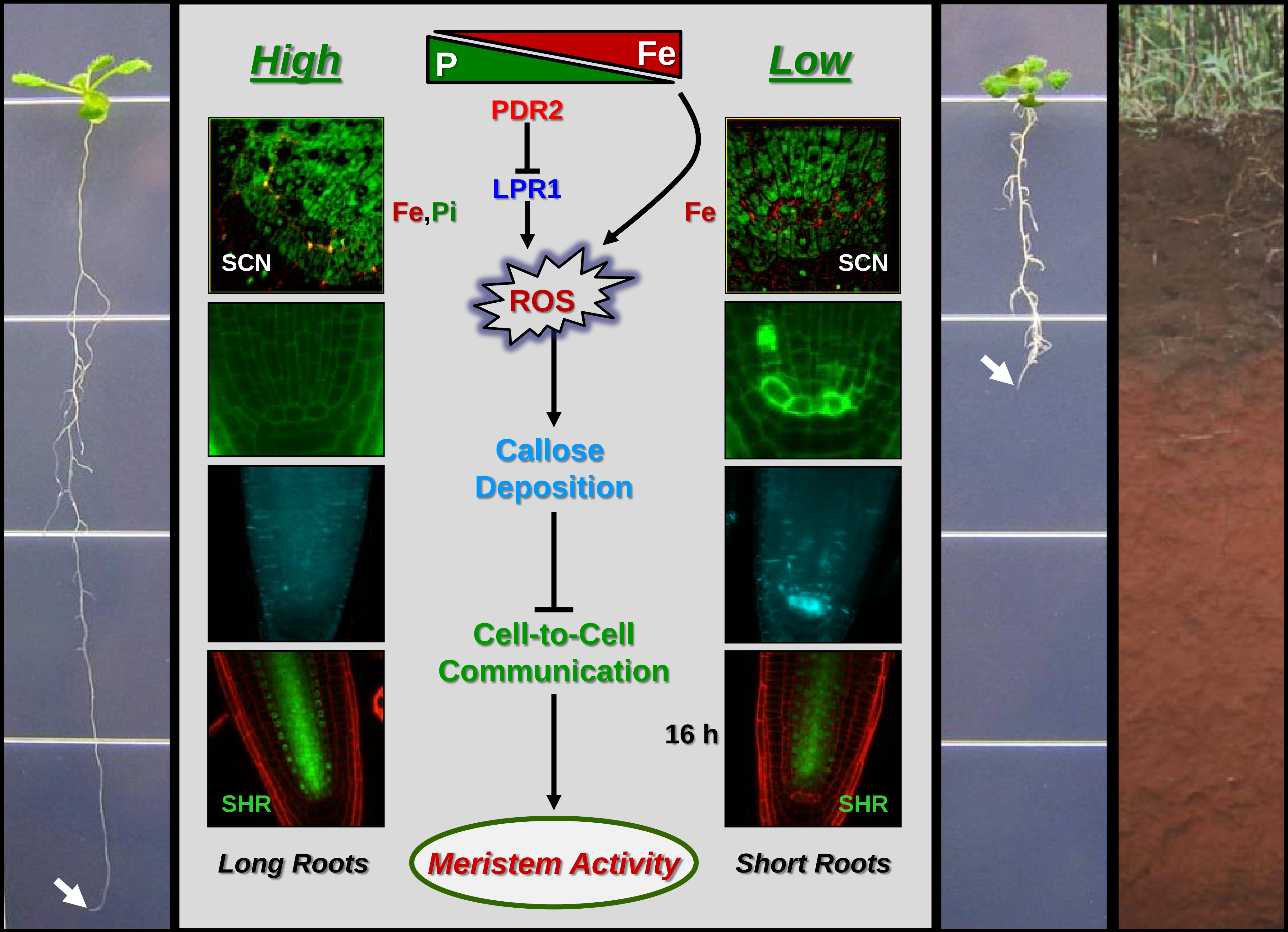




Double-Staining of Quiescent Center and Columella

Accelerated Loss of Stem Cell Identity in *pdr2*





High
P
Fe
Low
PDR2
LPR1
Fe,Pi
Fe
SCN
SCN
ROS
Callose
Deposition
Cell-to-Cell
Communication
16 h
SHR
SHR
Long Roots
Meristem Activity
Short Roots

Pflanzliche Anpassung an Phosphorverfügbarkeit

Prof. Steffen Abel
Leibniz-Institute für Pflanzenbiochemie, Halle (Saale)

Pillnitz, 9. November, 2016