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# Water and nutrients

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## OM7.1 BIOTECHNOLOGICAL APPROACHES TO REDUCE THE EFFECTS OF WATER DEFICIT ON CROP GROWTH

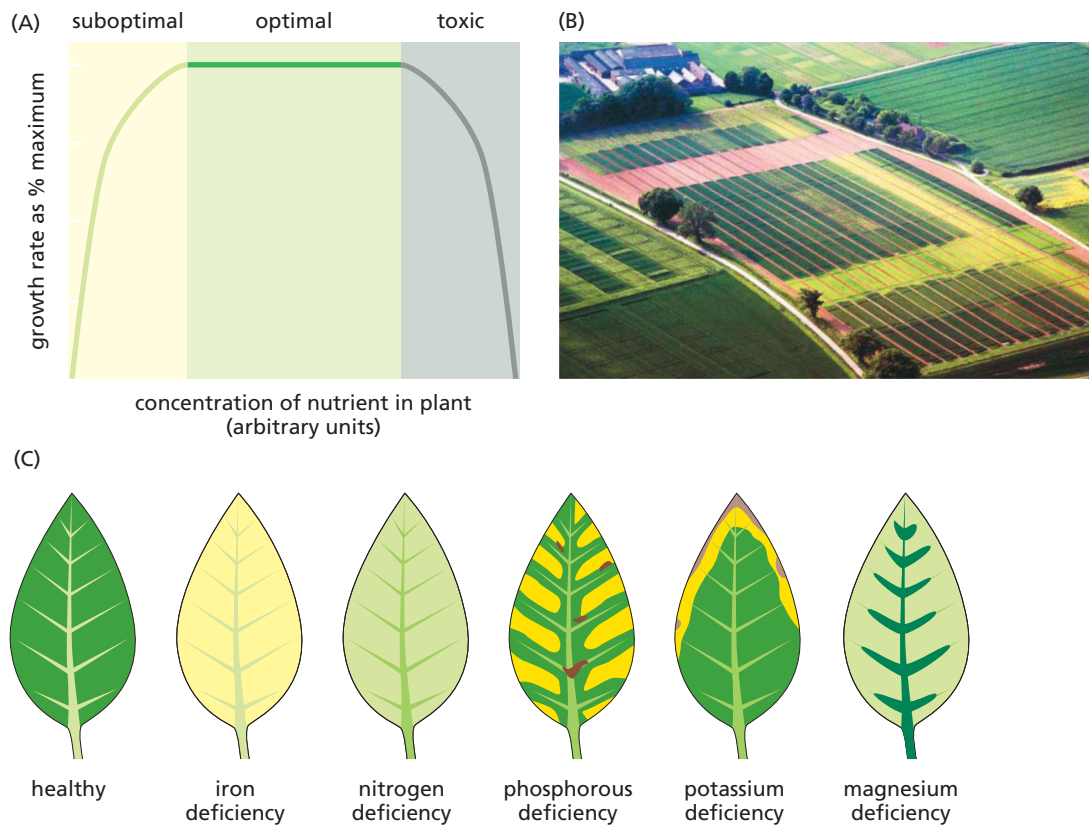
There is much interest in improving crop growth in conditions of water deficit by enhancing the accumulation of compatible osmolytes or LEA (late embryogenesis abundant) proteins. This approach - using transgenic plants with elevated or *de novo* expression of genes encoding LEA proteins or enzymes involved in synthesis of various osmolytes - has had success in some laboratory and controlled field trial conditions. For example, transgenic maize and sugar cane with elevated glycine betaine and transgenic rice with elevated LEA proteins had improved growth and yield under water deficit compared with control plants. It is important to remember, however, that crops experiencing water deficit may well also experience other environmental challenges such as high temperatures and damaging light levels. Broader strategies for improving performance in the field are being developed, using transcription factors that respond to multiple challenges. The expression of the sunflower transcription factor HaHB4 is induced by abscisic acid, water deficit, ethylene, jasmonic acid, and other environmental and hormonal factors. Its downstream targets include many genes involved in various pathways leading to abiotic and biotic stress tolerance. In extensive trials across a wide range of environmental conditions, transgenic wheat and soybean expressing HaHB4 had enhanced grain yield relative to control plants.

## OM7.2 OPTIMAL GROWTH OCCURS IN A WINDOW OF NUTRIENT CONCENTRATION

Nutrient requirements vary depending on plant growth stage. For example, requirements for mineral nutrients are high in young, rapidly growing plants but may decline when the plant switches from vegetative to reproductive growth. After fertilization of flowers, requirements may change depending on the nature of the fruit or seeds produced. In many monocarpic plants (plants that die when reproductive structures reach maturity), nutrients are remobilized from leaves to the developing fruits or seeds via the xylem or phloem, so the requirement for nutrient uptake by roots may decline to a low level at this stage. The import of  $K^+$  into developing juicy fruits such as grape and tomato supports the water influx needed for vacuolar and cellular expansion. Plant growth is suboptimal when nutrients are deficient or present in excess (**Figure OM7.2-1A**).

