

Advances in Soil Science

Advances in Soil Science

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Preface

The study of soils has taken on increased importance because a rapidly expanding population is placing demands on the soil never before experienced. This has led to an increase in land degradation. Land degradation is one of the most severe problems facing mankind. Volume 11 of *Advances in Soil Science* was devoted entirely to this critical area of soil science. The editors of that volume, R. Lal and B.A. Stewart, defined soil degradation as the decline in soil quality caused by its misuse by humans. They further stated that soil degradation is a major concern for at least two reasons. First, it undermines the productive capacity of an ecosystem. Second, it affects global climate through alterations in water and energy balances and disruptions in cycles of carbon, nitrogen, sulfur, and other elements. Through its impact on agricultural productivity and environment, soil degradation leads to political and social instability, enhanced rate of deforestation, intensive use of marginal and fragile lands, accelerated runoff and soil erosion, pollution of natural waters, and emission of greenhouse gases into the atmosphere. In fact, soil degradation affects the very fabric of mankind.

From the beginning of agriculture until about 1950, increased food production came almost entirely from expanding the cropland base. Since 1950, however, the yield per unit of land area for major crops has increased dramatically. Much of the increase in yields was because of increased inputs of energy. Between 1950 and 1985, the farm tractor fleet quadrupled, world irrigated area tripled, and fertilizer use increased ninefold. Between 1950 and 1985, total energy used in world agriculture increased 6.9 times.

Until recently, sustainability was seldom, if ever, mentioned in agricultural literature. Now, it is one of the most widely used terms. The high costs of irrigation development, escalating energy costs during the 1970s, public concern over potential negative impacts of fertilizer and pesticides on water supplies, soil erosion, soil compaction, and salinity problems, and other concerns have caused many people to question whether many of the present agriculture systems can be sustained. As a result, soil science is beginning to focus more on sustaining the resource base. The productivity level of an

agricultural soil at any time is the resultant of the interaction of degradative processes and conservation/reclamation practices that are occurring simultaneously. A sustainable system is any system where the benefits from the soil conservation practices are equal to or greater than the negative effects of the soil degradative processes.

This series, *Advances in Soil Science*, was established to provide a forum for leading scientists to analyze and summarize the available scientific information on a subject, assessing its importance and identifying additional research needs. This goal seems even more appropriate today than in 1982, when the idea of the series was formulated. Much is known about our soil resources. The principles learned and the technology developed need to be used to increase food production and sustain the productivity of the resource base. *Advances in Soil Science* fills a gap between the scientific journals and the comprehensive reference books. Scientists can delve in depth on a particular subject relating to soil science. Contributors are asked in particular to develop and identify principles that have practical applications to both developing and developed agricultures.

Advances in Soil Science is international in scope and covers all subjects relating to soil science. This volume continues that format in that it contains reviews of diverse interests written by scientists from Spain, The Netherlands, India, Federal Republic of Germany, and the United States. Although we consider our audience to be primarily scientists and students of soil science, the series provides technical information to anyone interested in our natural resources and man's influence on these resources. Research in the future must focus on systems that are resource efficient and environmentally sound. The need to optimize crop production while conserving the resource base has never been greater.

The quick acceptance of *Advances in Soil Science* by both authors and readers has been very gratifying and confirms our perception that a need did exist for a medium to publish soil science reviews. I want to thank the authors for their excellent contributions and cooperation. I also want to thank members of the Editorial Board for their help in selecting such competent authors and the Springer-Verlag staff for their kind assistance and counsel. Lastly, and most importantly, I want to thank the readers for their acceptance and use of *Advances in Soil Science*.

B.A. Stewart

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Vesicular–Arbuscular Mycorrhizae as Modifiers of Soil Fertility

J.M. Barea

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I. Introduction

It has become clear that microbial activity must be considered a key component among those conferring "soil fertility," i.e., the ability of a given soil to support plant development and nutrition (Pauli, 1967). The major components interacting to determine "soil fertility" are depicted in Figure 1. Accordingly, "fertility" can be considered an inherent property of a given soil. However, the plant itself is able to modify soil fertility in two different ways. One is based on the "rhizosphere effect" exerted by the plant, which can alter the fluxes of energy and the supply of substrates for soil microorganisms. The other way is based on the inherently different growth rates and metabolism of the different plant species that are known to "change" the capacity of the soil to provide each particular plant with nutrients (Hayman, 1975). In other words, the ability of a plant to exploit the nutritional supply of a given soil depends on the type of plant, mainly on the characteristics of its root system, and on the rates

