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Plant Mineral Nutrition

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Several inorganic minerals are essential for plant growth and these are usually obtained by roots from the soil. Availability of minerals in the soil is determined by the physical and chemical characteristics of the soil. Plants can directly influence nutrient availability around the root surface; this zone is called the rhizosphere. Plants adjust root architecture and exudation according to their nutrient requirements and under deficiency these changes can be a marker for nutrient status. Nutrients are taken up from the soil using plasma-membrane located transporter proteins and excess is stored in the cell vacuole or converted into polymerized storage forms. For crops it is essential to match nutrient supply to demand throughout the growth season to obtain the maximum yield. These nutrient storage forms can be used as agricultural indicators of crop nutrient status and the potential for fertilizer leaching losses. Membrane transporters provide a gateway for nutrient entry into plants, but the selectivity of these filters can breakdown when chemically similar minerals are present at very high concentrations. The minerals may not be essential for growth, but they can enter plant cells and cause toxicity.

Key concepts:

- Several mineral elements are essential for plant growth.

- These nutrients are usually obtained from the soil and their availability depends on the physical and chemical properties of the soil.
- Plants adjust their root growth according to their nutrient requirements and these changes can be a marker for nutrient status.
- It is necessary to matching nutrient supply to demand throughout the growth season to obtain maximum crop yield.
- Excess nutrients can be stored in the plant and these storage pools can be used as indicators of nutrient status.
- Root plasma membrane located transporters are the gateway for entry of nutrients into the plant and their selectivity is important for determining the toxicity of some elements.

Keywords: plant, plant mineral nutrition, soil, rhizosphere, homeostasis, nutrient status

Article contents

Introduction

Plants require some specific elements from the external environment and these are usually obtained by roots from the soil. Less typically nutrients can also be taken up across the surface of leaves or in specialised structures in the few types of plants that can catch and digest insects. The quantities of each element required by plants can be used to define them as being either macro- or micro-nutrients. **See also: Plant macro- and micronutrient minerals.** A complete list of the mineral nutrients found in plants is shown in Table 1, and this type of information is obtained by chemical analysis of the previously digested leaf or whole plants. Specific parts of the plant, like seeds, accumulate some microelements to much higher concentrations – for example, the zinc or iron levels can be ten to twenty times higher than the values given in **Table 1**.

< INSERT TABLE 1>

The elements that are essential for growth serve both structural and biochemical roles in the plant and many have multiple functions. It is difficult to specifically classify the role of each nutrient, but they can be placed into general types based on function (see **Table 1**). Type I nutrients are bound into the structure of carbon compounds, such as nucleic acids and proteins. Type II nutrients are required for energy storage and transport. Type III nutrients are linked with cell wall structure, and IV are integral as constituents of enzymes or other molecules required for metabolism (for example, chlorophyll and ferredoxin). Type V can activate enzymes or control their activity and type VI nutrients serve as major cellular osmotica.

Nutrient availability

The physical and chemical characteristics of the soil determine the availability of nutrients to uptake by plant roots. The nutrients dissolved in soil water are those that are generally available for uptake and this is why most plants can be successfully grown in hydroponics or water culture. In soil the plant can directly influence nutrient availability in the area around the root surface; this zone is called the rhizosphere. Root-mediated localised changes in pH and soil microbes can directly influence the water solubility of many nutrients (**see also: Rhizosphere**). For example, a more acidic rhizosphere pH dissolves soil mineral phosphorus, increasing solubility and making the nutrient available for uptake by plant roots (**see also: Phosphorus availability in the Environment**). A plant can adjust these root properties according to their nutrient requirements and under deficiency these changes can be a marker for nutrient status. Many plants (e.g. oilseed rape – *Brassica napus*) excrete organic acids under deficiency (e.g. phosphorus and iron) to increase the soil availability of these nutrients. Furthermore, some plant roots excrete specific enzymes and chelating molecules to improve soil nutrient availability, for example phosphatases for phosphate and siderophores for iron. Roots can encourage the growth of particular types of bacteria and fungi that can solubilise minerals in the soil making the nutrients more available for root uptake. These microbial populations receive carbon from the root to encourage their growth in the rhizosphere. There is good evidence that although the soil type is important, each type and even cultivar of plant can encourage a specific population of fungi and bacteria that can be a characteristic ‘fingerprint’ for that rhizosphere (Berg and Smalla, 2009). For example, alfalfa roots select in their rhizosphere for phenotypes of *Pseudomonas fluorescens* with enhanced motility (Martínez-Granero *et al*., 2006), although these have greater efficacy in biocontrol of fungal pathogens the bacteria release siderphores that bind iron and may make it available to plants. Comparing rice cultivars, some roots each showed characteristic rhizosphere selection of bacteria populations (Hardoim *et al*., 2011). Rhizosphere bacterial populations can convert nutrients into different forms that are more accessible for uptake by roots (e.g. fixing gaseous nitrogen or nitrification, converting ammonium to nitrite and nitrate), but they can also engineer the physical environment by generating local air-filled spaces or pores in the soil for gas exchange. In addition the rhizosphere bacteria can provide bridges that maintain contact between soil particles and the root to ensure water and dissolved nutrient delivery to the plant in drying soils. The cataloguing of soil and rhizosphere bacteria and fungi has been revolutionized by improvements in RNA and DNA sequencing and these techniques are independent of the ability to culture the microbes (Hirsch *et al*., 2010). **See also: Genomics and the Rhizosphere.**

