Fisiologia Vegetal - Nutrição

Segunda aula teórica de nutrição vegetal
2025-2026

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Nutrição Vegetal

O objectivo deste bloco de aulas teóricas é dar aos alunos os fundamentos básicos da nutrição vegetal

Objectivos da segunda aula:

1 – Hidroponia e soluções nutritivas
2 – Membrana cellular e transporte através da membrana
3 – Espaço livre aparente e espaço de Donan
4 – A equação de Nernst
5 – Funções de nutrientes
6 - Relação entre crescimento e disponibilidade de nutrientes

No fim da aula os alunos devem conseguir responder :
Porque é que uma planta pode ter deficiência mesmo com nutrientes no solo?
Como sabemos o que adicionar numa solução nutritiva?

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"17" is not arbitrary — but it's also not absolute in all contexts:

•It's a **minimum universal set**

•Some species may benefit from additional elements

•New roles are still being discovered (e.g. silicon in stress tolerance)

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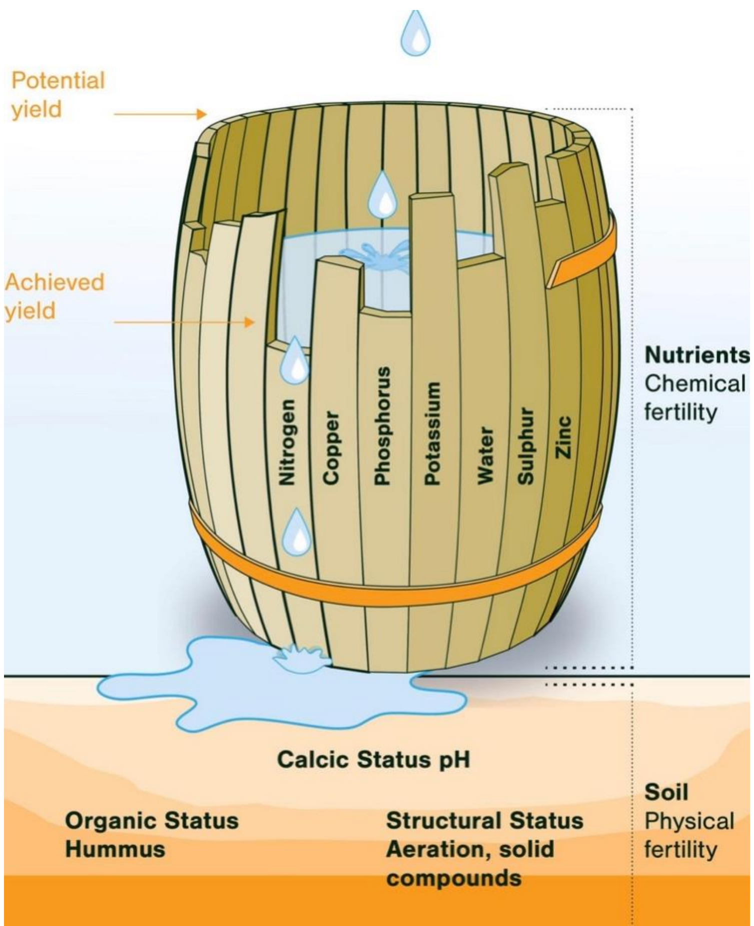
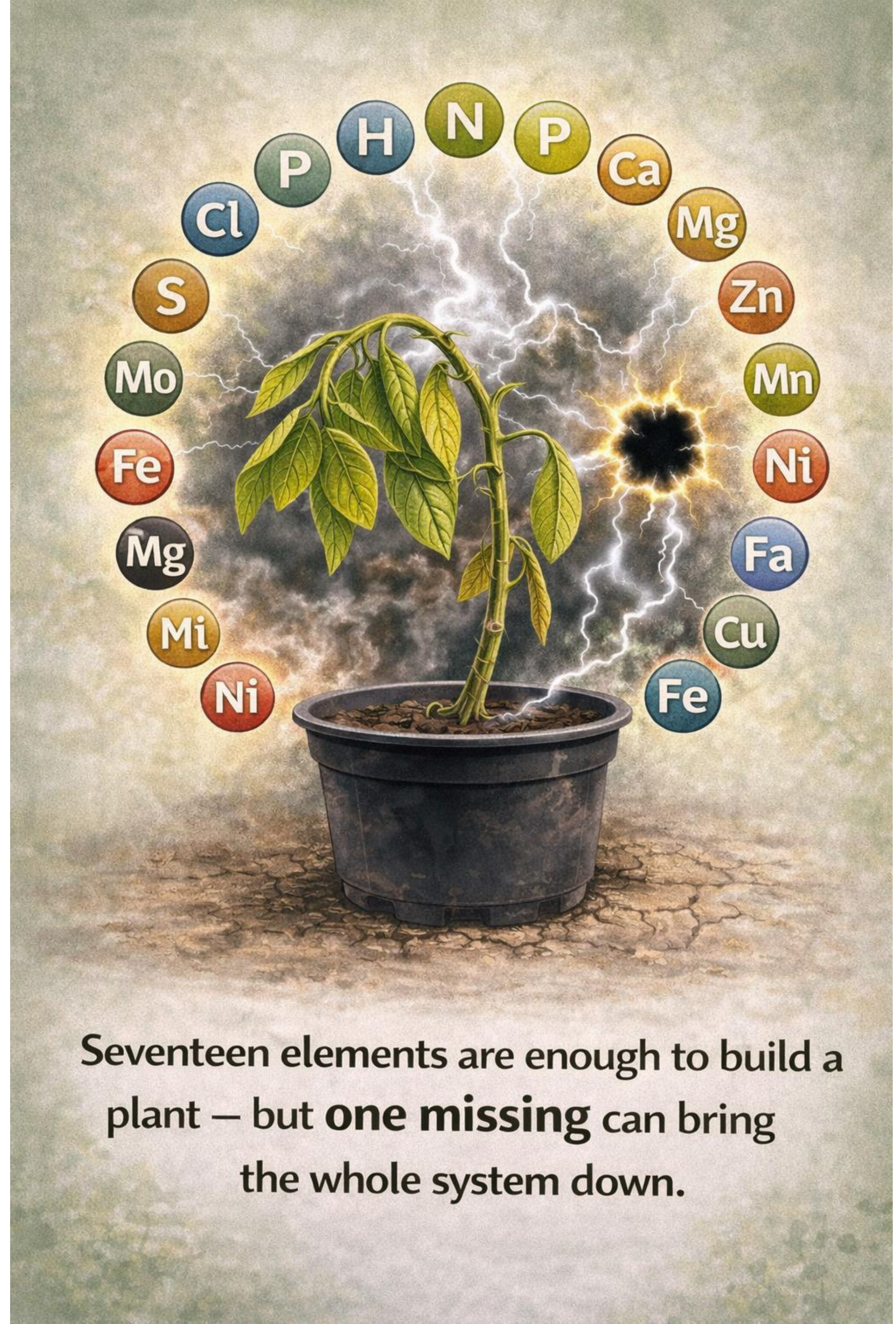


Potential yield
Achieved yield
Nitrogen
Copper
Phosphorus
Potassium
Water
Sulphur
Zinc
Nutrients
Chemical fertility
Calcic Status pH
Organic Status
Hummus
Structural Status
Aeration, solid compounds
Soil
Physical fertility



Cl
P
H
N
P
Ca
Mg
Zn
Mn
Ni
Fa
Cu
Fe
Ni
Mi
Mg
Fe
Mo
S
Seventeen elements are enough to build a plant – but **one missing** can bring the whole system down.

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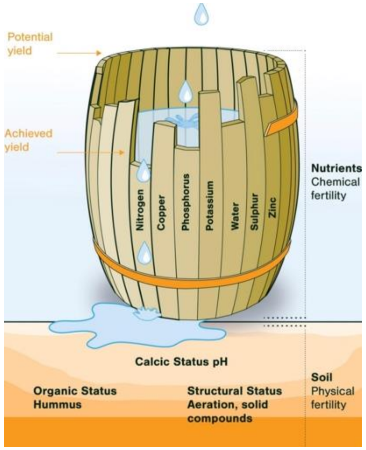
Nutrient deficiency symptoms in a plant are the expression of metabolic disorders resulting from the insufficient supply of an essential element.

These disorders are related to the roles played by essential elements in normal plant metabolism and function.



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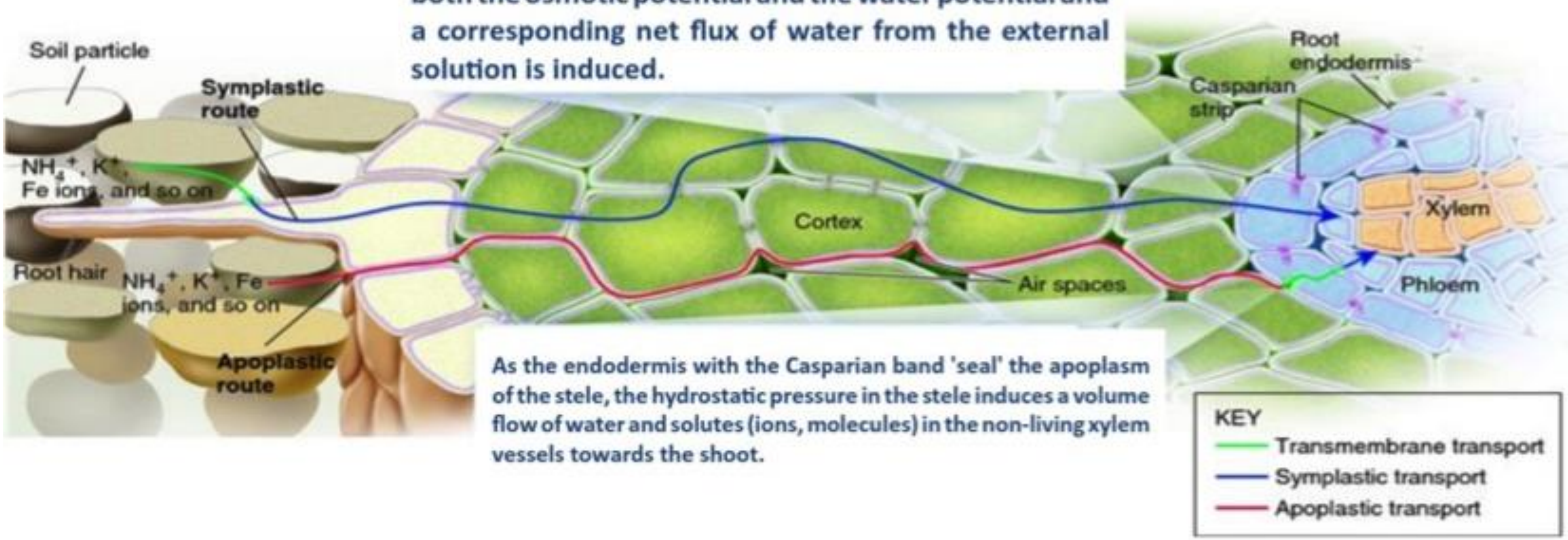
Classification of plant mineral nutrients according to biochemical function

Mineral nutrient		Functions
Group 1 Nutrients that are part of carbon compounds	N	Constituent of amino acids, amides, proteins, nucleic acids, nucleotides, coenzymes, hexoamines, etc.
	S	Component of cysteine, cystine, methionine, and proteins. Constituent of lipoic acid, coenzyme A, thiamine pyrophosphate, glutathione, biotin, adenosine-5'-phosphosulfate, and 3-phosphoadenosine.
Group 2 Nutrients that are important in energy storage or structural integrity	P	Component of sugar phosphates, nucleic acids, nucleotides, coenzymes, phospholipids, phytic acid, etc. Has a key role in reactions that involve ATP.
	Si	Deposited as amorphous silica in cell walls. Contributes to cell wall mechanical properties, including rigidity and elasticity.
	B	Complexes with mannitol, mannan, polymannuronic acid, and other constituents of cell walls. Involved in cell elongation and nucleic acid metabolism.
Group 3 Nutrients that remain in ionic form	K	Required as a cofactor for more than 40 enzymes. Principal cation in establishing cell turgor and maintaining cell electroneutrality.
	Ca	Constituent of the middle lamella of cell walls. Required as a cofactor by some enzymes involved in the hydrolysis of ATP and phospholipids. Acts as a second messenger in metabolic regulation.
	Mg	Required by many enzymes involved in phosphate transfer. Constituent of the chlorophyll molecule.
	Cl	Required for the photosynthetic reactions involved in O_2 evolution.
	Mn	Required for activity of some dehydrogenases, decarboxylases, kinases, oxidases, and peroxidases. Involved with other cation-activated enzymes and photosynthetic O_2 evolution.
	Na	Involved with the regeneration of phosphoenolpyruvate in C_4 and CAM plants. Substitutes for potassium in some functions.
Group 4 Nutrients that are involved in redox reactions	Fe	Constituent of cytochromes and nonheme iron proteins involved in photosynthesis, N_2 fixation, and respiration.
	Zn	Constituent of alcohol dehydrogenase, glutamic dehydrogenase, carbonic anhydrase, etc.
	Cu	Component of ascorbic acid oxidase, tyrosinase, monoamine oxidase, uricase, cytochrome oxidase, phenolase, laccase, and plastocyanin.
	Ni	Constituent of urease. In N_2-fixing bacteria, constituent of hydrogenases.
	Mo	Constituent of nitrogenase, nitrate reductase, and xanthine dehydrogenase.

Source: After Evans and Sorger 1966 and Mengel and Kirkby 1987.

Why do ions accumulate in the roots?

Ion release into the apoplasm of the stele decreases both the osmotic potential and the water potential and a corresponding net flux of water from the external solution is induced.



As the endodermis with the Casparian band 'seal' the apoplasm of the stele, the hydrostatic pressure in the stele induces a volume flow of water and solutes (ions, molecules) in the non-living xylem vessels towards the shoot.

THE JOURNEY OF AN ION: FROM OUTSIDE TO THE INSIDE OF A PLANT CELL

An ion encounters a series of physical and chemical barriers that control its movement and accumulation.

1 Bulk soil solution → Apoplast
The ion is in the soil solution and moves by mass flow and diffusion to the root surface.

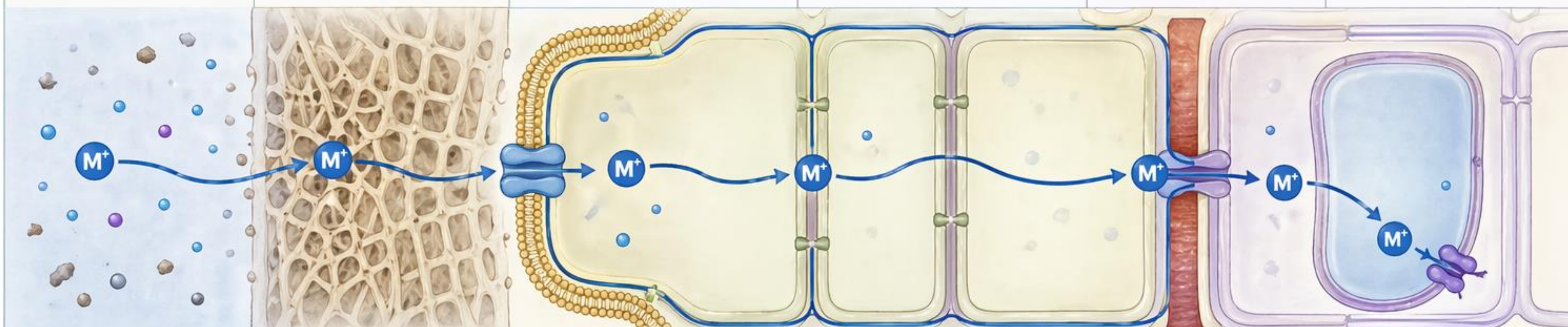
2 Cell wall (apoplast barrier)
Ion moves through the cell wall pores (apoplast pathway). Size exclusion is minimal for ions.