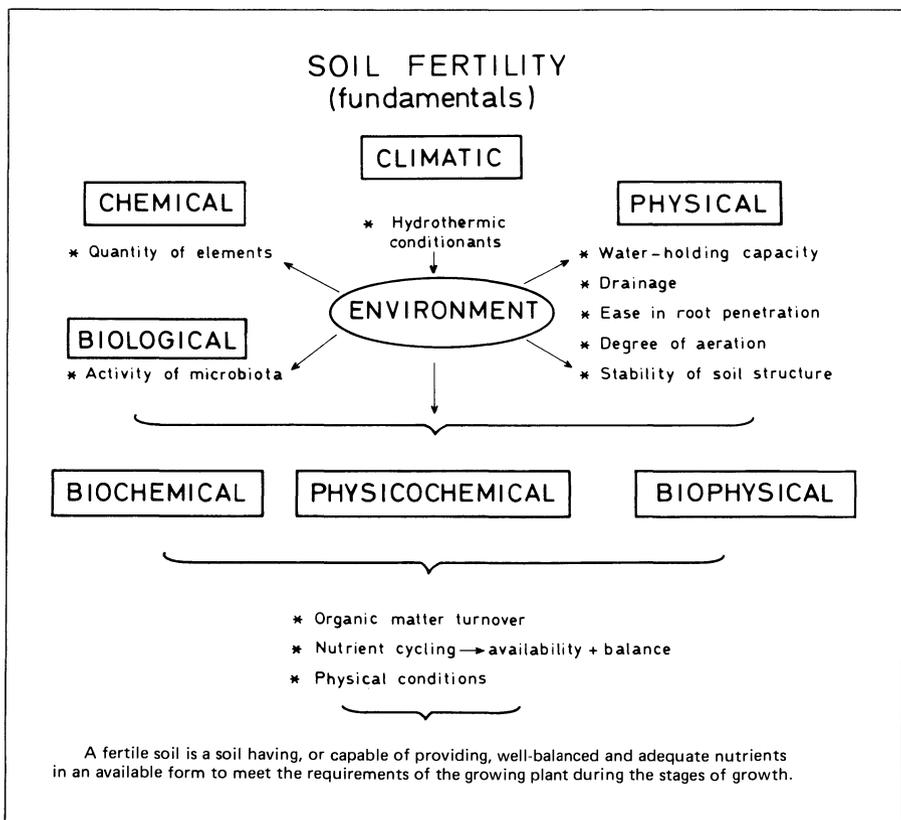


Figure 1. Summary of factors that affect soil fertility.

and patterns of exudation (Chapin, 1980; Clarkson, 1985). Thus, plants are able to “modify” the soil fertility.

It is widely known that a key determinant of the ability of a root system to acquire nutrients from the soil is the extent to which it is symbiotically colonized by appropriate mycorrhizal fungi. The mycorrhizal condition is actually the normal status of most terrestrial plants, and it greatly enhances the possibilities of the plant for nutrient uptake from soil (Mosse, 1973; Harley and Smith, 1983). The formation and activity of this symbiosis are in turn affected by the soil fertility level (Hayman, 1982; Gerschef-ske et al., 1988).

At this point it would be opportune to remember that soil microorganisms play vital roles in the root region, the rhizosphere, where they are invariably present and are stimulated by organic substrates supplied by the plant. The main beneficial activities of rhizosphere bacteria (actinomyces are considered bacteria) and fungi include the increased availability of plant nutrients, the improvement of nutrient uptake, the production of plant growth regulators, plant protection against root pathogens, and so on. According to their relationships with the plant, the microorganisms can be divided into three groups: saprophytes, parasitic symbionts (“pathogen”), and mutualistic symbionts (“symbionts”).

Particularly, the mutualistic symbiosis between photosynthetic plants and specific microorganisms plays a key role in both natural ecosystems and man-modified systems, mainly because the symbiotic microorganisms carry out functions for the plants that they are unable to perform for themselves (Barea and Azcón-Aguilar, 1983). The best-known examples of mutualistic symbiosis involving plant and microorganisms are (1) that established between bacteria and the roots of certain plant species to form N_2 -fixing nodules, the *Rhizobium*-legume association being the model case, and (2) the mycorrhizae, the study of which is the central subject of this review.