Root Uptake

Root architecture and membrane transporters are the main factors determining root acquisition of available nutrients. Plants can adjust their branching pattern and root hair development to exploit locally available patches of higher nutrient concentrations (see Figure 1). Roots show a foraging growth pattern and when they encounter a rich nutrient pocket in the soil their architecture changes to branch locally increasing the area for uptake and shortening the distance for diffusion (Mommer *et al*., 2012). The upper layers of soil usually contain the highest amounts of nutrients and so the top soil is frequently densely covered with roots. Phosphorus is an example of a nutrient that occurs in the top soil and bean roots proliferate in this layer to acquire this nutrient (Lynch and Brown, 2001). Primary roots grow deeper through the profile to exploit the water and nutrient (e.g. nitrate) supplies that are often located much lower in the soil. **See also; Roots and Root Systems.**

Plants have gene families of nutrient transporters that each specialise in the uptake of soil available nutrients, for example ammonium and nitrate (**see also: Plant Nitrogen Nutrition and Transport**). There are key steps in the uptake of nutrients, these are transport across the plasma membrane from the soil into the root cell, storage in the vacuole and loading of the long distance transport systems in plants (phloem and xylem), unloading into the growing tissues such as leaves or seeds. Each of these transport steps is mediated by specific transporter proteins and they are potential regulatory steps in the pathway for nutrient entry into the plant. This regulation can occur by changes in gene expression or by post-translational regulation of the protein. Often mutations in the transporter results in plants that demonstrate nutrient deficiency symptoms under normal supply conditions that would be adequate for a wild type plant. But sometimes the mutation is hidden because another transport in the family can step up expression to compensate for the missing function. Some of the plasma membrane transporters are also involved in sensing the external availability of nutrients and these have been described as 'transceptors' (Gojon *et al*., 2011). For a recent list of the plant nutrient transporter families check the ARAMEMNON website http://aramemnon.botanik.uni-koeln.de/. Although the gene families of nutrient transporters have selectivity for each type of nutrient this specificity can break down when concentrations of other ions become high enough (see *Deficiency and Toxicity* below). The selectivity and transport rate of a plasma membrane nutrient transporter can also be important for determining crop nutrient use efficiency, **see also: Improving Nutrient Use Efficiency in Crops.** Some nutrients are acquired by beneficial interactions or symbioses with bacteria and/or fungi, **see also: Root Nodules (Legume-Rhizobia Symbiosis); Plant-Fungal Interactions in Mycorrhizas.** In symbiosis with fungi, the plant benefits from the increased surface area provided for mining nutrients from the soil, this has obvious advantages for the acquisition of soil immobile minerals, like phosphorus, but also for water uptake. Together with bacteria, legumes can form a nitrogen-fixing nodule that supplies nitrogen to the plant taken from the air. A range of these symbiotic associations occur and their importance to each individual plant for nutrient acquisition depends on the local availability of nutrients. In some nutrient-poor soils a symbiotic relationship may be essential for the plant to grow and reproduce. These relationships can also be important for plants growing in toxic environments, for example there are some plants tolerate soils containing heavy metals by forming fungal mycorrhizal associations.

