Chapter Three
The Biology of Soil Fertility

How Plants Get Their Nutrients

What Nutrients do Plants Need?

Nutrients are substances that provide living organisms with the nourishment they need for growth and maintenance of life. Like people, plants need nutrients to survive and thrive. Unlike people, the list of essential nutrients required by plants is fairly limited. Some are needed in large amounts; these are called macronutrients. Others are only needed in small amounts, and maybe only at certain stages in the plant's life; these are called micronutrients. Each one of them, however, is essential for every plant's survival, to some degree or another. These essential plant nutrients, as well as their sources and important functions in plants, are summarized in Table 1[4].

Table 1: Essential Plant Nutrients		
Macronutrients		
Nitrogen (N)	Many essential functions; basis of amino acids, and thus proteins	NH_4^+, NO_3^-
Phosphorus (P)	Component of DNA/RNA; base for ATP (the energy molecule)	$H_2PO_4^-$
Potassium (K)	Regulator of water and CO_2 levels	K^+
Calcium (Ca)	Key component of cell walls; signaling; transport across cell membranes	Ca^{2+}
Magnesium (Mg)	Centre element in chlorophyll molecule – key to photosynthesis	Mg^{2+}
Sulfur (S)	A component of two important amino acids	SO_4^{2+}
Micronutrients		
Boron (B)	Cell walls; formation of pollen tubes; moving starch and sugar	$B(OH)_3$ (neutral)
Chlorine (Cl)	Operation of stomata; breaks H_20 apart for photosynthesis	Cl^-
Copper (Cu)	Key element in important enzymes (e.g., for respiration)	Cu^{2+}
Iron (Fe)	Important to respiration, chlorophyll, N fixation processes	Fe^{2+}, Fe^{3+}
Manganese (Mn)	Frees O_2 during photosynthesis by accepting electrons from H_2O	Mn^{2+}
Molybdenum (Mo)	Synthesis of P compounds; necessary for N fixation by microbial symbiotes	MoO_4^{2-}
Nickel (Ni)	Prevents urea accumulation in leaves	Ni^{2+}
Zinc (Zn)	Oxidation/reduction; growth hormones; several key enzymes	Zn^{2+}

NOTE: Not included in Table 1 are the three non-mineral elements – carbon, hydrogen, and oxygen – that make plant life (and all life, for that matter) possible. These elements comprise more than 95 per cent of a plant's weight, but are considered to be the basic constituents of plants, rather than nutrients. In general, they are not obtained from the soil, but from the air and water, via photosynthesis.

Nutrients in Soil – The Basic Chemistry

Each and every one of these nutrients is required by every plant if it is to grow and reproduce successfully. Some of the important functions of each nutrient are indicated in the table, but these are only included here for general interest, because they refer to the internal chemistry of the plant, rather than the chemistry and biology of the soil. What we are most concerned with here is how the plant manages to get these nutrients from the soil. First, however, we should talk about how these nutrients get into the soil in the first place, how they are held there (or not), and how they become available (or unavailable) to plants.

All of the essential plant nutrients, with the exception of nitrogen, are originally derived from the mineral component of soils – in other words, the rocks. Zinc, for instance, is found in mineral compounds all over the planet, usually in very small amounts. On average, soils contain about 50 parts per million (ppm) zinc within their mineral components. This means that one tonne of soil minerals (1000 kilograms, or one million grams) will contain, on average, 50 grams of zinc. This may seem like a very small amount, but it translates to about 150 kilograms (kg) of zinc per hectare (based on a depth of one half of a meter), and this is not all the zinc potentially available in a hectare of soil. More zinc can be found in the soil organic matter, because most of the zinc taken up by a plant is returned to the soil in the plant residues. This organics-based zinc is then recycled over and over. Finally, some nutrients arrive in the soil via atmospheric deposition (e.g., blown in from elsewhere on dust particles). The same processes apply to all of the other nutrients, except nitrogen, which is "fixed" in biochemical form by soil microbes (see **Chapter One, Figure 7**).