The aim of the present chapter is, in fact, to carry out a comprehensive study of how mycorrhizae change the supply of mineral nutrients that a given soil can supply, thereby modifying soil fertility. As an introduction, a brief review of some general and universally accepted principles, the mycorrhizal types, their morphology, and the processes of mycorrhizae formation is presented to achieve a conceptual background for nonspecialist readers. To facilitate a better understanding of the mycorrhizal effects, some ideas are then summarized concerning the processes of nutrient absorption by roots and their role at modifying the nutrient availability in a given soil. Current information on mycorrhizae functioning and its ecological conditionants is analyzed and summarized to constitute the core part of the review. A number of review articles are cited in this part of the review not only because of the conclusions they supply but also because they are a source of references, which have been reduced to a minimum in this part of the present chapter. Finally, the possibilities of application of mycorrhizae in agriculture, horticulture, fruit culture, and

forestry are discussed. The research requirement to demonstrate rationally stated hypotheses is suggested, and current trends on the subject are also outlined.

This study is therefore devoted to describing processes taking place in the root–soil interfaces; hence, according to Clarkson (1985), it can be considered an attempt to gain information in a critical research area: that linking plant physiology and soil science.

II. Mycorrhizae

A. General Concepts

1. Universality of the Symbiosis

It is widely known today that the roots of most flowering plants live associated, in a form of mutualistic symbiosis, with certain soil fungi by establishing the so-called mycorrhizae. The fungus biotrophically colonizes the root cortex, becoming an integral part of these organs, where an extramatricial mycelium develops that helps the plant acquire mineral nutrients from the soil. The symbiosis is considered the most metabolically active part of the absorbing organs of the autotrophic host plant, which in turn furnish the heterotrophic fungal associate with organic nutrients and with an ecologically protected habitat. Mycorrhizae are recognized as playing a key role in plant survival and nutrient cycling in the ecosystem. They can be found in nearly all soils of the world. All but a few vascular plant species (these belonging mainly to Cruciferae, Chenopodiaceae, Cyperaceae, and Juncaceae) are able to form mycorrhizae. The physiology of the plant is greatly affected by the presence of the fungal symbionts (Harley and Smith, 1983; Smith and Gianinazzi-Pearson, 1988).

2. Mycorrhizal Types

It is obvious that the universality of the symbiosis implies a great diversity in the taxonomic features of the fungi and plants involved. There are, in fact, great differences in the morphology of mycorrhizal group, and this is reflected in the resulting physiological relationships.

Five types of mycorrhizae can be recognized; their structural and nutritional features have been detailed before (Smith, 1980; Harley and Smith, 1983). Only a brief consideration to differentiate these groups is given here.

About 3% of the higher plants, mainly forest trees in the *Fagaceae*, *Betulaceae*, *Pinaceae*, *Rosaceae*, *Eucalyptus*, and some woody legumes, form ectomycorrhizae. The fungi involved are mostly higher basidiomycetes and ascomycetes, which colonize the cortical cells of the root, the lack of intracellular penetration being characteristic. In general, the fungus develops a sheath or mantle around the feeder roots.

In addition, three types of mycorrhizae can be grouped as endomycorrhizae, where the fungus can colonize the root cortex intracellularly. One of these is restricted to some species in the *Ericaceae* ("ericoid" mycorrhizae), the second to the *Orchidaceae* ("orchid" mycorrhizae), and the third, the vesicular–arbuscular (VAM), which is by far the most widespread type. There is a fifth group, the ectendomycorrhizae, formed by plant species in families other than *Ericaceae* but in the Ericales. They form a sheath and produce intracellular penetrations ("arbutoid" mycorrhizae). The ecological and economic interest of VAM can be simply deduced from the fact that about four-fifths of all land plants, including agronomically important crops, form this type of mycorrhizae. The nomenclature refers to typical structures, the "vesicles" and the "arbuscules," of the fungus in symbiosis.

B. Vesicular–Arbuscular Mycorrhizae

1. Occurrence and Distribution

Both the fungus and the VAM are distributed worldwide. The fungi belong to the class Zigomicotina, order Endogonales, family Endogonaceae. Morton (1988) systematizes about 150 species in the only six genera able to form VAM (*Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, *Sclerocystis*, and *Scutellospora*); none of these fungi has yet been successfully cultured axenically (Siqueira, 1987).