3 Plasma membrane (first selective barrier)
Ion crosses the plasma membrane of the epidermal/root hair cell through transporters or channels.

4 Cortex cells (apoplast or symplast)
Ion moves through the cortex. It can remain in the apoplast (through cell walls) or enter the symplast via plasmodesmata (cell-to-cell pathway).

5 Endodermis (Casparian strip)
The Casparian strip (blocks the apoplastic pathway) forces the ion to cross the plasma membrane.

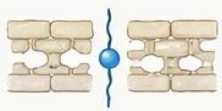
6 Plasma membrane (tonoplast barrier)
Ion enters the stele cells and, if needed, crosses the tonoplast to reach the vacuole (or remains in the cytoplasm).



SOIL SOLUTION | CELL WALL (APOPLAST) | PLASMA MEMBRANE (EPIDERMAL CELL) | CORTEX (PARENCHYMA CELLS) | ENDODERMIS (CASPARIAN STRIP) | STELE CELL (VASCULAR TISSUE)

1 Bulk soil solution
Ion is carried by mass flow and diffusion to the root surface.

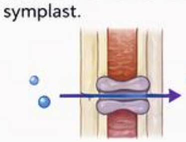
2 Cell wall (apoplast)
Ion moves through cell wall pores. The wall is not selectively restrictive for ions.



3 Plasma membrane
FIRST SELECTIVE BARRIER
Ion must cross the plasma membrane through specific transporters or channels. Selectivity and regulation begin here.

4 Cortex (apoplast or symplast)
Ion may continue in the apoplast (path around cells) or enter the symplast through plasmodesmata (path inside cells).

5 Endodermis (Casparian strip)
The Casparian strip blocks the apoplastic pathway. Ion must cross the plasma membrane to enter the symplast.



6 Tonoplast (vacuole)
LAST SELECTIVE BARRIER
Ion may be sequestered into the vacuole by transporters (tonoplast) or remain in the cytoplasm.

KEY
- M^+ Cation (e.g., K^+, Ca^{2+}, NH_4^+)
- Other ions (anions, cations)
- Apoplast pathway
- Symplast pathway

KEY TAKE-HOME MESSAGE
An ion does not move freely into the cell.
It faces multiple barriers, and selectivity is imposed primarily at cellular membranes (plasma membrane and tonoplast) through transport proteins.

BARRIERS SUMMARY
- Cell walls: porous, low selectivity for ions
- Plasma membranes: selective and regulated
- Casparian strip: blocks apoplastic bypass
- Tonoplast: controls vacuolar sequestration

Cell Wall Pore Size vs. Molecules and Ions

Are ions too big to pass through the cell wall?

Key idea: Most ions and small molecules are **MUCH smaller** than cell wall pores.
Therefore, the cell wall is **NOT** the main barrier for their movement.

SIZE SCALE (nanometers, nm)

0.1 nm — 1 nm — 10 nm — **5 nm** — 100 nm — 1,000 nm — 10,000 nm

IONS AND SMALL MOLECULES << 5 nm | **CELL WALL PORE SIZE LIMIT** < 5 nm | **CELL WALL STRUCTURES** >> 100 nm

K^+

0.66 nm

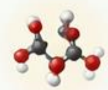
Freely passes through pores

Ca^{2+}

0.82 nm

Freely passes through pores

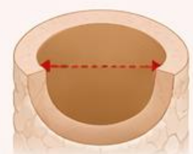
Sucrose



~1.0 nm

Freely passes through pores

Cell wall pore size limit



< 5.0 nm

Cortical cell wall (maize)

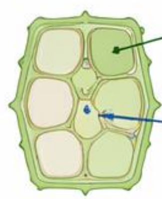
100–200 nm

Rhizodermal cell wall (maize)

500–3,000 nm

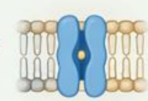
WHAT DOES THIS MEAN?

- Cell wall pores (<5 nm) are much larger than hydrated ions and small molecules (<1 nm).
- Movement in the apoplast (cell wall pathway) is not size-limited for ions like K^+ and Ca^{2+}.
- Selectivity must occur at the **plasma membrane.**



TAKE-HOME MESSAGE

Cell wall is permissive (not selective)



Plasma membrane is selective (controls entry)

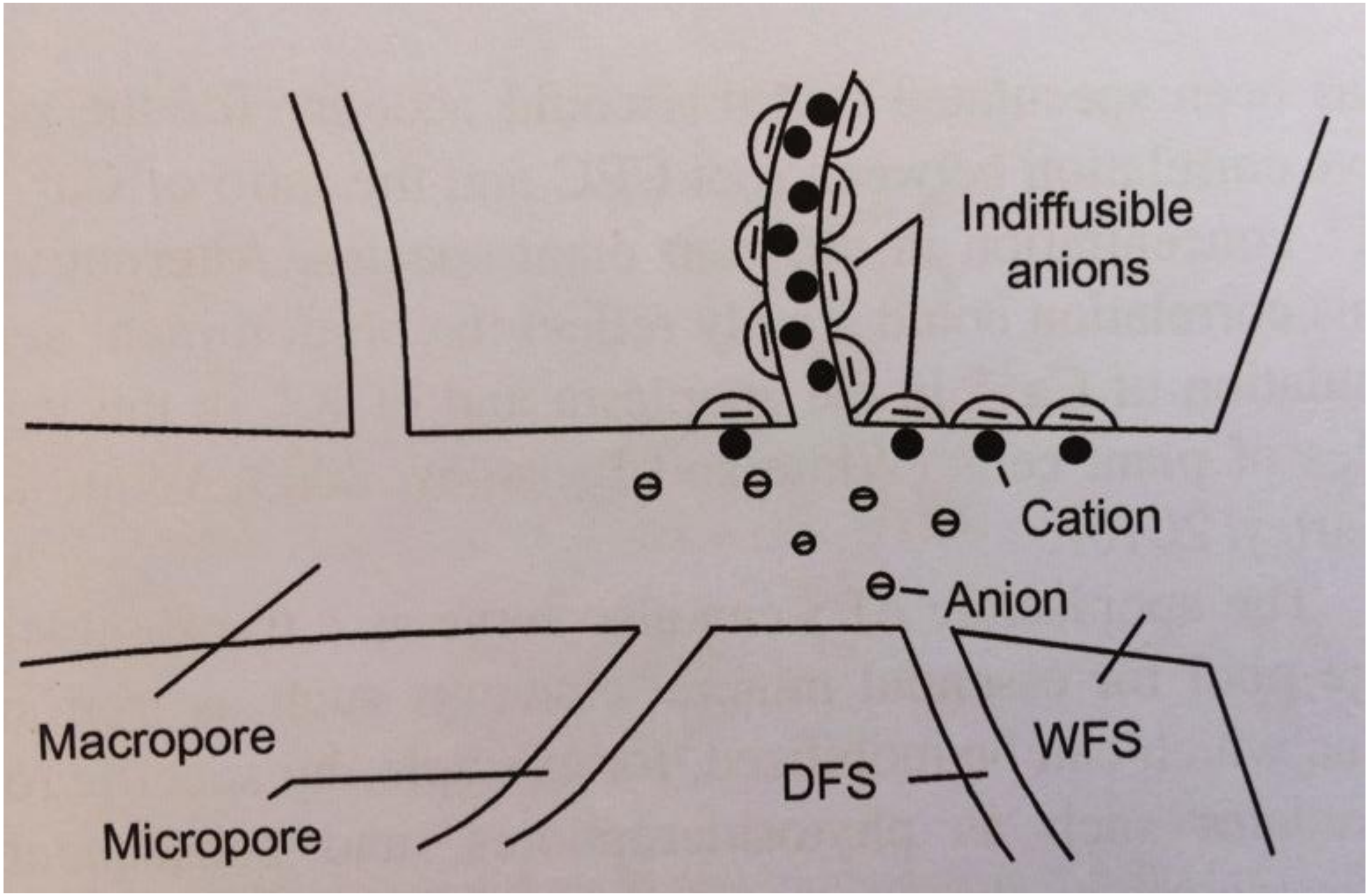
TABLE: DIAMETER OF CELL WALL PORES AND HYDRATED CATIONS

CELL WALL STRUCTURES	DIAMETER (nm)	MOLECULES / IONS	DIAMETER (nm)
Rhizodermal cell wall (maize)	500 – 3,000	Sucrose	~ 1.0
Cortical cell wall (maize)	100 – 200	K^+ (hydrated)	0.66
Pores in cell wall (limit)	< 5.0	Ca^{2+} (hydrated)	0.82

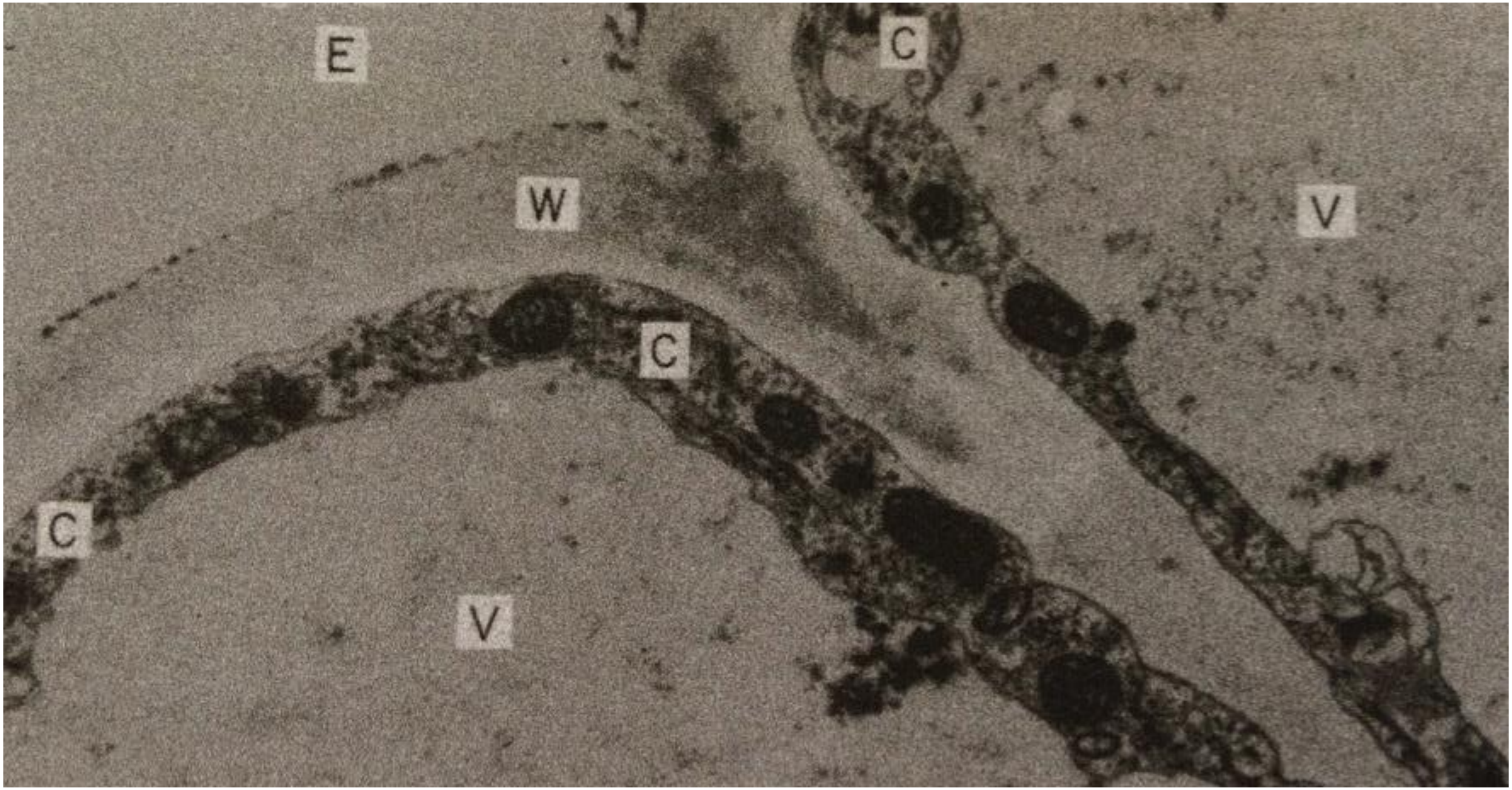
REMEMBER

If it fits through the pore, it can move in the apoplast.
If it needs selectivity, it must go through the membrane.

Donnan Free Space



Water Free Sapce (WFS) Donnan Free Space (DFS)


E
W
C
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C
V
V

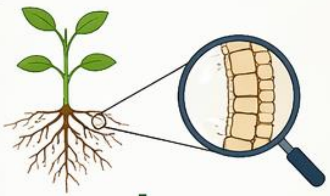
DONNAN SPACE

Why does the root accumulate ions?

Unequal distribution of charges across the plasma membrane creates an electrical potential difference that leads to ion accumulation in the cell (Donnan equilibrium).

THE QUESTION

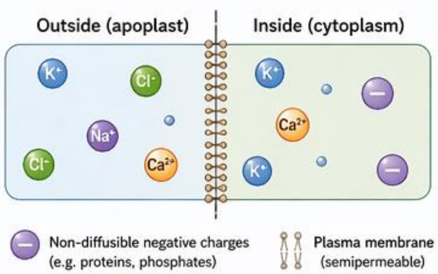
"Why does the root accumulate ions?"



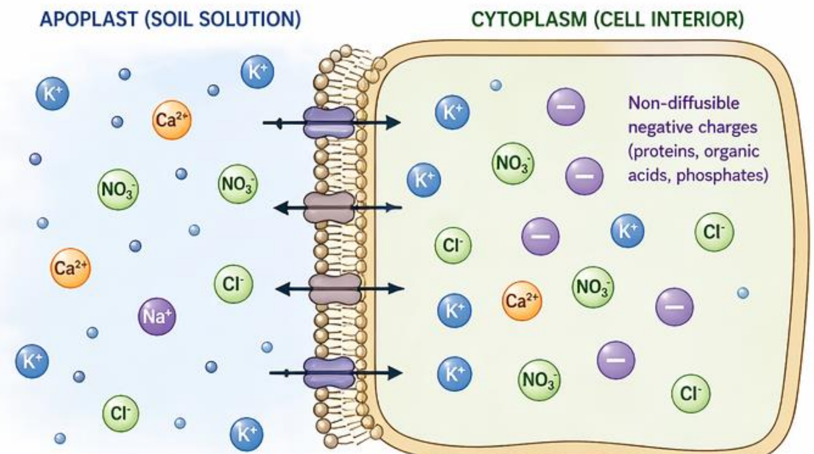
Because of charges and equilibrium!