It is very important to understand that nutrients in their mineral (rock) and organic-residue forms are not available to plants. Plants can only take up nutrients that are soluble in water. Fortunately, nature has many ways to free up nutrients, releasing them as ions (usually with an electrical charge) into the soil water (as shown in the right-hand column in Table 1). Nutrients are released from minerals by a number of mechanisms, some physical/chemical (e.g., organic acids in soil water) and some biological/chemical (release of specific enzymes by microbes and plants). Nutrients are released from organic residues through the action of microbes (more on this below).

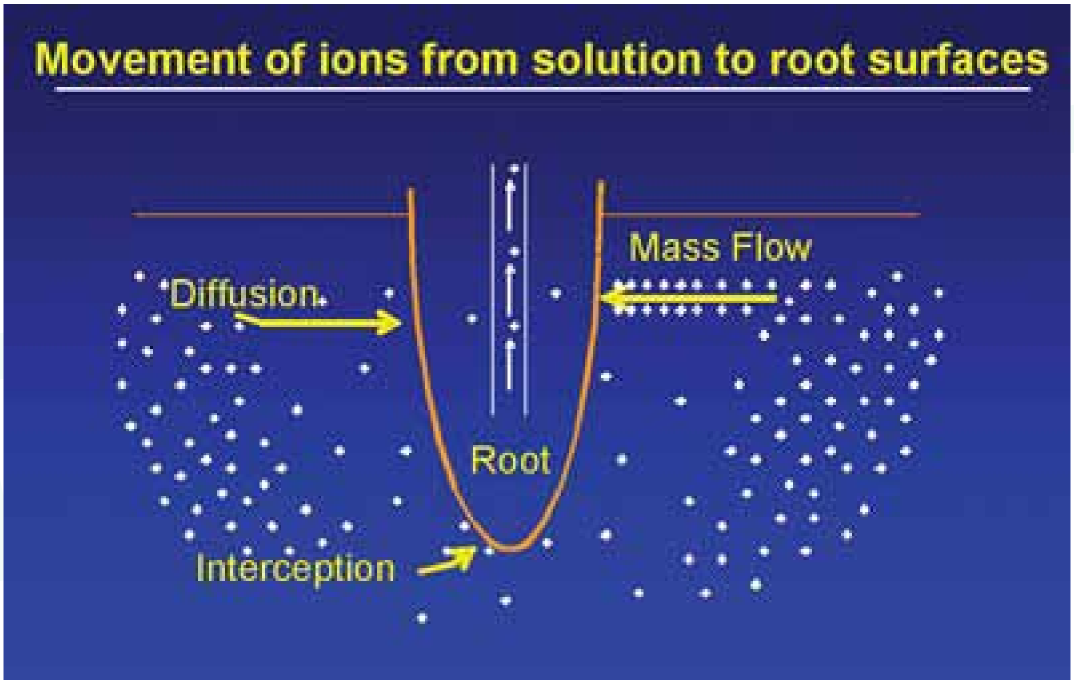
Ions are either positive or negative in charge (see **Table 1**). Some are cations (positive charged ions) and some are anions (negative charged ions). Cations are attracted to the negative charges on clay particles, or on particles of organic matter. To go back to our zinc example, since it is a cation, it is often adsorbed on soil particles. Molybdenum, on the other hand, is an anion and tends to stay in solution in the soil water.

As a general rule, soils usually contain far more nutrients than a plant needs. In fact, our relatively young Ontario soils contain enough nutrients to supply crops for thousands of years, even with the loss of some nutrients to harvest each year. However (and this is the rub): most of these are not plant-available, because they are tied up in minerals or (to a lesser extent) in soil organic matter. A small percentage of these nutrients is always available to plants, however, and these are either dissolved in soil water (this is called the "available pool"), or loosely attached to soil particles (the "exchangeable pool").

Soil tests tell us how much nutrients we have in the available and exchangeable categories. Farmers can then fertilize to a level that will ensure that their crops have all of the nutrients they need (all synthetic fertilizers are already in a plant-available form). But nobody is fertilizing natural ecosystems, so how do these plants get enough nutrients, on a regular, timely basis, to grow and reproduce?

How Plants Access their Nutrients

First of all, we have the older version, found in all of the earlier soil text books. It goes as follows. As plant roots and root hairs grow through the soil they access nutrients. This is essentially a random



Interception, diffusion and mass flow *(Figures 28)*
Source: https://cals.ncsu.edu/

process, known as interception. However, they also count on two routine, on-going physical processes to bring nutrients to their roots: diffusion and mass flow (see **Figure 28**).

