# Evolutionary adaptation of plants to phosphorus deficiency: the multifaceted role of cluster roots

Andrea Alciato, *The Book of Emblems*(1531)

Wikipedia: The genus *Protea* was named by Carl Linnaeus (1735), after the Greek god Proteus, associated with versatility, flexibility, adaptability etc.,

Proteoid roots - "clusters of rootlets which form lateral root "(*Purnell, 1960, Aust. J. Bot., 8, 38–50*)

*Dinkelaker et al. (1995) Bot. Acta 108, 183–200*

**Proteoid roots - root system of the Proteaceae plants**

**Cluster roots - root system of all other plants**

# Why focusing on phosphorus?

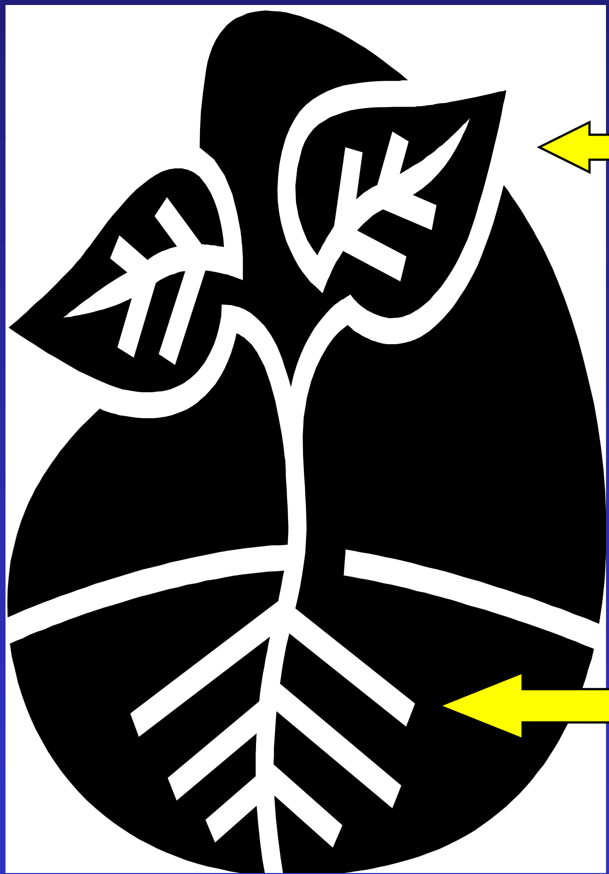
**Generally, phosphorus is the limiting nutrient for plant development**

**principally, because of its <u>low mobility</u>**

# Common disturbing problem

- Considerable P quantities exist in soil
- However, soil-phosphorus is not in the right form or the right site for plant utilization

# Common problem: the gap between the desired and the existing state



Cytoplasm-P concentration

5-10 m*M* (150-300 mg $L^{-1}$)

**Energy cost**

Rhizosphere-P concentration:

1 µ*M* (0.03 mg $L^{-1}$)

Very low soil-mobility

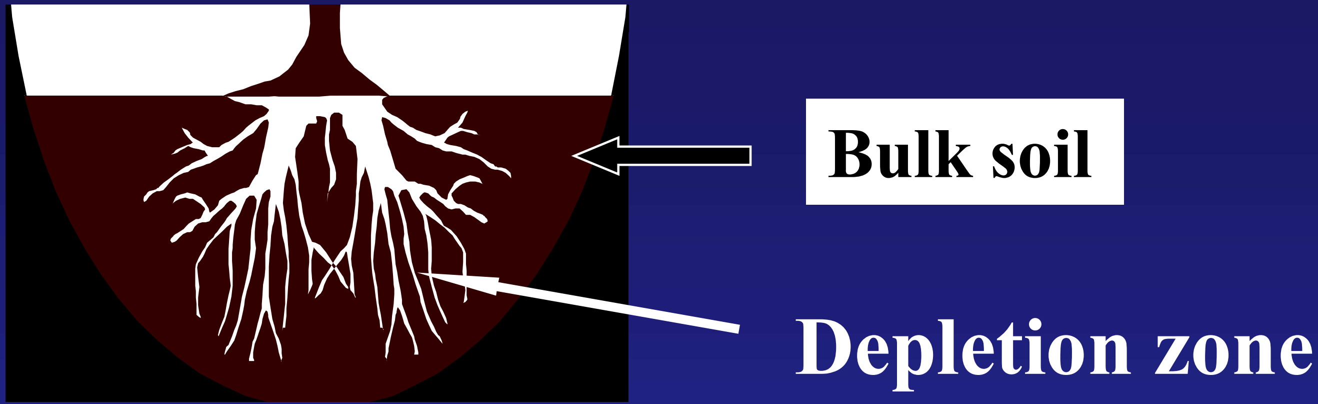
## Schematic presentation of the depletion zone

**Rhizosphere (Root area)**

**Bulk soil**

**The depletion zone**

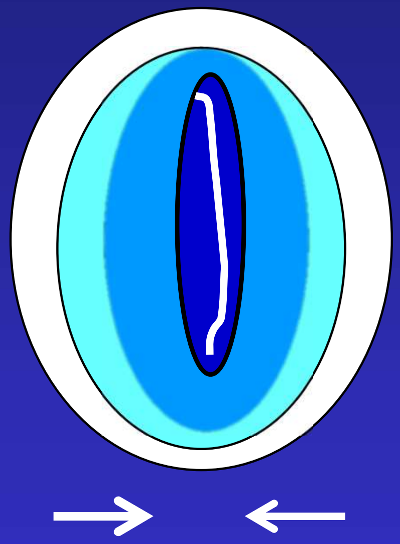
**Water and nutrients acquisition by roots leads to differences in water and nutrients concentration between the rhizosphere and the bulk soil**




**Nutrient transport from the soil solution to the root surface takes place by diffusion along the concentration gradient**

# Root-Soil interface

Fast process (seconds, minutes) – water and nutrient uptake by plant roots induced a depleted zone in the root-soil interface



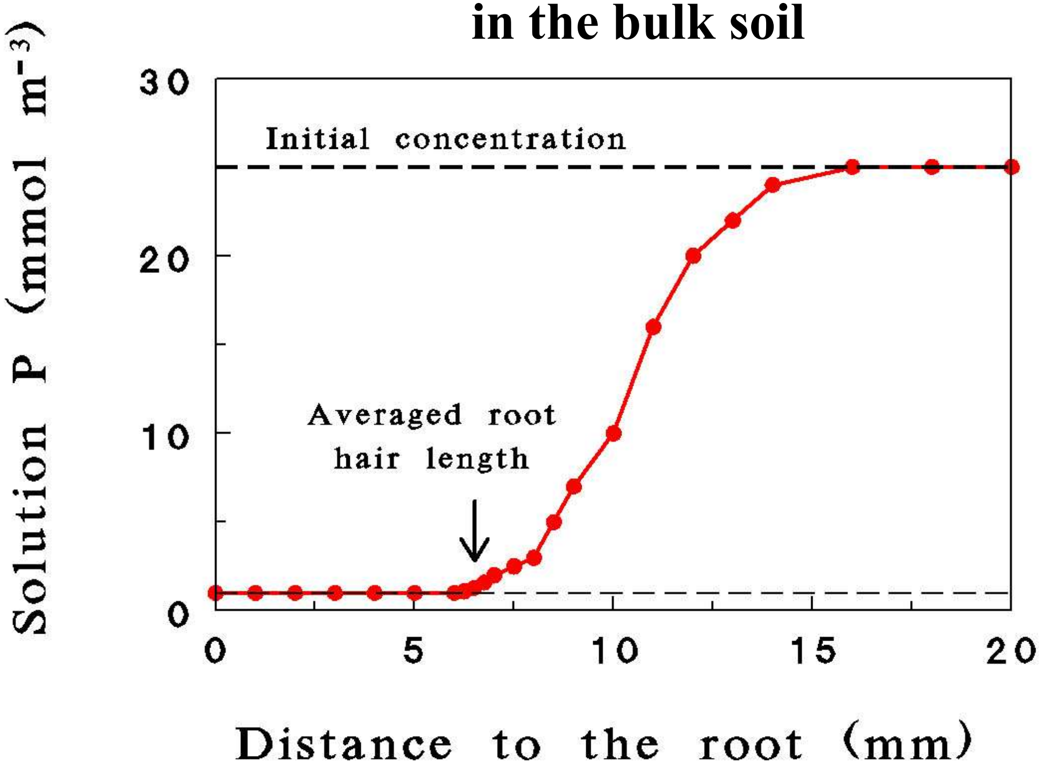
Reduced water and nutrient availability

Nutrient transport from the soil solution to the root surface takes place by very slow diffusion along the concentration gradient