WHAT IS THE DONNAN EFFECT?

When a membrane separates two solutions and one side contains non-diffusible charged molecules, mobile ions distribute unequally to maintain electrochemical equilibrium.



THE DONNAN EQUILIBRIUM IN ROOT CELLS



Because negative charges cannot cross the membrane, mobile cations (K^+, Ca^{2+}, NH_4^+) accumulate inside to balance the charge.

RESULTS

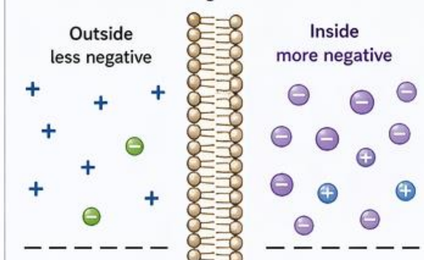
- Electrical potential develops (inside negative)
- Net accumulation of cations inside the cell
- Drives uptake of nutrients from the soil into the root

HOW IT WORKS (STEP BY STEP)

1. **Fixed negative charges** inside the cell (cannot cross the membrane).
2. **Mobile ions** can move, but negative ions are partially excluded.
3. **Cations** move in and accumulate to maintain electrical neutrality.
4. An electrical potential difference (inside negative) is established at equilibrium (Donnan equilibrium).

ELECTRICAL VIEW

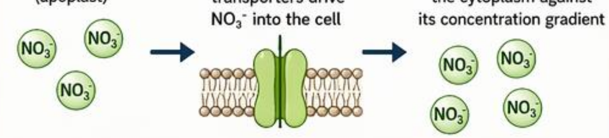
Inside becomes negative relative to outside.



Electrical potential (Ψ)
inside < outside

EXAMPLE: NITRATE UPTAKE

NO_3^- in soil solution (apoplast) → Positive potential and transporters drive NO_3^- into the cell → NO_3^- accumulates in the cytoplasm against its concentration gradient



KEY POINTS

- ✔ The root accumulates ions because of fixed charges.
- ✔ Donnan equilibrium creates an electrical potential.
- ✔ This potential drives nutrient uptake.
- ✔ It is a fundamental mechanism in plant nutrition.

IN A NUTSHELL

Fixed negative charges inside the cell

= Electrical potential → Ion accumulation

→ Efficient nutrient uptake by the root

MEMBRANE / TRANSPORT

Does the plant control what enters... or does everything enter?

Nutrient entry is NOT random.
Plants have selective mechanisms that regulate the uptake and transport of ions and molecules.

KEY QUESTION

Does the plant control what enters... or does everything enter?

✗ EVERYTHING ENTERS → would be toxic!

✓ THE PLANT CONTROLS → selectivity and regulation

WHY IS CONTROL NECESSARY?

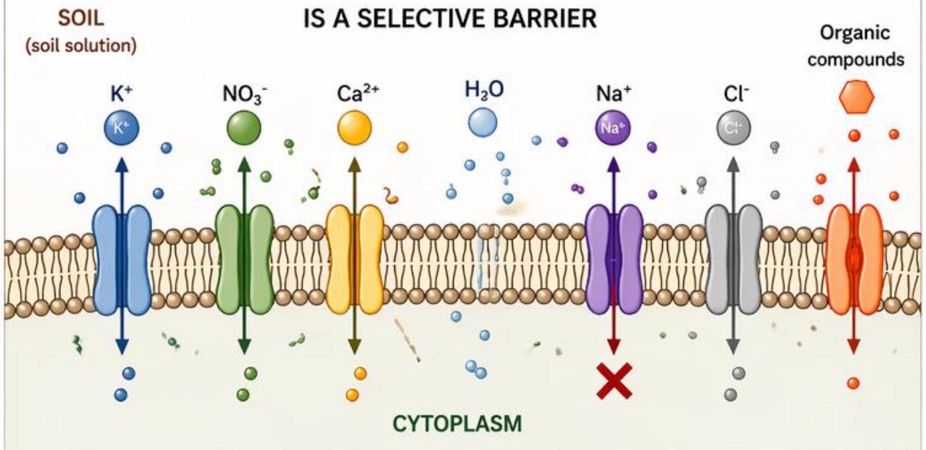
Avoid toxicity
e.g.: excess Na^+, heavy metals

Maintain ionic homeostasis
Balance of charges, osmolarity and pH

Optimize nutrient use
Energy is spent only when needed

Respond to the environment
Availability in soil, plant signals

THE PLASMA MEMBRANE OF ROOT CELLS IS A SELECTIVE BARRIER



MECANISMS OF TRANSPORT

Ion channels (passive)
Open or gated pores
Allow ions to pass down their electrochemical gradient

Transporters (facilitated diffusion)
Specific carriers for each ion or molecule

Pumps (active transport)
Use energy (ATP) to move ions against the gradient

Cotransporters (symport/antiport)
Move two ions together (e.g.: H^+/NO_3^-)

Transporters of compounds (carriers)
For sugars, amino acids, etc.

SELECTIVITY: HOW DOES THE PLANT DECIDE?

1. **Recognition**
   Proteins recognize specific molecules or ions.
2. **Regulation**
   Transporter activity changes according to:
   - nutrient availability
   - plant internal sattus
   - hormonal and environmental signals
3. **Gene expression**
   The plant adjusts the amount of transporters according to its needs.

REAL EXAMPLES

K^+ AKT1 channels allow K^+ entry only when the membrane potential is favorable.

NO_3^- NRT1.1 transporter brings NO_3^- coupled to H^+ (symport) driven by the H^+ gradient.

Na^+ H^+/Na^+ pumps expel Na^+ or sequester it into vacuoles to avoid toxicity.

KEY IDEA

The membrane is not a “passive filter”. It is an intelligent interface that controls the flow of nutrients.

IN SUMMARY

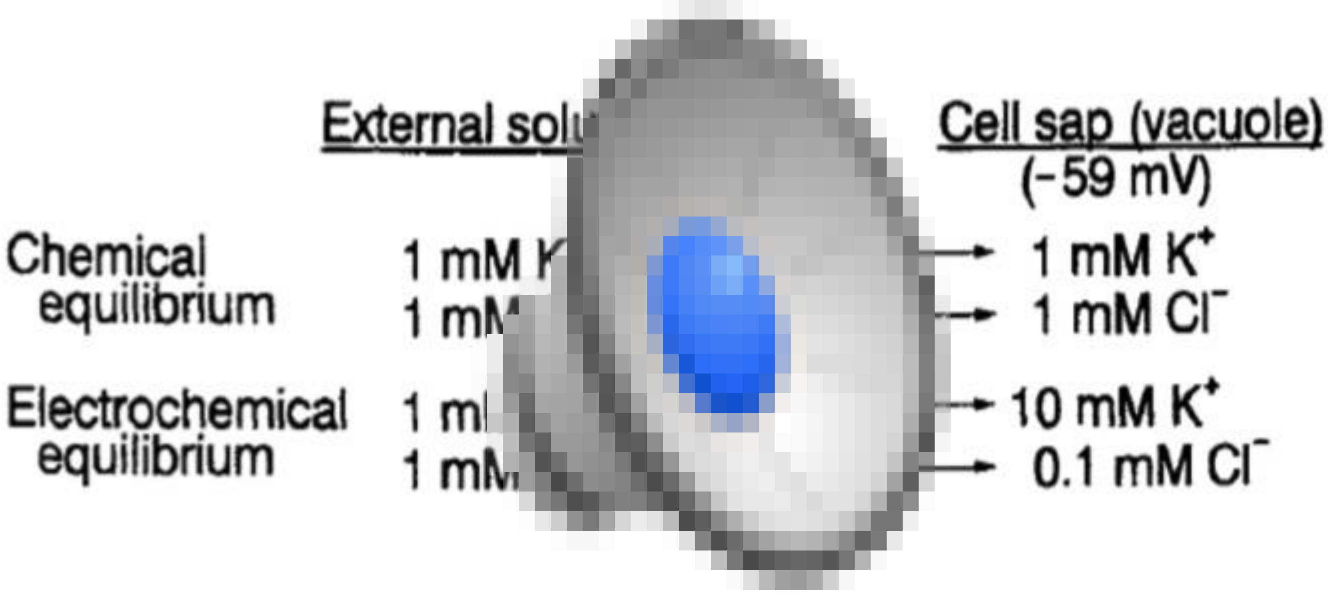
✓ Plants control what enters.
✓ Transport is selective, regulated and energy-efficient.
✓ Without this control, there is no growth or adaptation.

THINK LIKE A PLANT PHYSIOLOGIST

When a nutrient is missing in the plant, it may not be missing in the soil... it may be a transport problem.

A vida com 17 elementos

The Nernst equation:



$$E\ (\mathrm{mV}) = -59 \log \frac{\text{concentration inside (vacuole)}}{\text{concentration outside (external solution)}}$$

The Nernst equation:

	External solution		Cell sap (vacuole) (-59 mV)
Chemical equilibrium	1 mM K^+	⟷	1 mM K^+
	1 mM Cl^-	⟷	1 mM Cl^-
Electrochemical equilibrium	1 mM K^+	⟷	10 mM K^+
	1 mM Cl^-	⟷	0.1 mM Cl^-

$$E\ (\text{mV}) = -59 \log \frac{\text{concentration inside (vacuole)}}{\text{concentration outside (external solution)}}$$

FV- nutrição

Hydroponics

Composition of a modified Hoagland nutrient solution for growing plants

Compound	Molecular weight	Concentration of stock solution	Concentration of stock solution	Volume of stock solution per liter of final solution	Element	Final concentration of element	
	$g\ mol^{-1}$	mM	$g\ L^{-1}$	mL		μM	ppm
Macronutrients							
KNO_3	101.10	1,000	101.10	6.0	N	16,000	224
$Ca(NO_3)_2 \cdot 4H_2O$	236.16	1,000	236.16	4.0	K	6,000	235
$NH_4H_2PO_4$	115.08	1,000	115.08	2.0	Ca	4,000	160
$MgSO_4 \cdot 7H_2O$	246.48	1,000	246.49	1.0	P	2,000	62
					S	1,000	32
					Mg	1,000	24
Micronutrients							
KCl	74.55	25	1.864	2.0	Cl	50	1.77
H_3BO_3	61.83	12.5	0.773		B	25	0.27
$MnSO_4 \cdot H_2O$	169.01	1.0	0.169		Mn	2.0	0.11
$ZnSO_4 \cdot 7H_2O$	287.54	1.0	0.288		Zn	2.0	0.13
$CuSO_4 \cdot 5H_2O$	249.68	0.25	0.062		Cu	0.5	0.03
H_2MoO_4 (85% MoO_3)	161.97	0.25	0.040		Mo	0.5	0.05
NaFeDTPA (10% Fe)	468.20	64	30.0	0.3–1.0	Fe	16.1–53.7	1.00–3.00
Optional[a]							
$NiSO_4 \cdot 6H_2O$	262.86	0.25	0.066	2.0	Ni	0.5	0.03
$Na_2SiO_3 \cdot 9H_2O$	284.20	1,000	284.20	1.0	Si	1,000	28

Source: After Epstein 1972.

Note: The macronutrients are added separately from stock solutions to prevent precipitation during preparation of the nutrient solution. A combined stock solution is made up containing all micronutrients except iron. Iron is added as sodium ferric diethylenetriaminepentaacetate (NaFeDTPA, trade name Ciba-Geigy Sequestrene 330 Fe; see Figure 5.2); some plants, such as maize, require the higher level of iron shown in the table.

[a] Nickel is usually present as a contaminant of the other chemicals, so it may not need to be added explicitly. Silicon, if included, should be added first and the pH adjusted with HCl to prevent precipitation of the other nutrients.

FV- nutrição

Core Rules for Formulating a Nutrient Solution

1. Define target elemental concentrations (not compounds)

RULE: Design for plant requirements first, then choose salts to match those targets

1 DEFINE PLANT REQUIREMENTS

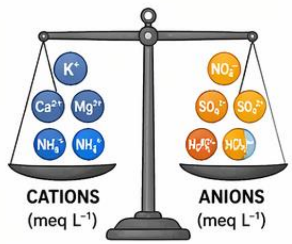
Choose target elemental concentrations (mg L^{-1}) based on crop species, growth stage, and literature guidelines.

EXAMPLE TARGETS (mg L^{-1})

N	150
P	30
K	200
Ca	120
Mg	40
S	60
Fe	2.0
Mn	0.5
Zn	0.3
Cu	0.05
B	0.5
Mo	0.05

2 CONSIDER ELEMENTAL RELATIONSHIPS

Maintain appropriate ratios and balance between cations and anions.



CHECK:
- ✓ Total cations ≈ total anions (meq L^{-1})
- ✓ Keep key ratios in range: K:Ca:Mg, NO_3:NH_4, NH_4:K, Ca:Mg, etc.

3 CALCULATE SALT REQUIREMENTS

Convert target elemental concentrations to the amount of each salt needed.

HOW:
1. Choose a salt as the source of the element.
2. Use stoichiometry to calculate how much salt provides the target element.
3. Accounts for % of element in the salt.

EXAMPLE

Target P = 30 mg L^{-1}
Use KH_2PO_4 (P = 22.7%)

Salt (mg L^{-1}) = $\frac{\text{Target P}}{\text{(P fraction in salt)}} = \frac{30}{0.227} =$ 132 mg L^{-1}

4 CHECK AND ADJUST

Recalculate the elemental concentrations contributed by all salts.

Verify that:
- ✓ All target elements are met
- ✓ No element is excessive or deficient
- ✓ Charge balance (meq L^{-1}) is maintained
- ✓ pH and EC are in the acceptable range

5 PREPARE THE SOLUTION AND VALIDATE

Dissolve salts in the correct order, make up to final volume, and verify.

ORDER OF ADDITION (example)

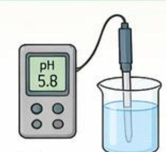
1. Calcium salts (e.g., $Ca(NO_3)_2$) ↓
2. Macronutrient salts (without phosphate) ↓
3. Phosphate source (KH_2PO_4, K_2HPO_4) ↓
4. Micronutrient mix ↓
5. Adjust pH ↓
6. Make up to final volume

KEY PRINCIPLES

- Design based on elemental needs, not on specific salts.
- Plants absorb elements, not compounds.
- Balance cations and anions (meq L^{-1}).
- Verify, adjust, and recheck all targets.
- Small changes in one element can affect others.

GOOD PRACTICES

- Use high-purity salts and clean water.
- Monitor pH (5.5–6.5) and EC.
- Recheck solution after mixing.
- Adjust based on plant response and tissue analysis.



BOTTOM LINE: Define elemental targets → balance → calculate salts → verify → prepare → monitor.