Diffusion is the scientific term for the tendency of substances in solution to move from areas of high concentration to ones of lower concentration. Nutrients in solution in soil water, for instance, will generally, over time, move towards plant roots. This is because the roots are regularly absorbing nutrients, lowering the concentration in the immediate area around them and creating what we call a concentration gradient.

Mass flow is a somewhat similar process but instead involves a water gradient. Plants are always drawing water up from their roots via transpiration. As the water goes out into the atmosphere from its leaves, the lowered pressure above pulls water up from the roots through passageways in the body of the plant. This creates a lower water pressure in the roots, which then are able to absorb water from the areas of higher pressure in the soil immediately around the roots. In turn, this soil becomes the low end of a water gradient moving away from the roots. As water moves from further afield along this gradient into the dry areas, it brings the nutrients it contains in solution with it. In essence, the plant is sucking water out of the soil, and the water is bringing dissolved nutrients with it.

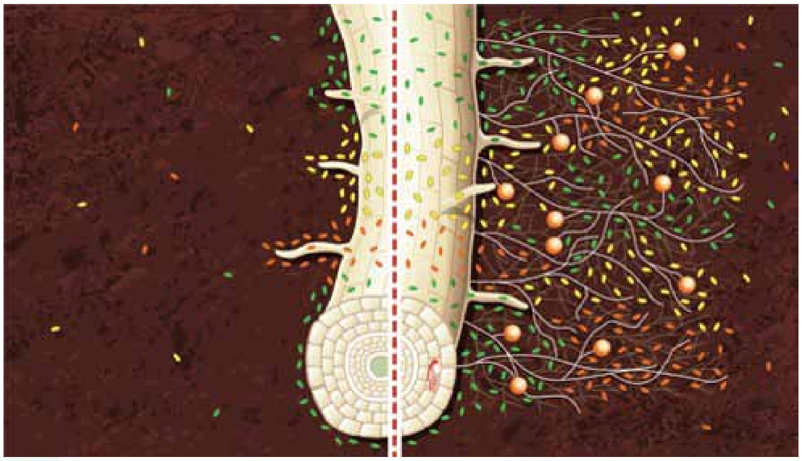
But what about those cations, attached to soil particles via an electric charge? Plant roots and microbes take care of of this problem by releasing hydrogen ions into the soil water. These ions replace cations on soil particles, essentially kicking them off the particle and back into solution, where interception, diffusion, and mass flow can deliver them to the plant.

Underground Carbon Trading Systems

The older version of how plants “eat”, summarized above, is certainly true. However, it is far from complete. As scientists have learned more about the soil food web and its relationship with plants, a newer understanding has developed. It turns out that microbes play very important roles, not just in liberating nutrients from organic matter and minerals, but also in getting those nutrients to the plant in a timely manner. Their work greatly enhances the relatively slow processes of interception, diffusion and mass flow. There are two main processes by which this quicker delivery is accomplished.

The Rhizosphere Effect and the Microbial Loop

The first process is the result of something scientists call the rhizosphere effect. All terrestrial plants exude carbon-rich substances from their roots into the rhizosphere (this term simply refers to the soil close to the roots). These exudates include sugars, carbohydrates, organic acids, and various other organic compounds produced by the plant from the simple sugars it created through photosynthesis. Because many of these substances are a great energy source for microbes, the rhizosphere is, to microbes, like a watering hole to desert animals – a crucial source of one of life's necessities. Accordingly, the population of bacteria and fungi are much higher around the roots of plants than they are in other parts of the soil (known as the bulk soil). This is the rhizosphere effect and this phenomenon has been well known by scientists for decades (see **Figure 29**).



The rhizosphere effect *(Figure 29)*

While some of these root exudates have specific single-focus purposes, such as directly breaking down minerals and releasing nutrients, or attacking disease organisms, (more on these other functions in later chapters), most of them appear to have another, broader purpose: to attract and "grow" microbes in the areas directly adjacent to their roots. Plants can devote more than 40 per cent of the chemical energy they fix through photosynthesis (materials collectively known as photosynthate) to this purpose – an incredibly high level of investment on their part. Why would they do this?