Nutrient deficiency is a major problem in arable farming and horticulture, leading to reduced photosynthesis and hence reduced growth. General symptoms of common nutrient deficiencies in arable crops are shown in **Figure OM7.2-1B, C**. Drone and satellite imaging techniques (based on multispectral imaging) can often detect nutrient deficiency in crops before symptoms are obvious at ground level. Deficiencies can arise for several reasons, including depletion of the soil by intense cropping, imbalances in the composition of applied fertilizers, and farming of naturally mineral-poor soils. In conventional farming, deficiencies are usually corrected or avoided by application of mineral fertilizers, often containing sources of nitrogen, phosphate, and potassium (“NPK” fertilizers). However this practice has led to pollution of water courses and loss of biodiversity in surrounding areas (discussed in, for example, Sections 16.2 and 18.4). While crop yields must be increased to feed the world’s increasing population, new means of maintaining soil fertility without the current levels of mineral fertilizer application are being sought. Approaches include: (i) precision farming, in which detailed crop yield and nutrient maps of arable land direct the location and amount of fertilizer applied; (ii) improved soil husbandry that reduces compaction, loss of organic matter, and depletion of diversity in the soil microbiome; and (iii) breeding for new cultivars using diverse germplasm from wild progenitors and land races to develop crops that perform optimally with lower nutrient inputs.

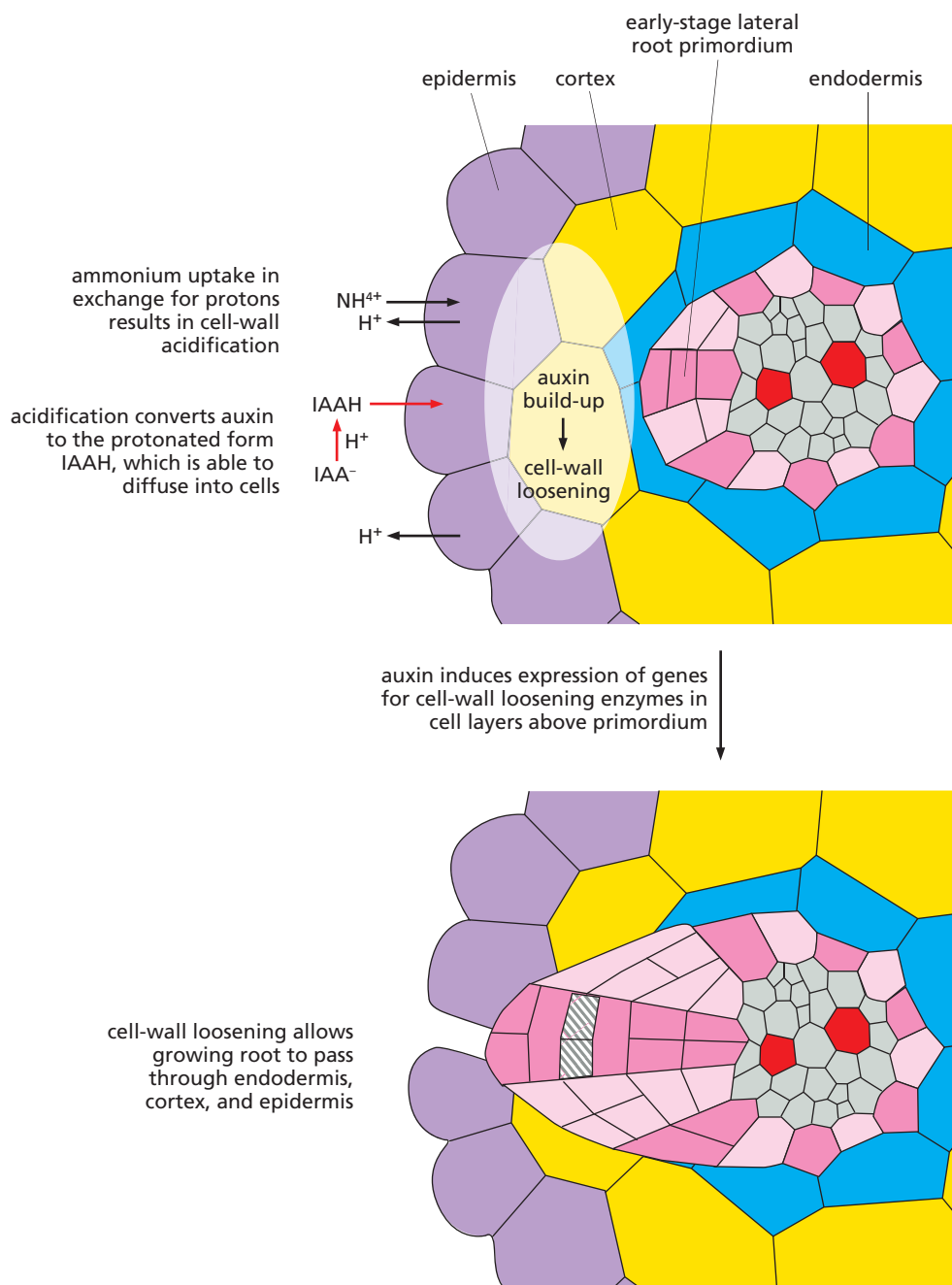
Although root uptake systems for nutrients are selective, some non-essential or toxic elements can also be taken up via these systems. For example, the  $K^+$  uptake system of the root is overwhelmed by the high levels of  $Na^+$  that occur in saline soils, potentially flooding root cells with  $Na^+$ . The  $Na^+$  ion cannot substitute for  $K^+$  in many cellular contexts, so high concentrations are toxic. (The mechanisms that allow plants in saline soils to avoid  $Na^+$  toxicity are described in Section 13.5.) In flooded soils, iron and sulfur may be reduced to soluble forms that accumulate to relatively high levels. Sulfite can be toxic to plants, and although many plants normally take up iron in its reduced form ( $Fe^{2+}$ ), high concentrations of  $Fe^{2+}$  are toxic. In naturally acidic soils, toxic elements such as aluminum ( $Al^{3+}$ ), lead, and cadmium – normally present in insoluble forms – can be solubilized from the soil or underlying rock and taken up by root transporters.