Design for plant requirements first, then choose salts to match those targets.

GOOD PRACTICES WHEN FORMULATING NUTRIENT SOLUTIONS

Goal: Provide balanced nutrition, avoid toxicity/deficiency, and maintain solution stability and plant health

1 DEFINE TARGET ELEMENTAL CONCENTRATIONS (NOT COMPOUNDS)

Base on plant requirements at the target growth stage.

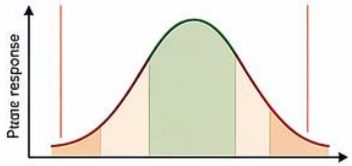
Example (mg L^{-1})

Macronutrients		Micronutrients	
N	150	Fe	2.0
P	30	Mn	0.5
K	200	Zn	0.3
Ca	150	Cu	0.05
Mg	50	B	0.5
S	60	Mo	0.05

✓ Work with elemental targets, not salt amounts.

2 RESPECT CONCENTRATION RANGES (TOXICITY vs DEFICIENCY)

Keep each nutrient within established physiological ranges.



✓ Stay within the optimal window for each nutrient.

3 CONSIDER PLANT TYPE AND GROWTH STAGE

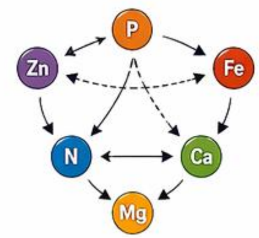
Adjust formulations to crop type, development stage, and production goals.

- More N in vegetative
- More P, K in flowering
- More K, Ca in fruiting

✓ C_3, C_4, CAM and species have different needs.

4 CONSIDER INTERACTIONS AND ANTAGONISMS

Balance nutrients to avoid antagonism and hidden deficiencies.



✓ Avoid excess of one nutrient that limits another.

5 USE HIGH-QUALITY, COMPATIBLE FERTILIZERS

Choose pure, soluble, and compatible fertilizers.

Good practices
- ✓ High purity (>98%)
- ✓ Fully water soluble
- ✓ Low impurities (Cl^-, Na^+, heavy metals)
- ✓ Compatible in solution

Avoid
- Insoluble residues
- Precipitates
- High Cl^- or Na^+ (unless tolerated)
- Unknown quality

✓ Test new fertilizers before large-scale use.

6 ADJUST FORMULATION BASED ON WATER QUALITY

Water chemistry affects nutrient availability and stability.

Key water parameters
- pH
- EC (salinity)
- Alkalinity (HCO_3^-)
- Hardness (Ca^{2+}, Mg^{2+})
- Sodium (Na^+)
- Chloride (Cl^-)

Actions
- Acidify high pH water
- Account for alkalinity
- Watch for precipitation (Ca, Mg, Fe, P)
- Adjust nutrient doses based on EC

✓ Analyze every new water source.

7 SEQUENCE AND MIX CORRECTLY

Add fertilizers in the right order to prevent precipitation.

General order of addition
1. Water
2. Calcium nitrate
3. Monopotassium phosphate (or phosphates)
4. Micronutrients (chelated)
5. Others (Mg, K, S, etc.)

Avoid mixing
- Ca^{2+} + PO_4^{2-}
- Ca^{2+} + SO_4^{2-} (concentrated)
- Fe^{3+} with phosphates
- Concentrated micronutrients together

✓ Add one at a time, mix well, then proceed.

8 MONITOR AND MAINTAIN PH AND EC

pH and EC strongly influence nutrient availability and plant uptake.

Target pH range

4.5 — 5.5 — 6.0 — 6.5 — 7.0 — 7.5

← Optimal for most crops 5.5 – 6.5 →

Monitor EC (salinity)

Adjust to crop tolerance

- Low EC: Deficiency risk
- Optimal EC: Best growth
- High EC: Stress risk

✓ Check pH and EC regularly and adjust as needed.

9 CHECK FOR PRECIPITATION AND SOLUTION CLARITY

Precipitates reduce availability and can clog systems.

- Good solution ✓
- Bad solution ✗

✓ If cloudiness or precipitate forms, reformulate/adjust pH or order of mixing.

10 VERIFY PLANT RESPONSE AND ADAPT

Plants are the ultimate test.

- Observe growth and color
- Check for deficiency/toxicity symptoms
- Tissue or sap analysis
- Adjust formulation as needed

✓ Nutrition management is an adaptive process.

KEY TAKE-HOME MESSAGE

Good nutrient solutions are based on science, not guesswork.
Define elemental targets, respect ranges, consider plant and water, manage interactions, monitor continuously, and adapt for optimal plant growth and productivity.

- Balanced nutrition
- Prevent toxicity
- Maximize growth and yield
- Protect water environment
- Improve efficiency and profitability

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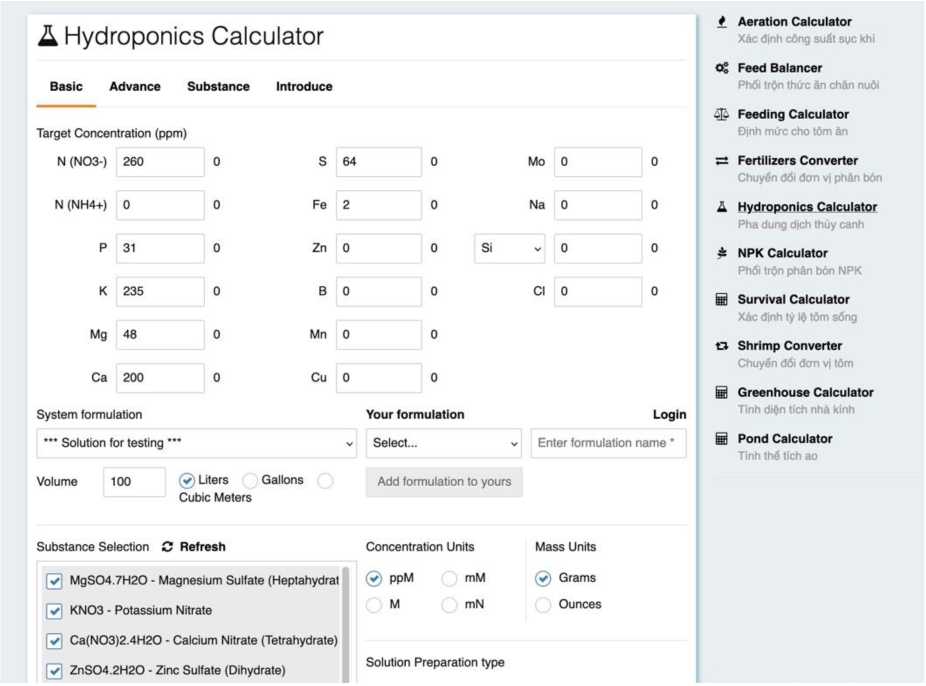
Core Rules for Formulating a Nutrient Solution



https://www.2lua.vn/agritec/hydroponics-calculator.html?hl=en

You can see the basics of an hydroponic calculator that
Combines plants needs with the available chemicals in order to rich a certain production.

Try!

Hidroponia

✓Estabelece através da **experimentação** o carácter **puramente mineral** da nutrição vegetal.

- ✓Análise da composição química das cinzas
- ✓Hidroponia

Lei do mínimo

Hidroponia

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Analysis of Plant Tissues Reveals Mineral Deficiencies

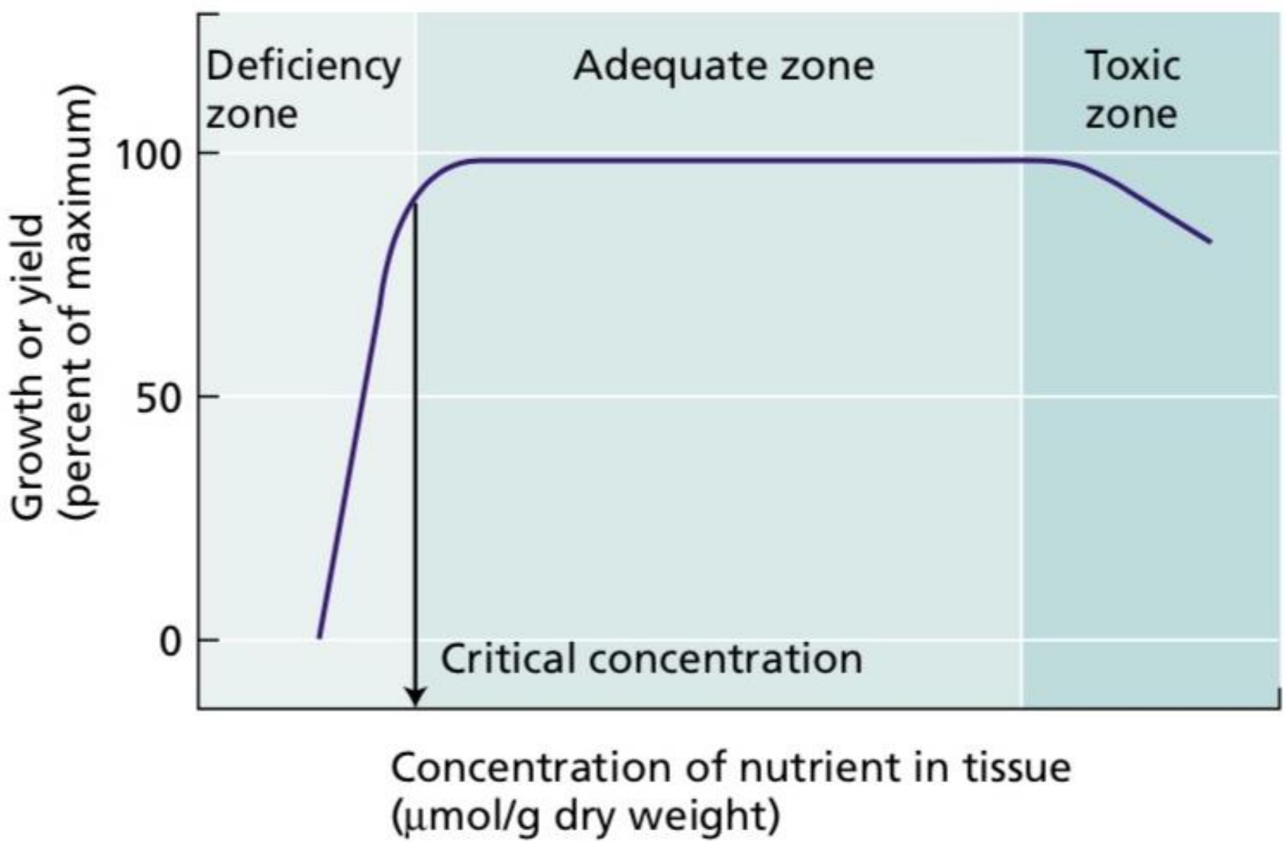

FIGURE 5.3 Relationship between yield (or growth) and the nutrient content of the plant tissue. The yield parameter may be expressed in terms of shoot dry weight or height. Three zones—deficiency, adequate, and toxic—are indicated on the graph. To yield data of this type, plants are grown under conditions in which the concentration of one essential nutrient is varied while all others are in adequate supply. The effect of varying the concentration of this nutrient during plant growth is reflected in the growth or yield. The critical concentration for that nutrient is the concentration below which yield or growth is reduced.

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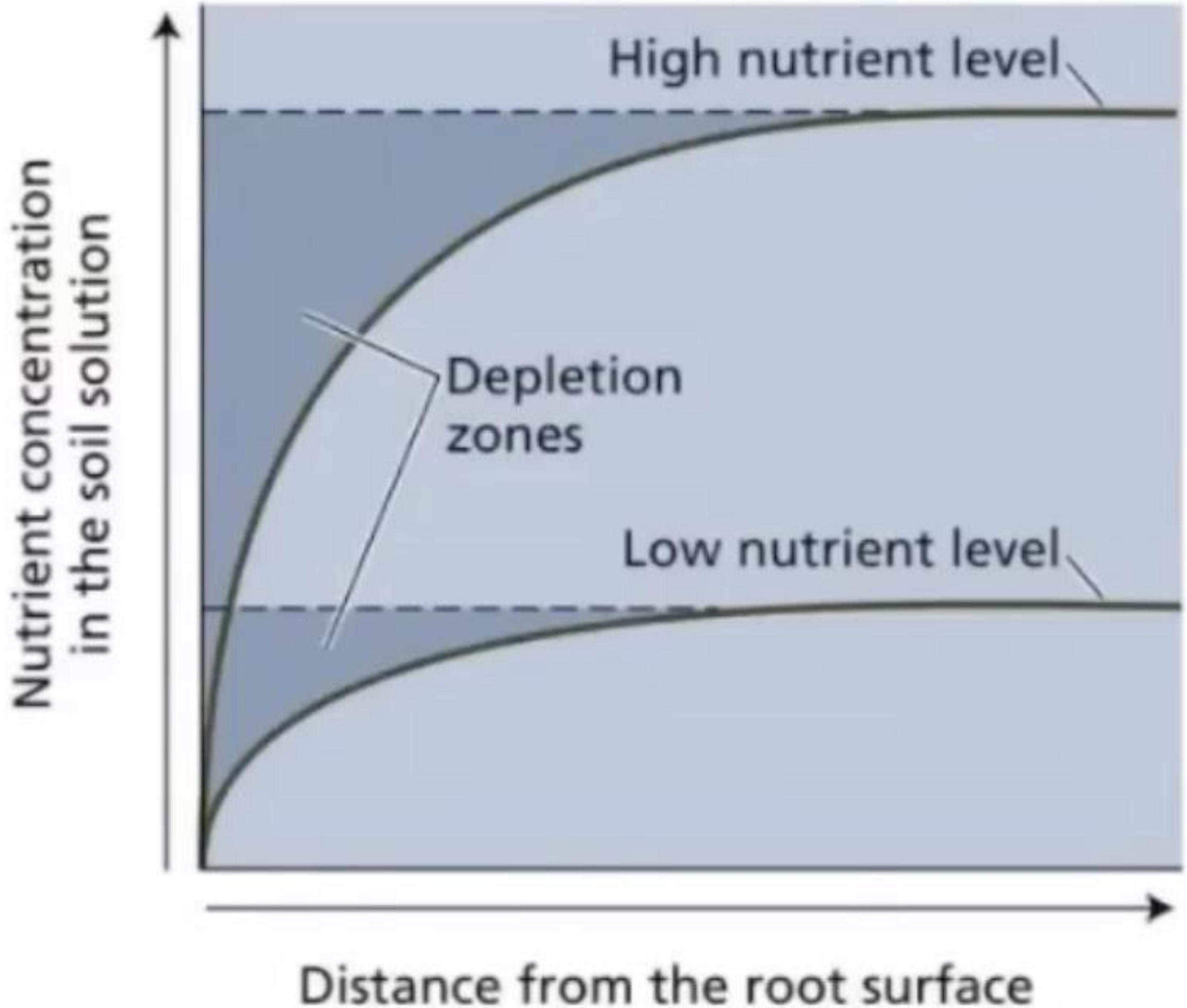
High nutrient level
Depletion zones
Low nutrient level
Nutrient concentration in the soil solution
Distance from the root surface

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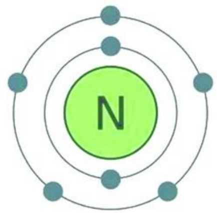
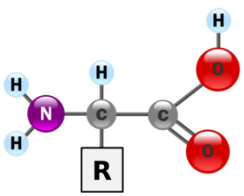
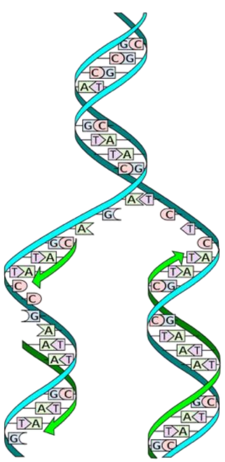
Group 1: Deficiencies in mineral nutrients that are part of carbon compounds



nitrogen deficiency rapidly inhibits plant growth.





most species show chlorosis (yellowing of the leaves), especially in the older

Under severe nitrogen deficiency, these leaves become completely yellow (or tan) and fall off the plant.

