1. Introduction

The soil supplies essential nutrients for plant growth. Many nutrients are limited in supply in soils due to chemical, physical, or biological reactions and constraints. In addition, other elements may be found in excess under a variety of circumstances. However, plants can actively affect the supply of nutrients from the soil, to increase the supply in low nutrient environments or reduce their concentration and/or absorption in extreme environments. Understanding these processes is critical in understanding plant nutrient relations.

2. Nutrient uptake by plants
2.1. Nutrient supply by the soil

The soil is a reservoir of nutrients contained in both inorganic (e.g., containing potassium, calcium, magnesium, iron) and organic particles (e.g., containing nitrogen, phosphorus, sulfur). Soils have a negative charge, the cation exchange capacity, that holds positively charged nutrients such as potassium, calcium, magnesium, and ammonium, preventing their leaching loss from the soil.

Agricultural soils have a very low positive charge, anion exchange capacity, so negatively charged nutrients, such as nitrate, are not held and leach from the soil into the groundwater. Phosphorus is negatively charged, but is specifically adsorbed to soil particles and, therefore, does not readily move downward to the groundwater.

2.2. Nutrient movement to the root surface

Nutrients move to plant roots by mass (bulk) flow and diffusion. In addition, as roots grow through the soil, they come in direct contact with and intercept nutrients associated with soil particles that are displaced by roots. The quantity of nutrients absorbed by plant roots through root interception depends on the soil volume occupied by the roots, the concentration of nutrients in the soil, and the root morphology.

Since the volume of soil occupied by roots is usually less than 1%, less than 1% of the soil nutrients can be supplied by root interception. As plants transpire water, water moves from the bulk soil to the roots by mass or convective flow.

The concentration of nutrients in the soil solution and the rate of transpiration determine the quantity of nutrients delivered to the root surface in this bulk flow of water. Factors that affect water use, such as species/crop, climate, and soil moisture level, will affect the contribution of mass flow to supplying nutrients to roots.

When the supply of a particular nutrient to the root surface by root interception or mass flow is not sufficient to meet plant demand, continued uptake by the plant depletes the concentration at the root surface.

The resulting concentration gradient that forms from the bulk soil to the root surface causes nutrients to diffuse along that gradient towards the root surface. Conversely, elements delivered to the root surface in excess of plant demand establish a concentration gradient away from the root surface and diffusion is then away from the plant root.

The rate of nutrient diffusion in the soil system depends on the concentration gradient and several factors that influence the diffusion coefficient. Diffusion coefficients for ions in water are similar, but in soil they differ significantly due to interactions between ions and the soil matrix.

For example, nitrate is not adsorbed by the soil, whereas phosphate is often highly adsorbed by the soil, which reduces its diffusion coefficient. The soil texture (% sand,
silt, and clay) and reactivity of nutrients with the soil, soil structure, and moisture content also affect the diffusion coefficient.

The soil structure includes the degree of compaction or bulk density and the nature of the soil aggregates; both these affect the size and distribution of soil pores and consequently the hydraulic conductivity and length of the diffusion path. As the water content of the soil decreases, air replaces water in the soil pores and the path length from the bulk solution to the root surface is greatly increased.

The relative quantity of a particular nutrient delivered by mass flow, diffusion, or through interception will depend on the nutrient and soil properties. Nutrients with a high concentration in the soil solution will be largely supplied by mass flow. Those with low concentrations, such as phosphorus, will be mainly supplied by diffusion.

Nutrient uptake by plants can be described and modeled by soil supply (soil solution concentration, ability to replenish or maintain that concentration, ability to diffuse through the soil), root morphology (growth rate, diameter, and proximity to other roots), root nutrient-influx (described by Michaelis-Menten kinetics), and water influx (transpiration) parameters.

For relatively immobile nutrients that are in low concentrations in the soil solution, such as phosphorus, plant uptake is supply-limited and root growth and soil supply parameters are more important in determining plant uptake. With more mobile nutrients, such as nitrate, root nutrient-influx parameters are more important in affecting uptake.

2.3. Nutrient uptake by plant roots

The chemical composition of plant tissues does not reflect the availability of nutrients in the soil solution. This difference results from selective uptake and transport of nutrients by the root system. Along the path from the soil to the leaf, there are several control points and processes that allow plants to accumulate and exclude elements from their leaves.

At the root surface, ions enter the cell wall and follow one of two parallel pathways for movement of nutrients from the root surface into the plant (Figure 1). One is through the apoplasm, the cell wall and intercellular spaces, and the other is transport across the cell membrane into the symplasm and then cell to cell through the plasmodesmata.

Ions can move from the root surface through the epidermis and cortex up to the endodermis, which is the inner most layer of cells of the cortex. The endodermis has a hydrophobic band of suberin in the walls, known as the Casparian band, which is a barrier to passive movement of ions into the stele.

To move from the cortex to the xylem at the Casparian band, ions must move through the plasma membrane of the endodermis, providing selectivity in ion transfer to the vascular system.
The cell wall is like a filter with pores that restricts the uptake or movement of organic molecules based on size. Low-molecular weight ions, organic acids, amino acids, and sugars can readily move through the pores of the cell wall.

However, high-molecular weight metal chelates, fulvic acids, and toxins or viruses and pathogens are too big to move through the cell wall pores. Since ions can readily pass through the cell wall, the wall does not function in the selectivity of ion uptake; selectivity of ion uptake occurs at the plasma membrane of individual cells.

The rate of nutrient uptake by roots depends on the concentration of the particular nutrient at the root surface, root properties or plant species, and requirements of the plant. At higher solution concentrations of nutrients, the rate of uptake is typically higher, but plants do exhibit selectivity in that they preferentially take up some elements and exclude others.

This is particularly the case in tolerance mechanisms in extreme environments discussed later. Plants can take up nutrients in excess of their needs, termed luxury consumption, and store these in the vacuole. However, there are feedback mechanisms that reduce ion uptake as internal concentrations increase, maintaining a balance between demand and acquisition.

There is tremendous genetic variation in the uptake and exclusion of ions by plants. Such variation can be harnessed to select nutrient efficient varieties, high in nutritionally
important elements, and soil stress-adapted varieties for use in low input agriculture or where soil conditions are sub-optimal. In addition, species or genotypes that accumulate elements can be used to remove selected elements from soils (see Phytoremediation below).

Bibliography