**Figure OM7.2-1 Nutrient requirements for optimal growth.** (A) Relationship between status of a given nutrient in the plant and its growth rate. (B) Appearance of field strips given different fertilizer treatments. Yellowing indicates nutrient deficiency. This field is part of a continuing experiment on the effects of fertilizer treatments, begun at Rothamsted Research UK in 1844. (C) Symptoms of some nutrient deficiencies common in arable crops. The differences in appearance and chlorophyll content of plants with different deficiencies potentially enable problems to be pinpointed with various robotic multispectral imaging devices, increasingly including satellite imaging. (B, courtesy of Rothamsted Research.)

### OM7.3 AMMONIUM AND LATERAL ROOT GROWTH

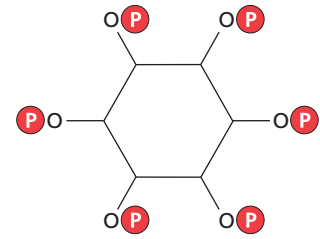
As described in the text, the capacity of NRT1.1 to transport auxin at low nitrate levels regulates lateral root growth. The capacity of ammonium transporters (AMTs) to transport ammonium in exchange for protons indirectly regulates auxin-promoted lateral root emergence (Figure OM7.3-1). Because AMTs exchange ammonium for protons, ammonium uptake acidifies the apoplast. This increases the protonation of auxin in the apoplast, permitting a greater flux of auxin across the plasma membrane into the cytosol of cell layers above the lateral root primordia in the outer layers of the stele. The increase in auxin in this location triggers expression of cell wall-loosening enzymes that facilitate emergence of the primordium through the primary root to become a new lateral root. Lateral roots are not initiated at low ammonium concentrations because the apoplastic pH is too high to permit sufficient auxin accumulation inside cells above the lateral root primordia. In summary, ammonium and nitrate transport promote initiation and elongation of lateral roots when nitrogen supply is plentiful, via two different means of auxin accumulation.



**Figure OM7.3-1 Ammonium transport indirectly promotes the induction and outgrowth of lateral roots.** Exchange of ammonium for protons at the cell surface acidifies the apoplast. Auxin (IAA) becomes protonated, allowing its passive diffusion into root cells. The auxin build-up above the lateral root initially induces the expression of cell wall-loosening enzymes, allowing the growing primordium to expand outward through the cell layers of the root.

## OM7.4 STORAGE OF PHOSPHATE AS PHYTATES

Many seeds, including nuts, grains, and pulses, and some vegetative tissues contain large stores of phosphate in the form of insoluble, crystalline phytates. Phytic acid (myo-inositol hexaphosphoric acid, **Figure OM7.4-1**) is synthesized in the endoplasmic reticulum during seed development. The negatively charged phosphate groups of the phytic acid associate with cations such as  $Mg^{2+}$  and  $K^+$ , resulting in large aggregations of phytic acid chelated with cations. The resulting crystalline phytate is exported in vesicles from the endoplasmic reticulum into protein bodies (see Section 6.2). During seed germination, phosphate is released by stepwise hydrolysis of the phosphate groups of the stored phytate by phytases. Phytates are antinutritional factors in the diets of humans and some farmed animal (including pigs and poultry but not ruminants). Their strong affinity for cations such as calcium, iron, and zinc in food stuffs can lead to deficiencies of these essential nutrients in phytate-rich diets.



phytic acid

**Figure OM7.4-1** Phytic acid.