Younger leaves may not show these symptoms initially because nitrogen can be mobilized from older leaves.

Thus a nitrogen-deficient plant may have light green upper leaves and yellow or tan lower leaves.

Group 1: Deficiencies in mineral nutrients that are part of carbon compounds

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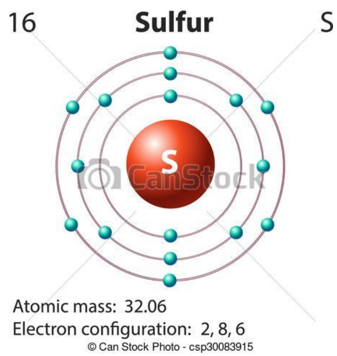
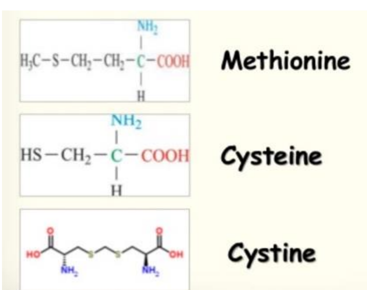
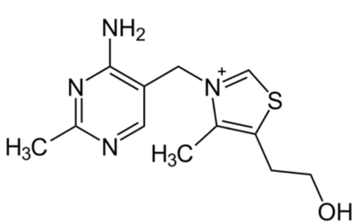


SULFUR. deficiency are similar to those of nitrogen deficiency, including chlorosis, stunting of growth, and anthocyanin accumulation.





Thiamine – vitamine B

This similarity is not surprising, since sulfur and nitrogen are both constituents of proteins.

However, the chlorosis caused by sulfur deficiency generally arises **initially in mature and young leaves, rather than in the old leaves as in nitrogen deficiency**, because unlike nitrogen, sulfur is not easily remobilized to the younger leaves in most species.

Group 2: Deficiencies in mineral nutrients important in energy storage or structural integrity

(P, Si, B)

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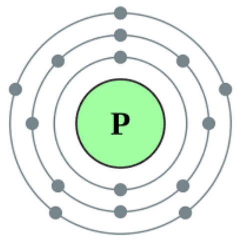
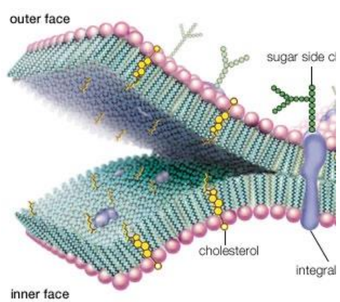
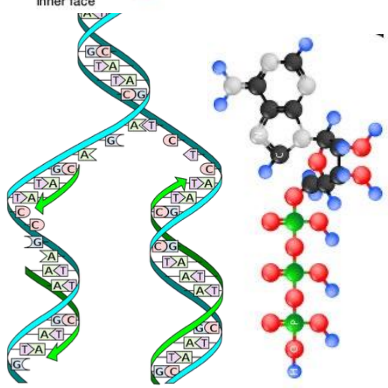


PHOSPHORUS. deficiency symptoms include stunted growth in young plants and a dark green coloration of the leaves, which may be mal- formed and contain small spots of dead tissue called **necrotic spots.**





As in nitrogen deficiency, some species may produce excess anthocyanins, giving the leaves a slight purple coloration.

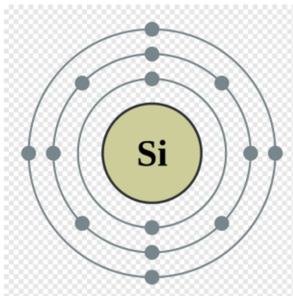
In contrast to nitrogen deficiency, the purple coloration of phosphorus deficiency is not associated with chlorosis.

In fact, the leaves may be a dark greenish purple. Additional symptoms include the production of slender (but not woody) stems and the death of older leaves. Maturation of the plant may also be delayed.

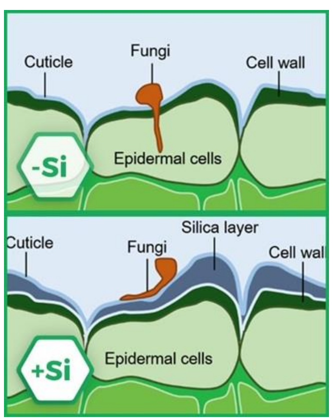
F526 × 656 V-nutrição

Group 2: Deficiencies in mineral nutrients important in energy storage or structural integrity

(P, Si, B)

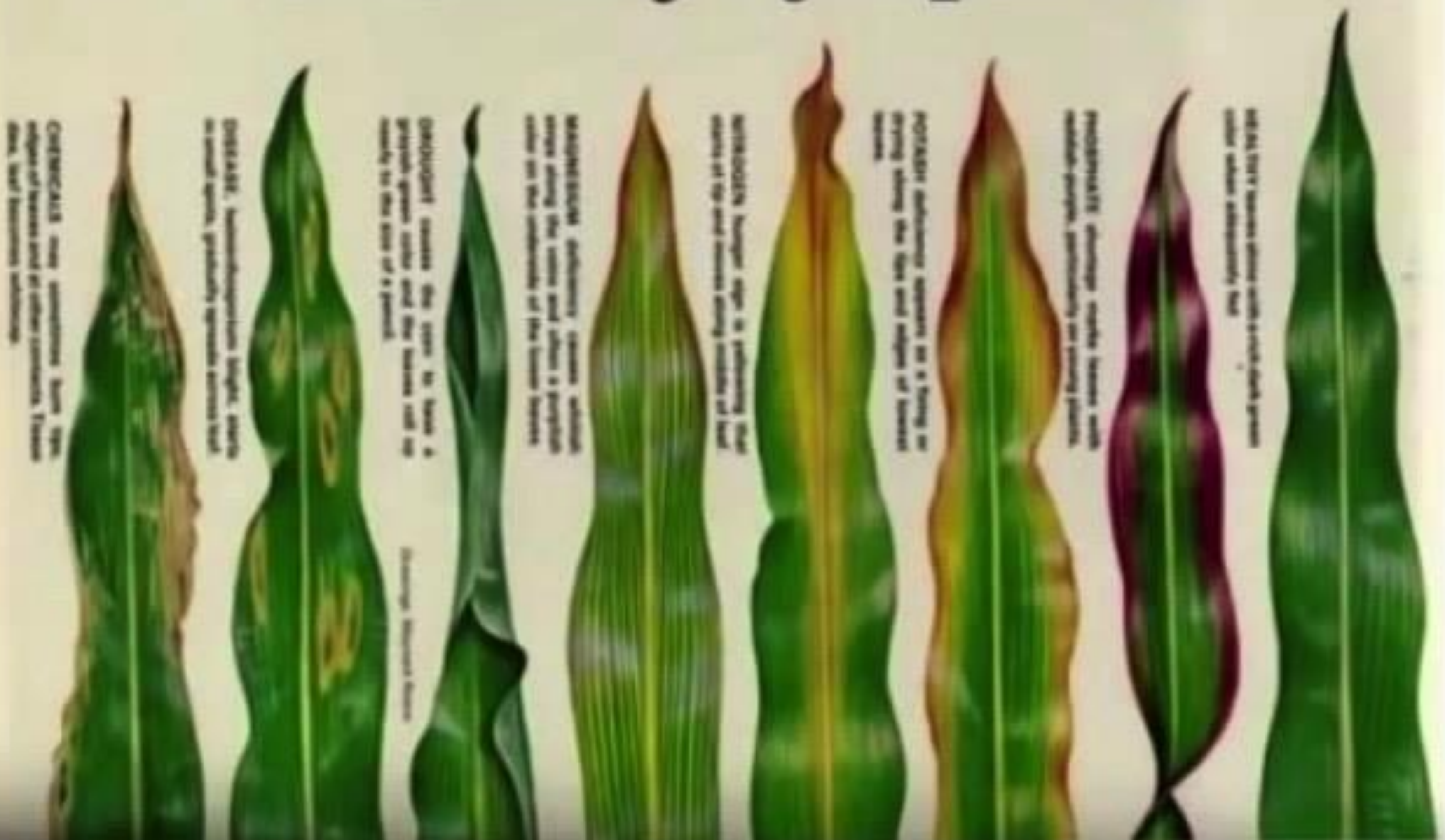


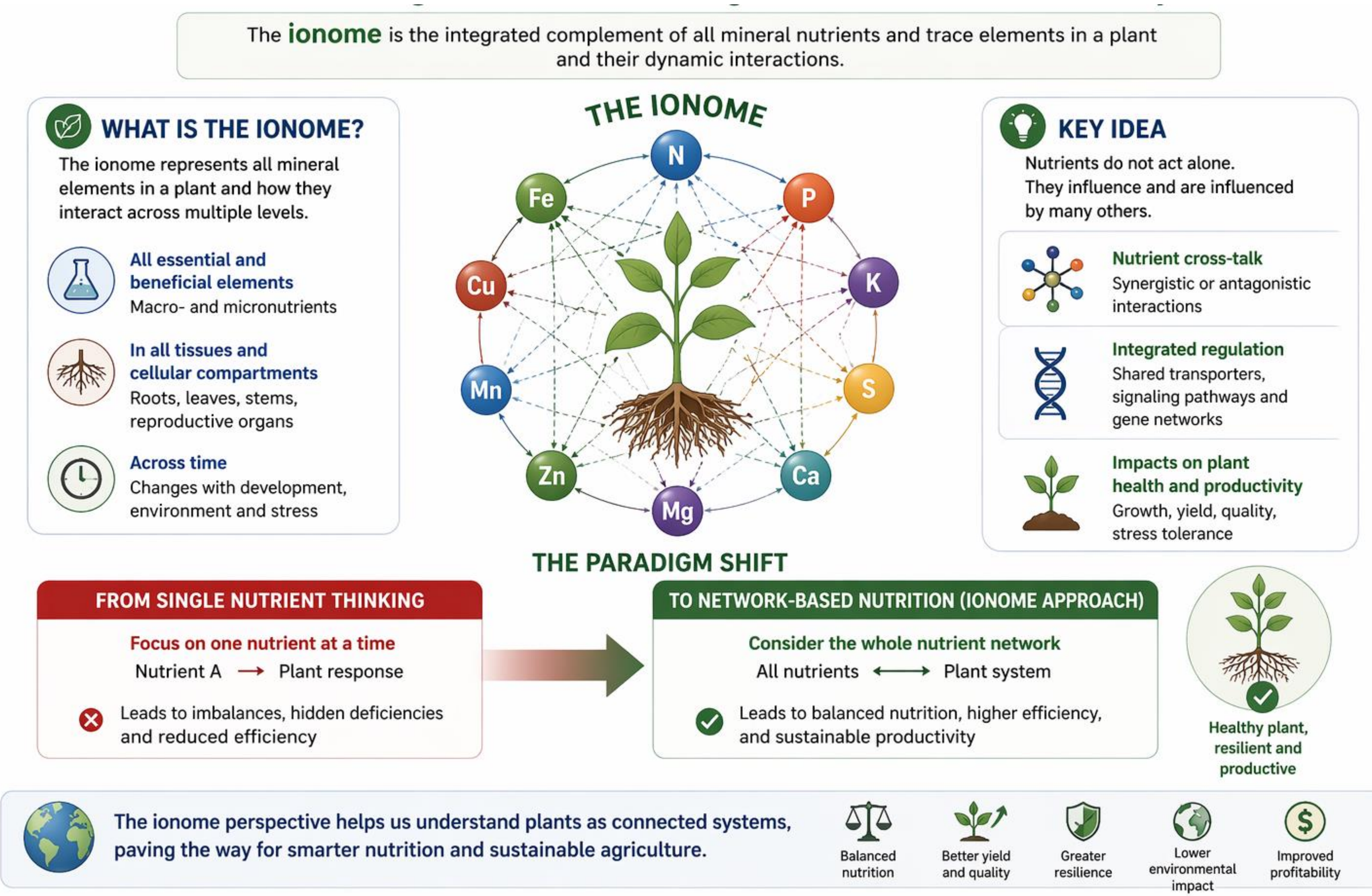
SILICON. Only **Equisetaceae plants** require silicon to complete their life cycle. Many other species accumulate substantial amounts of silicon within their tissues and show enhanced growth and fertility when supplied with adequate amounts of silicon (Epstein 1999).



Plants deficient in silicon are more susceptible to lodging and fungal infection. Silicon is deposited primarily in the endoplasmic reticulum, cell walls, and intercellular spaces as hydrated, amorphous silica ($SiO_2 \cdot nH_2O$). It also forms complexes with polyphenols and thus serves as an alternative to lignin in the reinforcement of cell walls. In addition, silicon can ameliorate the toxicity of many heavy metals.