Typical VAM-forming plants are legumes, cereals, temperate fruit trees, tropical timber trees, plantation crops; tropical, mediterranean, and "industrial" crops; and horticultural and ornamental crops (Barea and Azcón-Aguilar, 1983).

2. Characteristics of the Host–Fungus Relationships

Some properties of phenomena inherent to any symbiotic system are particularly relevant in VAM because the nutrient uptake by the plant can be strongly affected if associated with its suitable microsymbiont. Dependency, recognition phenomena, compatibility, and specificity are concepts that merit brief reference.

It seems (Pirozynski and Malloch, 1975; Malloch et al., 1980) that certain fungi played a critical role in the evolution of "plants" to colonize the land (Silurian and Devonian periods, 400 million years ago), because these fungi associated with such "plants" and helped them in the nutrient uptake processes. This may be plausible, since the Rhynie fossil (the earliest preserved plants—370 million years old) showed a fungal formation quite similar to modern VAM, suggesting a plant–VAM coevolution (Nicolson, 1975). These facts can explain the world wide spread of the VAM and several of their so-called "symbiotic properties," which are determined by (1) the ability of a plant to acquire nutrients through a fungus ("mycotrophy"), (2) the difficulties the fungus has in completing its life

cycle independently of the host, being a physiologically obligate symbiont (“fungal dependency”), and (3) the characteristics of the plant as expressed by its need to be mycorrhizal to develop (“mycorrhizal dependency of a plant”). Such dependency on VAM varies with the plant species, since some of these need VAM to survive, others to improve their growth, and others to reach their maximum yield (Hayman, 1983).

There is a lack of “specificity” (*sensu strictu*) in VAM. Roughly, any VAM fungi (VAMF) can colonize any suitable plant species, a single root system can support different VAMF species, and roots of different plant species can be linked by the mycelium of a single VAMF (Mosse et al., 1981; Harley and Smith, 1983; Gianinazzi-Pearson, 1984). Nevertheless, the different plant species, and even cultivars within the same species (Azcón and Ocampo, 1981), vary greatly in the level of “susceptibility” to VAMF. This indicates that the plant genotype controls the amount of root tissue that is colonized to become a VAM (Gianinazzi-Pearson, 1984; Buwalda et al., 1984). Since the different VAMF also differ in the level of colonization that they can reach in the root system of a given host plant, it follows that a certain type of “specificity” can be recognized in VAM. This raises the concept of “compatibility” in VAM, which must be associated with that of “symbiotic effectiveness” to establish that of “functional compatibility” (Gianinazzi-Pearson, 1984). The last refers to the phenotypic expression of a VAM as a result of the environmental influences on the expression of the genotypic equipment of both the plant and the fungus involved (see Smith and Gianinazzi-Pearson, 1988). According to Gianinazzi-Pearson (1984), there is evidence of fungus–plant “recognition,” as evidenced at several stages. Such evidence includes (1) cell-to-cell contact to form appresoria; (2) certain morphological and structural changes of the fungus, mainly cell wall composition, within the root tissues; (3) the integration of the physiology of both symbionts, and (4) the redistribution of enzymatic activities, especially those involved in nutrient exchange, between the components of the symbiosis.

III. Development of Vesicular–Arbuscular Mycorrhizae

A. The Processess of Vesicular–Arbuscular Mycorrhizae Formation

The VAM colonization originates from hyphae arising from soil-borne propagules (large resting spores of the VAMF or mycorrhizal root fragments) or from a VAM plant growing nearby. It seems that the network of VAM fungi mycelia in soil is an important source of inoculum. This can be reinforced by the fact that the hyphae can retain their infectivity after separation from the roots, even in dry soil (Jasper et al., 1989a,b). Consequently, soil disturbance disrupts the mycelium network and reduces infectivity.

On arrival of the fungal hyphae at the root surface, an appresorium is

usually formed on the cortical cells. The infection units ("internal mycelium associated with a single entry point"; Wilson, 1984) grow as the hyphae spread between and through cells of the cortical root layers. On reaching the inner cortex, the hyphae can grow into cells and, by repeated dichotomic branching, form some tree-like structures called "arbuscules." The life span of individual arbuscules is about 4–14 days. When the internal colonization is spreading, the extramatricial hyphae ramify. These may grow along the root surface, forming more penetration points, and also out into the surrounding soil, to form an extensive tridimensional network of mycelium.