# Soil-P concentration as a function of the distance from the root surface

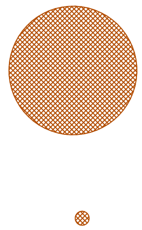
(*based on Jungk, 2002,* Dynamics of nutrient movement at the soil-root interface. In: *Plant Roots The Hidden Half*

**Phosphorus concentration in the vicinity of the root system is only <u>4%</u> from the concentration in the bulk soil**



# Diffusion coefficient of nutrient ion in water ($D_i$) and order of magnitude in soil ($D_e$; cm$^2$ s$^{-1}$) (based on *Barber, 1995*)

| | $D_i$ ($25^0$ C) | $D_e$ (soil) | Diffusive movement (cm/day) |
|---|---|---|---|
| $NO_3^-$ | $1.9 \times 10^{-5}$ | $10^{-6}$-$10^{-7}$ | 1.3 |
| $K^+$ | $2.0 \times 10^{-5}$ | $10^{-7}$-$10^{-8}$ | 0.13 |
| $H_2PO_4^-$ | $0.9 \times 10^{-5}$ | $10^{-8}$-$10^{-11}$ | 0.004 |



$De = Di\theta f(dCi/dCs)$ θ=moisture content

f=tortuosity → $f(\theta)$

# The plant is wiser than who grows it (and who investigate it)

**During the evolution plant developed several physiological mechanisms for overcoming phosphorus deficiency**

# Plant response to P–deficient soils

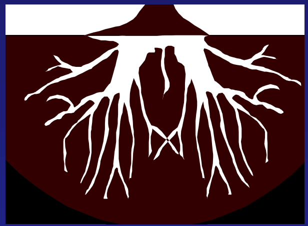
***Wissuwa 2003*. How do plants achieve tolerance to phosphorus deficiency?**
**Small causes with big effects**

**<u>In plant modification:</u>**
**Modifying the root system, i.e., improving the efficiency of nutrient acquisition**

**<u>Outdoor modification:</u>**
**Modifying the root environment, i.e., improving nutrient availability**

***Wissuwa, 2003, Plant Physiol., 133, 1947-1958***

# Plant adaptation to low nutrient availability: different physiological mechanisms



Increasing acquisition efficiency through modification of:

→ Root / Shoot ratio

← Roots allocation to shallow soil horizons

Root hair

**Proteoid roots**

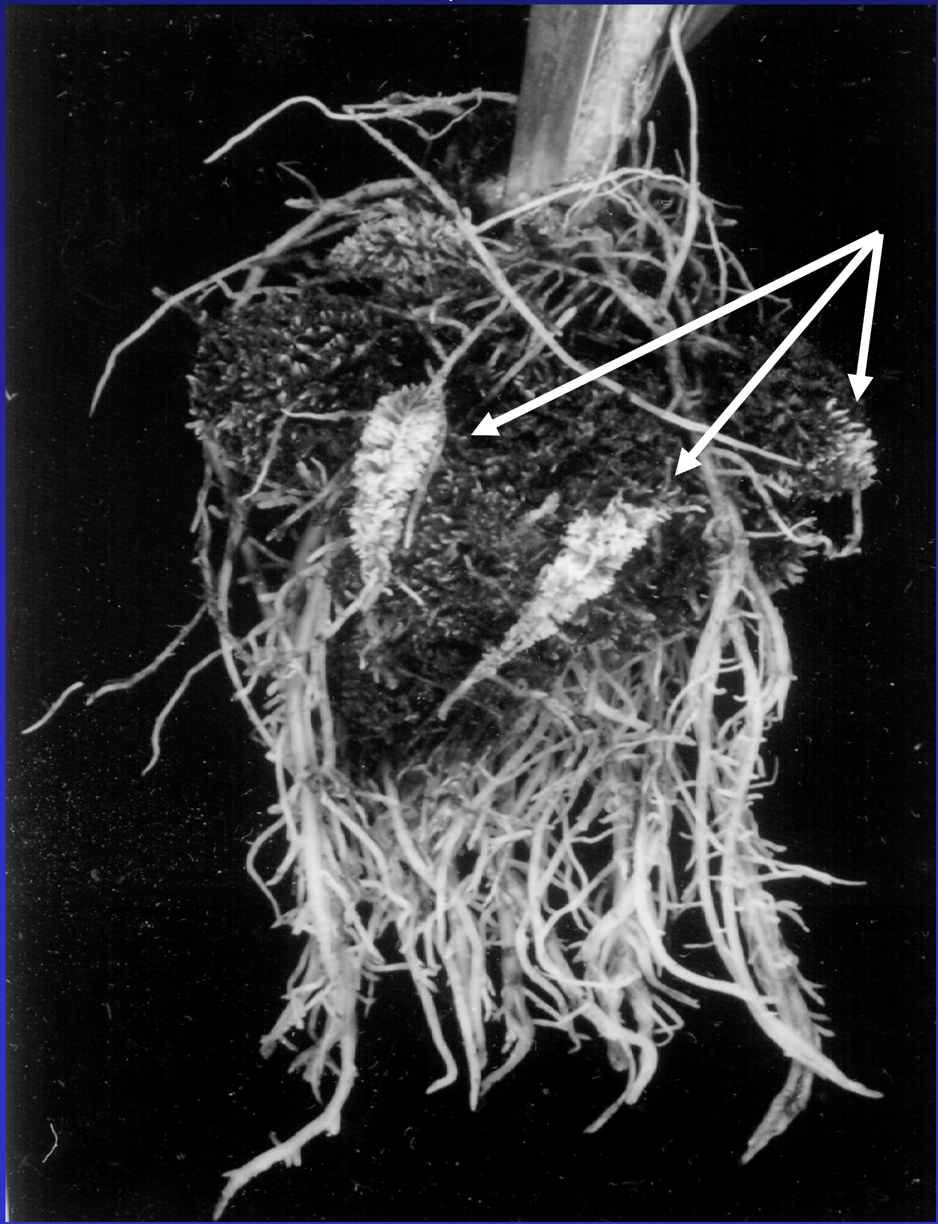
Mycorrhizal symbioses

Regulation the transcript of nutrient transporters

Rhizosphere modification with: organic acids, protons and enzymes

# Proteoid roots

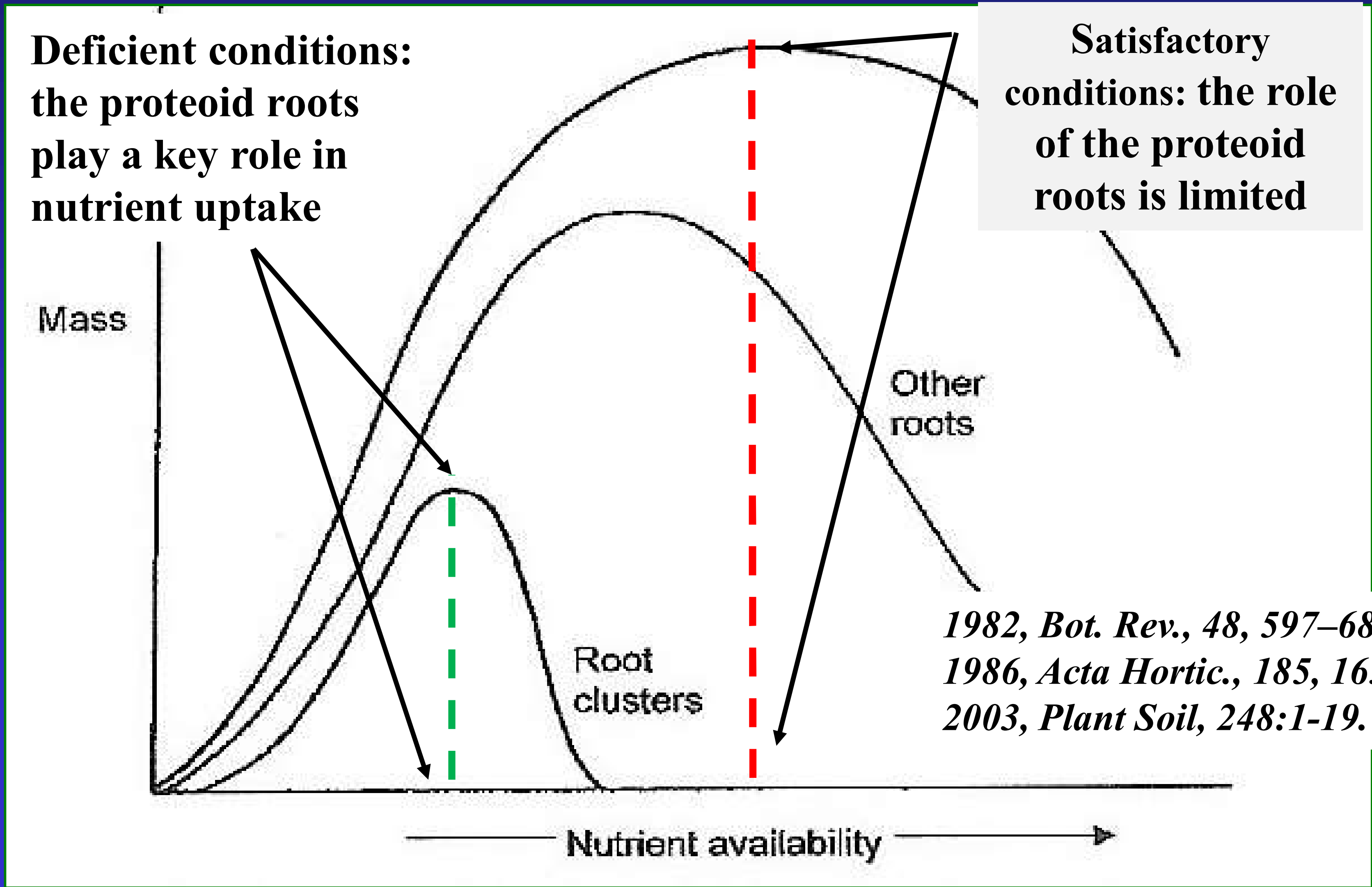
‘Safari Sunset’ (*Ben-Jaacov* 1995)



Proteoid roots - “clusters of rootlets which form lateral root”

# “The presence of abundant proteoid roots is a sign of a healthy plant” (*Lamont*, 1986)

# Idealized relationship between nutrients availability and root production (From *Lamont 2003*, adapted from *Lamont 1982*)




*1982, Bot. Rev., 48, 597–689*
*1986, Acta Hortic., 185, 163–173.*
*2003, Plant Soil, 248:1-19.*

# Mysterious problem during the 1960s – ’80s

**Phosphorus application to Proteaceae plants caused severe leaf chlorosis, necrosis, leaves abscission, growth impairment, and finally plant death**

## Nichols' query (*Sci. Hortic.*, *1979, 11, 197–206*)

**“why are phosphorus levels that are essential for most other plants toxic to the proteaceae?”**

**P toxicity?**

**P can be toxic to plants?**

# *Gardner et al. (1982a, b, 1983)*

**The availability of P and metal ions in the root environment of white lupin (*Lupinus albus* L.) was improved as a result of excretion of organic acids (mainly citric) and protons from the proteoid roots.**

**Role of proteoid roots: excretion of organic acids that enhance nutrient mobilisation towards the root**

*1982a, Plant Soil, 68, 19-32; 1982b, Plant Soil, 68, 33-41; Plant Soil, 70, 107-124.*

# White lupin as a plant model: the primary role of proteoid roots is associated with modification of the root environment

(*Dinkelaker et al., 1989*)

| Soil | pH | Citrate* | DTPA extractable (μmol/kg soil) Fe | Mn | Zn |
|---|---|---|---|---|---|
| Bulk | 7.5 | nd** | 34 | 44 | 2.8 |
| Proteoid root | 4.8 | 47.7 | 251 | 244 | 16.9 |

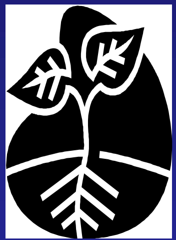
*(mmol/ g soil)
** not detectable

**Partial answer for Nichols' query**

*Plant Cell Env., 1989, 12:285-292.*

Improvement of micronutrients mobilisation toward roots

Increases of P concentration in the rhizosphere



Soluble complexes

$$\text{Citrate} + \text{M-P} \rightleftarrows \text{Citrate-M} + \text{P}$$

$$\text{Citrate} + \text{P}_{ads} \rightleftarrows \text{Citrate}_{ads} + \text{P}$$