Homeostasis, Storage and Measuring Nutrient Status

The interplay between plasma membrane uptake and nutrient storage forms is balanced to maintain cytoplasmic concentrations that are optimized for plant growth (Figure 2). Nutrient homeostasis is the regulation of supply to maintain an optimum environment for cellular biochemical reactions in the cytoplasm. The balance or homeostasis is important for a plant, yet very little is known about how this cellular equilibrium is sensed and regulated within individual plant cells. It has been proposed that changes in root cytoplasmic nutrient concentrations can signal nutrient status (e.g. nitrate, Miller and Smith, 2008; potassium, Walker *et al*., 1996).

Excess nutrients are usually stored in cell vacuoles and elemental analysis of whole tissue can be used to measure nutrient pools. For example, manganese (Mn) tissue accumulations can vary between plant species growing on the same soil. The general critical threshold concentration for the onset of Mn deficiency in leaves is in the range 10–20 mg kg^{-1} and it can particularly be a problem for plants to acquire the metal in alkaline soils (Marschner 1995). At the other extreme, some rare plants can hyper-accumulate leaf manganese to 10,000 mg kg^{-1} e.g. *Gossia* species (Fernando *et al*., 2009). **See also: Heavy Metal Adaptation.** Nutrients can sometimes be stored after conversion into specific forms, and the amounts of theses storage forms can also be used as indicators of a plant's nutrient status. For example, phosphorus can be stored as phytate in seeds, but the nutrient can be stored in all cells to a lesser extent as phosphate in the vacuole. Iron storage has been linked to accumulation of the protein ferritin, particularly in legume seeds like peas and beans, but this may result from iron toxicity rather than a direct role in storage of the metal (Briat *et al*., 2010). **See also: Iron in Plants.** Nutrient transporters at the vacuolar membrane mediate the storage and remobilization of nutrients, and like at the plasma membrane, there are specific families of proteins mediating these steps (Martinoia *et al*., 2012). The activity of these vacuolar transporters must be regulated in concert with those at the plasma membrane to achieve homeostasis and optimal cytoplasmic concentrations of nutrients for metabolism and growth. Very high concentrations of some nutrients can result in toxicity in plants (see Figure 2) and this occurs when the storage capacity is exceeded by the supply.

The nutrient status of plants can be identified by whole tissue digests followed by elemental analysis. Young leaf material is usually used for this analysis because this tissue is a good indicator of the whole plant nutrient status. The concentration in dry matter of a given nutrient can then be compared with tabulated values of the optimal range for each type of crop. As this laboratory analysis can be time consuming simpler assays have been developed that can be used by farmers in a field. Small deficiencies in nutrients may not present obvious symptoms, but can result in a sub-maximal crop yield for farmers. The general nutrient status of a crop can be assessed by the 'greenness' or chlorophyll content using hand-held or tractor mounted devices for measuring this parameter. Nitrogen supply is well-known to influence the greenness of a crop. Insufficient phosphorus supply can also influence on wheat leaf chlorophyll content and grain yield (Figure 3, left panels). The down-side of this chlorophyll assessment method is that other factors like pathogens or insect attack can complicate the measurement. Plant leaf or petiole sap analysis can be used as an indicator of nutrient status and portable equipment to measure nutrient concentrations in the field is available. Like whole tissue digests, sap analysis results can be compared with previously determined optimal nutrient concentrations to decide if the crop needs more fertilizer.

Deficiency and Toxicity

As nutrients concentrations are critical for the processes involved in metabolism and growth, a limited supply of any nutrient will result in sub-optimal stature and yield. Nutrient deficiencies result in stunted growth, but there are often other visual symptoms. Deficiency symptoms commonly include chlorosis, a yellowing of the leaf and stem tissues. The precise pattern of the chlorosis can indicate more specifically which nutrient is missing. For example, nitrogen deficiency results in a general chlorosis, but iron-deficient plants showing yellowing in the leaf between veins. When specific elements, like phosphorus, are deficient plants will develop a purple coloration due to the production of large amounts of anthocyanins (see Figure 3, right). These chemicals are produced when plants are stressed and they have a biochemically protective role in the cell. **See also: Anthocyanins.** Tissue death or necrosis follows chlorosis as deficiencies become more acute. In potassium-deficient plants necrosis occurs along leaf margins, but in manganese-deficient plants necrosis occurs between veins. For some nutrients such as iron, the deficiency symptoms show first in a young leaf; this suggests that the element is not easily translocated from old to young leaves. Nitrogen, potassium, and magnesium are easily loaded into the phloem and xylem and translocated from old leaves to younger developing leaves. For these nutrients the older leaves exhibit the deficiency symptoms. **See also: Plant macro- and micronutrient minerals.**