It turns out that they are essentially paying for a service – the fast, efficient delivery of nutrients to their root zones. It is similar to how we humans pay for the delivery of pizza. How does this delivery system work? As watering holes in the desert attract thirsty animals, so the exudate-rich rhizosphere attracts hungry bacteria and fungi. But they are not the only visitors. What predator doesn't know that watering holes are great hunting grounds? Because of the rhizosphere effect, microbial predators (remember the protozoa and nematodes in Chapter One?) find rich pickings in plant-root zones. As these protozoa and nematodes graze on the dense populations of bacteria and fungi in the rhizosphere, they leave their wastes behind, and these wastes are "microbial manure" -- chock full of plant-available nutrients.

In essence, plants are taking advantage of the following facts:

1 Bacteria and fungi break down soil organic matter, and many minerals as well, and absorb the nutrients in their bodies.

2 These bacteria and fungi are attracted to plant roots because of the carbon-rich exudates available there.

3 Predators, mainly the various types of protozoa and nematodes, consume bacteria and fungi to obtain these nutrients, as well as carbon (see **Figure 30**).

4 Because bacteria and fungi are nutrient-rich, relative to carbon, when compared to predators, excess nutrients are released by the predators in their wastes (i.e., microbial manures).

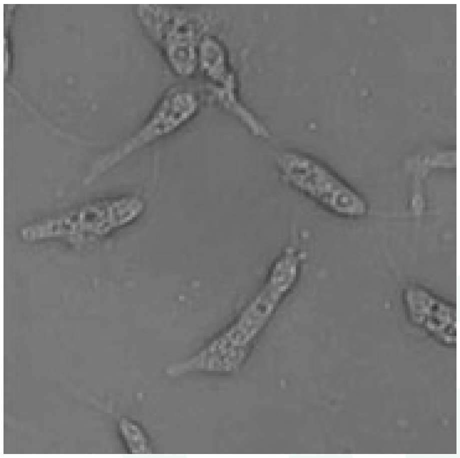
5 The nutrients in these microbial manures are in plant-available form (soluble ions).

6 Therefore, high numbers of microbes in the rhizosphere results in high levels of nutrient availability – and these nutrients are right where the plant needs them.

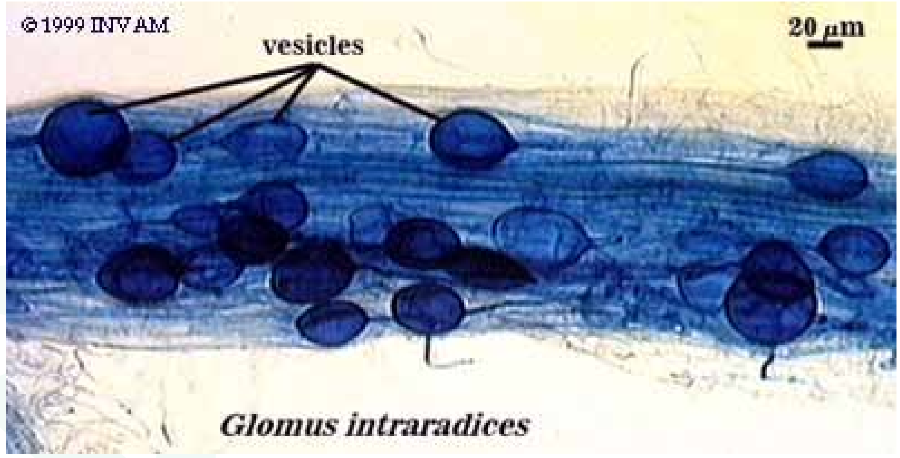
This has been called the microbial loop: plants devote much of their hard-earned photosynthate (carbon compounds) to soil, in effect trading this carbon for the fast, efficient delivery of nutrients right to their door, courtesy of the soil food web.

Mycorrhizal Fungi

The second underground carbon-trading system involves the mycorrhizal fungi described in Chapter



Predators Grazing in Rhizosphere *(Figure 30)*



Vesicular Arbuscular Mycorrhiza (VAM) *(Figure 31)*

2. These organisms establish connections with plant roots and use them to provide nutrients and water directly to the plant in return for sugars and other carbon-rich compounds. Unlike the system described above (the microbial loop), these fungi establish an actual physical connection with the roots.