When the colonization process is well established, the fungus may form "vesicles," oval-to-spherical structures with a storage (mainly lipids) function. Most VAMF form large resting spores on the external mycelium (see Harley and Smith, 1983; Bonfante-Fasolo, 1984; for a detailed description of the anatomy of VAM and the formation of the symbiosis).

Intracellular colonizations, as in the case of arbuscules, have a characteristic feature, which is that the fungus is always surrounded by the intact host-cell plasmalemma. Therefore, arbuscule formation represents a large surface of cellular contact between the two symbionts. This facilitates the interchange of metabolites between host and fungus. In fact, the arbuscule is considered the main site of transfer of mineral nutrients from the fungus (which had taken these up from soil) to the plant (see Smith and Gianinazzi-Pearson, 1988, for the development of host–fungus interfaces).

B. Quantitative Estimates

The spread of VAMF is usually measured as the proportion of the root length that is colonized by VAM hyphae. For comparison purposes, the estimates of the fungal development within and around roots must consider the rate of root growth and the size of the root system to get a realistic idea of VAM size. Time-course quantifications of the fraction of the root length that has been converted into VAM usually follow a characteristic sigmoidal curve (Tinker, 1975). The length of the lag phase depends on the density of viable propagules in the medium, the rate of germination, stimulation, and germ-tube growth (Sanders and Sheikh, 1983). The subsequent exponential phase of VAM development follows the spread of secondary infections, when the hyphae grow along and between roots. Then the VAM extent reaches a plateau, and the resulting percentage is usually less than 100%. The plant–fungus combination and the onset of environmental factors and/or conditions affect the extent and/or rate of the processes (Mosse et al., 1981; Sanders and Sheikh, 1983). The different phases of the VAM development can be modeled (see Smith and Walker, 1981; Buwalda et al., 1982; Sanders and Sheikh, 1983; Walker and Smith, 1984; Tinker, 1985; Sanders, 1986; as examples of modeling approaches).

From the point of view of the role of VAM as modifiers of soil fertility, the main quantitative estimate to be considered is that concerning the extent of the external hyphae growing in soil, associated with mycorrhizal roots (Abbott and Robson, 1985). Data recorded from different publications by Smith and Gianinazzi-Pearson (1988) indicate that most calculations reach values of 1 m cm^{-1} root on average, but values of 10–14 m cm^{-1} root have also been recorded.

IV. Root–Soil Interactions

A. Nutrient Uptake Processes

Plant growth is largely regulated by the supply of nutrients available to the root system and by the efficiency of the active absorption of the root cells on nutrient arriving at the surface of these cells. The magnitude of the supply of a given nutrient to the root surface depends on (1) the concentration of the corresponding ions in the soil solution, (2) the sorption–desorption capacity of the soil, which allows ions in the exchangeable pools to replenish the soil solution as these ions (nutrients) are being taken up by the plant, and (3) the efficiency of nutrient transport through the soil solution to the absorbing sites, either by mass flow or by diffusion (Tinker, 1980; Chapin, 1980). This is summarized in Figures 2 and 3.

In regard to the rate of nutrient movement to the root, it is important to realize that the bulk of the available forms of the major plant nutrients

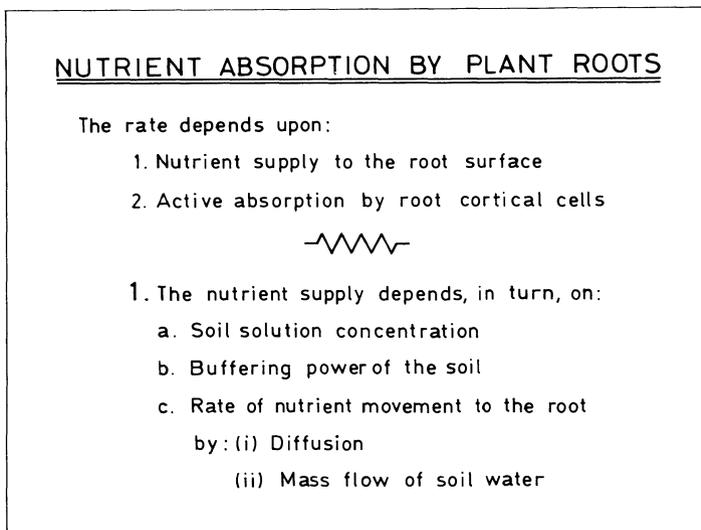


Figure 2. Summary of factors that affect nutrient absorption by plant roots.