As described above very high concentrations of some nutrients can result in plant toxicity (see Figure 2) although this rarely occurs in nature. The normal entry route for nutrients can become a way for toxic elements to enter plants. For example, transporters for the uptake of trace element metals can become a pathway for the entry of other toxic metals like cadmium and under saline conditions sodium can enter through potassium transporters as the external abundance of sodium relative to potassium is so high (**see also; Potassium in Plants**). The accumulation of these toxic elements in plants can be ameliorated by increasing the supply of the nutrient that usually enters the plant via this transporter system.

Future Prospects for Crop Nutrition

When a nutrient deficiency can be detected in a crop there is already likely to be a yield penalty. In other words, nutrient status detection in plants is too late; therefore new methods for measuring and predicting soil nutrient availability are important for the early diagnosis of impending nutrient limitations. This approach can ensure that the soil available nutrients are maintained at optimal levels for the crop, but not at levels that result in fertilizer leaching. The nutrient status of soil is usually assessed by taking core samples in the field, then measuring the extracted nutrients in the laboratory. The accuracy of this method depends on the type of extraction used, but often it overestimates the amount of the nutrient that is actually available for uptake by roots. New more accurate methods for measuring soil nutrient availability are important for improving crop nutrition.

Figure 4 shows some of the future possible strategies for improving nutrient use by crop roots. For example, the inoculation of soil with specific types of bacteria tailored for each crop may be a way of enhancing the nutrient availability. Choosing the appropriate type of bacteria can encourage root growth and health, promoting nutrient cycling in the rhizosphere. Soil and seed could be inoculated using beneficial microbes, with the species mix tailored for each type of crop. In addition, the ability of the plant to host particular types of bacteria may be enhanced by the root exudate composition. There is some evidence that modern crop cultivars may have lost some of the chemical exudates found in ancestral varieties than can influence nutrient availability in the rhizosphere. For example, root exudates can contain nitrification inhibitors blocking the conversion of ammonium into nitrate (Subbarao *et al*., 2009). The plasma membrane transporters that mediate the uptake of nutrients by roots may also be targets for improved acquisition of nutrients. This may be achieved by increasing the affinity of the transporter for the nutrient or by modifying the regulation of transporter activity, for example by phosphorylation state of the protein. Root architecture is another potential target as increasing root area provides a larger area for the nutrient acquisition. Some nutrients are acquired by beneficial symbioses with bacteria and fungi, these relationships are especially important in nutrient poor environments. These symbioses are important for water and nutrient acquisition and there is scope for encouraging their development more in agricultural soils.

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Glossary

homeostasis, nutrients, plant mineral nutrition, critical nutrient concentrations.

Table 1. Mineral concentrations of typical whole plants. Modified from Epstein and Bloom, Mineral Nutrition of Plants (2005).

Element	**Chemical symbol**	**Concentration in dry matter**		**Function and main roles in plant (with group classification)**
		ppm or %	µmol g^{-1}	
Macronutrients				
Nitrogen	N	1.5%	1000	Chlorophyll, nucleic acids & proteins (I, VI)
Potassium	K	1%	250	Enzyme activator, osmotic balance (V, VI)
Phosphorus	P	0.2%	60	Energy supply [e.g. ATP], nucleic acids (I, II)
Sulphur	S	0.1%	30	Nucleic acids & proteins (I)
Calcium	Ca	0.5%	125	Cell walls, enzyme activator, signalling (III,V)
Magnesium	Mg	0.2%	80	Chlorophyll (IV,V)
Silicon	Si	0.1%	30	Cell walls (III)
Micronutrients				
Nickel	Ni	0.05 ppm	0.001	Enzyme component [e.g. urease] (IV)
Molybdenum	Mo	0.1 ppm	0.001	Enzyme component [e.g. nitrogenase] (IV)
Cobalt	Co	0.1 ppm	0.002	Nitrogen fixation in legumes (IV)
Copper	Cu	6 ppm	0.1	Respiration & oxido-reduction (IV, V)
Zinc	Zn	20 ppm	0.3	Enzyme activation (IV,V)
Sodium	Na	10 ppm	0.4	C4 photosynthesis in some plants (IV)
Manganese	Mn	50 ppm	1.0	Chlorophyll synthesis, energy transfer (IV, V)
Boron	B	20 ppm	2.0	Cell wall stability (III)
Iron	Fe	100 ppm	2.0	Chlorophylll synthesis, energy transfer (IV, V)
Chlorine	Cl	100 ppm	3.0	Photosynthesis, osmotic balance (V, VI)

Figure legends

Figure 1. The pattern of barley root development showing localised increased growth where nitrate is available at higher concentrations. This pattern of development depends on the type of nutrient, but this localised proliferation can be observed by many different species in response to the major nutrients.