There are many different species of mycorrhizal fungi. These fall into several general types, the most well-known of which are ectomycorrhizal and endomycorrhizal. The ecto type do not penetrate plant roots; they set up their trading sites on the plant root surfaces. They are associated with conifer trees and some deciduous trees, and so are of limited interest to farmers. The endo type, on the other hand, infect plant roots, setting up shop inside them.

One type of endo, known as vesicular arbuscular mycorrhiza (VAM), creates vesicles (small compartments) inside plant roots. These vesicles are typically arranged in tree-like structures (see **Figure 31**). This is where the commonly used acronym "VAM" comes from: "vesicular" is for the vesicles, "arbuscular" means tree-like, and "mycorrhiza" is the shortened form of "mycorrhizal fungi". VAM is the type of endomycorrhizal fungi found most commonly in agricultural fields.

The hyphal networks established by these fungi can be quite extensive. These networks explore and mine areas that plant roots cannot reach, greatly extending the feeding area of the plant. Most agricultural plants (e.g., corn, soy, wheat, most vegetables) establish mycorrhizal associations, although not all with the same species and not all to the same extent or degree. The main crop exception in agriculture are the brassicas, which do not establish any mycorrhizal associations whatsoever.

Mycorrhizal fungi can be extremely beneficial to farmers, as they help crops in a number of important ways. Below is a brief summary of the potential benefits:

- greater access to nutrients (particularly phosphorus, but many others as well), delivered directly to the plant
- drought protection, as the fungi also deliver water to the plant when it is most needed;
- disease suppression (see Chapter Four)
- better soil aggregation and structure (see Chapter Two)
- increased carbon sequestration (see Chapter Five)
- weed suppression.

With respect to the last point above: many annual weeds are either non-mycorrhizal or have only a weak association with these fungi. This can be a great help to farmers in managing weeds, as long as the VAM are kept alive and well in the soil. The plants that have mycorrhizal partners (the crop) have an advantage over the many weeds that do not; the latter can actually be starved of phosphorus by the fungi, who will deliver it all to their plant partners.

How to manage your soils to ensure good levels of mycorrhizal fungi is a topic covered in Chapter Seven.

Summary

Plants need certain essential nutrients in order to grow and reproduce. These include the six macronutrients – nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur – as well as the eight micronutrients – boron, chlorine, copper, iron, manganese, molybdenum, nickel and zinc. With the exception of nitrogen, which is fixed from the atmosphere by microbes, all of these come originally from the mineral component of soils. They are released over time by various mechanisms and can be found in ionic form in soil water, or loosely attached to soil particles. Plants can only absorb those nutrients that are dissolved in water. Nutrients are also recycled in the soil by microbes as they break down organic residues.

It used to be thought that plants had only three ways to access these nutrients: interception by roots; diffusion of nutrients along a concentration gradient; and mass flow. We now know that these processes are important but only part of the story. Microbes are not only involved as decomposers; they are also a fundamental part of two types of underground carbon trading systems. Using these systems, plants are able to access more nutrients more quickly (and with more control over the process). The overall idea is that plants offer the products of photosynthesis (substances such as sugars rich in carbon) to the soil food web in return for access to nutrients.

There are two types of carbon trading system underground. In the first, known as the microbial loop, plants put out their carbon-rich offerings through their root systems, as plant-root exudates. These exudates attract very large numbers of bacteria and fungi, which are themselves rich in nutrients due to their consumption of organic material and their ability to free up nutrients directly from minerals. As they congregate around the plant roots, predators (protozoa and nematodes) consume them in large numbers, releasing excess nutrients in the root zone in plant-available form. In the second system, plants form associations with a type of fungus known as mycorrhizal fungi. This is a more direct trading system, where plants provide the sugars to the fungus and the fungus provides nutrients and water to the plant. Both of these systems enhance the ability of plants to access the nutrients they need quickly and in sufficient quantities.

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4 This is not to say that plants don't use other elements – they do. However, only the nutrients listed in Table 1 are absolutely essential. Of course, scientists are always learning more about plants, and the list of essential nutrients will probably increase in number in the future, as it has in the past.