Guide to Nutrient Deficiency Symptoms




The ionome is the integrated complement of all mineral nutrients and trace elements in a plant and their dynamic interactions.
WHAT IS THE IONOME?
The ionome represents all mineral elements in a plant and how they interact across multiple levels.
All essential and beneficial elements
Macro- and micronutrients
In all tissues and cellular compartments
Roots, leaves, stems, reproductive organs
Across time
Changes with development, environment and stress
THE IONOME
N
P
K
S
Ca
Mg
Zn
Mn
Cu
Fe
KEY IDEA
Nutrients do not act alone.
They influence and are influenced by many others.
Nutrient cross-talk
Synergistic or antagonistic interactions
Integrated regulation
Shared transporters, signaling pathways and gene networks
Impacts on plant health and productivity
Growth, yield, quality, stress tolerance
THE PARADIGM SHIFT
FROM SINGLE NUTRIENT THINKING
Focus on one nutrient at a time
Nutrient A → Plant response
Leads to imbalances, hidden deficiencies and reduced efficiency
TO NETWORK-BASED NUTRITION (IONOME APPROACH)
Consider the whole nutrient network
All nutrients ⟷ Plant system
Leads to balanced nutrition, higher efficiency, and sustainable productivity
Healthy plant, resilient and productive
The ionome perspective helps us understand plants as connected systems, paving the way for smarter nutrition and sustainable agriculture.
Balanced nutrition
Better yield and quality
Greater resilience
Lower environmental impact
Improved profitability

Interactions between Ions in the Rhizosphere

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New Phytologist

Review

Tansley review

Linking the key physiological functions of essential micronutrients to their deficiency symptoms in plants

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Cross-Talks Between Macro- and Micronutrient Uptake and Signaling in Plants

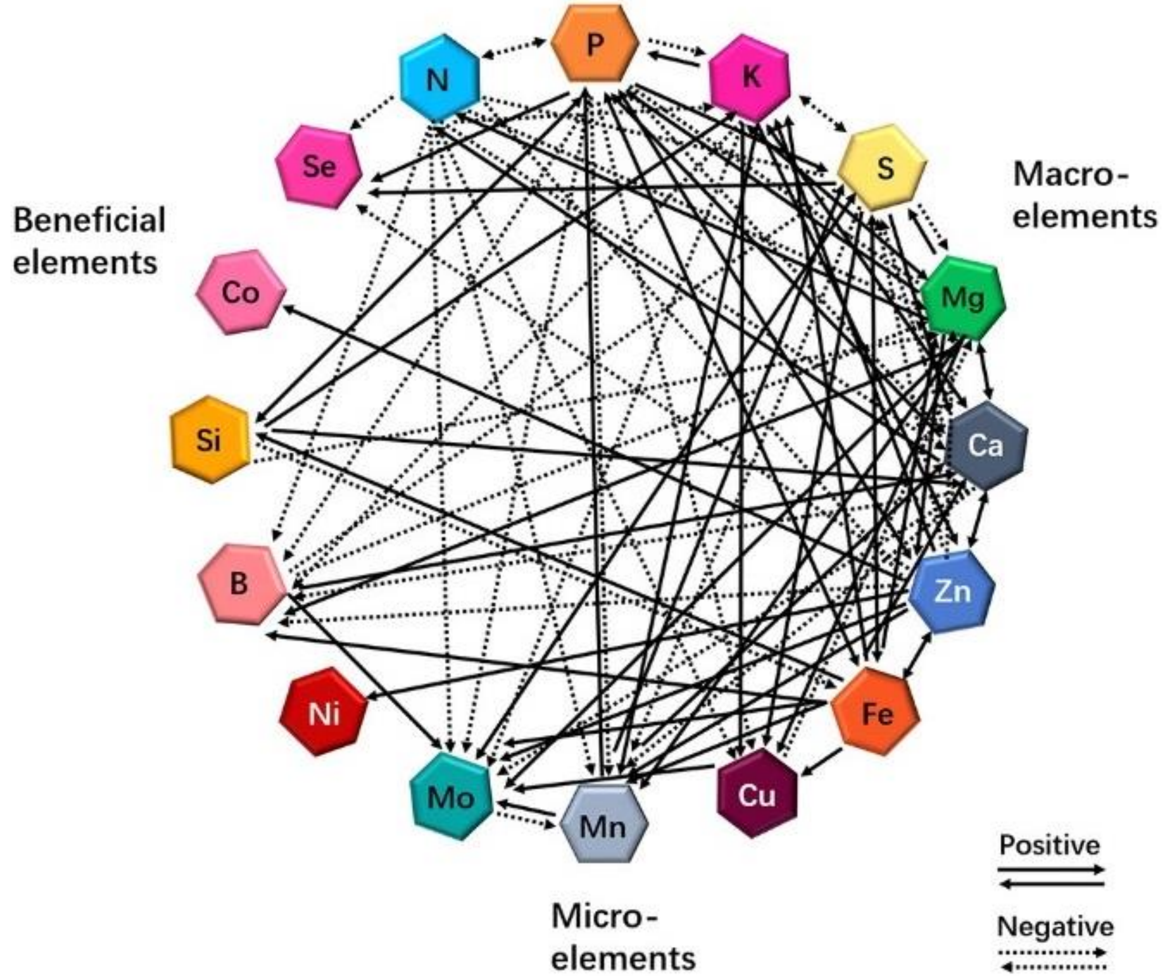
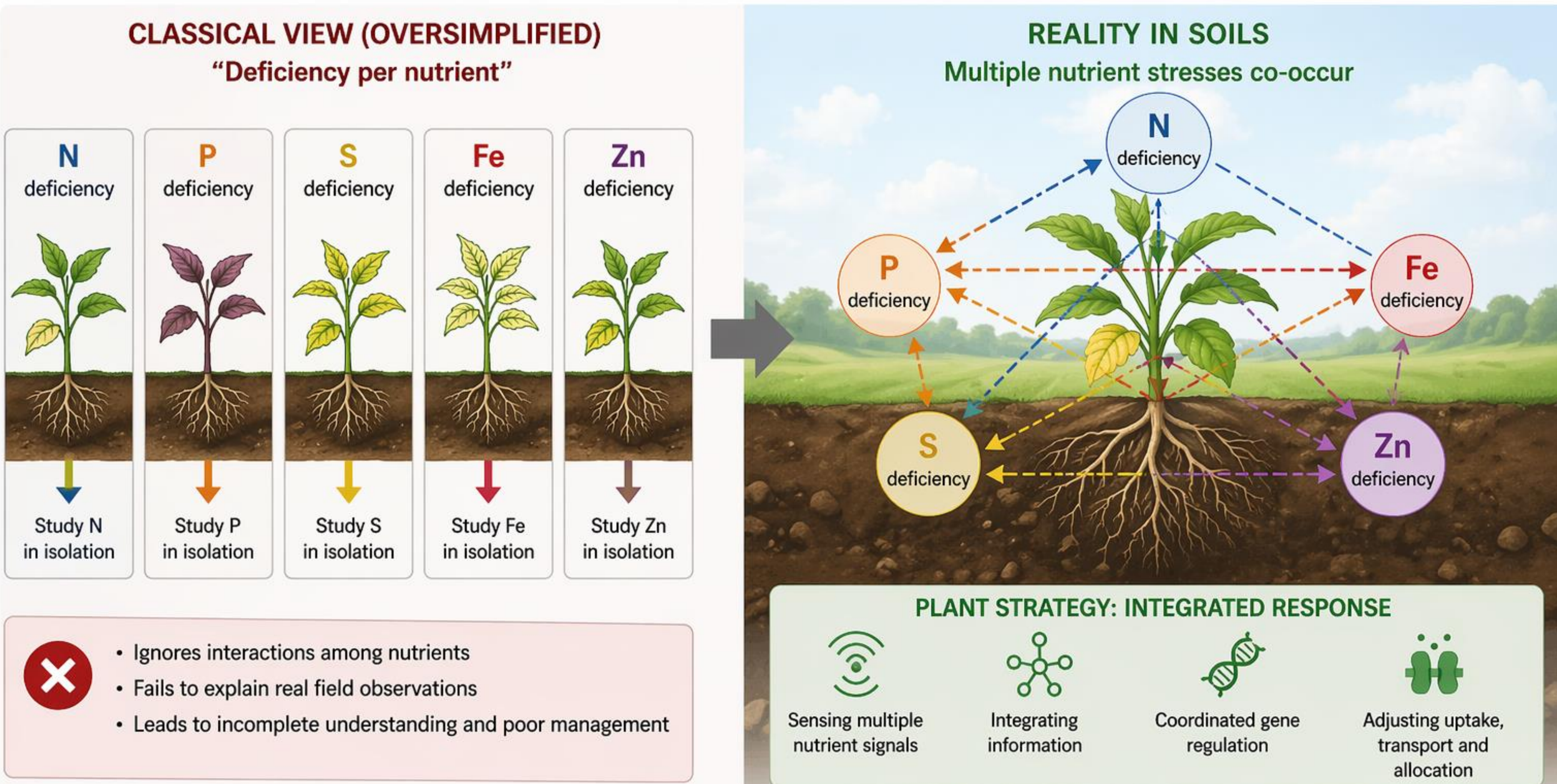


FIGURE 1 | Cross-talks between macro- and micro-elements or beneficial elements in plants in response to individual mineral deficiency. Interactions resulting from single-element deficiency (any one of 16 elements) lead to enhanced (solid lines) or decreased (dashed lines) uptake of other minerals. Updated from the previous publications (Bokor et al., 2015; Rai et al., 2015; Maillard et al., 2016; Courbet et al., 2019; Chaiwong et al., 2020; Zhou et al., 2020; Ji et al., in press).

doi: 10.3389/fpls.2021.663477

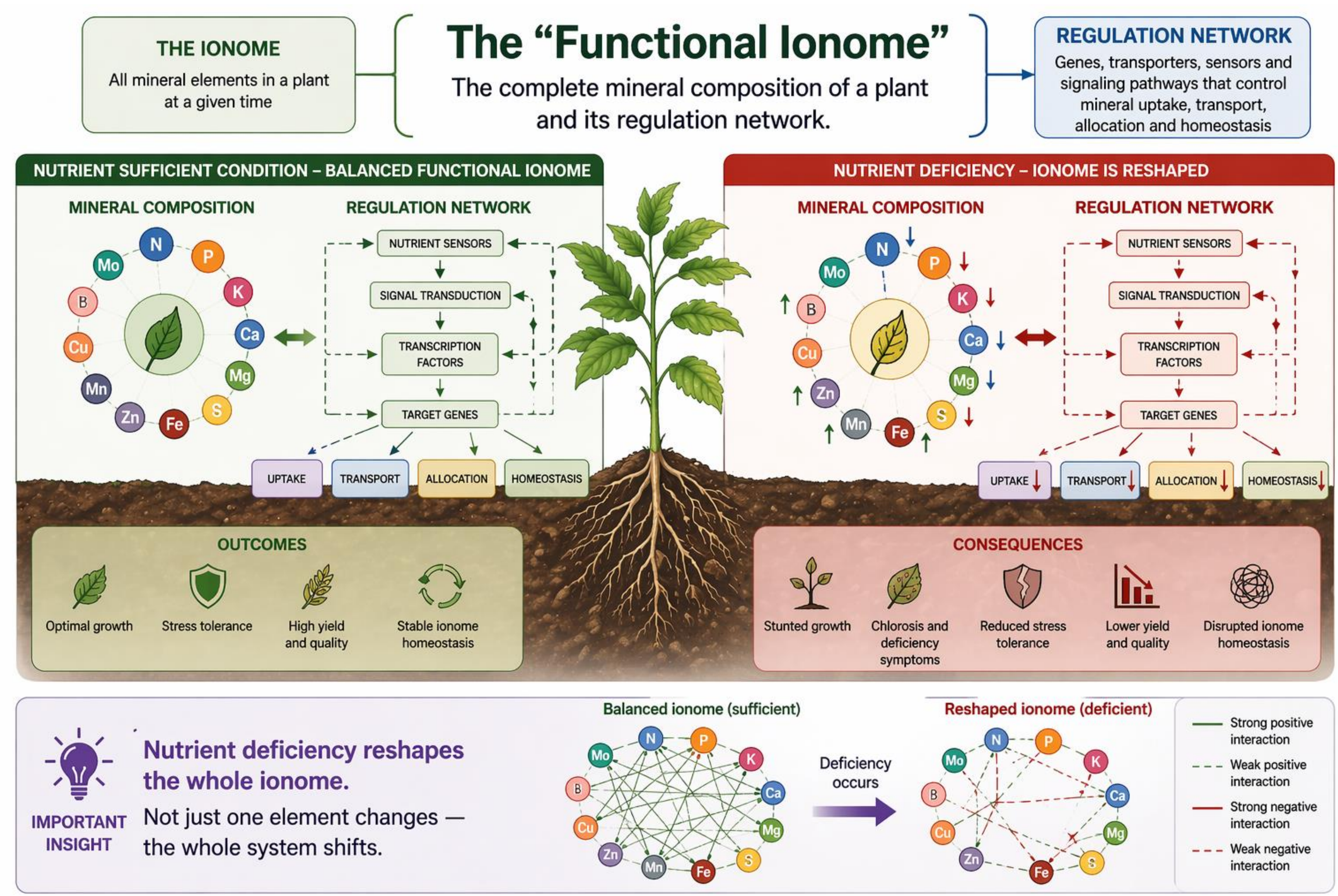
1. Plants Experience MULTIPLE Nutrient Stresses Simultaneously

In real soils, N, P, S, Fe, Zn deficiencies co-occur.
Plants evolved mechanisms to coordinate responses, not isolate them.

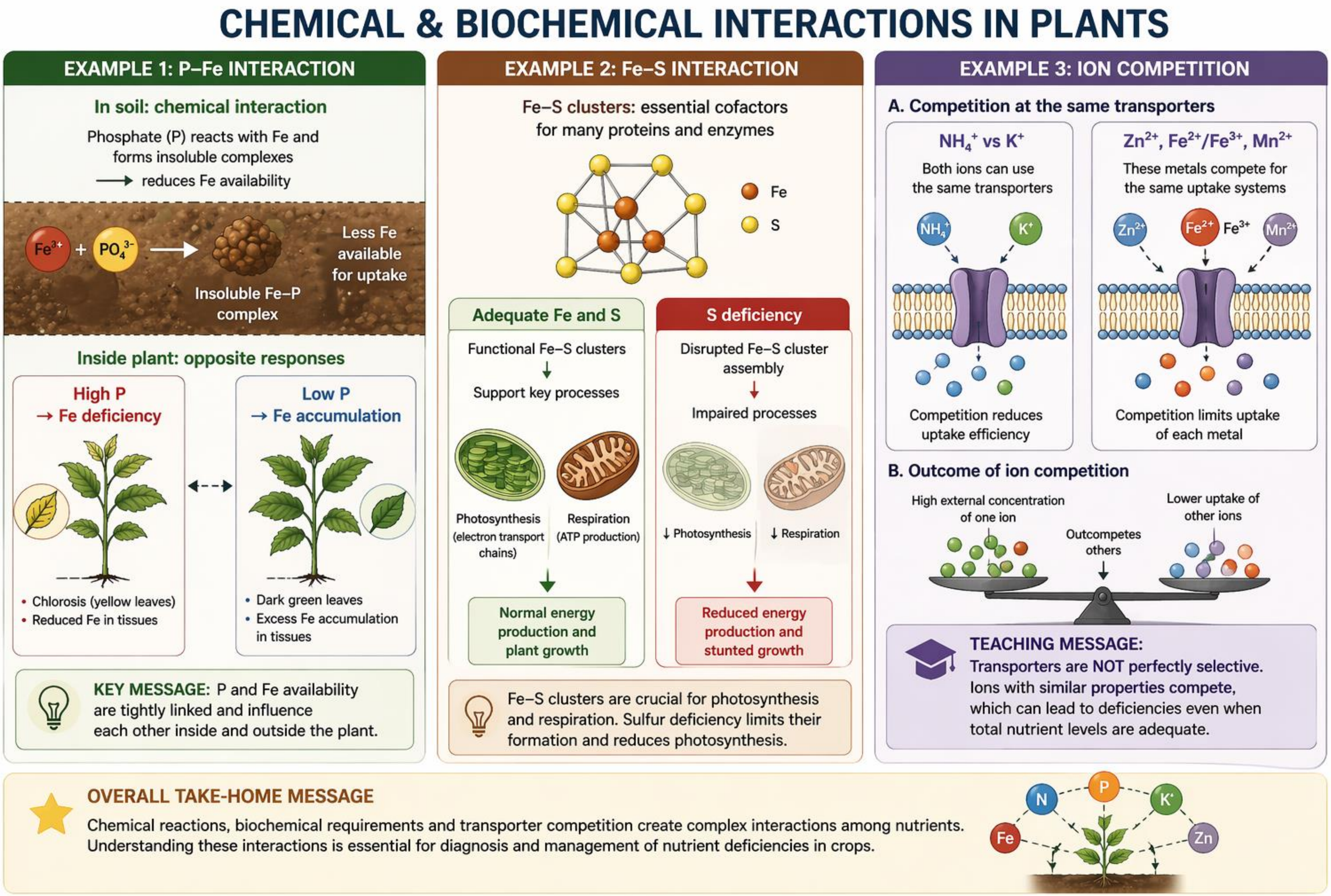


TEACHING POINT: Plants do not respond to nutrients one by one. They coordinate responses to multiple, interacting nutrient stresses.