M = Metal, M-P = Soil Metal-P complex

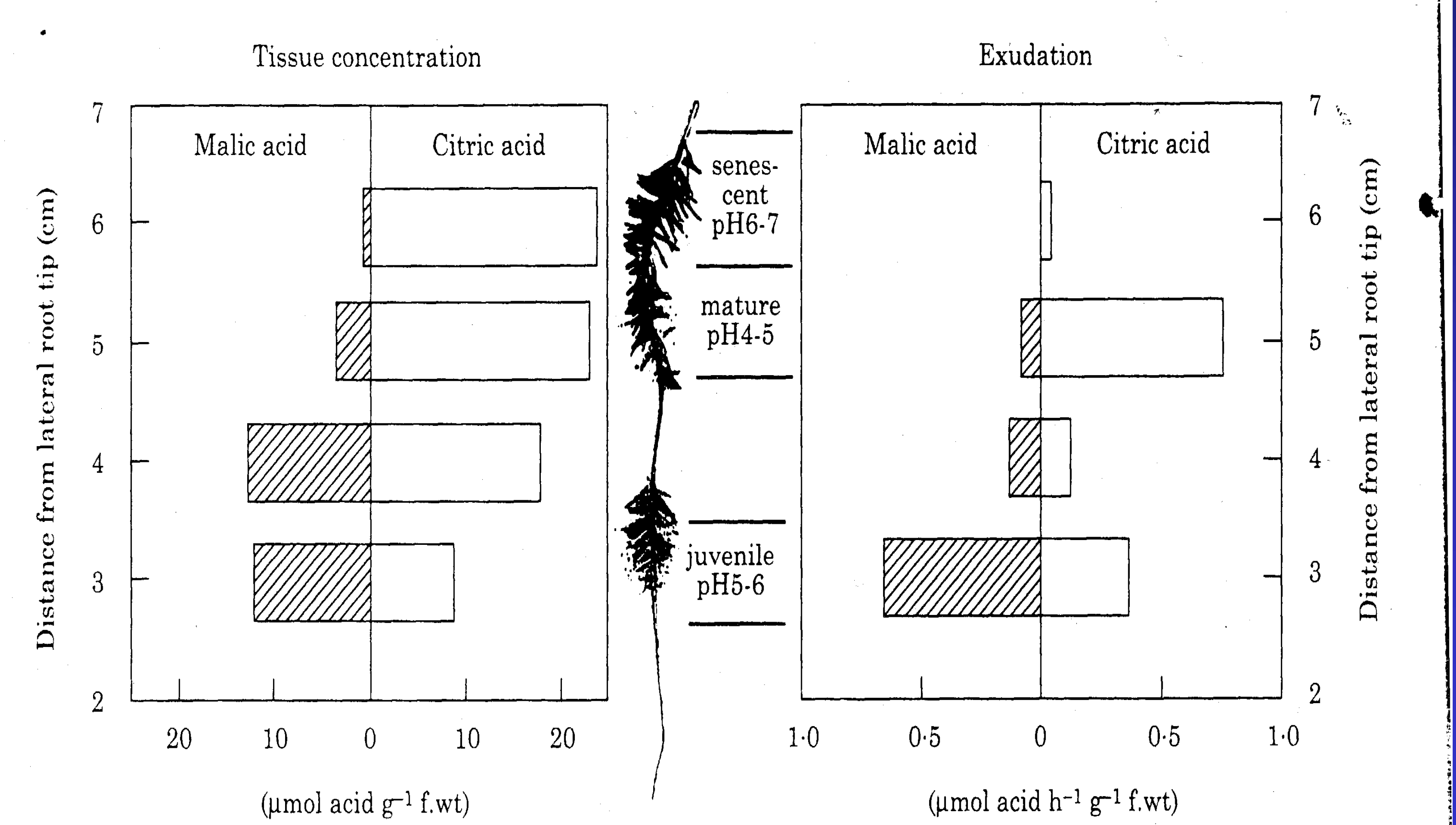
$P_{ads}$ - P adsorbed onto surface sites

# P deficiency-induced changes in carboxylate metabolism

(*Neumann et al., 2000,* Ann. Bot., *85*, 909–919)

**Cluster root formation in white lupin (*Lupinus albus* L.) is induced mainly by phosphorus starvation and seems to be regulated by the endogenous P status of the plant**

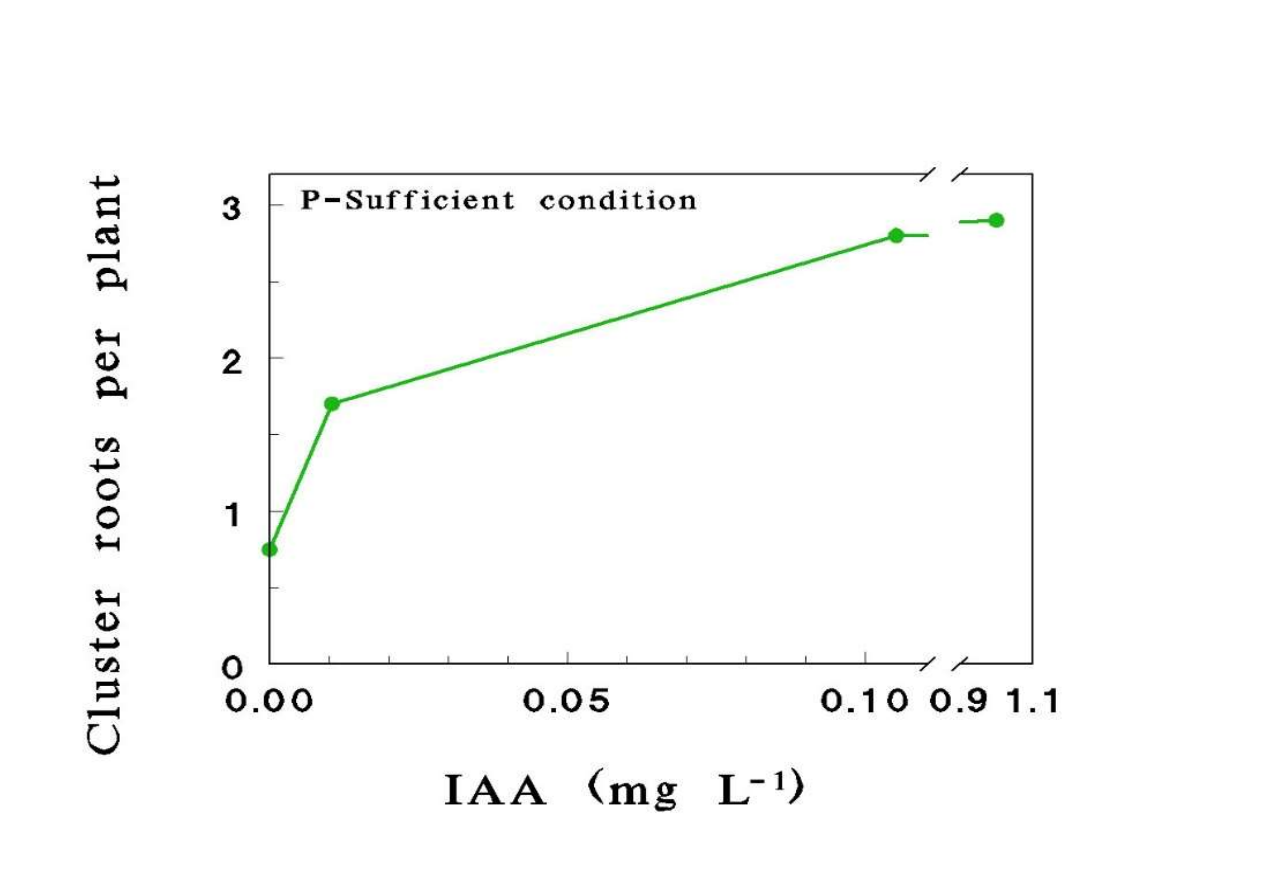
# Spatial variation of malate and citrate in tissue concentrations, root exudation and rhizosphere pH in different development stages of cluster roots in white lupin (*Neumann et al., 2000,* Ann. Bot., *85*, 909–919)