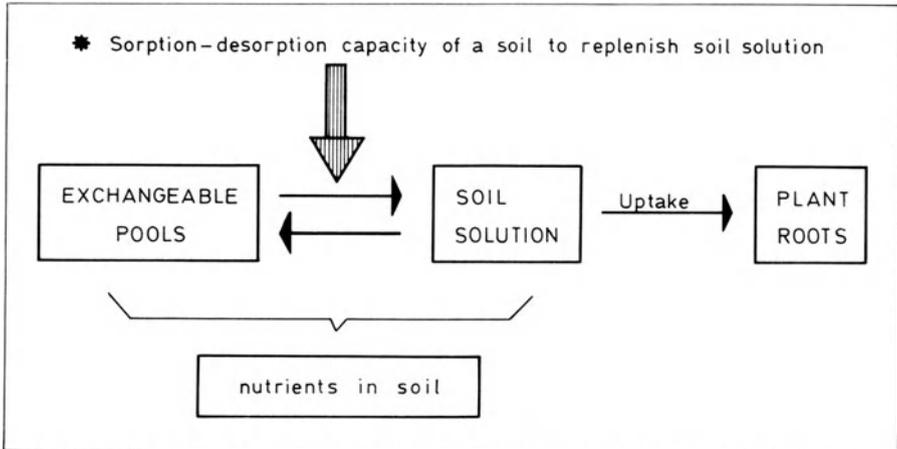


Figure 3. Buffering power of the soil.

(N, P, K) that are in the soil solution at low concentration (Nye and Tinker, 1977) move to the root surface by diffusion (Chapin, 1980). Therefore, the rate-limiting step in the absorption of low-mobility phosphate, ammonium, and potassium is actually the diffusion of these ions through the soil solution. Because the rate of diffusion of these ions is much lower than that of absorption once they arrive at the root surfaces, regions depleted of the nutrient frequently develop around roots (Chapin, 1980; Tinker, 1980; Hayman, 1983; Clarkson, 1985). This is illustrated in Figure 4.

Root properties greatly affect nutrient acquisition (Clarkson, 1985). First, plant metabolism exerts its influence through processes such as secretion of H^+ or HCO_3^- loss of substrates by root exudation, lysates, and sloughing of cells or tissue debris, and secretion of chelating substances, O_2 , etc. Even plant shoots influence root activity by affecting the rate of photosynthesis by depleting mineral nutrients, by controlling (through feedback mechanisms) the source-to-sink equilibrium in the shoot-to-root relationship, and by synthesizing carriers and related substances (Chapin, 1980).

The characteristics of the root system as a whole, and of the root surfaces in particular, greatly affect the nutrient intake of the plant (mean uptake per unit root length). As reviewed by Clarkson (1985), two main properties of a root system modify nutrient inflow: (1) its size and distribution (i.e., morphological and geometric features) and (2) the capacity of the root surface for nutrient uptake (i.e., kinetic properties). It is known that the use of the nutrients present in the soil solution by the root follows a Michaelis-Menten pattern, expressed by the parameters K_m (indicating affinity) and I_{max} (related to V_{max} , which indicates capacity); this is summarized in Figure 5.