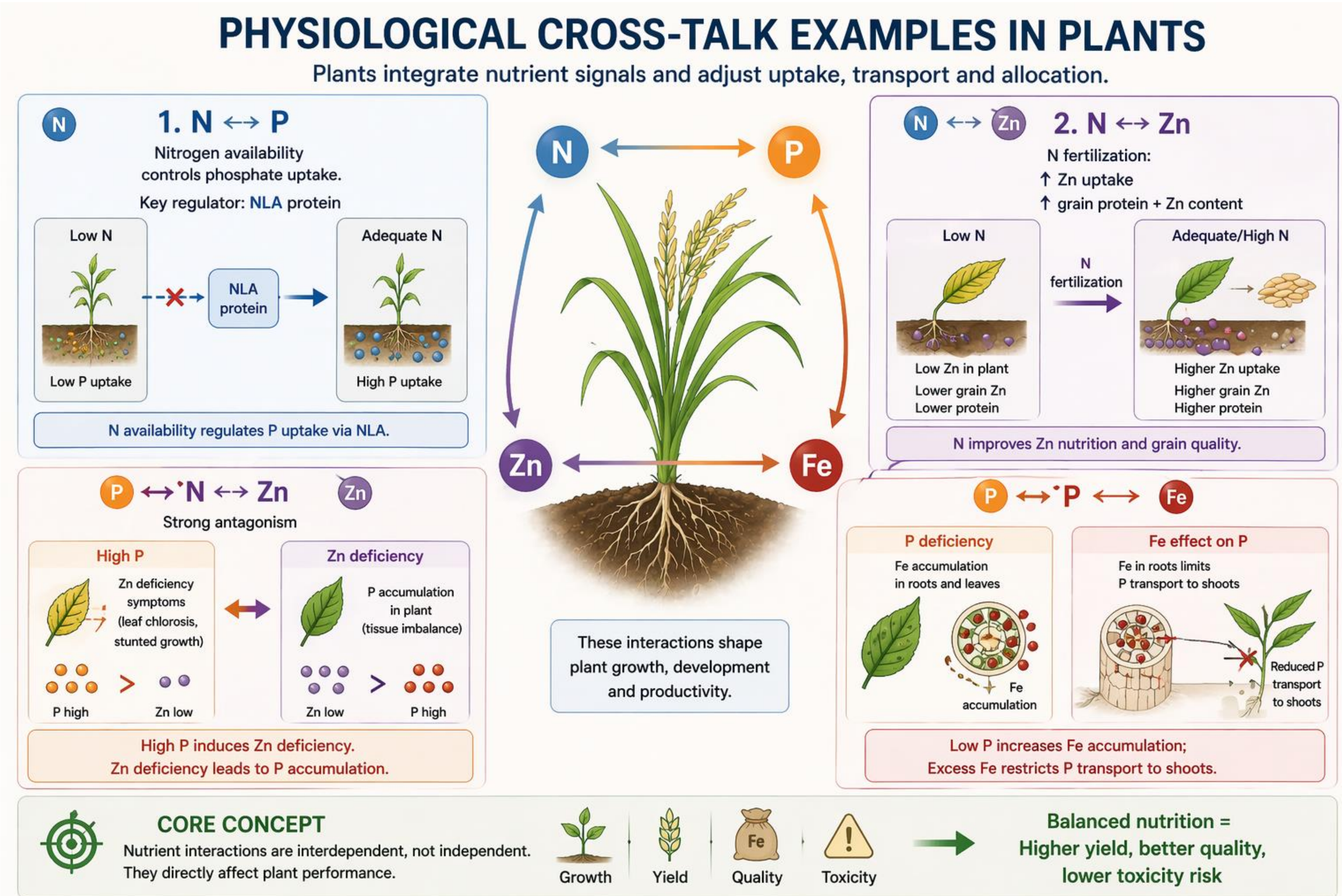
Think "NETWORK", not "ISOLATED NUTRIENTS".



THE IONOME
All mineral elements in a plant at a given time
The "Functional Ionome"
The complete mineral composition of a plant and its regulation network.
REGULATION NETWORK
Genes, transporters, sensors and signaling pathways that control mineral uptake, transport, allocation and homeostasis
NUTRIENT SUFFICIENT CONDITION – BALANCED FUNCTIONAL IONOME
MINERAL COMPOSITION
N
P
K
Ca
Mg
S
Fe
Zn
Mn
Cu
B
Mo
REGULATION NETWORK
NUTRIENT SENSORS
SIGNAL TRANSDUCTION
TRANSCRIPTION FACTORS
TARGET GENES
UPTAKE
TRANSPORT
ALLOCATION
HOMEOSTASIS
NUTRIENT DEFICIENCY – IONOME IS RESHAPED
MINERAL COMPOSITION
REGULATION NETWORK
NUTRIENT SENSORS
SIGNAL TRANSDUCTION
TRANSCRIPTION FACTORS
TARGET GENES
UPTAKE
TRANSPORT
ALLOCATION
HOMEOSTASIS
OUTCOMES
Optimal growth
Stress tolerance
High yield and quality
Stable ionome homeostasis
CONSEQUENCES
Stunted growth
Chlorosis and deficiency symptoms
Reduced stress tolerance
Lower yield and quality
Disrupted ionome homeostasis
IMPORTANT INSIGHT
Nutrient deficiency reshapes the whole ionome.
Not just one element changes — the whole system shifts.
Balanced ionome (sufficient)
Deficiency occurs
Reshaped ionome (deficient)
Strong positive interaction
Weak positive interaction
Strong negative interaction
Weak negative interaction



CHEMICAL & BIOCHEMICAL INTERACTIONS IN PLANTS
EXAMPLE 1: P–Fe INTERACTION
In soil: chemical interaction
Phosphate (P) reacts with Fe and forms insoluble complexes
→ reduces Fe availability
Fe^{3+} + PO_4^{3-} →
Insoluble Fe–P complex
Less Fe available for uptake
Inside plant: opposite responses
High P → Fe deficiency
• Chlorosis (yellow leaves)
• Reduced Fe in tissues
Low P → Fe accumulation
• Dark green leaves
• Excess Fe accumulation in tissues
KEY MESSAGE: P and Fe availability are tightly linked and influence each other inside and outside the plant.
EXAMPLE 2: Fe–S INTERACTION
Fe–S clusters: essential cofactors for many proteins and enzymes
Fe
S
Adequate Fe and S
Functional Fe–S clusters
Support key processes
Photosynthesis (electron transport chains)
Respiration (ATP production)
Normal energy production and plant growth
S deficiency
Disrupted Fe–S cluster assembly
Impaired processes
↓ Photosynthesis
↓ Respiration
Reduced energy production and stunted growth
Fe–S clusters are crucial for photosynthesis and respiration. Sulfur deficiency limits their formation and reduces photosynthesis.
EXAMPLE 3: ION COMPETITION
A. Competition at the same transporters
NH_4^+ vs K^+
Both ions can use the same transporters
NH_4^+
K^+
Competition reduces uptake efficiency
Zn^{2+}, Fe^{2+}/Fe^{3+}, Mn^{2+}
These metals compete for the same uptake systems
Zn^{2+}
Fe^{2+} Fe^{3+}
Mn^{2+}
Competition limits uptake of each metal
B. Outcome of ion competition
High external concentration of one ion
Outcompetes others
Lower uptake of other ions
TEACHING MESSAGE:
Transporters are NOT perfectly selective. Ions with similar properties compete, which can lead to deficiencies even when total nutrient levels are adequate.
OVERALL TAKE-HOME MESSAGE
Chemical reactions, biochemical requirements and transporter competition create complex interactions among nutrients. Understanding these interactions is essential for diagnosis and management of nutrient deficiencies in crops.
N
P
K^+
Fe
Zn



PHYSIOLOGICAL CROSS-TALK EXAMPLES IN PLANTS
Plants integrate nutrient signals and adjust uptake, transport and allocation.
N
1. N ↔ P
Nitrogen availability controls phosphate uptake.
Key regulator: NLA protein
Low N
NLA protein
Adequate N
Low P uptake
High P uptake
N availability regulates P uptake via NLA.
N
P
Zn
Fe
N ↔ Zn
2. N ↔ Zn
N fertilization:
↑ Zn uptake
↑ grain protein + Zn content
Low N
N fertilization
Adequate/High N
Low Zn in plant
Lower grain Zn
Lower protein
Higher Zn uptake
Higher grain Zn
Higher protein
N improves Zn nutrition and grain quality.
P ↔ N ↔ Zn
Zn
Strong antagonism
High P
Zn deficiency symptoms (leaf chlorosis, stunted growth)
P high
Zn low
Zn deficiency
P accumulation in plant (tissue imbalance)
Zn low
P high
High P induces Zn deficiency.
Zn deficiency leads to P accumulation.
These interactions shape plant growth, development and productivity.
P ↔ P ↔ Fe
P deficiency
Fe accumulation in roots and leaves
Fe accumulation
Fe effect on P
Fe in roots limits P transport to shoots
Reduced P transport to shoots
Low P increases Fe accumulation;
Excess Fe restricts P transport to shoots.
CORE CONCEPT
Nutrient interactions are interdependent, not independent.
They directly affect plant performance.
Growth
Yield
Fe
Quality
Toxicity
Balanced nutrition =
Higher yield, better quality,
lower toxicity risk

MOLECULAR INTEGRATION OF NUTRIENT SIGNALS IN PLANTS

Nutrient signaling is a network, not isolated pathways

CORE IDEA

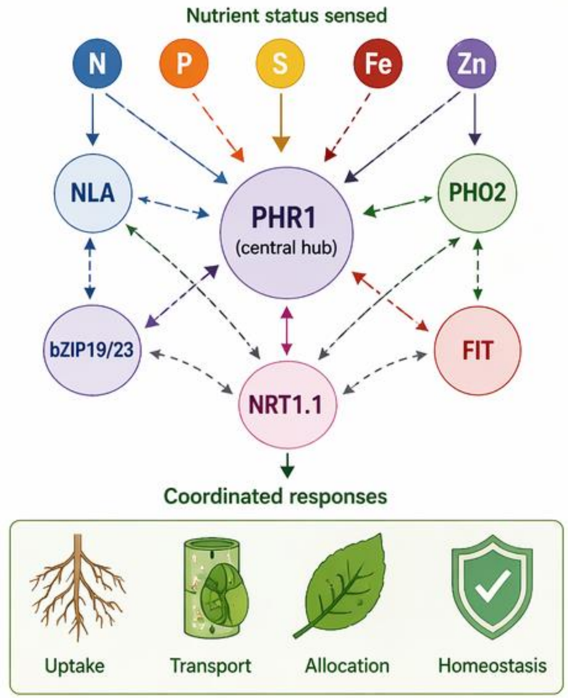
Plants use **master regulators** that integrate signals from multiple nutrients to coordinate uptake, transport, allocation and homeostasis. → One regulator can control many nutrients. Signals converge on hubs to produce coordinated responses.

KEY MASTER REGULATORS INTEGRATING MULTIPLE NUTRIENTS

PHR1	Central integrator (main hub)	Regulates genes for uptake, transport and homeostasis of:	P, Fe, Zn, S
NLA	Nitrate-dependent regulation	Links N status to phosphate uptake	N, P
PHO2	Phosphate signaling	Controls phosphate starvation responses	P
NRT1.1	Nitrate sensor / transceptor	Regulates root architecture and interacts with	N
bZIP19/23	Zn deficiency response	Activate Zn deficiency genes; interact with P and Fe signaling	Zn
FIT	Iron uptake regulation	Activates Fe uptake genes; coordinated with	Fe, P

These regulators form an interconnected network with feedback and feedforward loops.

SIGNAL CONVERGENCE ON HUBS



Integration ensures balanced nutrition, optimal growth and stress tolerance. → Disruption leads to imbalances and disorders.

EXAMPLES OF GENE REGULATION BY MASTER REGULATORS

PHR1	Activates genes for P uptake (PHT1), Fe homeostasis (FERs), Zn transport (ZIPs), and S transport (SULTRs).	PHT1, FER, ZIP, SULTR
NLA	Under high N, promotes PHO2 expression and phosphate uptake.	PHO2, PHT1
PHO2	Induces phosphate starvation genes; represses growth under low Pi.	IPS1, PHT1, miR399
FIT	Activates Fe uptake genes (IRT1, FRO2) under Fe deficiency; interacts with P signaling.	IRT1, FRO2
bZIP19/23	Activate ZIP genes for Zn uptake; modulated by P and Fe status.	ZIP1, ZIP3, ZIP4
NRT1.1	Senses nitrate and regulates root growth and other nutrient signaling pathways.	RTPs, ARF7/19