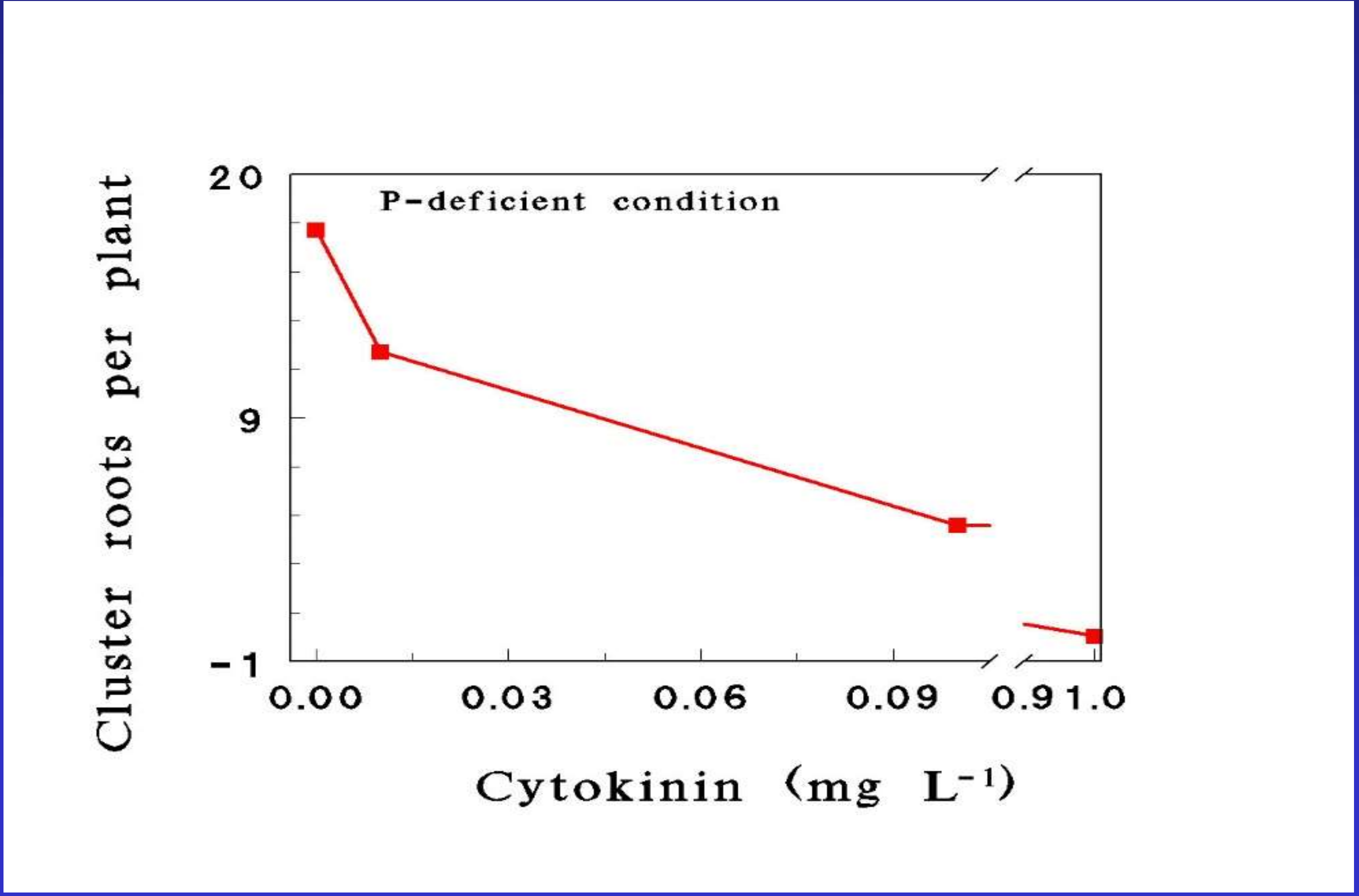

G. 7. Spatial variation of tissue concentrations and root exudation of major carboxylates (malate, citrate) and rhizoplane pH in different ...elopmental stages of cluster roots in white lupin grown in hydroponic culture for 35 d without P supply. Means of three replicates (each including four root segments) are presented (adapted from Neumann *et al*, 1999).

# Endogenous phyto-hormones such as auxin and cytokinins may act as antagonist to P-starvation response

# Exogenous addition of auxin (IAA) on cluster root of white lupin grown under P-sufficient conditions (*Neumann et al., 2000,* Ann. Bot., *85*, 909–919)



# Exogenous addition of cytokinin (kinetin) on cluster root of white lupin grown under P-deficient conditions (*Neumann et al., 2000,* Ann. Bot., *85*, 909–919)



# Effect of plant-P status on citrate synthesis in normal and proteoid roots of white lupin

*(Johnson et al., 1994, Plant Physiol., 104, 657–665)*

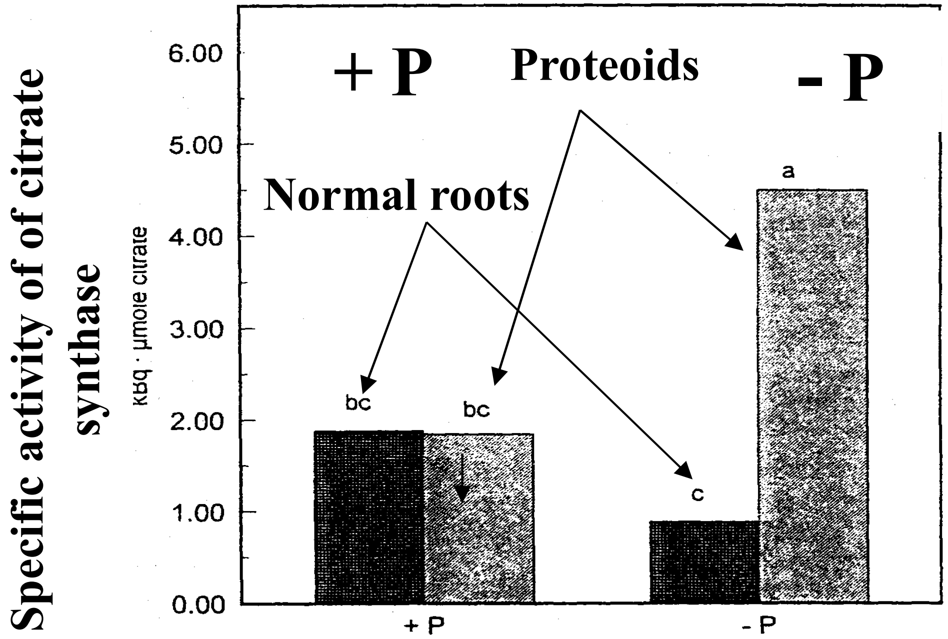



**Figure 6.** The specific radioactivity of citrate (kBq $\mu mol^{-1}$ of citrate) from excised normal and proteoid roots of *L. albus* plants grown with +P and −P. The interaction of P treatment and root tissue was significant according to analysis of variance ($P \leq 0.05$). Each bar represents the treatment mean ($n = 9$); bars labeled with the same letters are not different as determined by LSD ($P \leq 0.05$).

# Effect of plant-P status on the specific activity of PEPC (phosphoenolpyruvate carboxylase) in white lupin organs *(Johnson et al., 1994, Plant Physiol., 104, 657–665)*