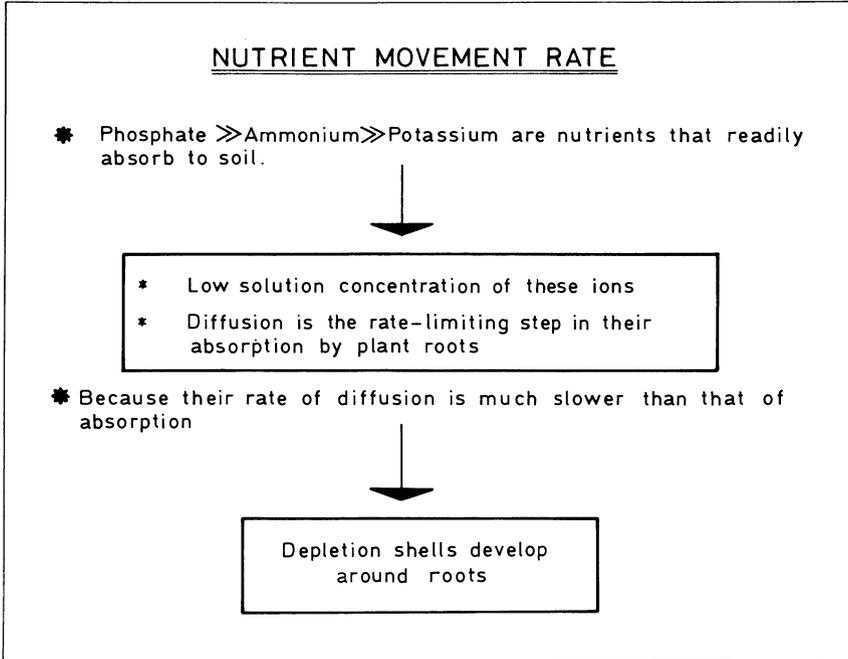


Figure 4. Motility of nutrients in soil.

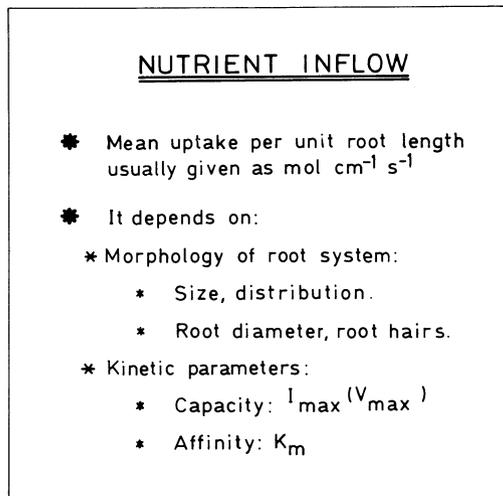


Figure 5. Summary of factors that affect nutrient inflow.

B. Vesicular–Arbuscular Mycorrhizae as Modified Root Systems

The development of an extensive network of extramatricial hyphae by the VAM in the soil surrounding the root, together with the capacity of these hyphae for nutrient absorption and transport to the cortical root cells, indicates that VAM modify the nutrient uptake properties of a root system. Actually, it is widely accepted that VAM play a recognized role in nutrient cycling in the ecosystem (Harley and Smith, 1983). Because the external mycelium extends several centimeters from the root surface, it can bypass the depletion zone surrounding the root and exploit soil microhabitats beyond the nutrient-depleted area where rootlets or root hairs cannot thrive (Rhodes and Gerdemann, 1980). This is discussed in detail later. It is evident that VAM have a greater exploring ability than the root and overcome limitations on acquisition of ions that diffuse slowly in the soil solution to the rhizosphere. The quantitative features of hyphal growth in soil have already been considered (Section III.B), and it is obvious that the size of the extramatricial mycelium is critical in defining its uptake characteristics. In addition, the turnover of hyphal development and the activity of these hyphae are also important (Smith and Gianinazzi-Pearson, 1988).

It is obvious that these facts allow one to envisage the VAM as a modified root system greatly improved for nutrient uptake. Besides, as discussed below, there is some evidence that VAM can alter the kinetic properties of the root in regard to its absorption abilities (Harley and Smith, 1983; Bolan et al., 1987a).

It is commonly accepted that plants with profusely branched root systems having fine rootlets less than 0.1 mm in diameter and long root hairs (graminoid roots) are less dependent on VAM than those with coarse roots (magnolid roots) having rootlets more than 0.5 mm in diameter (Baylis, 1975). This reinforces the idea that VAM represent a complement of the root system, being more critical when the latter is less developed or when the environment is stressed, nutrient-poor, or competitive (Mosse et al., 1981).

V. Vesicular–Arbuscular Mycorrhizae and Acquisition of Phosphate by Plants

A. Phosphate Transport by VAM, a Key Factor in Plant Nutrition

A great deal of work, recently reviewed (Barea and Azcón-Aguilar, 1983; Harley and Smith, 1983; Abbott and Robson, 1984; Hayman, 1986; Smith and Gianinazzi-Pearson, 1988) shows that VAM enhance plant growth as a result of improved mineral nutrition of the host plant, and this has been confirmed with the use of isotopic tracers. Mycorrhizal plants not only