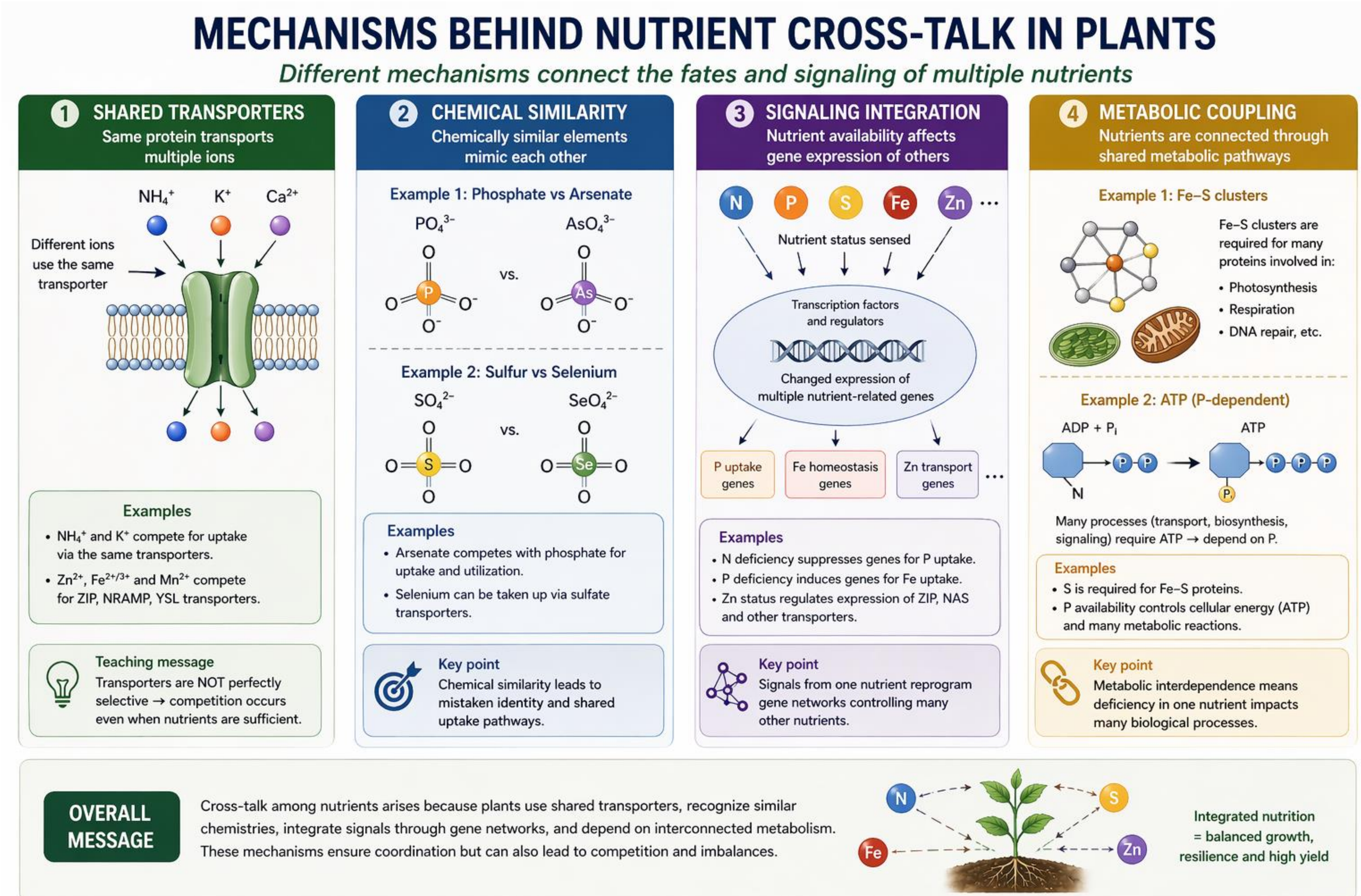
IMPACT ON CROP PERFORMANCE

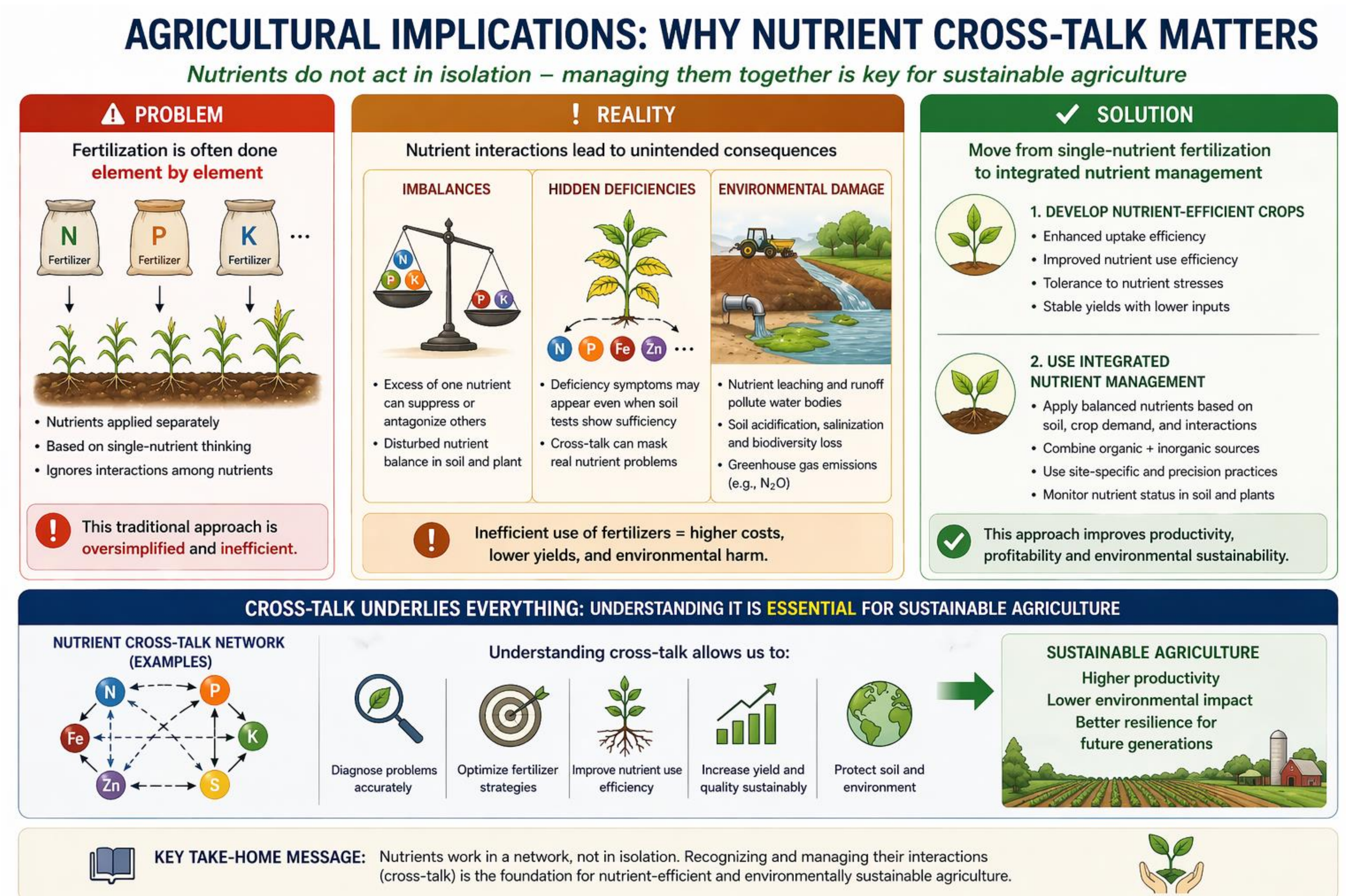
- Better nutrient use efficiency
- Higher yield
- Improved quality
- Greater stress resilience
- Lower risk of toxicity

TEACHING MESSAGE

Nutrient signaling is controlled by an integrated gene network. Understanding these regulators is key to developing nutrient-efficient, high-yielding, and stress-resilient crops.

NUTRIENT SIGNALING = NETWORK, NOT LINEAR PATHWAYS


MECHANISMS BEHIND NUTRIENT CROSS-TALK IN PLANTS
Different mechanisms connect the fates and signaling of multiple nutrients
1 SHARED TRANSPORTERS
Same protein transports multiple ions
NH_4^+
K^+
Ca^{2+}
Different ions use the same transporter
Examples
• NH_4^+ and K^+ compete for uptake via the same transporters.
• Zn^{2+}, $Fe^{2+/3+}$ and Mn^{2+} compete for ZIP, NRAMP, YSL transporters.
Teaching message
Transporters are NOT perfectly selective → competition occurs even when nutrients are sufficient.
2 CHEMICAL SIMILARITY
Chemically similar elements mimic each other
Example 1: Phosphate vs Arsenate
PO_4^{3-}
vs.
AsO_4^{3-}
Example 2: Sulfur vs Selenium
SO_4^{2-}
vs.
SeO_4^{2-}
Examples
• Arsenate competes with phosphate for uptake and utilization.
• Selenium can be taken up via sulfate transporters.
Key point
Chemical similarity leads to mistaken identity and shared uptake pathways.
3 SIGNALING INTEGRATION
Nutrient availability affects gene expression of others
N P S Fe Zn …
Nutrient status sensed
Transcription factors and regulators
Changed expression of multiple nutrient-related genes
P uptake genes
Fe homeostasis genes
Zn transport genes
…
Examples
• N deficiency suppresses genes for P uptake.
• P deficiency induces genes for Fe uptake.
• Zn status regulates expression of ZIP, NAS and other transporters.
Key point
Signals from one nutrient reprogram gene networks controlling many other nutrients.
4 METABOLIC COUPLING
Nutrients are connected through shared metabolic pathways
Example 1: Fe–S clusters
Fe–S clusters are required for many proteins involved in:
• Photosynthesis
• Respiration
• DNA repair, etc.
Example 2: ATP (P-dependent)
ADP + P_i
ATP
Many processes (transport, biosynthesis, signaling) require ATP → depend on P.
Examples
• S is required for Fe–S proteins.
• P availability controls cellular energy (ATP) and many metabolic reactions.
Key point
Metabolic interdependence means deficiency in one nutrient impacts many biological processes.
OVERALL MESSAGE
Cross-talk among nutrients arises because plants use shared transporters, recognize similar chemistries, integrate signals through gene networks, and depend on interconnected metabolism. These mechanisms ensure coordination but can also lead to competition and imbalances.
N S Fe Zn
Integrated nutrition = balanced growth, resilience and high yield

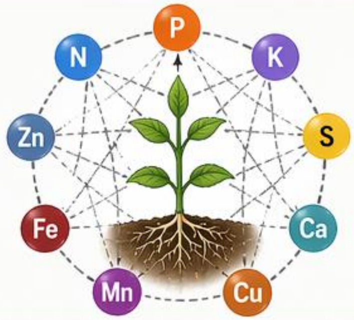

AGRICULTURAL IMPLICATIONS: WHY NUTRIENT CROSS-TALK MATTERS
Nutrients do not act in isolation – managing them together is key for sustainable agriculture
PROBLEM
Fertilization is often done element by element
N Fertilizer
P Fertilizer
K Fertilizer
...
• Nutrients applied separately
• Based on single-nutrient thinking
• Ignores interactions among nutrients
This traditional approach is oversimplified and inefficient.
REALITY
Nutrient interactions lead to unintended consequences
IMBALANCES
N P K
P K
• Excess of one nutrient can suppress or antagonize others
• Disturbed nutrient balance in soil and plant
HIDDEN DEFICIENCIES
N P Fe Zn ...
• Deficiency symptoms may appear even when soil tests show sufficiency
• Cross-talk can mask real nutrient problems
ENVIRONMENTAL DAMAGE
• Nutrient leaching and runoff pollute water bodies
• Soil acidification, salinization and biodiversity loss
• Greenhouse gas emissions (e.g., N_2O)
Inefficient use of fertilizers = higher costs, lower yields, and environmental harm.
SOLUTION
Move from single-nutrient fertilization to integrated nutrient management
1. DEVELOP NUTRIENT-EFFICIENT CROPS
• Enhanced uptake efficiency
• Improved nutrient use efficiency
• Tolerance to nutrient stresses
• Stable yields with lower inputs
2. USE INTEGRATED NUTRIENT MANAGEMENT
• Apply balanced nutrients based on soil, crop demand, and interactions
• Combine organic + inorganic sources
• Use site-specific and precision practices
• Monitor nutrient status in soil and plants
This approach improves productivity, profitability and environmental sustainability.
CROSS-TALK UNDERLIES EVERYTHING: UNDERSTANDING IT IS ESSENTIAL FOR SUSTAINABLE AGRICULTURE
NUTRIENT CROSS-TALK NETWORK (EXAMPLES)
N P Fe K Zn S
Understanding cross-talk allows us to:
Diagnose problems accurately
Optimize fertilizer strategies
Improve nutrient use efficiency
Increase yield and quality sustainably
Protect soil and environment
SUSTAINABLE AGRICULTURE
Higher productivity
Lower environmental impact
Better resilience for future generations
KEY TAKE-HOME MESSAGE: Nutrients work in a network, not in isolation. Recognizing and managing their interactions (cross-talk) is the foundation for nutrient-efficient and environmentally sustainable agriculture.

FINAL TAKE-HOME MESSAGES

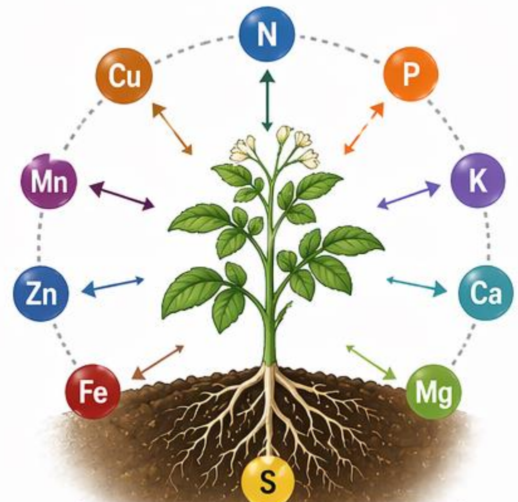
Understanding nutrient cross-talk is the key to healthy plants and sustainable agriculture

1 Plants regulate nutrients as a system, not individually

Plants sense the status of multiple nutrients and coordinate uptake, transport, allocation and storage.



✓ Plants function through an integrated nutrient network (the "ionome").



The nutrient status of one element influences many others.

2 Nutrient interactions can be:

Synergistic (positive)
One nutrient improves the uptake or use of another.

N improves Zn uptake and increases grain protein + Zn content.

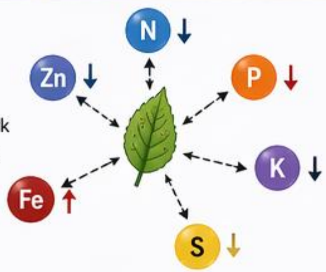
Antagonistic (negative)
One nutrient reduces the availability or uptake of another.

High P reduces Fe uptake (Fe deficiency symptoms).

✓ Interactions can be positive or negative depending on levels and environmental conditions.

3 A deficiency in one nutrient alters many others

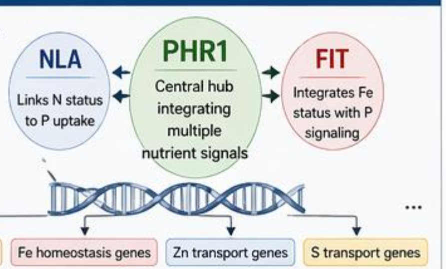
Deficiency triggers changes across the entire nutrient network (not just the deficient nutrient).



✓ Nutrient deficiencies cause ripple effects through the whole system.

4 Key regulators (PHR1, NLA, FIT) integrate signals

Master regulators receive nutrient signals and control the expression of target genes for multiple nutrients.



✓ These regulatory hubs coordinate uptake, transport, storage and utilization to maintain nutrient homeostasis.

5 Future agriculture depends on: Managing nutrient networks, not just fertilizers

From single-nutrient fertilization...

- More input
- Lower efficiency
- Environmental damage

✗

...to integrated nutrient management

✓

- Balanced nutrition and soil health
- Higher yield and quality
- Lower environmental impact
- Stronger resilience to stresses

KEY TAKE-HOME MESSAGE: Nutrients work in networks, not in isolation. Understanding and managing their interactions (cross-talk) is essential for developing nutrient-efficient crops and achieving sustainable agriculture.

FV- nutrição

Fim da segunda aula