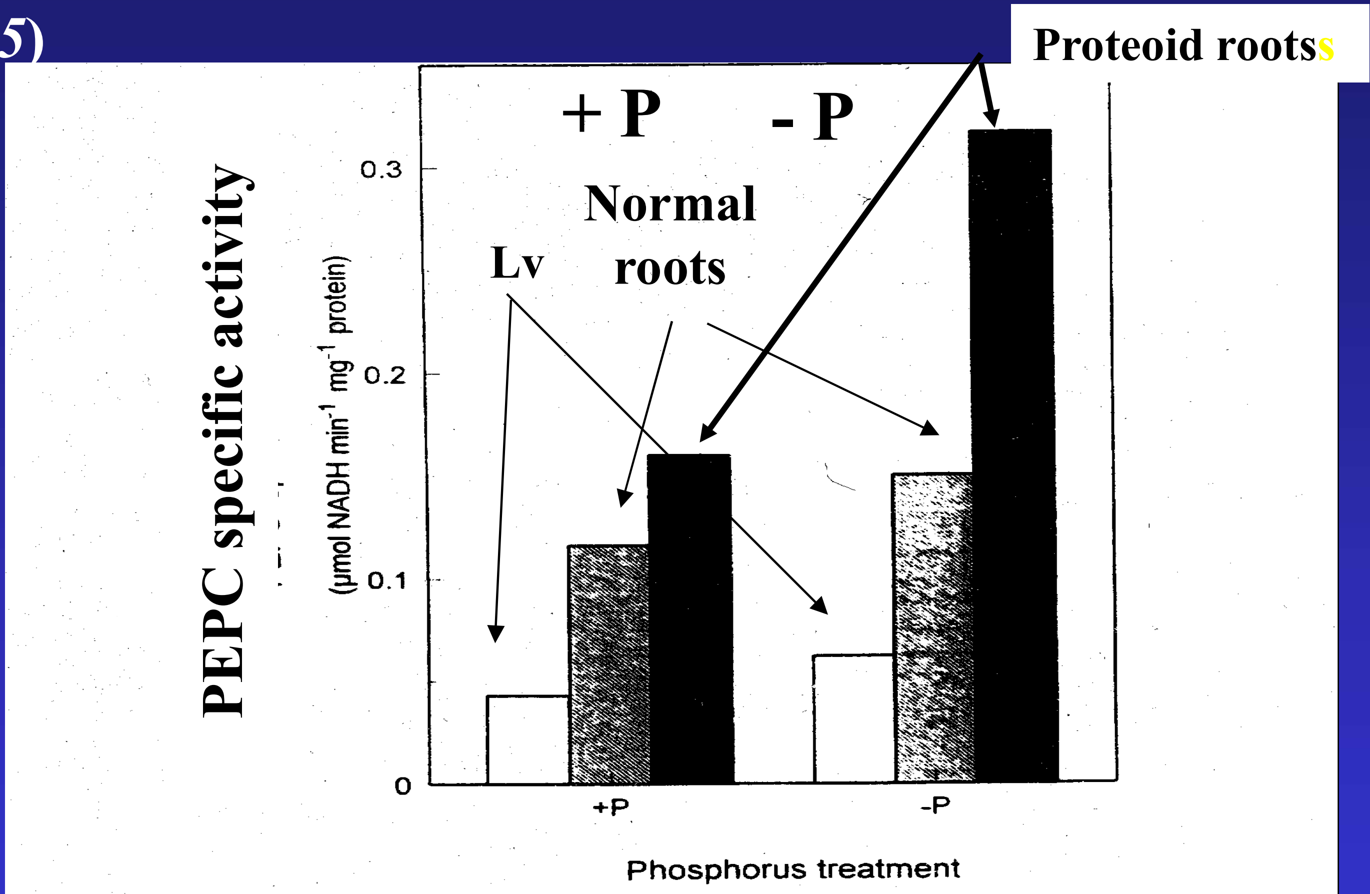
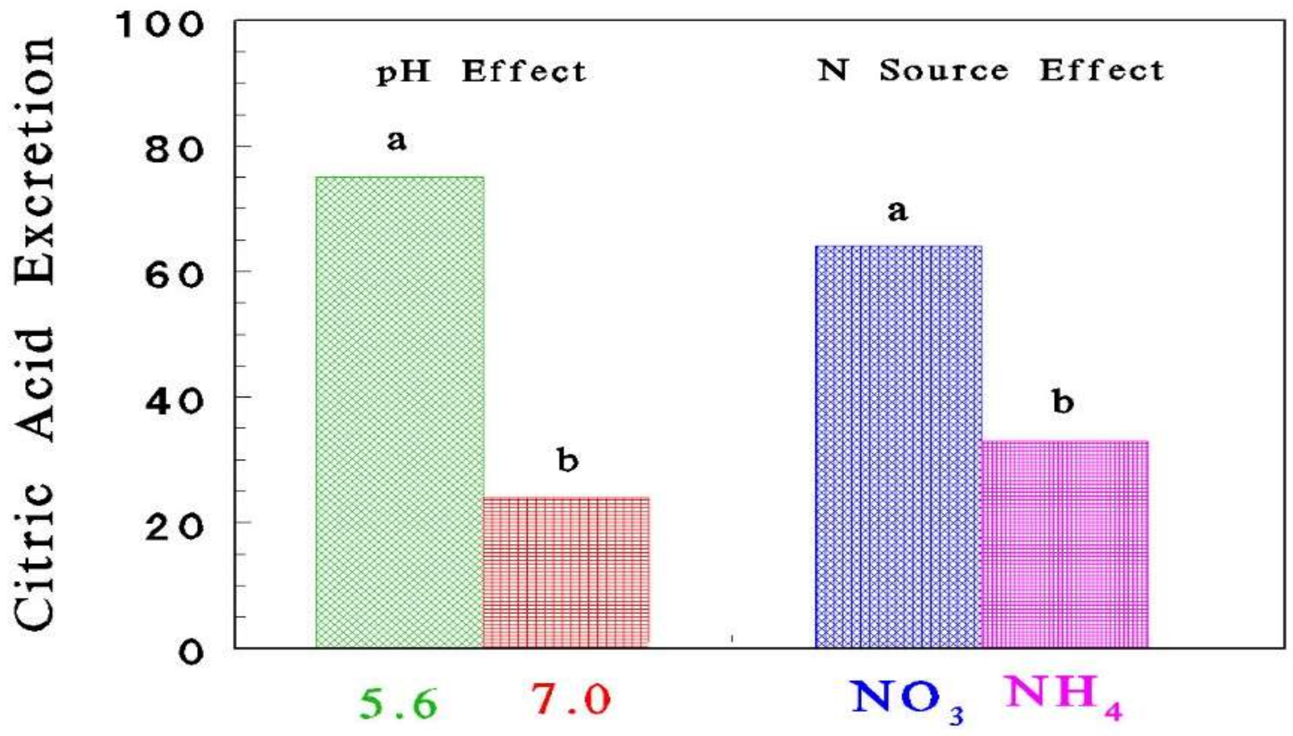



**Figure 3.** In vitro specific activity of PEPC (μmol NADH $min^{-1}$ $mg^{-1}$ protein) determined spectrophotometrically at $A_{340}$ for leaves (white bars), normal roots (hatched bars), and proteoid roots (black bars) of *L. albus* plants grown with either 1 mM P (+P-treated) or without P (−P-treated) for 14 DAE. Each bar represents the treatment mean ($n$ = 6). $LSD_{\alpha=0.5}$ = 0.09 for all interactions.