Figure 2. Diagram representation showing the relationship between plant growth and tissue concentration. The blue graph line represents the relationship between plant growth and the nutrient concentration in tissue. Redrawn from E. Epstein and A. J. Bloom, Mineral Nutrition of Plants: Principles and Perspectives, 2d ed., Sinauer, Sunderland, Mass., 2005).

Figure 3. The influence of varying phosphorus supply on wheat leaves and yield (left) and visual leaf symptoms in strawberry (right). Wheat figure shows the effects of phosphorus supply on chlorophyll (upper) and grain yield (lower). Figures reproduced from Buchanan *et al*., (2002) Chapter 23.

Figure 4. Some future strategies for improving crop nutrient acquisition.

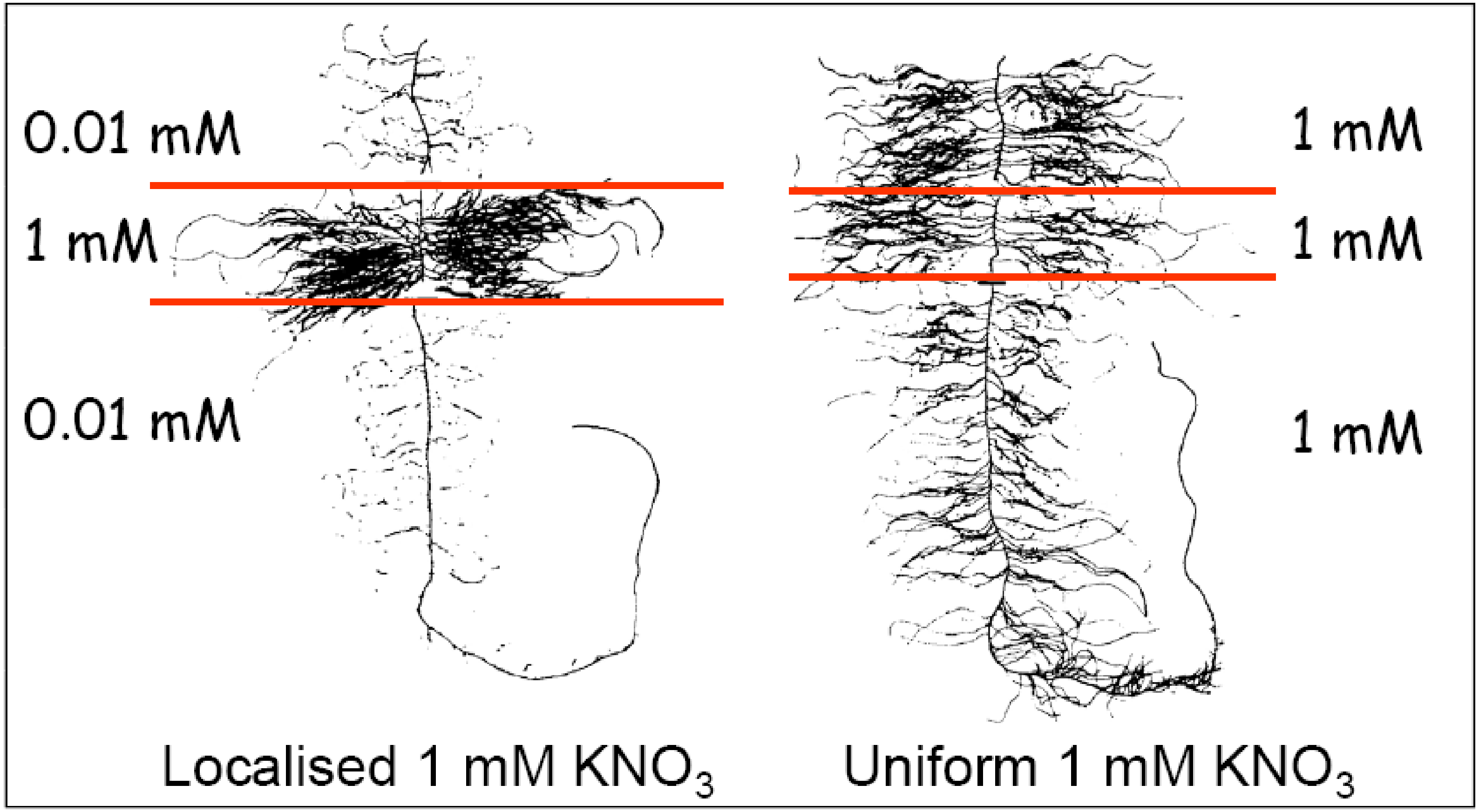

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Figure 1

Figure 2

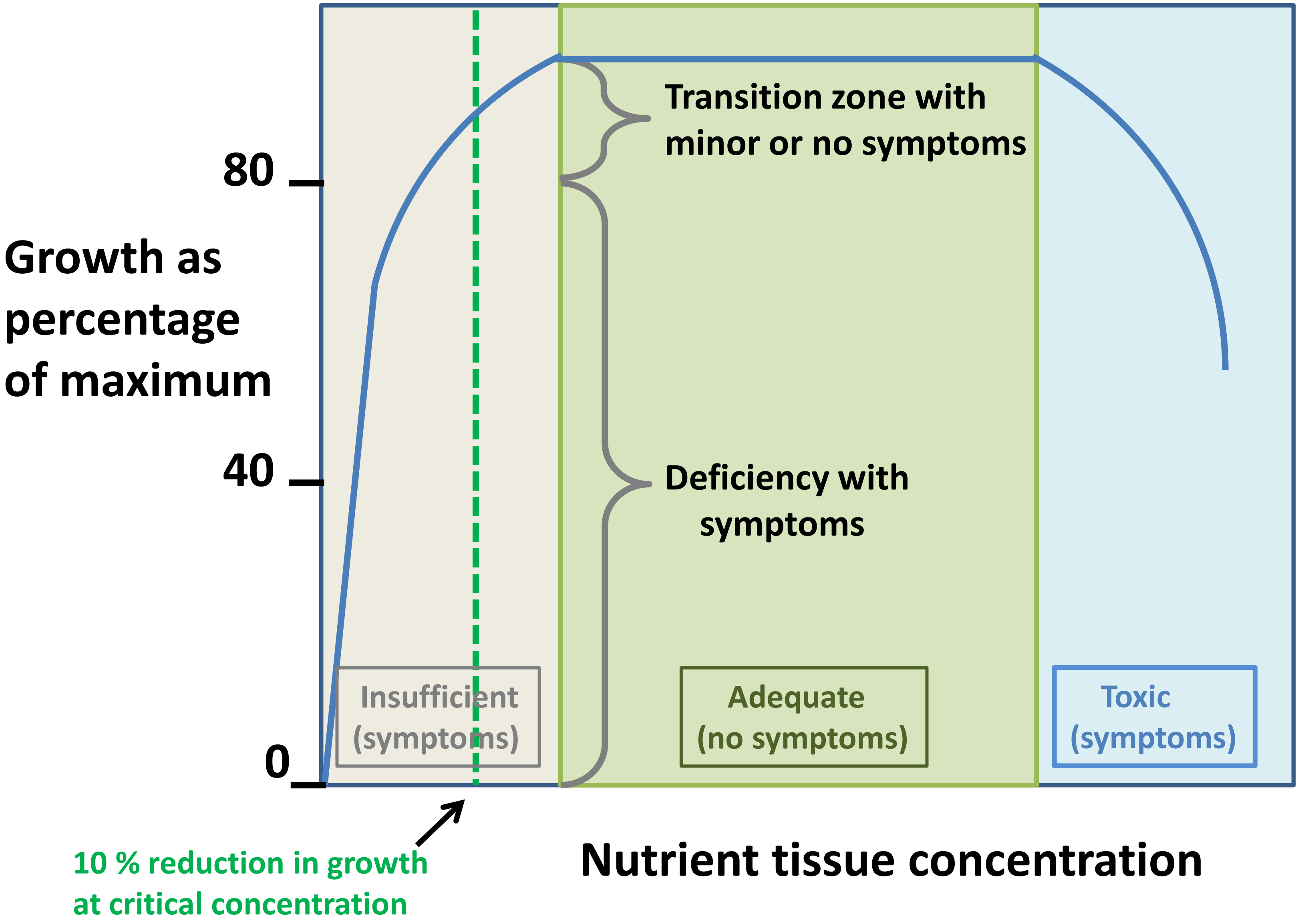
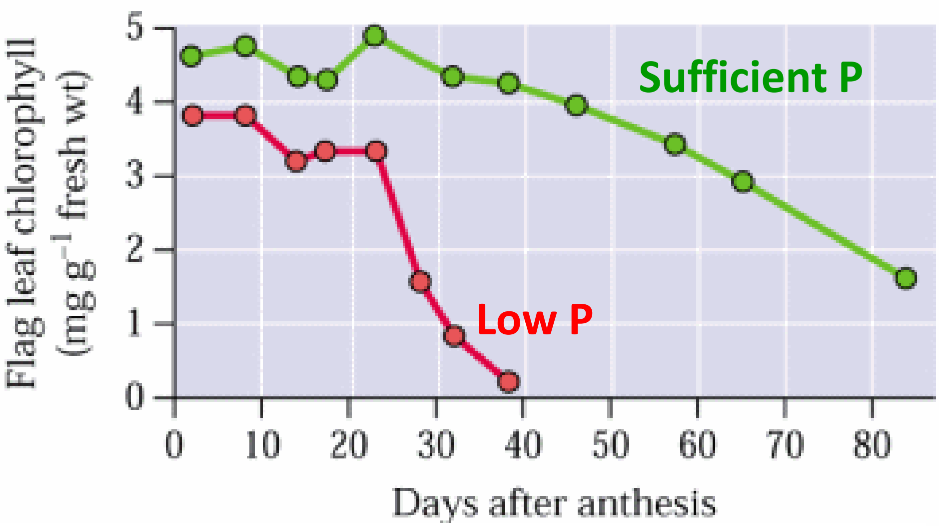
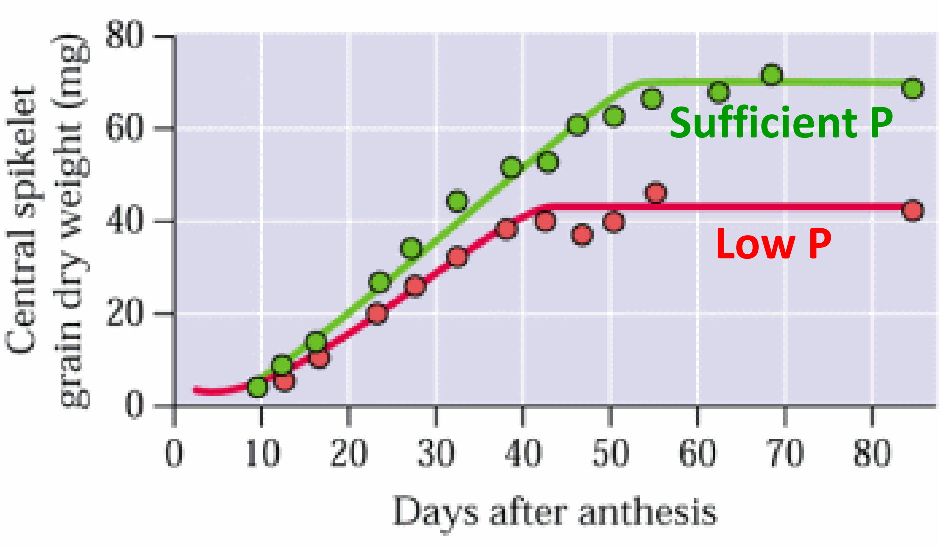

Transition zone with
minor or no symptoms
80
Growth as
percentage
of maximum
40
Deficiency with
symptoms
0
Insufficient
(symptoms)
Adequate
(no symptoms)
Toxic
(symptoms)
10 % reduction in growth
at critical concentration
Nutrient tissue concentration

Figure 3

P nutrition affects wheat leaf chlorophyll



P nutrition affects wheat grain yield



Strawberry leaf with sufficient P

Strawberry leaf showing P deficiency

Root strategies for improving nutrient acquisition

- **Rhizosphere** - exudates, acidification, enzymes, specific types of microbes)
- **Uptake** - transporters, regulation
- **Root architecture** - root hairs, laterals, surface, depth, penetration
- **Symbioses** - mycorrhization, nodulation

Figure 4