# The effect of phosphorus on growth and cluster-root formation in the Chilean Proteaceae: *Embothrium coccineum*

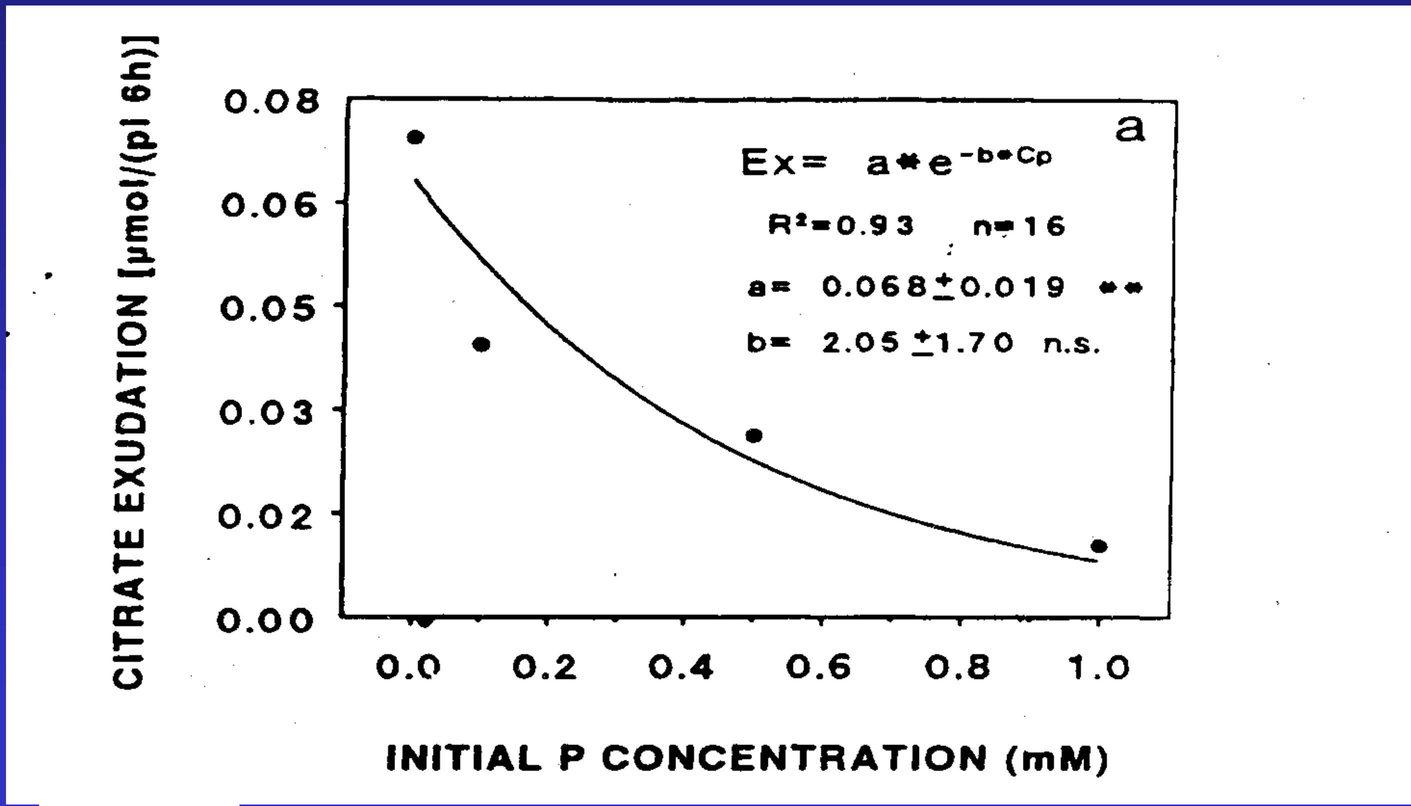
# Effects of pH and $NH_4^+/NO_3^-$ ratio on citric acid excretion from *L.* 'Safari Sunset' plants (*Silber et al., 2000, HorScience*, 35, 647-650)

)



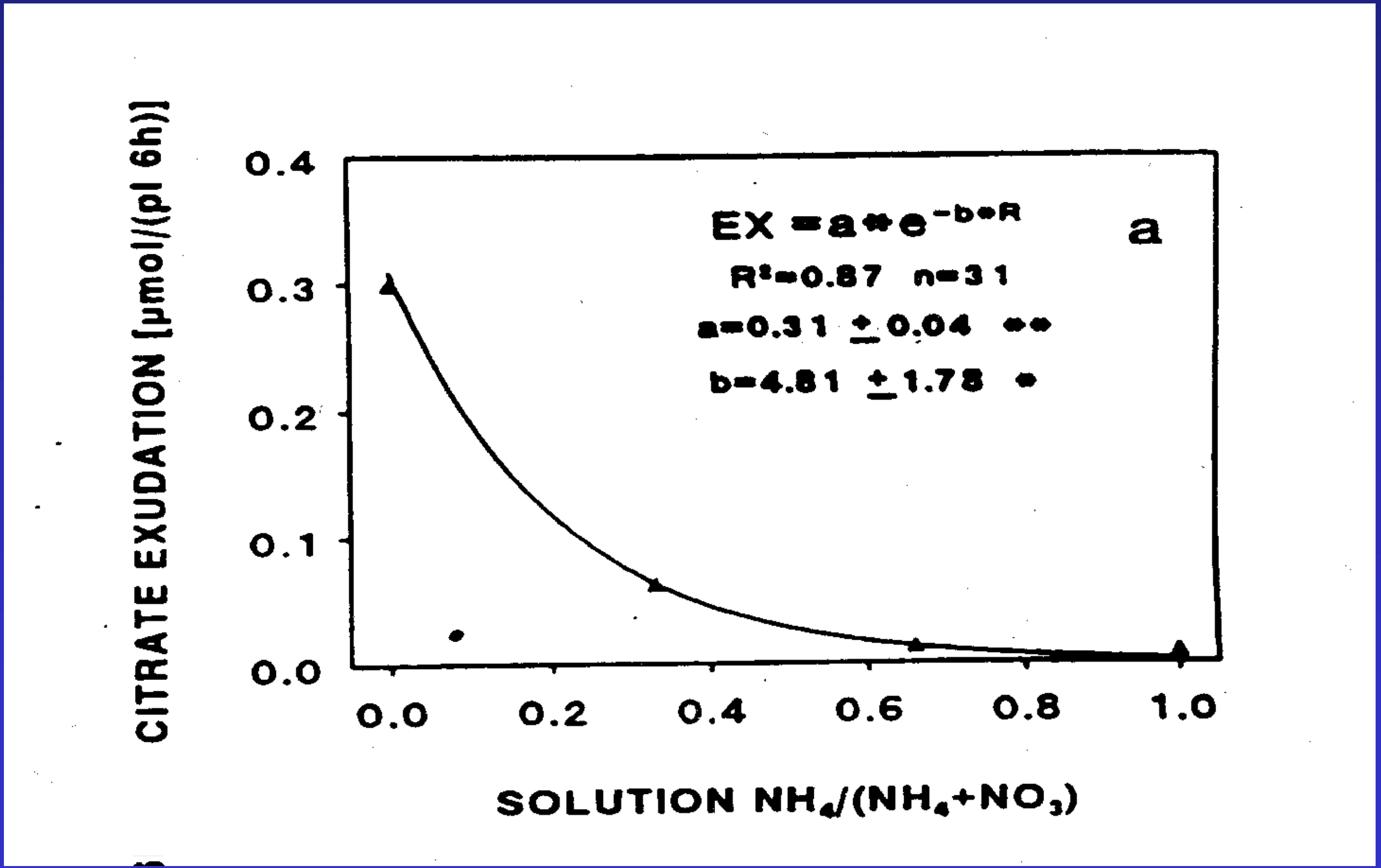

*Silber et al., 2000, HorScience*, 35, 5647-650

# Citrate exudation from tomato roots as a function of initial P concentration in the nutrient solution (*Imas et al., 1997, Plant Soil, 191, 35-39*)



# Relationships between $R_N$ and

**Carboxylic acids exudated from tomato roots: (a) citric acid; and (b) dicarboxylic acids.** (*Imas et al., 1997, Plant Soil, 191, 27-34*)



# An old savant once said:

**Nothing is gratis in our world. You have to pay for goodies you get**

# Costs-Benefits of plant adaptation to nutrient deficiency – formation of proteoid roots (after *Lynch et al., 2005, Plant Soil, 269, 45-56*)

**Costs:**

Decay of photosynthesis products (up to 50%)

⇩

Carbohydrates allocated to roots, fungus, root exudation, etc.

**Carbon** ↓

**Benefits:**

Improved nutrient acquisition

⇩

Photosynthesis improvement

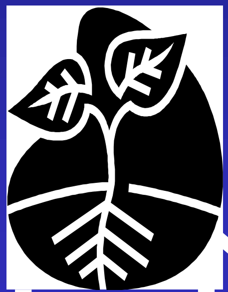
Enhancement of biomass production

**Carbon** ↑

# "P toxicity": P-induced micronutrients deficiency

**P fertilisation:** Elevating plant-P level

**Impairment of metal uptake by roots**



Mycorrhizal infection

Organic exudates

Reduction of root:shoot ratio, root hairs and changes in root architecture

### Possible conclusion

- Omitting P from the fertilisation system (???)
- Adding all the necessary nutrients (including micronutrients) through the fertilisation system

# Rhizoeconomics: Carbon costs of phosphorus acquisition (*Lynch & Ho,Plant Soil, 2004*)

- The activity of proteoid roots is primarily influenced by the P status in the plant, and their formation is depressed at high plant-P level
- Commonly, proteoid roots are abundant only in plants exposed to a poor nutrient solution

# Proteoid roots are a sign of a healthy plant (*Lamont, 1986*) ?

Under intensive agricultural systems

**No !!!**

**We are not selling roots!!!**

**In modern agricultural systems it is more efficient to supply all plant demands via fertilisation methods**

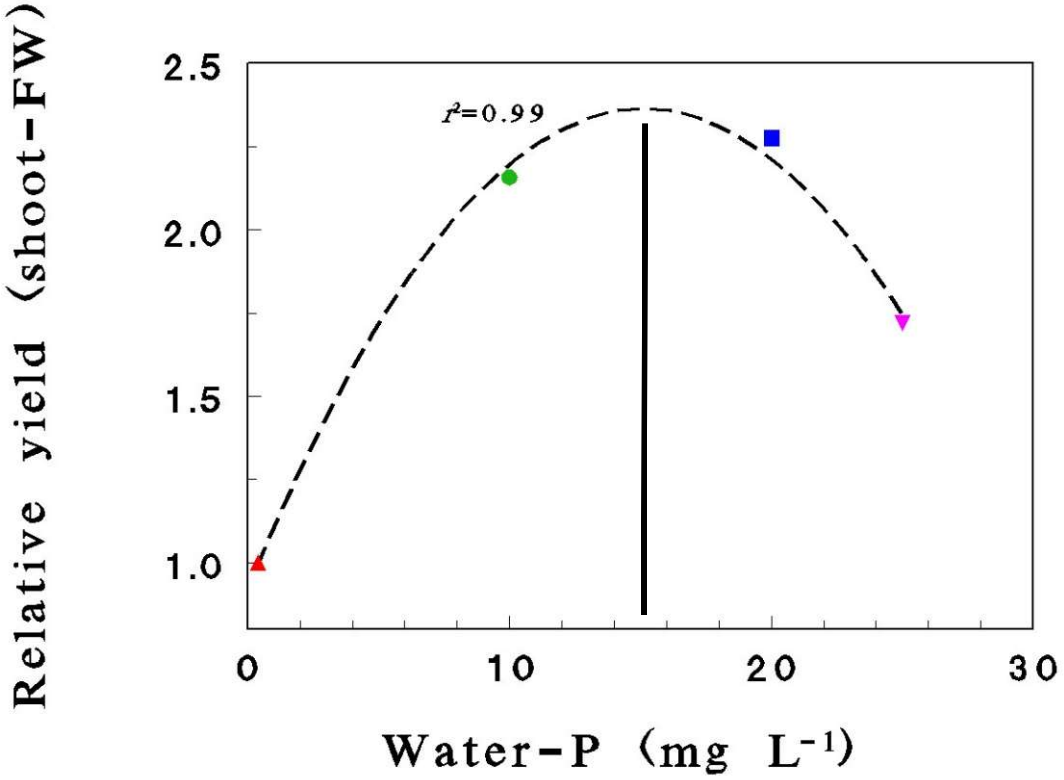
**Proteoid roots indicate deficient nutrients regime**

*1986, Acta Hortic., 85, 163–173.*

# Relationships between yield and water-P concentration

'L. 'Safari Sunset' respond to P nutrition is not exceptional

**Maximum yield: Solution-P of 10-20 mg L$^{-1}$**

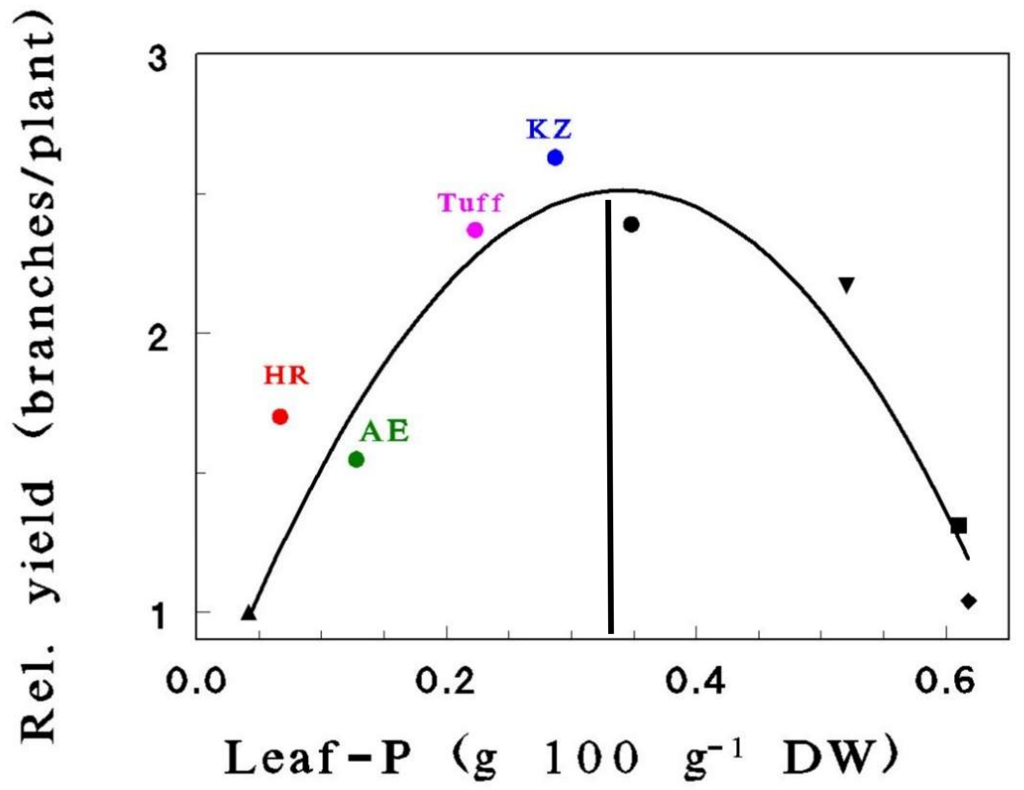



(*Silber et al., 2000, Agric. Sci., 135, 27-24*)

# Relationships between yield of L. 'Safari Sunset' and leaf-P concentration

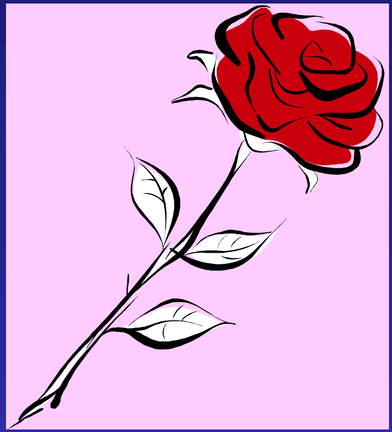
**L. 'Safari Sunset' respond to P nutrition is similar to many other horticultural plants**

**Maximum yield: leaf-P of 0.25-0.35 g 100 $g^{-1}$ DW**




*(Silber et al., 2000, Agric. Sci., 135, 27-24)*

# Thank you




avnersilber@gmail.com

972-54-7800064